

Can measurements of foraging behaviour predict variation in weight gains of free-ranging cattle?

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ABSTRACT

Context. Technologies are now available to continuously monitor livestock foraging behaviours, but it remains unclear whether such measurements can meaningfully inform livestock grazing management decisions. Empirical studies in extensive rangelands are needed to quantify relationships between short-term foraging behaviours (e.g. minutes to days) and longer-term measures of animal performance. **Aims.** The objective of this study was to examine whether four different ways of measuring daily foraging behaviour (grazing-bout duration, grazing time per day, velocity while grazing, and turn angle while grazing) were related to weight gain by free-ranging yearling steers grazing semiarid rangeland. **Methods.** Yearling steers were fitted with neck collars supporting a solar-powered device that measured GPS locations at 5 min intervals and used an accelerometer to predict grazing activity at 4 s intervals. These devices were used to monitor steers in four different paddocks that varied in forage biomass, and across two grazing seasons encompassing a wide range of forage conditions. Steer weight gain (kg/steer.day) was measured in each paddock during each of three ~60 day time intervals, and daily foraging behaviours were measured during 15–21 days in each interval. **Results.** A model based on only two daily measurements of foraging behaviour, mean grazing bout duration (calculated at a 5 min resolution) and mean velocity while grazing explained 62% of the variation in animal weight gain. **Conclusions.** Daily measurements of foraging behaviour vary substantially in response to varying foraging conditions in space and time, and can effectively serve as indicators of variation in cattle weight gain. **Implications.** On-animal sensors that monitor foraging behaviour have the potential to transmit indicators to livestock managers in real time (e.g. daily) to help inform decisions such as when to move animals among paddocks, or when to sell or transition animals from rangeland to confined feeding operations.

Keywords: accelerometer, average daily gain, forage limitation, grazing bout duration, grazing velocity, semiarid rangeland, shortgrass steppe, weight gain.

Introduction

Free-ranging livestock in extensive rangelands often experience substantial spatiotemporal variability in the biomass and quality of available forage. In response, animals adjust their foraging behaviours at multiple temporal scales, ranging from bite formation and rate, to the length of foraging bouts, and the amount of time spent foraging within a day, week or season (e.g. Brosh *et al.* 2006; Laca 2008; Braghieri *et al.* 2011). Understanding the magnitude of change in daily foraging behaviours in response to forage quality and daily intake may enable forage behavior measurements to be used as indicators of animal performance (Searle *et al.* 2007; Carvalho *et al.* 2015). Over the past two decades, the ability to measure subdaily to daily foraging behaviours has advanced rapidly through development of technologies to remotely monitor animal movement pathways *via* GPS collars, and simultaneously monitor other types of activity (e.g. heart rate and movements associated with grazing activity) *via* sensors (Brosh *et al.* 2006; Ungar and Rutter 2006; Ungar *et al.* 2011; Augustine and Derner 2013; Barwick *et al.* 2020; Raynor *et al.* 2021). One key advance has been the ability to monitor and classify diurnal animal location

and foraging activity (e.g. Raynor *et al.* 2021; Suparwito *et al.* 2021). If daily foraging behaviours can provide reliable indicators of animal performance across paddocks and management systems, they could be used by managers for timing herd rotations among paddocks, assessing optimal stocking densities on the basis of current forage conditions, and determining supplement needs or ideal timing to move livestock among types of extensive rangelands or to confined finishing operations (Peel 2003; Da Trindade *et al.* 2012; Imaz *et al.* 2020).

Recent studies of diurnal foraging activity have begun to quantify variation in time spent grazing and distance travelled per day for different cattle breeds using the same forage conditions, as well as variation within a breed between wet and dry seasons (Aharoni *et al.* 2013; Spiegel *et al.* 2019). In some cases, shifts in behaviour or differences among breeds may be expressed only under conditions when forage biomass and/or quality is low (Braghieri *et al.* 2011; Aharoni *et al.* 2013). However, the direction and magnitude of these changes may be difficult to predict. During periods of higher forage quality and/or biomass, animals may be able to forage more selectively, and that might change the length of grazing bouts, short-term intake rate (e.g. g per minute), and grazing time per day (Carvalho *et al.* 2015). However, increased diet quality could also be achieved with slower, more selective searching and prehension bites (i.e. area-restricted search; Kareiva and Odell 1987), with little change in short-term intake, but a reduction in time spent ruminating and increased grazing time per day. For example, cattle grazing desert grasslands substantially increased grazing time per day when grazing lush, green herbage, as compared with dry-season forage (Brosh *et al.* 2006). Empirical studies in extensive rangelands are needed to unravel the complex interactions among foraging behaviours expressed over minutes to days, and how they relate to measures of animal performance. Improved understanding of which behavioural measurements are most sensitive to changing forage conditions could additionally assist development of on-animal sensors that could detect impending changes in animal performance and transmit these indicators to livestock managers in real time.

