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Linking foraging behaviour of free-ranging, lactating beef cows with diet quality and weight gain in semi-arid rangeland

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ABSTRACT

Monitoring free-ranging livestock foraging behaviour and health with on-animal sensors has emerged as a potential means to enhance adaptive management for ranching operations. We evaluated the use of GPS collars collecting animal locations at 5-min intervals and estimating activity (grazing, walking, or stationary) via a 3-axis accelerometer to quantify foraging behaviour of lactating *Bos taurus* beef cows with calves on a ~7600 ha working ranch in a sagebrush grassland ecotone in northeast Wyoming. We used this sensor data to quantify five metrics of foraging behaviour at a daily time step including (1) mean velocity while grazing (VG), (2) mean grazing bout duration (GBD), (3) mean turn angle while grazing (TAG), (4) total daily grazing time (TTG) and (5) total daily travel distance (TD), and related these metrics to measurements of cattle diet quality, weight gain, and stock density. While foraging behaviour metrics varied among individual cows, we found that daily estimates of VG, GBD, TAG and TD were all significantly related to stock density and variation in remotely-sensed estimates of dietary crude protein content. Over longer time periods of weeks to months, cattle diet quality and weight gain were significantly related to VG (positive correlation; $R^2 = 0.42 – 0.87$), and GBD (negative correlation; $R^2 = 0.58 – 0.78$). These findings indicate that ranchers have the ability to influence diet quality and animal performance via (1) the rotation of herds among pastures of varying composition and quality, and (2) changes in herd size relative to pasture size (i.e., animal density). Furthermore, our results indicate there is substantial potential utility for near-real-time monitoring of foraging behaviour as an indicator of animal performance via the combination of GPS tracking, accelerometer data, and a method to wirelessly transmit data to the internet. However, operationalizing such a system will likely depend on continuing improvements in sensor durability and data management efficiency, and reductions in sensor and data transmission costs.

1. Introduction

In extensive rangeland settings where livestock forage on diverse plant communities across heterogeneous terrain, livestock movements and grazing distribution have been quantified using global positioning system (GPS) collars since the 1990's (Bailey et al., 2018). More recently, studies have begun to combine the use of GPS tracking and behavioural monitoring via accelerometers, heart rate monitors, and other types of on-animal sensors at temporal resolutions that are fine enough to quantify daily foraging patterns in rangelands (Brosh et al., 2006; Brennan et al., 2021; Sprinkle et al., 2021; Augustine et al., 2023; Cibils et al., 2023). This combination of movement tracking and activity monitoring now makes it possible to quantify variation in foraging behaviour among different breeds of beef cattle (Nyamuryekung'e et al., 2021; McIntosh et al., 2021; Cibils et al., 2023;), among individuals within a breed relative to specific traits (Sprinkle et al., 2021), and among individuals relative to seasonal and spatial variation in forage conditions and herd size (Augustine et al., 2022; 2023). These studies are revealing the wide range of factors influencing foraging behaviour, which in turn can influence animal growth rates as well as the effect of

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grazing on vegetation dynamics (Carvalho et al., 2015). However, the use of on-animal sensors in extensive rangeland settings is still limited by many challenges associated with sensor durability, data curation and transmission to the internet, and the calibration and interpretation of high-frequency spatiotemporal data collected by various types of sensors (Bailey et al., 2018; Trotter, 2019; Nyamuryekung'e, 2024).

While it has long been recognised that foraging behaviours are likely to reflect variation in the quality and quantity of forage being consumed (Stobbs, 1973; Chacon et al., 1976; Carvalho et al., 2015), studies have only recently begun to quantify the relationships between specific metrics of daily or sub-daily foraging behaviours and measures of animal performance such as diet quality, weight gain, or milk and wool production. Several studies have quantified lactating cow (*Bos taurus* and *Bos indicus*) foraging behaviour in Mediterranean and desert grasslands using GPS collars (Henkin et al., 2012; Aharoni et al., 2013; Cibils et al., 2023). In addition, studies in semi-arid grasslands of the North American Great Plains have shown that metrics quantifying the foraging behaviour of yearling steers are associated with variation in weight gain and diet quality (Brennan et al., 2021, Augustine et al., 2022; 2023). Furthermore, changes in stock density (steer herd size relative to pasture size) can significantly alter foraging behaviour in ways that reduce diet quality and animal weight gain (Augustine et al., 2023). However, to our knowledge, no studies have quantified similar foraging behaviours for beef cows in this region. Cows may forage differently than steers due to their nutrient requirements relative to gestation and lactation, the maternal association with their calf, as well as their pre-existing knowledge of complexity of plant communities and terrain within pastures to which they return each year. Moreover, rangeland ecosystems can include substantial topographic, edaphic, and vegetation heterogeneity that could impact foraging behaviour in ways not captured by previous studies conducted in more homogeneous systems.

Key questions with regard to the use of measurements from on-animal sensors include (1) which aspects of foraging behaviours we might seek to quantify, and (2) how to calculate them in ways that are related to measures of animal performance. One frequently measured variable is the total time that an animal spends grazing per day (TTG), which is expected to be related to an animal's daily intake rate, and also to be constrained by digestive processes when an animal is consuming low-quality forage. For example, the time that cows spent foraging per day in a Mediterranean grassland declined from 9 – 12 h during periods of high forage quantity and quality to as little as 4–6 h per day during dry seasons with limited forage quantity and low quality (Henkin et al., 2012). Other metrics evaluated in prior studies of yearling steers included (1) velocity while grazing (VG), which increased as animals foraged more selectively (Augustine et al., 2022), (2) mean duration of grazing bouts during a day (GBD), which increased as forage quality and quantity declined (Orr et al., 2001; Augustine et al., 2022), and (3) mean turn angle while grazing (TAG), which is a measure of the tortuosity of grazing pathways and increased as animals foraged more selectively (Augustine et al., 2023).

We examined seasonal and interannual variation in foraging behaviour, weight gain, and diet quality of lactating beef cows with calves on a ~7600 ha working ranch in a sagebrush grassland ecotone in northeast Wyoming with the primary research question: Are foraging behaviour metrics good predictors of weight gains and diet quality for cow-calf pairs in this rangeland? To answer this question, we used two years of daily GPS collar data from cow-calf pairs being rotated through multiple, variously-sized pastures, combined with periodically collected cattle weights and faecal samples analyzed for diet quality. Our first research objective was to evaluate whether the four daily metrics discussed previously (TTG, VG, GBD, and TAG) have utility in predicting variation in cow-calf weight gain. In addition, we examined a fifth metric, total distance travelled per day (TD), to determine whether it could be used as a proxy for VG because TD can be more readily quantified from GPS data only. Our second research objective was to evaluate whether the same foraging behaviour metrics can predict variation in beef cow diet quality, as measured via faecal samples.

