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Predicting spatial-temporal patterns of diet quality and large herbivore performance using satellite time series

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Abstract

Adaptive management of large herbivores requires an understanding of how spatial-temporal fluctuations in forage biomass and quality influence animal performance. Advances in remote sensing have yielded information about the spatial-temporal dynamics of forage biomass, which in turn have informed rangeland management decisions such as stocking rate and paddock selection for free-ranging cattle. However, less is known about the spatial-temporal patterns of diet quality and their influence on large herbivore performance. This is due to infrequent concurrent ground observations of forage conditions with performance (e.g., mass gain), and previously limited satellite data at fine spatial and temporal scales. We combined multi-temporal field observations of diet quality (weekly) and mass gain (monthly) with satellite-derived phenological metrics (pseudo-daily, using data fusion and interpolation) to model daily mass gains of free-ranging yearling cattle in shortgrass steppe. We used this model to predict grazing season (mid-May to October) mass gains, a key management indicator, across 40 different paddocks grazed over a 10-year period ($n = 138$). We found strong relationships between diet quality and the satellite-derived phenological metrics, especially metrics related to the timing and rate of green-up and senescence. Satellite-derived diet quality estimates were strong predictors of monthly mass gains ($R^2 = 0.68$) across a wide range of aboveground net herbaceous production. Season-long predictions of average daily gain and cattle off-mass had mean absolute errors of 8.9% and 2.9%, respectively. The model performed better temporally (across repeated observations in the same paddock) than spatially (across all paddocks within a given year), highlighting the need for accurate vegetation maps and robust field data collection across both space and time. This study demonstrates that free-ranging cattle performance in rangelands is strongly affected by diet quality, which is related to the timing of vegetation green-up and senescence. Senescing vegetation suppressed mass gains, even if adequate forage was available. The satellite-based pseudo-daily approach presented here offers new opportunities for adaptive management of large herbivores, such as identifying within-season triggers to move livestock among paddocks, predicting wildlife herd health, or timing the grazing season to better match earlier spring green-up caused by climate change and plant species invasion.

KEYWORDS
cattle mass gain, Central Plains Experimental Range, diet quality, Landsat, long-term agroecosystem research network, MODIS, rangeland ecology, remote sensing, STARFM

INTRODUCTION

Understanding linkages between primary and secondary productivity is a central focus of both ecological theory and the management of rangelands, which includes a diverse array of grassland and shrubland ecosystems worldwide. Rangelands are characterized by substantial temporal and spatial variability in precipitation and temperature, both within and among years (Augustine, 2010; Knapp & Smith, 2001). This variability affects forage resources and their heterogeneous spatial–temporal distribution (Ganskopp and Bohnert 2009, Browning et al., 2018), which directly influences seasonal performance of livestock (Vavra & Raleigh, 1976) and wild ungulates (Garel et al., 2011; Owen-Smith, 2002). Free-ranging livestock provide a good model system for studying large herbivores since managerial control enables high-quality and high-frequency data collection. While the mechanistic links among diet quality, forage quantity, and livestock performance are well known (Van Soest, 1994), information about how spatial-temporal variability in forage (e.g., the abundance, timing, and duration of access to high-quality forage) affects free-ranging livestock performance remains elusive. This is largely due to the lack of data at a sub-seasonal time step (Rouquette, 2016), as it is labor intensive to monitor animals at frequent intervals while concurrently collecting forage condition data for the area they have been grazing (Ganskopp & Bohnert, 2009).

This lack of knowledge presents challenges for implementing adaptive rangeland management strategies that seek to mitigate the effects of fluctuating forage conditions on large herbivore performance, while also meeting rangeland health and conservation objectives (Williams, 2011). To date, decision-making for adaptive rangeland management has largely relied on (1) coarse-scale, field-derived, correlative relationships, including using growing season precipitation and large-scale climate patterns to predict forage production (Chen et al., 2017) or livestock performance (Derner et al., 2008), and (2) fine-scale, individual site monitoring of key variables on the ground such as rangeland health indicators (Pyke et al., 2002). To support adaptive management on rangelands, new tools are needed that can (1) assess changes in forage conditions throughout the growing season across diverse plant communities and (2) link performance of large herbivores with spatial-temporal changes in forage conditions.