We examined the use of a GPS tracking collar combined with an accelerometer to quantify grazing behaviours that may be associated with measures of animal weight gain. Our first objective was to examine the degree to which grazing

time per day varies in relation to the temporal resolution of the calculation of grazing activity, as well as in response to spatiotemporal variation in forage conditions both early in the growing season when vegetation was green and actively growing, and later when vegetation was senescing. Our second objective was to examine how additional measurements of daily foraging behaviour, such as movement rate, complexity of the foraging pathways, and length of foraging bouts could be used along with grazing time per day to predict variation in cattle weight gain. We hypothesised that behavioural measurements of foraging selectivity could potentially serve as better indicators of forage limitation and/or animal performance than would time spent grazing per day.

Materials and methods

Study area

All research was conducted at the United States Department of Agriculture (USDA)–Agricultural Research Service’s Central Plains Experimental Range (CPER), a Long-Term Agroecosystem Research network site that encompasses approximately 6400 ha of shortgrass steppe in north-eastern Colorado (40°50’N, 104°43’W). Mean annual precipitation was 340 mm and mean growing-season precipitation (April–August) was 241 mm. The CPER was subdivided into paddocks that vary from 65 to 390 ha in size, and they have been grazed by cattle since the station was established in 1939. Topography consisted of gently undulating plains at a mean elevation of 1640 m. Soils consisted of deep, well drained, fine sandy loams to loamy sands on alluvial flats and upland plains (Kelly *et al.* 2008). All research followed the Institutional Animal Care and Use Committee protocol (#CPER-4) approved March 2019 by the USDA–Agricultural Research Service in Fort Collins, CO, USA.

Cattle foraging behaviour was studied during 2019 and 2020 in four 130-ha paddocks that were selected to represent a gradient from high to low standing forage biomass and total herbaceous productivity during the growing season (Table 1, Fig. 1). Paddock 1 contained soils associated with the Sandy Plains ecological site (USDA 2007a) and was dominated by C₃ perennial grasses (*Pascopyrum smithii* and *Hesperostipa comata*) combined with an understorey of C₄

Table 1. Description of the four study paddocks at the Central Plains Experimental Range in north-eastern Colorado, USA.

Paddock	Forage biomass	Plant community	Stocking rate (animal equivalents/ha)
1	High	C ₃ midgrass	Moderate (0.21)
2	Moderate	C ₄ shortgrass/C ₃ midgrass	Moderate (0.19)
3	Low	C ₄ shortgrass	Heavy (0.27)
4	Low	C ₄ shortgrass/C ₃ midgrass	Moderate (0.19) + prairie dogs