Previous studies with wild ruminant ungulates demonstrated that animal movement patterns and growth rates are correlated with forage conditions estimated from satellites based on the shape of the normalised difference vegetation index (NDVI) curve (e.g., Merkle et al., 2016; Middleton et al., 2018). Our third research objective was to examine how foraging behaviour metrics are related to changing forage conditions in this rangeland by testing how satellite-derived estimates of forage conditions were related to cattle foraging behaviour at a daily time step. Specifically, we evaluated how estimates of dietary crude protein (CP) content derived from the model calculated from annual time series of NDVI following the approach of Kearney et al. (2022a), are related to each of the cattle foraging behaviour metrics. Our fourth research objective was to evaluate whether animal stocking density (numbers of animals per unit land area at a given time) or herd size (numbers of animals per pasture) influenced the relationship between daily behaviour metrics and forage conditions. We expected stocking density to be negatively related to foraging behaviour patterns associated with higher selectivity (Augustine et al., 2023).

2. Material and methods

2.1. Study Area

We studied black Angus cow-calf pairs on a ~7600 ha working ranch in the Thunder Basin ecoregion of northeastern Wyoming USA, where the vegetation consists of herbaceous plant communities typical of the northern mixed grass prairie coexisting with a sparse sagebrush shrub overstory of *Artemisia tridentata* subsp. *wyomingensis* (Porensky et al., 2018). Common graminoids include C_3 perennial graminoids (*Pascopyrum smithii, Hesperostipa comata, Carex filifolia*), C_3 annual grasses (*Bromus tectorum, Vulpia octoflora*), and the C_4 perennial grass *Bouteloua gracilis*. The ranch consists of a mosaic of privately owned land interspersed with public grazing allotments that are part of the Thunder Basin National Grassland administered by the United States Forest Service within the United States Department of Agriculture. Mean annual precipitation averages ~320 mm and is highly variable among and within years. Annual precipitation was 424 mm in 2019, 196 mm in 2020, and 406 mm in 2021. Mean annual temperature is 6 °C and summer high temperatures average 27 °C. The most common ecological sites include Loamy (R058BY122WY), Shallow Loamy (R058BY162WY), Clayey (R058BY104WY), and Shallow Clayey (R058BY158WY) (USDA, 2015).

Pastures on the ranch vary from 71 to 2172 ha, with larger pastures including a combination of flat plains, rugged badlands, drainages with intermittent streams, and ridgelines with ponderosa pine trees (*Pinus ponderosa*). Calving occurs in May. During May – Sept, the cow-calf pairs are rotated among smaller pastures (71 – 398 ha), with cows subdivided into four or five smaller breeding herds separately grazing pastures with different bulls in August. These breeding herds are brought back together into a single herd in early September. At the end of September during the two years of our study (2019 and 2021), the cow-calf pairs were rotated to a large pasture (2172 ha) where they remained until weaning in December or January. For each pasture used in the grazing rotation each study year, we calculated stock density by dividing the number of cows by the pasture size. Stock density was calculated assuming 1.1 animal units (AU) per cow. Research in 2020 was disrupted by the global COVID-19 pandemic, and no foraging behaviour data were collected.

2.2. Cattle measurements

In 2019, the study period ran from July 31 to December 12. We collared 11 cows (2–9 years old) with MOOnitor GPS collars (www.moonitorcows.com) from a total herd of 128 cow-calf pairs, and individually weighed these cows and their calves on July 31, September 28, and at weaning on December 12 (Table 1). The second study period ran from May 7, 2021, to January 24, 2022 (referred to as the 2021 study season). During 2021, we collared 12 (2–10 years old) out of 16 individually weighed cows from a total herd of ~128 pairs. Numbers varied slightly during 2021 as animals were occasionally removed from or added to the study herd. Cows collared in 2021 were different individuals than those collared in 2019. Collared cows and their calves were individually weighed on July 2, July 29, September 1, and September 29 of 2021 and at weaning on January 24, 2022 (Table 1). Collars collected data from May 7 to December 12 of 2021, after which length of daylight became too short to support power needed for full daily operation of the collars. Animal use and welfare was approved by the University of Wyoming – Institutional Animal Care and Use Committee (IACUC) under protocol 20190509DS00363.

We collected faecal samples from each of the collared cows over a 1- or 2-day period every 2 – 4 weeks over the course of the two study years. Samples were obtained from fresh faecal pats on the ground immediately after observation of defecation. Samples were stored and analyzed for each individual cow on each sampling date, and results were averaged for each sampling date. Samples were kept on ice in the field and then frozen and shipped to the Grazingland Animal Nutrition Laboratory (Texas A&M University, Temple, TX, USA). Samples were analyzed to estimate crude protein (CP) content of the diet consumed by cows, based on Near Infra-red Reflectance Spectroscopy (Lyons and Stuth, 1992). In 2019, half of the samples were lost in transit by the shipping company.

2.3. Remote sensing of diet quality

We used satellite data from the Harmonised Landsat-Sentinel (HLS) time series to predict changes in dietary CP content over time. The HLS data provide imagery (surface reflectance) at 30-m spatial resolution every one to three days over the study period. NDVI was calculated from the red and near infra-red HLS reflectance bands and then a gap-filling and smoothing procedure used by Kearney et al. (2022b) was applied to generate a daily estimate of NDVI at 30-m resolution. From this, we extracted the average daily NDVI for each of the nine pastures grazed during each year. We used a previously calibrated model that predicts CP in the diet of free-ranging cattle as a function of five indices calculated from the NDVI curve. This model was developed using six years of field data where faecal samples were collected weekly throughout the growing season from cattle grazing pastures with the same dominant plant species as this study area (Kearney et al., 2022a). For each pasture and date, we used the NDVI time series to calculate (1) the integrated area under the NDVI curve from the start of the growing season to the given date (iNDVI), (2) the average daily rate of change in NDVI over the preceding 30 days (NDVI_d30), (3) the number of days elapsed since the peak daily rate of change in NDVI (t_peak_NDVI), and (4) the integrated drop in NDVI since NDVI first began to decline (iNDVI_dry). We then used an updated version of the random forest model reported by Kearney et al. (2022a) – which was refit using the NDVI curve instead of absorbed photosynthetically active radiation (APAR) – to estimate dietary CP content in each pasture on each date (Fig. 1) as a function of NDVI, NDVI_d30, iNDVI, t_peak_IRG, and iNDVI dry. We tested the relationship between dietary CP predicted by the remote sensing model against dietary CP measured via faecal sampling (see above) on 23 different dates (8 in 2019 and 15 in 2021), and found they were significantly correlated ($r^2 = 0.50$, $F_{1,21} = 21.03$, $P = 0.0002$)

Table 1
Average daily weight gains (kg/animal/day) of free-ranging cow-calf pairs in northeastern Wyoming for two intervals during 2019 and four intervals during 2021–2022. Cows calved in May each year, and calves were weaned in December of 2019 and January of 2022. Numbers in parentheses show 1 standard error and N = number of cow-calf pairs weighed individually in each time period.