A subset of decision tools for adaptive rangeland management, such as the Livestock Early Warning System (LEWS; Stuth et al., 2004), the Grassland Production Forecast (Grass-Cast; Peck et al., 2019) and others, have begun to fuse applied ecological relationships with remote sensing and predictive modeling. Tools based on remotely sensed data have the unique ability to provide "wall-to-wall" predictions across large or remote areas common to rangelands. Lacking, however, are tools relevant for management decision-making at finer temporal (daily to monthly) and spatial (paddock or ranch) scales. Many managers use rotational grazing strategies employing adaptive triggers based on field-observed vegetation (e.g., growth stage, height) and animal behavior to move livestock to the next paddock (Teague & Barnes, 2017). However, it is difficult to collect field observations frequently across large spatial extents, and relationships between vegetation-based triggers and livestock performance (e.g., mass gains, a key management outcome) are rarely well quantified. Furthermore, remote-sensing applications to rangelands have focused primarily on quantifying forage production (e.g., Eisfelder et al., 2012; Gaffney et al., 2018; Jansen et al., 2018; Zhou et al., 2019), while estimates of forage quality are less common.

Existing forage quality assessments from remote sensing often use airborne hyperspectral (Pullanagari et al., 2018) or high resolution satellite imagery (Adjorlolo et al., 2014), which are cost prohibitive, thus limiting their temporal resolution and the ability to link forage quality with large herbivore performance within the grazing season. Remote-sensing applications with high temporal frequency but low spatial resolution (≥250 m) have captured broad patterns in diet quality, distribution, and performance of large herbivores (Geremia et al., 2019; Hamel et al., 2009; Middleton et al., 2018; Tolleson et al., 2020). Yet these spatially coarse images are poorly correlated with point-based forage quality measurements (Garroutte et al., 2016; Kawamura et al., 2005) making it difficult to link them to fine-scale (e.g., paddock-scale) animal performance and adaptive management decision-making. Recent advances in data fusion techniques permit satellite-based images to be produced pseudo-daily (i.e., some data points are interpolated) at moderately high spatial resolution (30 m) with freely available data (Gao et al., 2015). This time-series data can be used to link fine-scale field data on forage conditions with animal performance, even when data have been collected at different temporal frequencies.

We sought to (1) develop a robust model to predict weekly diet quality (an integrated indicator of paddock-scale forage quality derived from fecal samples) using phenological metrics derived from a pseudo-daily 30-m satellite time series, (2) predict sub-seasonal performance (mass gains) of individual free-ranging yearling cattle based on these diet quality predictions, along with forage production predicted using an existing satellite-based model, and (3) use the relationships among diet quality, forage production, and sub-seasonal mass gains to predict season-long mass gains in independent sites.

METHODS

We combined daily satellite observations with field data sets collected at varying temporal scales to predict pseudo-daily and season-long cattle mass gains (Figure 1). To do this, we first predicted daily diet quality and forage production (biomass) from phenological metrics derived from the satellite time series. We then predicted daily mass gain from the diet quality and biomass estimates and compared predicted season-long mass gains against field data.

Study area

We conducted this study at the USDA-Agricultural Research Service Central Plains Experimental Range (CPER) in north-central Colorado, USA (40°49′ N, 107°46′ W), a Long-Term Agroecosystem Research (LTAR) network site covering approximately 6,270 ha. The study area consists of shortgrass steppe vegetation, with a mix of perennial warm-season (C_4) and cool-season (C_3) grasses and graminoids. The dominant warm season grass is blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths. The most common perennial cool-season graminoids are needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve), and needle-leaf sedge (*Carex duriuscula* C.A. Mey.). Mean annual precipitation is 341 mm with 70% occurring May–September.

Paddocks included in this study ranged from 75 to 260 ha, with most being ~130-ha "half-sections" (Appendix S1: Table S1), and were grazed by free-ranging British-breed yearling steers from mid-May to early October (135 days). Nonmigratory pronghorn antelope (*Antilocapra americana*) are the dominant wild ungulate in the area. Landscape-scale aerial surveys indicate they are present at densities of ~1.0–1.5 pronghorn/km^2 (Pojar et al., 1995), and their presence was unlikely to influence results. Black-tailed prairie dogs (*Cynomys ludovicianus*) are the dominant small-mammalian herbivore in the region, but prairie dogs were excluded from paddocks included in this study using lethal control.