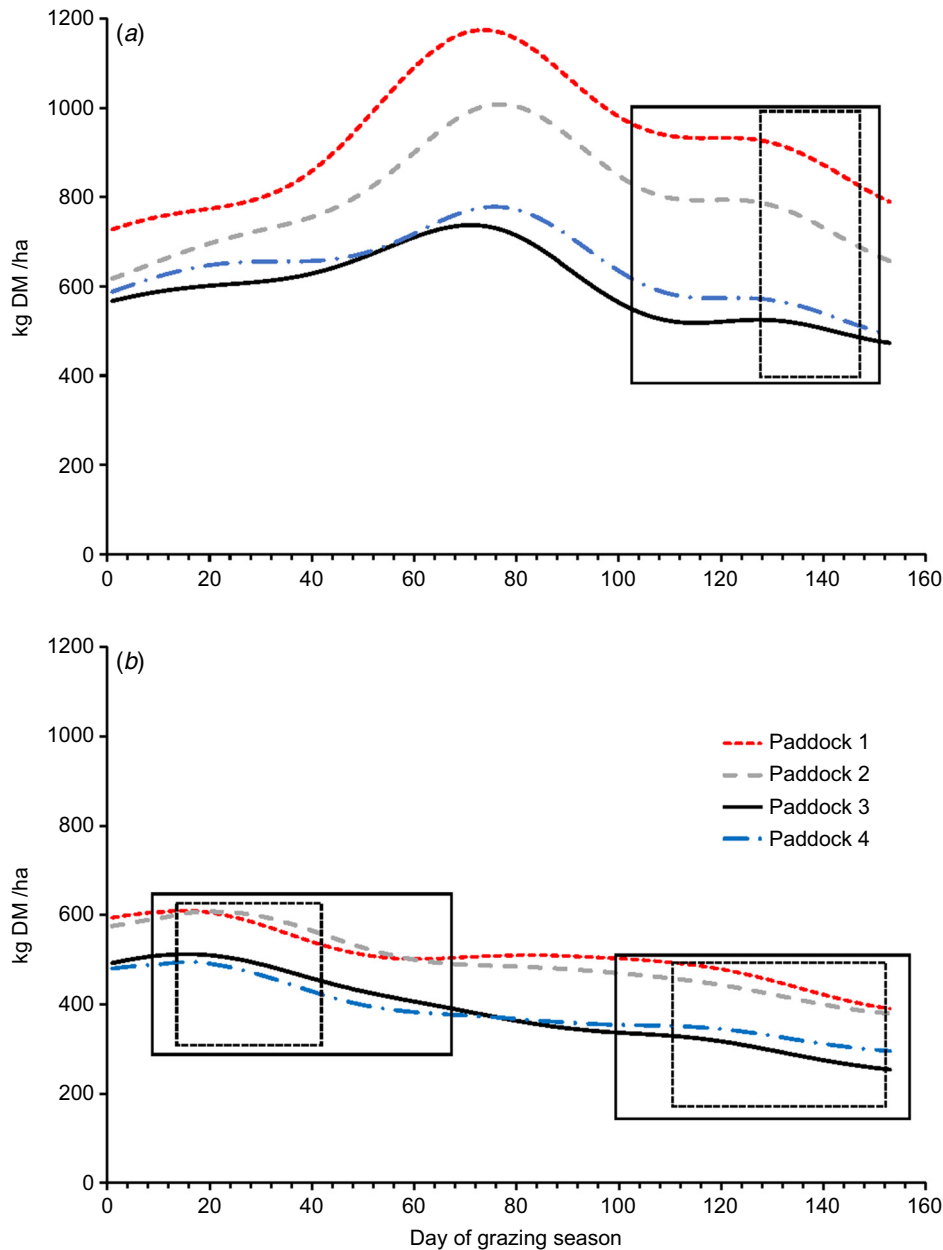


Fig. 1. Daily estimates of standing forage biomass derived from the Harmonized Landsat–Sentinel remote-sensing product for four study paddocks at the Central Plains Experimental Range in north-eastern Colorado, USA, in (a) 2019 and (b) 2020. Solid black boxes show the time period over which average daily weight gain of steer was measured, and dashed boxes within the solid boxes show associated time periods when cattle foraging behavior was quantified using a GPS collar and activity sensor. Day 1 on the x-axis is 1 May.

shortgrasses (*Bouteloua gracilis* and *B. dactyloides*) that had been grazed at a moderate growing-season stocking rate for the past 30 years. Prior measurements during near-average production years of 2016–2018 (Augustine *et al.* 2020) found that this soil type and plant community yielded mean herbaceous vegetation production of 1050 kg DM/ha.

The remaining three paddocks had soils associated with the Loamy Plains ecological site (USDA 2007b). Paddocks 2

and 3 were consistently grazed at moderate and heavy growing-season stocking rates respectively, since 1939, as part of a long-term stocking-rate experiment (Porensky *et al.* 2017). Paddock 2 was dominated by C₄ shortgrasses coexisting with a subdominant layer of C₃ perennial grasses. During 2016–2018, this soil and plant community yielded net herbaceous production of 770 kg DM/ha (Augustine *et al.* 2020). In Paddock 3, the history of heavy grazing (~50%

greater than in Paddock 2) has maintained a C₄-dominated plant community where C₃ perennial grasses are rare (Porensky *et al.* 2017). During 2003–2013, this history of heavy grazing reduced herbaceous production, on average, by 25% compared with moderately grazed paddocks (Irisarri *et al.* 2016). Paddock 4 was grazed by cattle at a moderate stocking rate for the past 30 years, and was dominated by C₄ shortgrasses with subdominant C₃ perennial grasses (as in Paddock 2). In addition, Paddock 4 had been grazed by black-tailed prairie dogs (*Cynomys ludovicianus*), which are a colonial, burrowing rodent that consumes a similar diet as does cattle. The proportion of Paddock 4 occupied by prairie dog colonies has fluctuated since the mid-1990s in response to disease outbreaks (Augustine and Derner 2021). During 2018, prairie dog colonies occupied 48% of Paddock 4, which has been shown to substantially reduce standing forage biomass when compared with areas not occupied by colonies during average-precipitation years (Augustine and Springer 2013). It was therefore expected that the daily standing forage biomass over the course of the growing season in the four study paddocks would follow the order of 1 > 2 > 3 = 4.

Forage conditions

Kearney *et al.* (2022) recently calibrated a model that uses the Harmonized Landsat–Sentinel dataset (Claverie *et al.* 2018) to generate smoothed daily estimates of standing herbaceous biomass at a 30 × 30 m pixel resolution for this site. The model was calibrated specifically to the vegetation, soils, and weather patterns in our study area by using 8 years of previous ground-based vegetation biomass measurements (Kearney *et al.* 2022). This model was used to estimate daily standing herbaceous biomass for each of the four study paddocks during the 2019 and 2020 growing season. The model estimates standing biomass (including live and dead) of grasses and forbs only and does not include cactus or shrubs, which are generally not eaten by cattle.

Forage quality was measured by conducting direct observations of grazing steers in Paddocks 1 and 2 during 10 min grazing bouts, as part of a continuous bite-monitoring study described by Raynor *et al.* (2021). At the conclusion of each day of direct observations conducted in a paddock, technicians collected hand-plucked samples of each of the types of bites that they observed, where bite types were classified by plant functional group and bite depth, following Agreil and Meuret (2004) and Bonnet *et al.* (2015). After the hand-plucked samples were oven dried, a composite forage-intake sample was generated by weighting a pooled sample of bite types by the number of bites collectively observed for that type during a given observation day. Six of these weighted daily forage samples were obtained for each paddock and study period combination. Samples were analysed for crude protein and total digestible nutrient content by near-infrared spectroscopy (NIRS) at Ward

Laboratories (Kearney, NE, USA), using calibrations developed by the NIRS Forage and Feed Testing Consortium (www.nirsconsortium.com). Due to the labour-intensive nature of forage-sample collection method, forage-quality samples were not collected in Paddocks 3 and 4.