Time Interval	Average Daily Weight Gain			N
	Cows	Calves	Total (sum)	
07/31/2019–09/28/2019	0.29 (0.08)	1.03 (0.09)	1.33 (0.11)	11
09/28/2019–12/12/2019	−0.21 (0.07)	0.57 (0.06)	0.36 (0.08)	11
07/02/2021–07/29/2021	0.44 (0.30)	1.09 (0.06)	1.54 (0.31)	16
07/29/2021–09/01/2021	0.77 (0.17)	0.99 (0.05)	1.76 (0.18)	16
09/01/2021–09/29/2021	−0.78 (0.18)	1.11 (0.05)	0.32 (0.17)	16
09/29/2021–1/24/2022	−0.09 (0.04)	0.89 (0.03)	0.72 (0.05)	16

2.4. Foraging behaviour metrics

Collars were set to collect GPS fixes every 5-min, and additionally recorded the cow's predicted activity state (resting, grazing, or walking) at 4-sec intervals derived from a proprietary algorithm applied to measurements recorded by a 3-axis accelerometer. We previously tested these predictions with direct observations of free-ranging cattle wearing these collars, and found they correctly predicted observed grazing behaviour with an overall error rate of 8.6 %, a false positive rate of 8.5 %, and a false negative rate of 8.8 % (Augustine et al., 2022). For each 5-min interval between GPS fixes recorded by the cattle collars, we classified the interval as 'grazing' or 'non-grazing' based on whether more than 50 % of the 4-sec activity predictions from the accelerometer were classified as grazing or not. For each day in which a collar successfully collected data for > 95 % of the day, we then calculated five behavioural metrics at the daily time step. We note that in both years of study, some collars failed to operate due to damage from cattle rubbing on fences, water tanks and other objects in the pastures, and also from internal failure of sensors in collars without visible damage for unknown reasons. Sample sizes of collars that operated successfully for each time interval used in the diet quality and weight gain analyses are summarised in Tables S1 and S2.

The behavioural metrics were as follows. First, we used the GPS fix data to calculate the mean velocity for each 5-min interval during which the majority of the 4-sec intervals were classified as grazing, and then calculated the mean velocity while grazing each day (VG, in m/sec). Second, we calculated the total travel distance (TD, in metres) per day as the sum of distance moved in all 5-min intervals that were classified as grazing plus all intervals classified as walking. In order to remove "apparent movement" associated with GPS fix errors when the animal is stationary, this calculation did not include the distance between fixes when the animal was classified as stationary. Third, we calculated the mean grazing bout duration within a day (GBD, in minutes), where a bout was defined as a continuous string of 5-min intervals of grazing, separated from other grazing bouts by at least one 5-min interval of non-grazing activity. However, if the animal stopped grazing for a single 5-min interval, and then resumed grazing, the bout was assumed to continue. This method of calculating GBD corresponds closely to that used by Orr et al. (2001). Fourth, for each series of three consecutive GPS fixes where the animal was classified as grazing for the entire 10-min time period, we calculated the angle between the vector connecting the first and second fix and the vector connecting the second and third fix. The absolute value of this angle was then subtracted from 180°, and is referred to 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°. Fifth, we calculated the total time spent grazing each day (TG, in minutes) at two temporal resolutions, by summing all of the 5-min intervals classified as grazing, and by summing all of the 4-sec intervals classified as grazing.

2.5. Analytical approach

We examined temporal variation in each of these behavioural metrics, as we sought to examine whether they are sensitive to variation in forage conditions, and may serve as useful indicators of animal performance. For the four metrics that did exhibit variation in response to rotations and forage conditions (see Results), we then conducted the

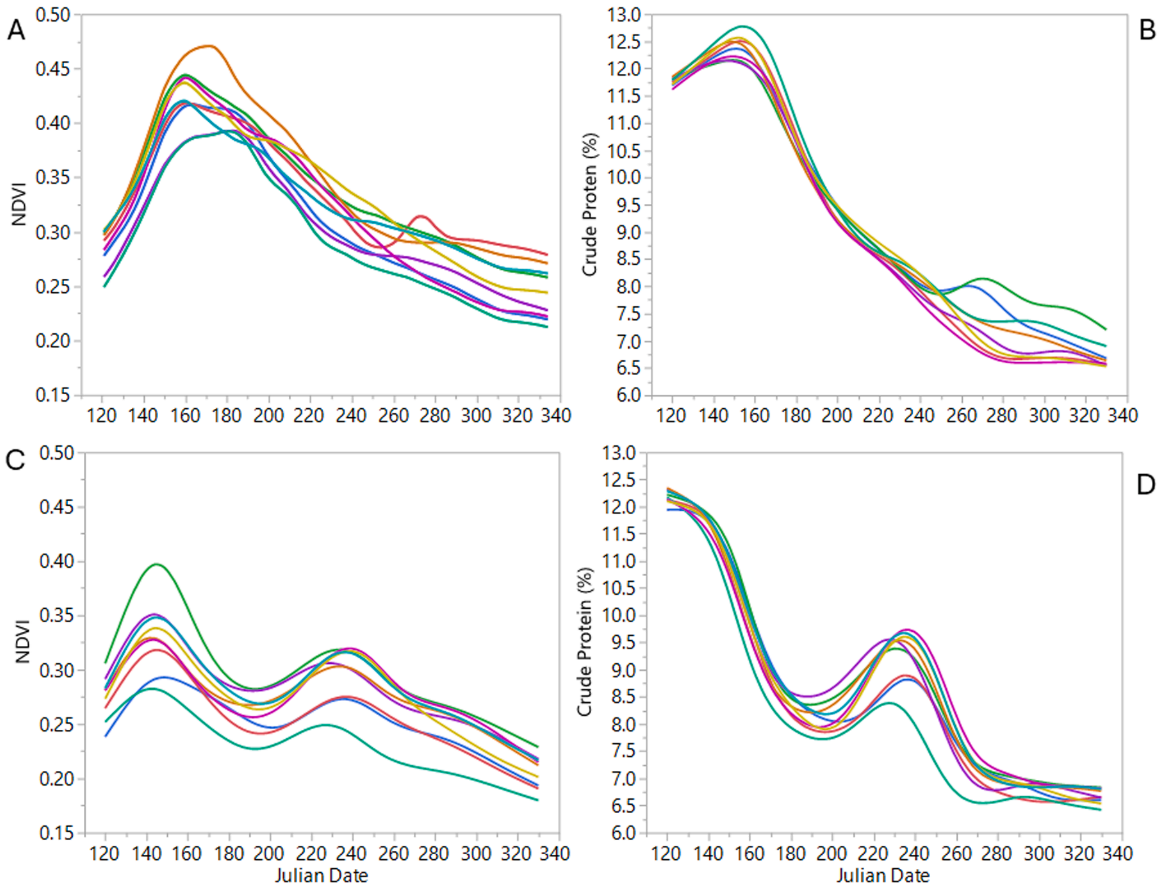

Fig. 1. Temporal variation in vegetation greenness (NDVI) and remotely sensed estimates of dietary crude protein content (%) in northeast Wyoming rangeland in 2019 (A, B) and 2021 (C, D). Different colours show patterns for different pastures among which cattle wearing GPS collars were rotated in 2019 and 2021.