Data acquisition

Weekly diet quality data

We used two measures of diet quality derived from analyses of cattle fecal samples, crude protein (CP) and digestible organic matter (DOM), as indicators of paddock-scale forage quality. Fecal samples were collected from three to five animals per paddock (10%–25% of animals in each herd) weekly during each grazing season from 2014 to 2019 across 10 different paddocks (Appendix S1: Table S1). Samples were analyzed at the Grazingland Animal Nutrition Lab (GANlab) using near infrared spectroscopy (Lyons et al., 1995; Lyons & Stuth, 1992). Not every herd was sampled every week or every year, resulting in a total of 199 samples.

Monthly cattle mass gain data

We calculated paddock-scale average daily gain (ADG, $kg \cdot head^{-1} \cdot d^{-1}$) from 2000 to 2019 for yearlings weighed approximately every 28-days during the grazing season across six different paddocks with stocking densities of 0.08–0.27 animal units (AU)/ha, where one AU is equivalent to a 454-kg animal. It is worth noting that AU's change as a function of both the number of cattle within a paddock and the size of individual animals, the latter of which changes within a single grazing season. This becomes important to consider when using sub-seasonal mass data for fast-growing yearlings. For paddock-scale ADG, we first calculated ADG for each individual yearling as the difference between the masses obtained at the end and beginning of each period, divided by the number of days in each period, and then averaged for all individuals in the paddock. We excluded data from 2013 due to data collection inconsistencies.

Most of the monthly mass data (97%) came from three paddocks where cattle were weighed every year, whereas in the other three paddocks, monthly masses were only measured during 2017–2019 (Appendix S1: Table S1). Apart from the 2013 data, which were not comparable to data from other years, we chose to use all available mass gain data for CPER to maximize spatial-temporal