Cattle stocking rates and measurements of liveweight and foraging behaviour

Study paddocks were stocked with yearling steers that entered in mid-May and grazed until early October each year. Steers were mixed-European breeds provided by local ranchers, and were weighed individually at the beginning and end of the grazing season. Steers were weighed without overnight restriction of water or food; however, weights were corrected for estimated overnight shrinkage following Derner *et al.* (2016). Steers were additionally weighed 53 days before the end of the 2019 grazing season, 59 days after the start of the 2020 grazing season, and 60 days prior to the end of the 2020 season, to obtain seasonal estimates of average daily weight gain (ADG) that corresponded to the time periods when cattle foraging behaviour was measured (see below and Table 1). Each year, stocking rates were set prior to the grazing season by a group of stakeholders that included local ranchers, land managers, and representatives of non-governmental organisations (Wilmer *et al.* 2018). Generally, yearling steers at our study site gain ~125–130 kg liveweight during the May–October grazing season; hence, it was assumed that one yearling steer = 1.03 animal equivalents (AE), as recommended by McLennan *et al.* (2020) for livestock of moderate productivity. On the basis of stakeholders' recommendation, the moderate stocking rate on Paddock 1 (Sandy Plains) was 0.21 AE/ha, and on Paddocks 2 and 4 (Loamy Plains), it was 0.19 AE/ha over 136 and 137 day periods in 2019 and 2020 respectively. The heavy stocking rate for Paddock 3 (Loamy Plains) was 0.27 AE/ha, or ~50% above moderate.

In 2019, MOOnitor GPS collars (www.moonitorcows.com) were deployed on four randomly selected steers in each study paddock from 5 to 30 September, which corresponded to a period of low and senescent forage biomass, when it was anticipated that cattle weight gain may vary substantially among paddocks. Collars were set to collect GPS fixes every 5 min, and additionally recorded the steer's predicted activity state (resting, grazing, or walking) at 4 s intervals derived from a proprietary algorithm applied to measurements recorded by a three-axis accelerometer. In 2020, MOOnitor collars were deployed on four randomly selected steers in each paddock at the beginning of the grazing season, when vegetation was green and increasing in biomass (albeit at rates lower than during average precipitation years), and again at the end of the grazing season, when vegetation was senescent and at unusually low biomass in Paddocks 3 and 4 (<400 kg DM/ha; Fig. 1). In 2019, some collars failed to collect data (including all collars in Paddock 2)

because problems with the connection of the neck straps to the solar panels and GPS receiver caused them to shift sideways rather than being centred on the steer's neck (Supplementary Fig. S1), which prevented sufficient daily charging. This strap connection was modified in 2020, but some collars still occasionally shifted to where they were not centred on the neck, resulting in incomplete charging on some days, depending on the steer's orientation to the sun and weather conditions. Such days were not included in analyses.

To assess the validity of predictions generated by the activity sensors, direct visual observations of steer behaviours were conducted during each of the three deployment intervals (late summer of 2019, early and late summer of 2020). Following [Augustine and Derner \(2013\)](#), visual observations occurred during daylight hours, typically beginning during morning hours and continuing until early afternoon, with the goal of encompassing bouts of both grazing and resting within a given day. Cattle activity was classified into categories consisting of grazing (including grazing while walking), travelling (walking without grazing), standing, bedding, grooming, drinking, or consuming mineral supplements. Activity timing and duration were recorded every 30 s. When an animal changed activity, observers noted the precise transition time. If the new activity persisted for >15 s, then the transition was recorded on the field data sheet. If the animal resumed prior activity in <15 s, the interlude was ignored.

Data analyses

To evaluate concordance between activity sensor predictions and direct observations of grazing steers, both data types were summarised at 1 min intervals and were linked on the basis of time stamps. For direct observations, if the minute interval included only one 30 s grazing period, it was still classified as grazing. For activity sensor output, each minute was classified as 'grazing' when >50% of the 4 s intervals in that minute were classified as grazing.

To examine daily grazing behaviour, the activity data recorded at 4 s intervals were used to calculate the time spent grazing each day in hours ($\text{GHrs}_{4\text{sec}}$, in hours) and the mean grazing bout duration ($\text{GBD}_{4\text{sec}}$, in seconds) each day, where a grazing bout was defined as a continuous string of 4 s intervals of grazing. For example, if the sensor measured that an animal was grazing for 20 consecutive 4 s intervals, then was not grazing for one or more subsequent 4 s intervals, the bout duration was 80 s. In addition, the 4 s records of grazing activity were used to classify each 5 min interval between the GPS fixes as either a grazing interval (>50% of the 5 min interval spent grazing) or non-grazing interval (<50% spent grazing). A 5 min resolution version of grazing time per day ($\text{GHrs}_{5\text{min}}$, in hours) was calculated as the sum of 5 min grazing intervals, and a 5 min resolution of the mean grazing bout duration ($\text{GBD}_{5\text{min}}$, in minutes) was calculated 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. 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 6 min or more, and demonstrated that grazing-bout duration of sheep varied inversely with forage quality. For all analyses, data were used only from days when the MOOnitor device successfully collected GPS and activity data for $\geq 99\%$ of the 4 s intervals.