following three types of analyses, each at a different temporal resolution. First, for each time interval where we calculated average daily weight gain of the cow-calf pairs (two intervals in 2019, four intervals in 2021), we also calculated the value of the daily foraging behaviour metrics averaged across all collars in that interval (see Table S1 for sample sizes), and examined simple linear regression models relating the behavioural metrics to mean weight gain of the collared animals. Second, to relate foraging behaviour to estimates of diet quality derived from faecal samples, we calculated mean values of the behavioural metrics for the last day of each faecal sampling session combined with the preceding nine days, averaged across all of the cows for which faecal samples were collected (see Table S2 for sample sizes). We also calculated the mean dietary CP content averaged across all cows sampled in a given session. This produced 11 intervals where we estimated both 10-day behavioural metrics and associated diet quality (four in 2019 and seven in 2021). We then examined simple linear regression models relating the mean of behavioural metrics to mean dietary CP content measured from faecal samples. Third, at the timestep of individual days, we examined generalised linear mixed models to determine whether remotely-sensed estimates of diet CP content combined with stock density or herd size could explain daily variation in each of the four foraging behaviour metrics (fit in this case as the response variable). In these daily models, we included individual animal ID as a random effect. Fixed effects included the daily satellite-derived CP estimate matched to each day of the foraging behaviour metric, and either animal density or herd size in that pasture on that day. We fit a quadratic relationship for CP since we expected a non-linear relationship, with CP becoming more influential on behaviour as it declines below the level of 7 % where rumen function is compromised (van Soest, 1994). Regarding the latter two variables, we fit separate models with either stock density or herd size, and report the model that both maximised R^2 and minimised the Akaike Information Criterion, corrected for small sample sizes (AICc).

3. Results

In 2019, study cows averaged 496 ± 26 kg (mean ± 1 SE) on July 31, with variation in weight (384 – 625 kg) correlating with age (2 – 9 years). During July 31 – Sept 28, cows gained an average of 0.29 kg/day while their calves gained 1.33 kg/day (Table 1). From September 28 until weaning on December 12, cows lost 0.21 kg/day while their calves gained 0.57 kg/day (Table 1), with a mean calf weaning weight of 192 ± 13 kg. Excluding one calf with abnormally low growth rate (likely attributed to some confounding but unknown health factor), mean weaning weight in 2019 was 202 ± 9 kg. Vegetation growth was unimodal in 2019, with greenness reaching a peak in early June (ranging from 0.39 – 0.47 across study pastures, Fig. 1A), and predicted dietary CP content reaching a peak in the second week of June (Fig. 1B); greenness and CP content then declined continuously from late June to December (Fig. 1A,B).

In 2021, study cows averaged 531 ± 20 kg on July 29, with variation in weight (409 – 670 kg) again correlating with age (2 – 10 years). Both cows and calves gained weight rapidly during July 2 – July 29, and July 29 – September 1; calves continued to gain at a lower rate while cows experienced weight loss during September 1 – September 29 and September 29, 2021 – January 24, 2022 (Table 1). Mean calf weaning weight on January 24, 2022, was 275 ± 10 kg. Vegetation growth was bimodal in 2021 (in contrast to the unimodal pattern from 2019), with both greenness and CP content reaching a peak in early June, where NDVI was ~20 % lower and predicted dietary CP content was ~8 % lower than the peak in 2019 (Fig. 1C,D). Greenness and CP content declined from early June to late July, and then increased rapidly again in August, with CP content reaching a second peak in late August and early September and then declining thereafter (Fig. 1C,D).

In both 2019 and 2021, the cattle rotated through nine different pastures during the period of GPS collar operation. Due to variation in pasture size and herd size, stock density varied widely each year, from 0.06 to 1.00 AU/ha. Of the five foraging behaviour metrics that we evaluated, TTG was the only one that did not vary temporally in relation to plant phenology or pasture rotations ($P = 0.97$ in 2019 and 0.18 in 2021; Fig. S1). Mean TTG, calculated by summing all the 5-min intervals in which the cow was predicted to be grazing for more than 50 % of the interval, was 11.3 + 0.18 (mean + 1 SE) and 10.8 ± 0.24 h per day in the two years, respectively (Fig. S1). However, our estimates of TTG were sensitive to the temporal resolution of the calculation. When we summed all 4-sec intervals in which the animal was predicted to be grazing, mean TTG declined significantly across all individuals compared to the 5-min resolution calculation (paired t-tests, $P < 0.001$) to 9.8 ± 0.18 and 9.5 ± 0.26 h per day in 2019 and 2021, respectively. Given the lack of any consistent temporal variation in TTG, we did not consider this metric in subsequent analyses examining relationships among weight gain, diet quality (field sampled or remotely sensed), foraging behaviour, and stock density.

The other four foraging behaviour metrics exhibited clear temporal variation within each year (Figs. 2 and 3). Mean VG and TD both declined significantly ($P < 0.001$) over time in both years. In contrast, mean GBD increased significantly ($P < 0.001$) over time each year. Turn angle while grazing (TAG) increased significantly over time in 2019 ($P < 0.001$; Fig. 2), but did not vary over time in 2021 ($P = 0.17$; Fig. 3). We evaluated how each of these behavioural metrics varied at three different temporal resolutions.

When we fit simple linear models for average daily weight gain (ADG; summed for each cow-calf pair; Table 1) as a function of each of the four behavioural metrics, variation in ADG was strongly and positively correlated with both VG ($R^2 = 0.87$; $P = 0.007$; Fig. 4A) and TD ($R^2 = 0.95$, $P = 0.0008$; Fig. 4B), and was also strongly negatively correlated with GBD ($R^2 = 0.78$, $P = 0.019$; Fig. 4C). In contrast, ADG was not related to TAG ($P = 0.12$). When we considered linear models with any combination of two predictors, none of the models had significant relationships for both predictors ($P > 0.1$). Due to the limited sample size, we did not consider more complex models.

Relationships between field collected dietary CP and foraging behaviour metrics were very similar to those for ADG. Variation in dietary CP showed a similar positive relationship with both VG ($R^2 = 0.42$; $P = 0.031$; Fig. 4D) and TD ($R^2 = 0.43$; $P = 0.028$; Fig. 4E), a negative correlation with GBD ($R^2 = 0.58$, $P = 0.006$; Fig. 4F), and no relationship with TAG ($P = 0.63$). When we considered linear models with any combination of two predictors, none of the models had significant relationships for both predictors ($P > 0.1$).