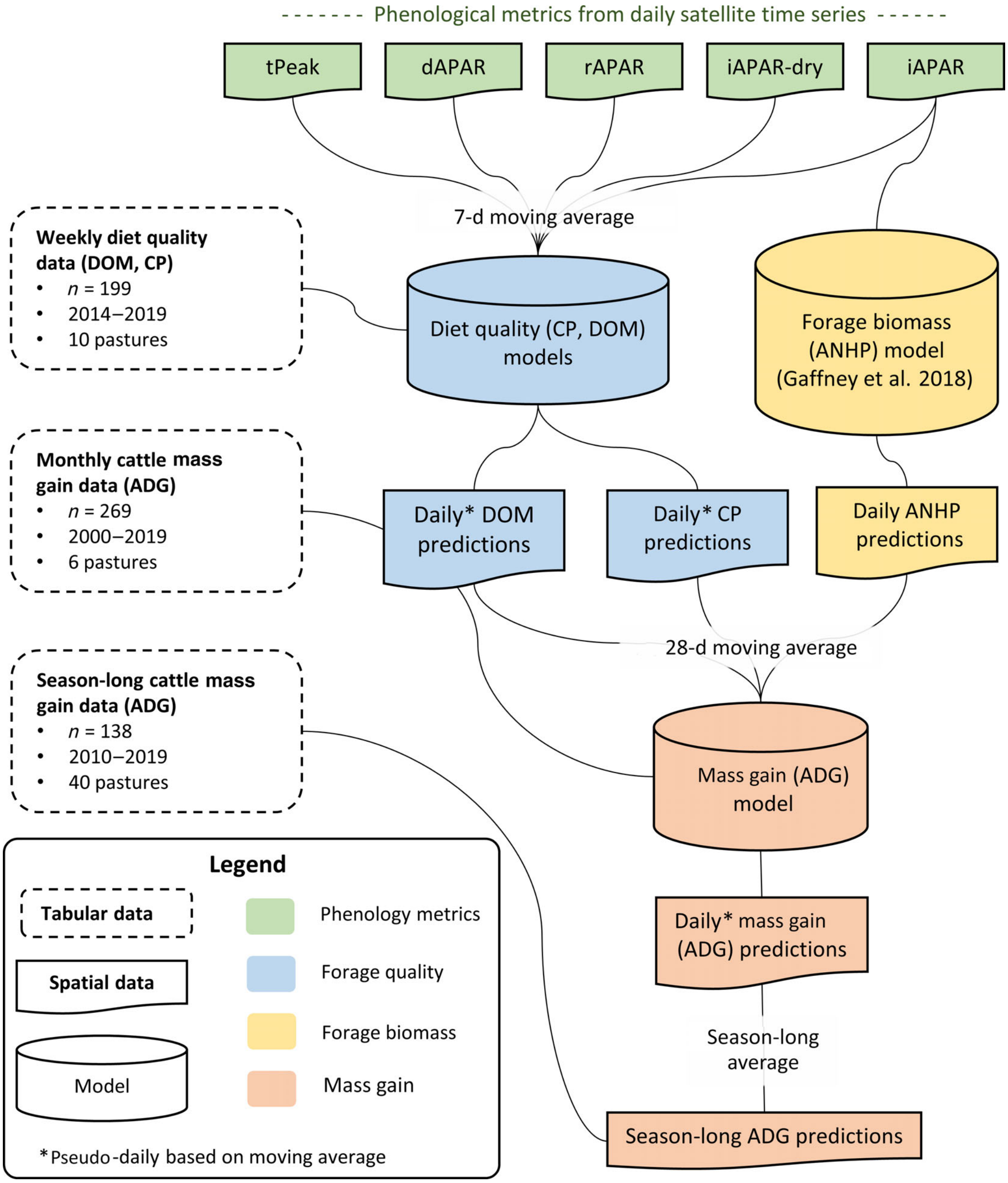

FIGURE 1 Overview of the modeling and validation methods and data sets used. CP, crude protein; DOM, digestible organic matter; ADG, average daily gain. See *Satellite time-series and phenological metrics* for variable descriptions

coverage and avoid potential bias from subjective decisions to subset the data. This resulted in 269 paddock-scale estimates of monthly ADG, with robust temporal, but limited spatial, coverage.

Season-long cattle mass gain data

We calculated paddock-scale ADG for the entire grazing season from 2010 to 2019 (excluding 2013) by averaging seasonal ADG of each yearling, determined as the difference between the end and starting masses divided by the number of days in the grazing season. This data set was available for 40 paddocks spanning a range of soil types, plant communities, and topographic positions. We note that there was spatial overlap among a small number of paddock boundaries across different years since some fence lines were moved in 2012 and 2014 (see Appendix S1: Table S1).

Satellite time-series and phenological metrics

We used a time series of daily 30-m NDVI (normalized difference vegetation index) observations produced by fusing surface reflectance imagery from Landsat and

MODIS using the Spatial and Temporal Adaptive Reflectance Fusion Model (STARFM; Gao et al., 2006). We converted the NDVI time series to absorbed photosynthetically active radiation (APAR) following methods described in Gaffney et al. (2018) using average incoming PAR, calculated for each day of the year for 2014–2019 using data from an onsite meteorological station.

To model diet quality, we produced five phenology-related metrics from the daily APAR time series (Figure 2), all of which can be calculated for any day during the growing season. As a simple measure of green vegetation, we calculated raw APAR (rAPAR), the APAR value for a given day. In temperate climates, peak forage quality has been linked to a peak in the instantaneous rate of green-up (IRG), which can be calculated as the maximum of the first derivative of a double-logistic regression fit to an NDVI time series (Bischof et al., 2012; Merkle et al., 2016). Therefore, we calculated the time since peak IRG (tPeak) in days, using the APAR time-series to calculate IRG. Since multimodal green-up curves are not uncommon in our study area, we also wanted to represent the degree to which APAR was increasing or decreasing on a given day, which we calculated as the cumulative change in APAR over the last 30 days (dAPAR). Diet quality is not just related to cover and greenness, but also structure and senescence (Drescher et al., 2006), which are related to biomass accumulation throughout the growing season. To represent live and dead biomass, we used two metrics developed from the cumulative change in APAR during the growing season. First, we calculated integrated APAR (iAPAR) as the cumulative sum of APAR since the start of the growing season, which is strongly related to aboveground live biomass production in this system (Gaffney et al., 2018). Second, we created a new metric to estimate senesced biomass (iAPAR-dry). For each day that the first derivative of APAR was negative, we calculated the percent decrease in the maximum APAR observed up until that day and multiplied this by the integrated APAR observed on that day. We then took the cumulative sum of these values up until the observed day. Thus, this metric represents an approximation of the cumulative biomass that has senesced (i.e., converted from a living to a non-living state).