The GPS fix data were used to calculate the mean velocity for each 5 min interval during which the majority of the 4 s intervals were classified as grazing (VG, in m/s). In addition, for each series of three consecutive GPS fixes where the animal was classified as grazing for the entire 10 min time period, the 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, this 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° .

The weight gain of each collared steer was calculated on the basis of liveweight measured at the start and end of each study period ([Table 1](#)). Each weight-gain interval was approximately 60 days, which encompassed the collar deployment intervals ([Table 1](#)). Models of cattle weight gain were fit as a function of all possible combinations of the foraging behaviour measurements, and an information-theoretic approach was used for model selection ([Anderson 2008](#)), where Akaike's information criterion with a correction for a small sample size (AICc) was used. All statistical analyses were performed using JMP v13.2.1 from the SAS Institute, Inc. (Cary, NC, USA).

Results

Forage conditions

In 2019, peak biomass varied among paddocks from ~700 to 1100 kg DM/ha in the middle of the growing season, and then senesced rapidly during the second half due to dry conditions. Paddocks 1 and 2 contained substantially more standing forage biomass than did Paddocks 3 and 4 during late summer, when measurements of cattle weight gains and foraging behaviour were conducted ([Fig. 1a](#)). Forage quality in Paddocks 1 and 2 (not measured in Paddocks 3 and 4) was especially low in this study period, compared with early summer of 2020 ([Table 2](#)). In 2020, biomass increased marginally during the first 20 days and remained green and highly digestible throughout the early summer study period, reaching a peak of 500–600 kg DM/ha, with Paddocks 1 and 2 supporting ~100 kg DM/ha more

Table 2. Time periods when measurements of cattle weights and cattle foraging behaviour occurred for yearling steers grazing shortgrass rangeland at the Central Plains Experimental Range in north-eastern Colorado, USA, and variation in total digestible nutrients and crude protein content of forage consumed by steers in Paddocks 1 and 2.

Study period	Cattle weigh date		Days	Collar date		Number of steers with data	Mean number of days with data	Total digestible nutrients (%)		Crude protein (%)	
	Start	End		On	Off			Paddock 1	Paddock 2	Paddock 1	Paddock 2
(1) Late summer, 2019	8/8/2019	30/9/2019	53	6/9/2019	26/9/2019	9	18	67.6 (1.4)	57.5 (1.3)	11.3 (1.2)	8.4 (0.6)
(2) Early summer, 2020	11/5/2020	9/7/2020	59	16/5/2020	11/6/2020	14	15	69.7 (0.9)	67.0 (1.1)	17.9 (0.6)	16.4 (0.7)
(3) Late summer, 2020	6/8/2020	5/10/2020	60	20/8/2020	2/10/2020	13	21	63.3 (1.0)	63.9 (1.7)	11.0 (0.6)	12.0 (0.8)

The number of steers and days with data refer specifically to the data collected by cattle collars.

biomass than did Paddocks 3 and 4 (Fig. 1b). Due to lower rainfall and forage growth in 2020, study paddocks had especially low forage biomass during the late-summer study period (Fig. 1b), with levels in Paddocks 3 and 4 approaching conditions at which supplemental feed is recommended to maintain cattle weight gain in our study system (Bement 1969). Forage quality in Paddocks 1 and 2 at this time was much reduced compared with that in early summer (Table 2).

Collar operation and activity sensor validation

The collars successfully collected GPS fix and activity sensor data for nine steers in late summer of 2019, 14 steers in early summer of 2020, and 13 steers in late summer of 2020 (Table 1).

Concurrent visual observations and collar-based measurements of grazing activity were obtained for three, six, and five steers in late summer 2019, early summer 2020, and late summer 2020 respectively, to determine the reliability of the collar-based measurements. Two of these direct observation periods were only 40 min long. The remaining 12 periods ranged from 203 to 345 min (mean = 297 min), for a total of 3648 min of concurrent measurements. Of these minutes, 2173 min were correctly classified as a grazing interval, 1160 min were correctly classified as a non-grazing interval, 203 min were falsely classified as grazing, and 112 min were falsely classified as non-grazing intervals. This yielded a false positive rate of 8.5% (95% CI = 4.3%), false negative rate of 8.8% (95% CI = 7.2%), and overall error rate of 8.6% (95% CI = 3.6%), which is slightly lower than error rates reported for other grazing activity sensors (Ungar *et al.* 2011; Augustine and Derner 2013).