Despite considerable variation at the daily time step (e.g. mean daily coefficient of variation was 0.30 for GBD and 0.21 for VG; Figs. 2, 3), we found that daily measurements of all four metrics (GBD, VG, TAG, and TD) were quadratically related to the remotely-sensed estimates of dietary CP content, and also linearly related to stock density (Table 2). At the daily time step, none of the behavioural metrics covaried strongly with one another ($-0.21 < r < 0.55$), but VG and TD were moderately correlated ($r = 0.55$; Fig. S2). Most notably, we found that VG increased most rapidly (from a mean of 3–5 m/min) as estimated dietary CP increased from 6.5 % to 9 %, and then levelled off as dietary CP increased above 10 % (Fig. 5). In contrast, mean daily GBD was greatest (averaging above 100 min) when dietary CP content was below 7.5 %, and lower (averaging 80 min or less) across the range of CP content from 8 – 12 % (Fig. 5). Models that included stock density were more

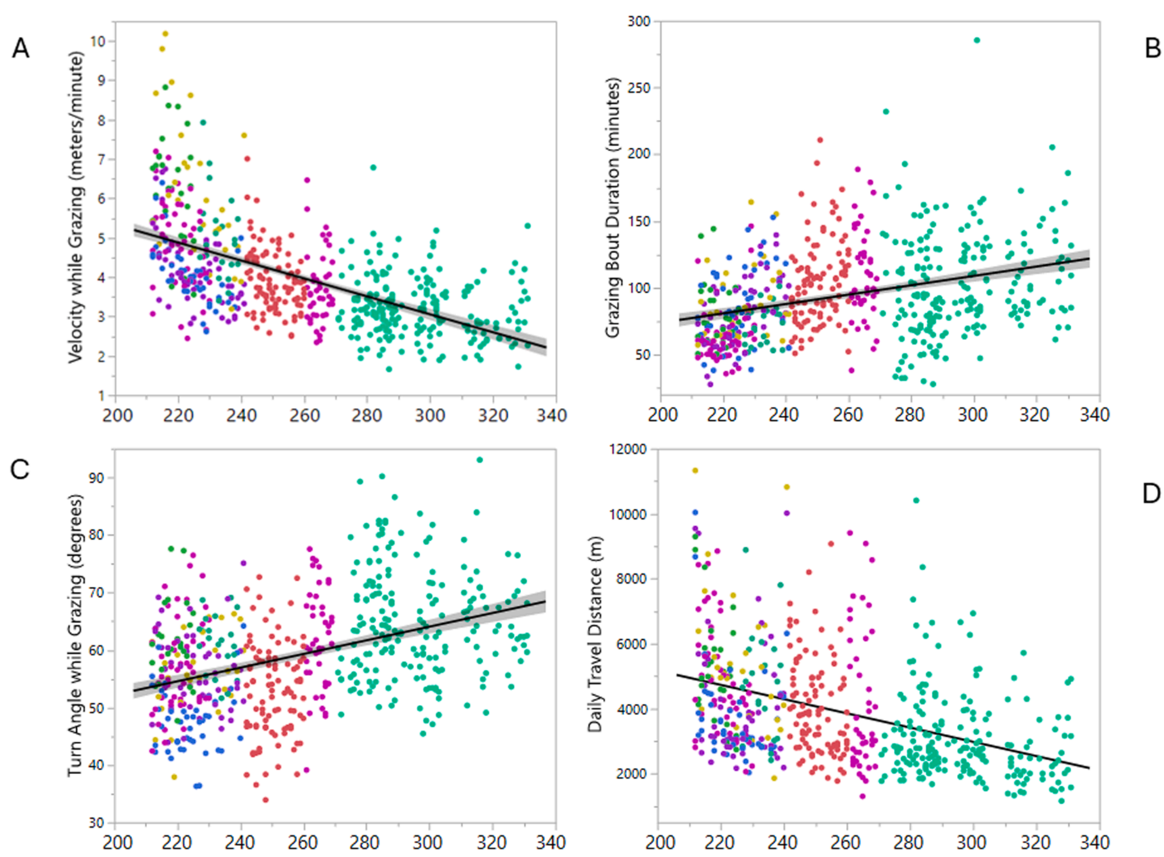

Fig. 2. Temporal patterns of four daily foraging behaviour metrics for free-ranging cattle quantified via GPS collars in northeast Wyoming rangeland during 2019. Different colors indicate different pastures occupied by the cattle over the time period.