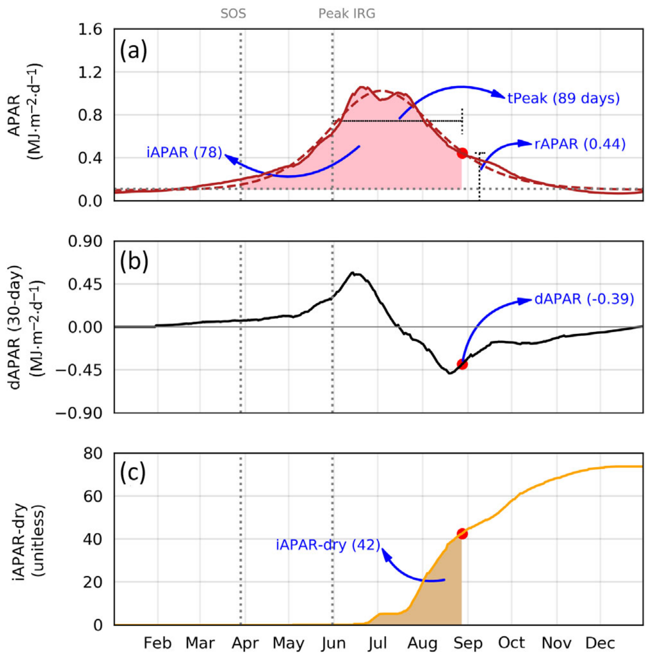

FIGURE 2 Schematic example of phenological metrics for 28 August 2011 (an "average" year) for paddock 31E. (a) The APAR time series, where the solid line is the observed APAR; dashed line is a fitted double logistic curve; rAPAR is "raw" values of greenness; tPeak is days since the instantaneous rate of green-up (IRG) peaked; and iAPAR is integrated APAR since the start of season (SOS), an indicator of live biomass accumulation. (b) The 30-day moving cumulative sum of the first derivative of APAR (dAPAR), an indicator of the rate of greening. (c) An indicator of senesced biomass accumulation (iAPAR-dry), which is an integration of APAR decline

Since the diet quality and cattle mass gain data were only available at the paddock scale, we calculated all metrics from the mean daily APAR time series of each paddock after removing extreme pixel values, identified as values outside the upper 99th and lower first percentiles.

Data analysis

Diet quality model

We trained random forest models to predict CP and DOM using the five phenological metrics. Random forests are a type of machine learning algorithm built from an ensemble of decision trees, which can achieve high predictive accuracy and account for complex relationships among input variables (Breiman, 2001). We chose to use a random forest model since we expected nonlinear and threshold-type relationships with metrics, along with interactions between metrics. We used 10-fold cross validation, stratified by 28-day periods, to determine the optimal number of features to use at each branch-split based on minimizing the mean squared error (MSE), and set the minimum number of samples per split and per leaf to two. We report the mean root mean squared error (RMSE) and explained variance (R^2) for the cross-validated model fit (training data) and validation (test data; RMSE-CV and R^2-CV), along with their standard deviations.

Forage biomass model

We used a linear regression model developed by Gaffney et al. (2018) to calculate net aboveground herbaceous productivity (ANHP; kg/ha) from iAPAR. While ANHP is likely more representative of total biomass production to date, rather than current standing biomass, we chose this as an indicator of forage biomass since the model was developed from field data collected at this experimental site. We averaged the coefficients of four spatial models (2013–2016) developed by Gaffney et al. (2018), resulting in the following equation:

$$\text{ANHP} = -26.47 + 2.07(\text{iAPAR}).$$

Monthly cattle mass gain model

We trained a multivariate linear regression model to predict monthly ADG using the satellite-derived estimates of diet quality (CP and DOM) and forage biomass (ANHP). We fit broken line regressions for CP and DOM, since thresholds are known to exist for both CP and DOM, below which mass gain declines precipitously (Van Soest, 1994). We used a second-order polynomial for ANHP to allow for a nonlinear relationship between ADG and forage biomass (Irisarri et al., 2019). We included interactions between all variables, as well as an interaction between each variable and stocking density. This allowed for two hypothesized interactions: (1) differences in stocking density change the slope of the relationship between forage biomass and mass gain (Irisarri et al., 2019) and (2) as cattle gain mass during the grazing season, their energy requirements increase, thus changing the relationship between forage biomass, DOM, and mass gain (Caton & Olson, 2016). We report RMSE and R^2 of the model, along with their mean and standard deviation from 10-fold cross-validation (RMSE-CV, R^2-CV), stratified by 28-day periods.