Daily foraging behaviour measurements versus ADG

We found that GHrs_{4sec} and GHrs_{5min} were closely correlated ($r^2 = 0.91$, $P < 0.001$; Fig. S2), with similar means of 10.7 h/day and 10.6 h/day respectively. However, estimates from 5 min intervals varied more widely, from 6.1 to 15.9 h/day,

while estimates from the 4 s intervals varied only from 7.2 to 14.9 h/day. The regression largely followed the 1:1 line for values from 8 to 13 h, but the 5 min estimates were greater than expected (above 1:1 line) for days with grazing times greater than 13 h, and lower than expected (below 1:1 line) for days with grazing times less than 8 h. This result indicated that GHrs_{4sec} was more accurate than GHrs_{5min}; hence, we considered only GHrs_{4sec} in all models of weight gain. GHrs_{4sec} varied significantly among the three study periods, with increased daily grazing time in early summer of 2020 with green, highly digestible vegetation (11.7 ± 0.18 h; mean \pm s.e.), compared with late summer of 2019 (10.0 ± 0.21 h) and 2020 (10.4 ± 0.16 h) with senescent vegetation.

We also found that GBD_{4sec} and GBD_{5min} were correlated, but much less strongly than was grazing time ($r^2 = 0.31$, $P < 0.001$). The lower correlation reflects that they are measuring two different but related behaviours, where the 4 s estimate is measuring how frequently the animal stops taking bites, typically to search for its next set of bites. The 5 min estimate is primarily a measure of how frequently the animal stops a grazing bout entirely, often arising from a combination of the animal raising the head to survey its environment, searching for or walking to a new area in which to graze, or stopping to rest and ruminate. Because of their low correlation, we considered models with both estimates, but only included one or the other in any given model.

Models of ADG based on the two different procedures to measure duration showed that GBD_{5min} performed better than GBD_{4sec} (Table 3). In addition, single-predictor models based on TAG, GHrs_{4sec} and VG all performed better than did the null model (reducing AICc by 2.88, 2.94, and 20.16 respectively, compared with the null; Table 3). When we fit all possible models on the basis of the main effects, including all possible combinations of two or more of these four behavioural measurements (GBD_{5min}, TAG, GHrs_{4sec}, and VG), the model based only on GBD_{5min} and VG provided the best fit to the data (Table 2). These two

Table 3. Comparison of 11 linear regression models predicting average daily weight gain as a function of mean daily grazing-bout duration calculated at a 5 min resolution (GBD_{5min}), grazing hours per day at a 4 s resolution ($GHrs_{4sec}$), mean velocity while grazing (VG), and mean turning angle while grazing (TAG) for yearling steers grazing shortgrass rangeland at the Central Plains Experimental Range in north-eastern Colorado, USA, on the basis of Akaike's information criteria statistics calculated with a correction for small sample sizes (AIC_c).

Model	AIC_c	ΔAIC_c
GBD_{5min}, VG	158.49	0.00
GBD_{5min} , VG, TAG	161.04	2.54
GBD_{5min} , VG, $GHrs_{4sec}$	161.04	2.55
GBD_{5min} , VG, $GHrs_{4sec}$, TAG	163.72	5.23
VG	170.11	11.62
VG, $GHrs_{4sec}$	171.98	13.49
VG, TAG	172.59	14.10
GBD_{5min}	172.69	14.20
GBD_{4sec}	179.47	20.97
TAG	187.32	28.83
$GHrs_{4sec}$	187.38	28.89
Null	190.26	31.77

The final selected model is shown in bold.

measurements of daily grazing behaviour were able to predict 62% of the variation in ADG (Fig. 2), where

$$\text{Average daily gain (kg/steer.day)} = 0.438 - 0.0049GBD_{5min} + 0.132VG.$$

The standard error for the estimate of the intercept was 0.288, and for the estimates of the coefficients for GBD_{5min} and VG were 0.0012 and 0.029 respectively.

Discussion

There are several technologies available that may have application for summarising daily foraging behaviour measurements and transmitting them to smart devices through satellite transmissions (e.g. www.moonitor.com), cell phones (in areas with adequate coverage), or through non-cellular, long-range and low-power wireless, wide-area networks (employed by companies developing virtual fence technologies in Australia, Europe, and North America). These technologies create the potential to monitor changes in forage conditions within paddocks and/or animal performance via changes in foraging behaviour. Here, we examined how four measurements of daily grazing behaviour varied across paddocks with varying forage biomass and sward composition,

and across two grazing seasons within a semiarid, temperate rangeland.

First, for daily time spent grazing, we found the temporal resolution at which grazing time is calculated to be an important factor. Using an activity sensor that classified each 4 s interval as grazing or non-grazing, our estimates of daily grazing time rarely exceeded 14 h or were less than 7 h. In contrast, when each 5 min interval was classified as grazing or non-grazing, the frequency of daily grazing times above or below these extremes increased. This result suggests that using accelerometers to classify behaviour at subminute time scales may provide more robust estimates of grazing time than do measurements conducted at 5 min or 10 min intervals (e.g. as estimated by 2-axis mechanical sensors; Augustine and Derner 2013). At the 4 s resolution, daily grazing time varied significantly among the study periods, and explained more variation in animal weight gain than did a null model (Table 2). When cattle are grazing a sward dominated by green leaves, initial depletion of the sward can lead to an increase in daily grazing time as the animals compensate for declining bite size (Benvenuti *et al.* 2016). However, as the quality of available forage declines due to plant maturation and senescence, grazing time per day can decline substantially as intake is restricted by digestion rate. In this study, we found that grazing time per day declined by ~1.5 h when steers were grazing senescent, low-quality vegetation late in the growing season. Brosh *et al.* (2006) reported an even larger decline in daily grazing time of ~5–6 h between growing and dormant seasons in arid Israeli rangelands. Daily grazing time did not improve predictions of animal weight gain when added to a model that already included grazing bout duration and velocity while grazing. Thus, the importance of shifts in daily grazing time as an indicator of animal performance may depend on a variety of factors such as the magnitude of the change in forage conditions, diversity and composition of the rangeland, and breed or genetic strain of the animals (Aharoni *et al.* 2013; Spiegel *et al.* 2019).