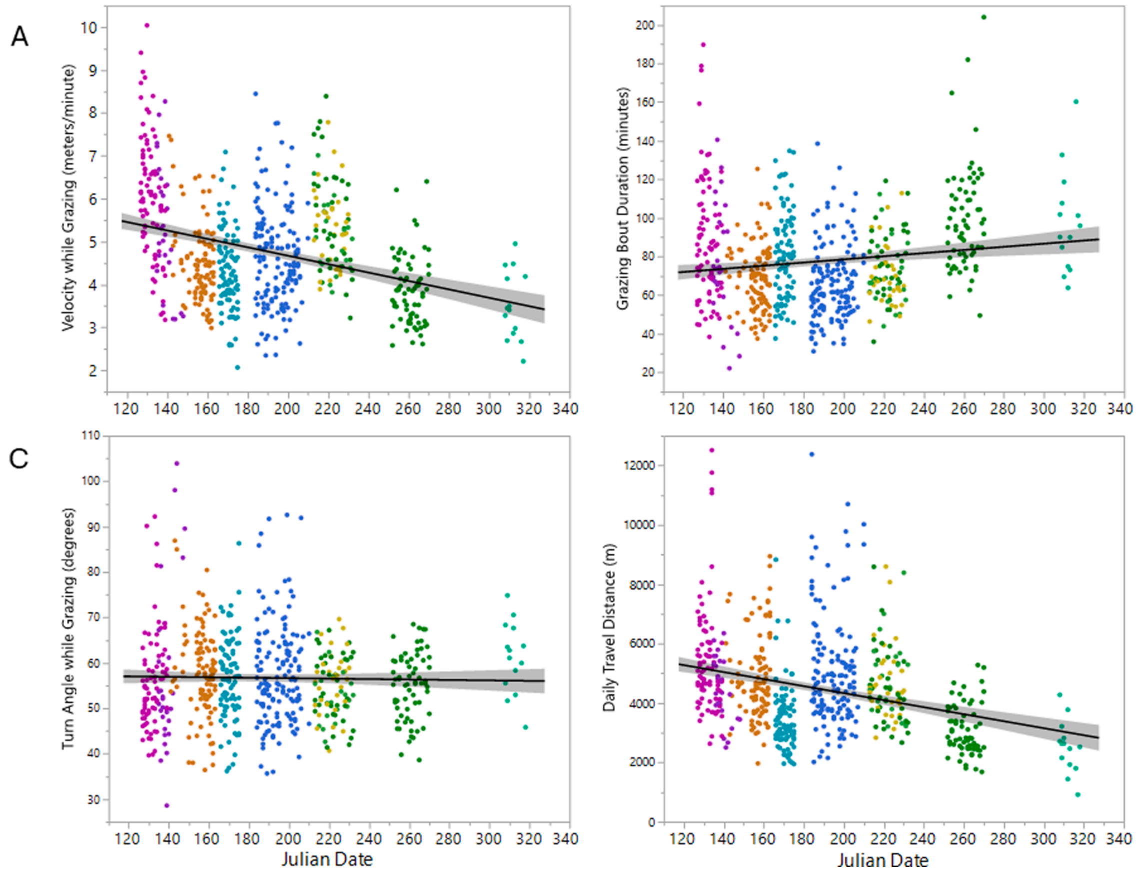

Fig. 3. Temporal patterns of four daily foraging behaviour metrics for free-ranging cattle quantified via GPS collars in northeast Wyoming rangeland during 2021. Different colors indicate different pastures occupied by the cattle over the time period.

parsimonious (Δ AICc >26) than models with herd size for all four behavioural metrics. We found VG, TAG, and TD declined and GBD increased with increasing stock density (Fig. 5).

4. Discussion

Our findings from a working ranch in an extensive semiarid rangeland collectively show that foraging behaviour measured via on-animal sensors can provide useful indices of cattle performance at temporal scales varying from days to months. In both study years, vegetation growth patterns varied substantially over the course of the season, with a single pulse of primary productivity in 2019 and two production pulses in 2021. These patterns were in turn associated with variability in cattle weight gain within and between years (Table 1). While the foraging behaviour metrics varied substantially among individuals on any given day (Figs. 2, 3), we found that day-to-day variation in foraging behaviour was significantly related to variation in satellite-based estimates of diet quality, as well as longer-term variation in animal performance (Table 2, Figs. 4, 5). We also found that variation in foraging behaviour was coupled with variation in stock density, which changes as a result of rotating herds among pastures of different sizes. These findings indicate that changes in stock density due to grazing rotation may trigger changes in foraging behaviour that ultimately affects the selected diet and hence animal performance, consistent with prior findings (Augustine et al., 2023). Changes in behaviour may also occur through the rotation of herds among pastures of varying vegetation composition and quality, and temporal changes in forage quality and quantity associated with plant growth, consumption, and senescence, all of which are expected to ultimately be reflected in animal weight gain.

Our results highlight VG and GBD as particularly valuable indicators of variation in dietary CP and animal weight gain (Fig. 4). These findings are consistent with prior work in semiarid, shortgrass rangelands of Colorado (Augustine et al., 2022), where VG was also positively and GBD was negatively correlated with weight gain of yearling cattle. The current study found that VG and GBD together did not explain more variation in weight gain or dietary CP of cow-calf pairs than either did singularly, suggesting that fewer metrics may be needed to characterise animal performance in this system. VG and GBD also exhibited similar (but inverse) relationships to satellite-based indicators of forage conditions and stock density (Table 2). The relationships indicated that as forage quantity and predicted diet quality decline, VG decreases and GBD increases. Likewise, as stock density increases, VG decreases and GBD increases. These findings are indicative of animal competition affecting diet quality and animal weight gain outcomes. Results support our hypotheses that when forage conditions are poorer and/or stock density is higher, cattle are less selective (i.e., move slower and graze in longer bouts), leading to lower diet quality and weight gain (Augustine et al., 2022; 2023).

In the current study, we also quantified daily travel distance (TD), which includes travel while grazing (correlated with VG) as well as travel while walking without grazing (not necessarily correlated with VG). Over the entire dataset, TD and VG covaried to a moderate degree ($r = 0.55$). Both explained a similar degree of variation in dietary CP and animal weight gain (Fig. 4), but VG was much more strongly related to remotely sensed estimates of diet quality and stock density (Table 2). This is not surprising, as increased VG is hypothesised to reflect increased search distances between bites while animals are grazing, and to be associated with an increase in selective foraging (Augustine et al., 2022; 2023). In contrast, TD includes travel not associated with grazing, and hence may be more affected by factors such as pasture configuration and the distribution of salt and water sources (Ganskopp, 2001; Hennig et al., 2022). Overall, our results indicate that metrics derived from

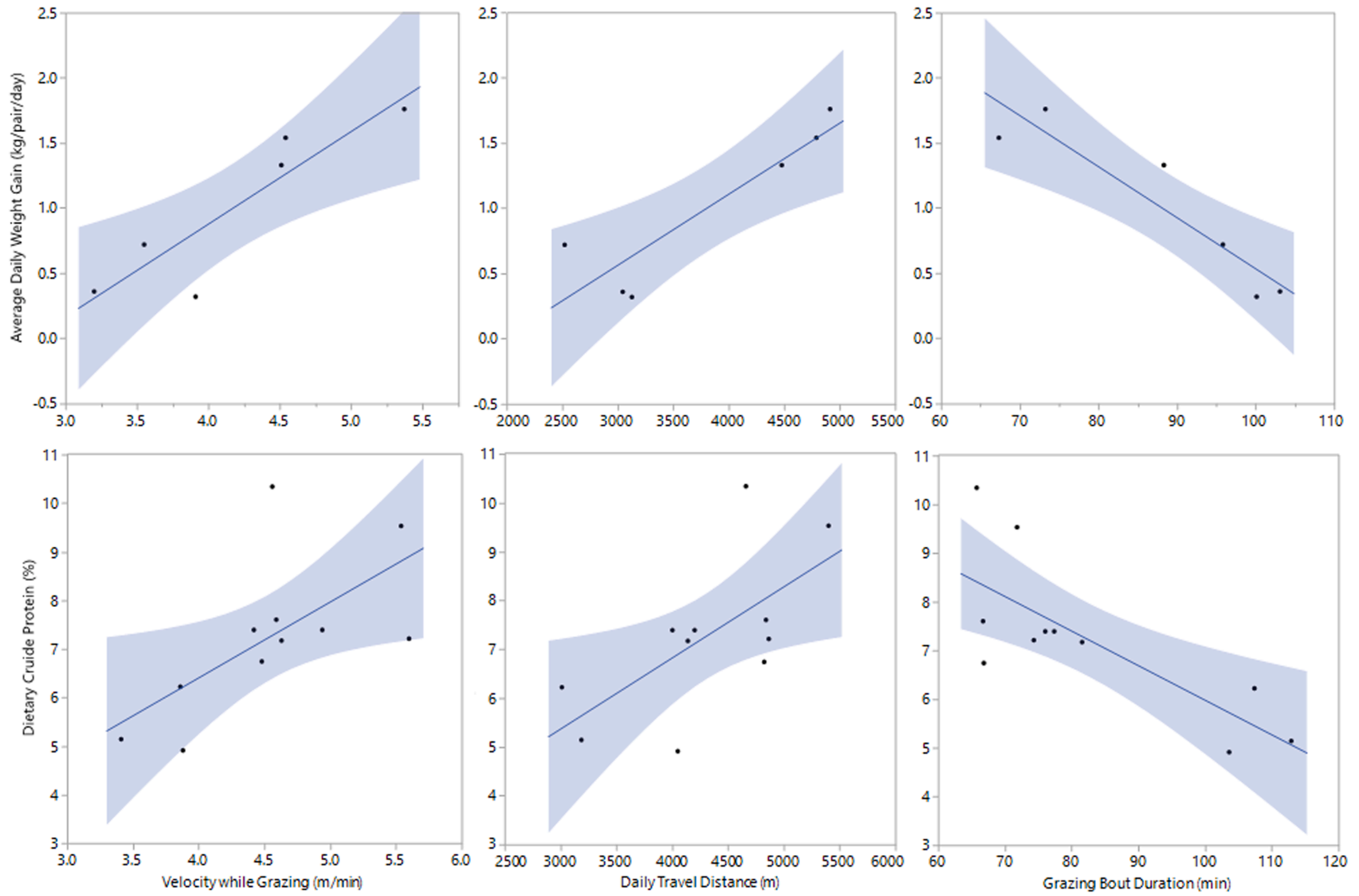

Fig. 4. Relationships between each of three daily metrics of foraging behaviour (velocity while grazing, travel distance, and grazing bout duration) averaged over six time intervals (see Table 1 for interval dates) versus weight gains measured during the same time periods (A-C), followed by relationships between each of three metrics of foraging behaviour averaged over 11 different 10-day time intervals versus dietary crude protein estimated from faecal samples collected at the end of each 10-day interval (D-F), for free-ranging cow-calf pairs in northeastern Wyoming.

Table 2
Results of four generalised linear mixed models examining the degree to which daily measures of foraging behaviour (Velocity while Grazing, VG, Grazing Bout Duration, GBD, Turn Angle while Grazing, TAG, and Travel Distance, TD) are related to daily, remotely sensed estimates of dietary crude protein content and either stock density (animal units per ha) or herd size (animals per pasture) for lactating cows rotated through pastures of varying sizes in northeastern Wyoming during 2019 and 2021.

Velocity while Grazing, VG	Estimate	Std Error	DF Den	t Ratio	Prob> |t|	R^2
Intercept	−0.261481	0.254285	318.9	−1.03	0.30	0.46
Dietary Crude Protein Content	0.6290763	0.029765	1246	21.13	< .0001	
Dietary Crude Protein Content^2	−0.085721	0.011107	1249	−7.72	< .0001	
Stock Density	−3.122152	0.360066	1237	−8.67	< .0001	
Grazing Bout Duration, GBD						
Intercept	156.3144	6.63627	340.5	23.55	< .0001	0.29
Dietary Crude Protein Content	−10.01222	0.790458	1240	−12.67	< .0001	
Dietary Crude Protein Content^2	3.4906236	0.295133	1249	11.83	< .0001	
Stock Density	41.65783	9.558001	1224	4.36	< .0001	
Turn Angle while Grazing, TAG						
Intercept	70.6096	2.28662	328.2	30.88	< .0001	0.22
Dietary Crude Protein Content	−1.49030	0.26969	1244	−5.53	< .0001	
Dietary Crude Protein Content^2	0.58550	0.10066	1249	5.82	< .0001	
Stock Density	−9.5049	3.26183	1232	−2.91	0.0036	
Travel Distance, TD						
Intercept	−329.6075	371.1029	515.8	−0.89	0.37	0.23
Dietary Crude Protein Content	618.10238	46.82786	1156	13.2	< .0001	
Dietary Crude Protein Content^2	−117.0851	17.56492	1226	−6.67	< .0001	
Stock Density	−2352.893	564.1429	1085	−4.17	< .0001	

on-animal sensors that distinguish between grazing vs. walking without grazing provide more robust information on the animals' foraging environment, compared to total daily movement. At the same time, daily travel distance appears to be an acceptable predictor of some animal performance outcomes, and may also be cheaper and easier to implement because it does not require the use of accelerometers. However, we caution that predicting activity states from GPS data alone reduces classification accuracy compared to predictions with an accelerometer

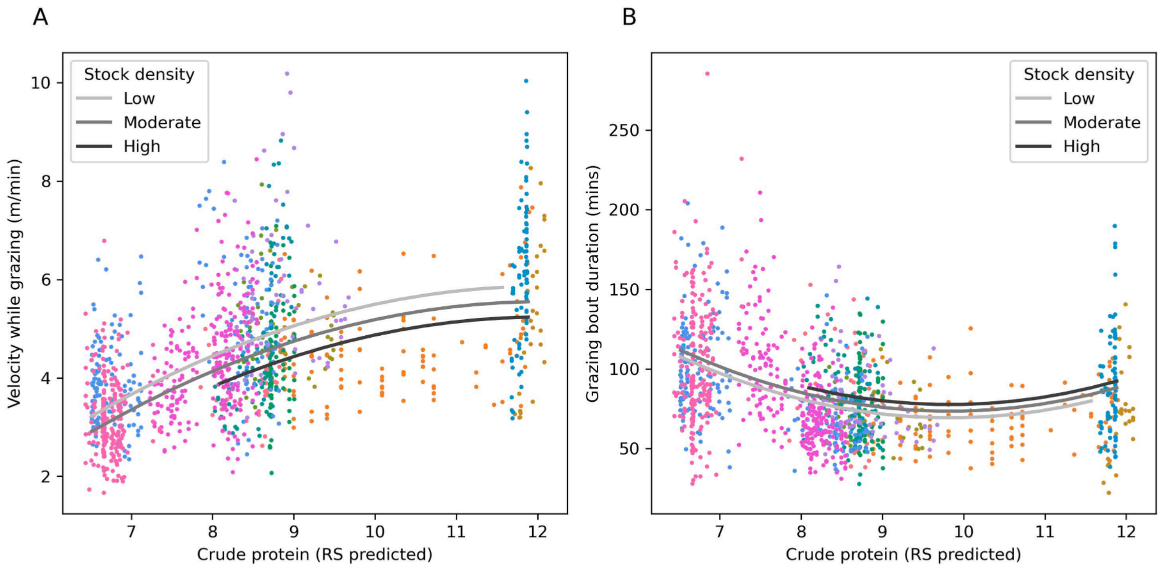

Fig. 5. Relationships between remotely sensed estimates of dietary crude protein content and the daily velocity, VG, of lactating cows while grazing (A), as well as their mean daily grazing bout duration, GBD, (B) in rangeland of northeastern Wyoming. Lines show the relationships as modelled by the generalised mixed models fit in this study (see Table 2). Stock density categories are based on the range of observed stock densities in the study and set at: Low = 0.1, Moderate = 0.2 and High = 0.3 animal units ha^{-1}. Note that lines are only shown within the range of dietary crude protein observed at each stock density. Different colors indicate different pastures occupied by the cattle during the study.