Second, grazing-bout duration provided a valuable indicator of differences in animal weight gain. We calculated bout duration at two different temporal resolutions because we expected that they would represent two different levels of foraging selectivity. If the start and end of a bout is defined as a switch between grazing and non-grazing activity for just a 4 s interval, then 'bouts' can become longer when the animal rarely pauses between bites or feeding stations to search for the next bite or station. In contrast, if a 'bout' ends when the animal stops grazing for 5 min or more, then bouts can become longer as the animal engages in a few long, continuous periods of intense grazing each day (often an hour or more), rather than several bouts shorter than an hour, which are punctuated by longer searches for the next feeding patch (e.g. collection of feeding stations). We found that GBD_{5min} was a better predictor of animal weight gain than was any other foraging-behaviour

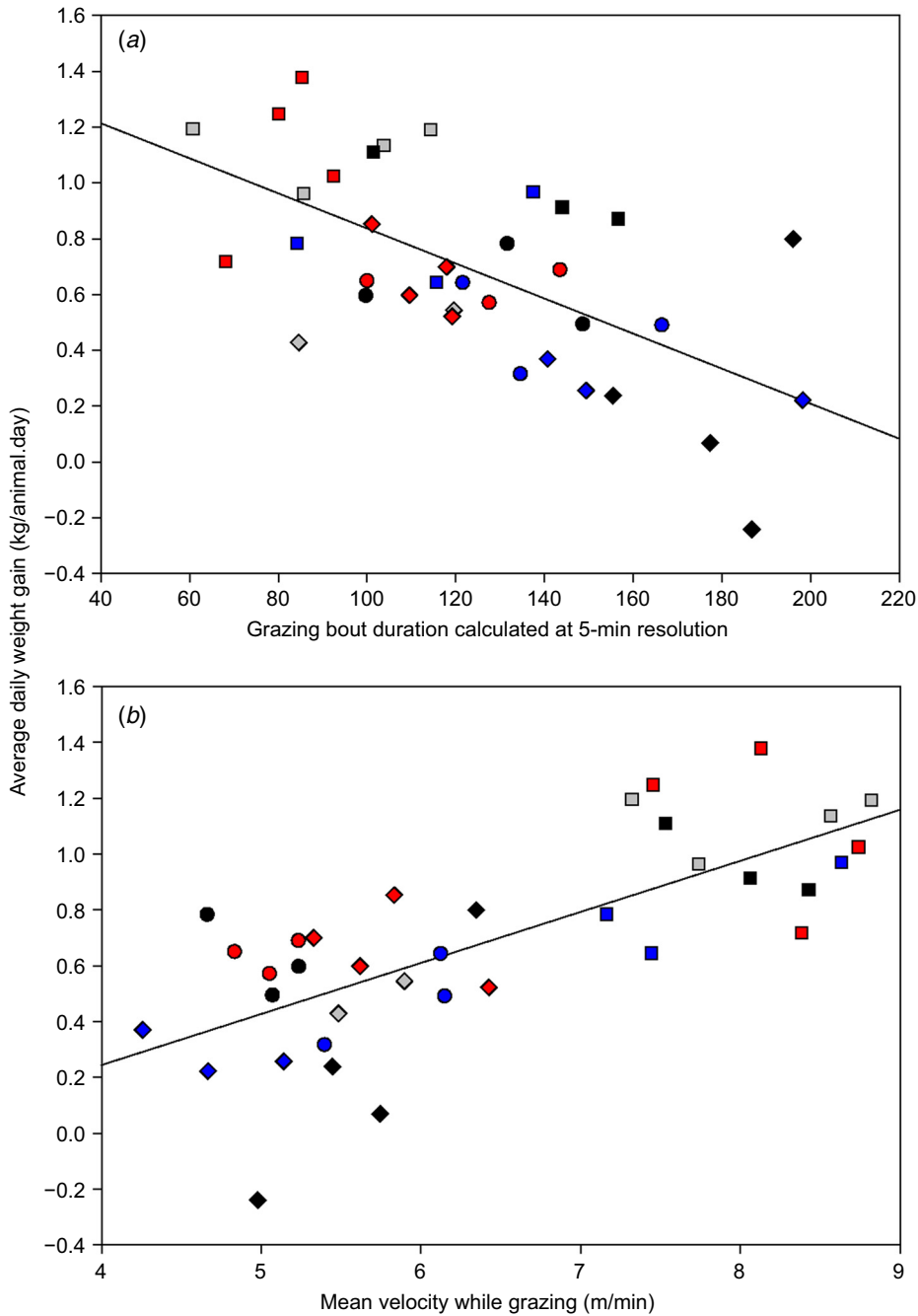


Fig. 2. Relationships between average daily weight gain of yearling steers (kg/animal.day) during a given study period versus (a) mean grazing bout calculated daily at a 5 min temporal resolution ($GBD_{5\text{-min}}$) for that entire study period, and (b) mean velocity of the animal while grazing shortgrass rangeland of north-eastern Colorado, USA. Symbol colours correspond to Paddocks 1 (red), 2 (grey), 3 (black), and 4 (blue) from Fig. 1. Symbol shapes correspond to late summer of 2019 (circles), early summer of 2020 (squares), and late summer of 2020 (diamonds).