(Brennan et al., 2021; Cunningham et al., 2024), and it remains unclear how this will affect the estimation of foraging behaviour metrics. We also note that mean VG for lactating beef cows in this study varied from ~ 2.5–5.5 m/min over the growing season. In contrast, VG for yearling steers in prior studies was higher, varying from ~4.5–10 m/min over the growing season (Augustine et al., 2022; 2023). This difference may be related to the larger body size, greater intake requirements, and hence less selective foraging by adult cows compared to yearling steers.

Management of the cow herd sometimes induced substantial changes in stock density as animals were rotated among pastures of widely varying sizes, as well as subdivided into multiple small breeding herds during August each year. We evaluated the influence of stock density in all models of foraging behaviour at a daily time step, as prior work showed that VG and TAG both declined with increased stock density for yearling steers, and these changes were directly linked to reduced animal weight gains (Augustine et al., 2023). Consistent with previous findings for steers, both VG and TAG were significantly negatively associated with stock density for lactating cows (Table 2). In other words, both steers and cows graze in more linear pathways (i.e., reduced TAG) and at slower speeds with increased stock density. This reflects less selective grazing due to inter-animal competition resulting in reduced diet quality and lower weight gains.

Finally, we found that TTG did not vary dramatically within or across years of study. This is surprising, given that prior studies have documented significant decreases in TTG as forage quantity and quality decline in the dormant season in Mediterranean grasslands (Henkin et al., 2012; Aharoni et al., 2013). In the Mediterranean climate, a large reduction in TTG (from ~10 to 5 – 6 h) was associated with a substantial decline in forage CP content (Henkin et al., 2012). Perhaps this magnitude of forage quality decline limited passage rates through the rumen to such an extent that cattle were forced to substantially reduce TTG. In our current study, we speculate that the presence of cool-season grasses (which maintain some photosynthetic activity into the fall and early winter period) may enable cattle to maintain high enough dietary CP content to minimise digestive constraints and thereby maintain TTG at a constant level (Fig. S1). We also note that our estimates of TTG were sensitive to the time step at which grazing activity is measured, with TTG measured at 4-second intervals (9.3 – 9.8 hrs per day) averaging more than an hour less than TTG measured at 5-minute intervals (10.8 – 11.3 hrs per day). This finding highlights the critical need to consider how "grazing" is defined and quantified in comparative studies of foraging behaviour (Ungar and Horn, 2025). Despite the lack of seasonal or yearly variation in TTG, we still found that other foraging behaviours, especially VG and GBD, were sensitive to variation in animal weight gain and diet quality.

While our results suggest there is potential utility for real-time monitoring of foraging behaviour via the combination of GPS tracking, accelerometer data, and a method to wirelessly transmit data to the internet, operationalizing such a system for practical use by ranchers will need to address numerous hurdles. First, sufficiently durable GPS receivers and accelerometers need to be available at low enough prices to instrument a sufficient proportion of animals within a herd. Costs of devices we have tested combined with breakage rates are currently too prohibitive to justify deployment on typical working ranches in the western US. In addition, data will need to be acquired from a sufficient proportion of animals in a herd to average across inevitable variability in individual animal behaviour unrelated to forage conditions. In this study, we only successfully tracked 3 – 9 % of the cows in the herd, due to the expense of the devices and device failure over the course of each year. Second, means to transmit data from collars to the internet include via satellite, cell phone, or long-range, wide-area network (LoRaWAN) transmissions, all of which incur additional costs and logistical challenges. Power source is another important consideration; the solar panels used on collars in this study were sufficient to power devices most of the year, but collar operation became intermittent as day length declined in the winter, and when overcast or cloudy conditions persisted for multiple days. While we did detect consistent temporal patterns in foraging behaviour when collars were operational, algorithms to interpret such indices may require calibration to specific management regimes (Augustine et al., 2023), breeds (Cibils et al., 2023), and animal classes (this study vs. Nyamuryekung'e et al., 2022). We are only just beginning to understand the degree to which these factors influence quantitative measures of foraging behaviour. One way to reduce device costs may be to classify behaviours only based on GPS locations, thus alleviating need for the accelerometer. However, previous analyses indicate this will significantly reduce the accuracy of classifying stationary vs. grazing vs. walking behaviours (Augustine and Derner, 2013; Cunningham et al., 2024). In this study, we found that a metric derived from location data alone (travel distance) was moderately predictive although not as robust as metrics that rely on accelerometer data. In cases where livestock managers are already using virtual fencing collars that collect animal locations and transmit data to the internet, adding an accelerometer to quantify grazing activity could enable near-real-time transmission of highly predictive behavioural metrics to the manager.

Given the cost and complexity of on-animal GPS collars and resultant data, we explored the potential for satellite-derived metrics to be used as indicators of expected foraging behaviour, diet quality, and animal weight gain. Remotely sensed estimates of dietary CP content explained about 50 % of the variation in VG, which explained about 80 % of the variation in animal weight gain. Kearney et al. (2022a) demonstrated that animal weight gain of yearling steers could be estimated directly from satellite time series in the shortgrass prairie of northeastern Colorado. Our study confirms that some relationship between satellite imagery and animal performance exists for cow-calf pairs too, though we did not attempt to predict animal weight gain directly. While GPS-derived behaviour metrics provide more fine-grained information and insight into how cattle are actually grazing, and hence are likely a better predictor of animal weight gain across variable vegetation communities, satellite time series can provide additional near-real-time monitoring of expected trends in cattle behaviour and performance.

5. Conclusion

On-animal sensors that monitor foraging behaviours of free-ranging beef cattle have the potential to provide useful measures of cattle performance. Here, we showed that the velocity of beef cows while grazing and the mean duration of grazing bouts were significantly, linearly related to direct measures of the animals' diet quality and weight gain at temporal scales of weeks to months. Furthermore, velocity while grazing and stock density were associated with remotely sensed estimates of diet quality. Our results indicate there is potential utility for near-real-time monitoring of foraging behaviour as an indicator of animal performance via the combination of GPS tracking, accelerometer data, and a method to wirelessly transmit data to the internet. However, operationalizing such a system will likely depend on continuing improvements in sensor durability and data management efficiency, and reductions in sensor and data transmission costs.

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CRediT authorship contribution statement

Augustine David: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Justin D. Derner:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **J. Derek Scasta:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization. **David W. Pellatz:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Sean P. Kearney:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Lauren M. Porensky:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Monte J. Reed:** Writing – review & editing, Resources, Methodology, Investigation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2025.106802.

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