measurement. One potential explanation is that when animals are given access to swards with both larger and more digestible bites, they can increase diet quality by being more selective in which feeding patches they choose, with an associated increase in time periods of 5 min or more

spent searching for the next feeding patch. In addition, animals with access to larger and more digestible bites can increase short-term intake rate and thereby reach satiety and gut fill more rapidly, thereby reducing grazing bout length (Orr et al. 2001). Although our findings are specific

to the shortgrass rangeland grazed by these study steers, they suggest grazing bout duration be examined more widely as a key indicator of changes in animal performance.

Third, we found that animal velocity while grazing was an important indicator of variation in animal weight gain. When vegetation was green and growing early in 2020, grazing velocities were consistently ≥ 7.2 m/min, but during late-summer conditions with senescent, low-quality forage, velocities were reduced to < 6.5 m/min (Fig. 2b). Steers may have increased their velocity while grazing high-quality vegetation, so as to increase encounter rates with high-quality bites, and thereby increase diet quality without a reduction in short-term intake rate. To our knowledge, this is the first demonstration that grazing velocity, when used in combination with grazing bout duration, can be a second key indicator of animal performance. Given the increasing prevalence of GPS tracking studies of cattle at 5 min or shorter time steps, we also encourage evaluation of this indicator across a broad spectrum of rangelands and livestock types.

Fourth, we hypothesised that mean turning angle while grazing might increase with improved weight gain, because animals that are foraging more selectively (and hence acquiring higher-quality diets) may move in more convoluted pathways, which could be reflected in the turn angle. Under the conditions of our study, we found no strong correlation between turn angle and animal performance. However, our study examined only steers grazing at relatively low stock densities (3.8–5.8 ha/animal), and we suggest that turn angle while grazing could still potentially be sensitive to management approaches that employ higher stock densities, or paddocks with greater diversity of forage patch types. We also note that our turn angles were calculated at a 5 min time step, which may be too coarse to detect how foraging pathway tortuosity co-varies with diet quality. We encourage future studies to still consider turn angle while grazing as a potential indicator of animal performance, and, in particular, to continue to evaluate how grazing pathway complexity may be related to changes in stock density and vegetation diversity.

Overall, our findings support the idea that foraging behaviour measurements could serve as an indicator of changes in animal performance, but substantially more evaluation is needed to test this idea and develop weight gain predictions in varying types of rangelands, and across varying combinations of circumstances. We acknowledge that other technologies to monitor animal performance, such as walk-over weigh scales at water locations, remote sensing of forage biomass and quality, and faecal analyses of diet quality may be more effective under certain conditions. At the same time, the use of multiple indicators of cattle performance, including foraging behaviour measurements, could increase manager confidence and timeliness in their decision-making, as well as provide insights as to why animal performance is declining during the grazing season. Additionally, for applications based on foraging behaviour

measurements to be useful and economical, the economic benefits of changes in management decisions would need to exceed costs of the technology. Such measurements may be most economical when used in combination with other emerging technologies, such as virtual fencing, which already require that the livestock wear a collar designed to communicate remotely with livestock managers. Behavioural measurements may also be most valuable under extensive rangeland conditions where livestock are not visited or observed frequently by managers. We encourage future studies to evaluate the measurements presented here across diverse types of rangelands worldwide, using research designs that encompass spatial variation in forage conditions associated with differing soils, plant communities (of varying heights and plant densities), and grazing management strategies, as well as temporal variation among seasons and years that differ in plant phenology and production levels.

Conclusions

We showed that daily measurements of cattle foraging behaviour can serve as indicators of changes in cattle weight gains associated with spatial and temporal variation in forage conditions. In the case of yearling steers grazing shortgrass rangeland in central North America, mean daily grazing-bout duration and velocity while grazing were the most valuable predictors of variation in individual weight gain, whereas grazing time per day and mean turn angle while grazing did not additionally improve predictions of weight gain. Given ongoing technological advances in on-animal sensors that can monitor animal foraging behaviour, these findings provide a pathway to provide cattle managers with daily updates of indicators of animal performance.

Supplementary material

Supplementary material is available [online](#).

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Data availability. Data supporting this publication are available online at data.nal.usda.gov/dataset/data-from-can-measurements-of-foraging-behaviour-predict-variation-in-weight-gains-of-free-ranging-cattle (<https://doi.org/10.15482/USDA.ADC/1524788>).

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