Season-long cattle mass gain

We used the season-long mass gain data to evaluate the predictive ability of our models across broader spatial and temporal inference spaces. We predicted season-long cattle mass gains by first predicting daily mass gain for each day of the grazing season using the previously developed models. We predicted CP and DOM for each day using a 7-day moving average, since these models were developed from weekly averages. We predicted ANHP for each day using the iAPAR observed for that day. We then used a 28-day moving average of predicted CP, DOM, and ANHP to predict "pseudo-daily" mass gain using the monthly mass gain model, which was built from approximately 28-day averages. We calculated the initial stocking density from the number of cattle and the average cattle mass at the start of the grazing period for each paddock. We then updated the stocking density for each day of the season based on the predicted mass gain for that day in each paddock, continuing until the end of the grazing season to arrive at a final cattle off-mass. We calculated the final ADG for the entire grazing season as the average predicted ADG, starting 28 days into the growing season. We did this to account for the 28-day moving average and the fact that monthly mass gain measurements used to create the model were never available within the first 28 days of the season.

We evaluated the overall performance of season-long predictions of ADG and cattle off-masses using metrics related to fit, error, and bias. To estimate fit, we calculated the Pearson's correlation coefficient between predicted and observed ADG and off-masses. To estimate error, we calculated the mean absolute error (MAE) in the original units and as a percentage of the overall mean observed values. We estimated bias using the mean percent error (MPE), which shows the degree to which errors tend to be over- or underestimated.

In addition to evaluating the overall fit of the predicted season-long mass gains, we also evaluated the predictions spatially (i.e., for all available paddocks within a given year) and temporally (i.e., for an individual paddock across all available years). Finally, we evaluated two factors that we expected would drive variability in our season-long predictions. First, in high forage production years associated with above-average precipitation, forage quality declines due to lower leaf : stem ratios and livestock mass gains diminish at this site (Derner & Hart, 2007). To test if this was captured in our model, we plotted prediction fit metrics against ANHP at the end of the grazing season across years. We also suspected predictions may perform differently in paddocks with different vegetation types. To test this, we plotted prediction fit metrics against sand content, the primary driver of vegetation community differences at this site (Augustine et al., 2017), across paddocks.

RESULTS

Weekly diet quality

The random forest model predicted weekly CP better than DOM, though both showed good model fit (Table 1, Appendix S1: Figure S1). For CP, the cross-validated root mean squared error (RMSE-CV) of predictions was 10.4% of the range of field-measured values while, for DOM, it was 11.3%. The most important variables in the diet quality models were related to the time since peak green-up (tPeak), the rate of greening or browning (dAPAR), and the senescent biomass accumulation (iAPAR-dry; Table 1). Raw greenness (rAPAR) and live biomass accumulation (iAPAR) were comparatively less important. For DOM, senescent biomass accumulation (iAPAR-dry) was the most important variable, with a score of nearly twice the next most important variable. For CP, time since peak green-up (tPeak) was the most important, followed by the rate of greening (dAPAR) and senescent biomass accumulation (iAPAR-dry).

TABLE 1 Results of random forest models predicting weekly crude protein (CP) and digestible organic matter (DOM) from the five satellite-derived phenological variables

	CP (%)	DOM (%)
Model fit		
RMSE	0.51	0.79
R^2	*0.95*	*0.93*
Model validation		
RMSE-CV[a]	0.95 (0.15)	1.54 (0.26)
R^2-CV[a]	0.81 (0.11)	0.68 (0.10)
Variable importance		
rAPAR	0.09	0.09
tPeak	0.33	0.21
dAPAR	0.26	0.19
iAPAR	0.09	0.09
iAPAR-dry	0.23	0.41

Note: See *Satellite time-series and phenological metrics* for variable descriptions.

[a]Values are the mean and standard deviation, computed using cross validation.

Partial dependence plots revealed that predicted CP was highest close to peak green-up, indicated by tPeak values near zero, and when APAR was high and increasing, indicated by high values of dAPAR (Figure 3a). It was lowest when time since peak green-up (tPeak) was high, APAR was low and decreasing but becoming flat, and senescent biomass accumulation (iAPAR-dry) was high. Predicted DOM followed a similar pattern but was especially sensitive to changes at the lower bounds of iAPAR-dry, with predicted values quickly decreasing as senescent biomass accumulation increased (Figure 3b).

Monthly cattle mass gain

The model predicting monthly ADG from satellite-derived CP, DOM, and ANHP showed reasonably good model fit (Figure 4; see Appendix S1: Table S2 for

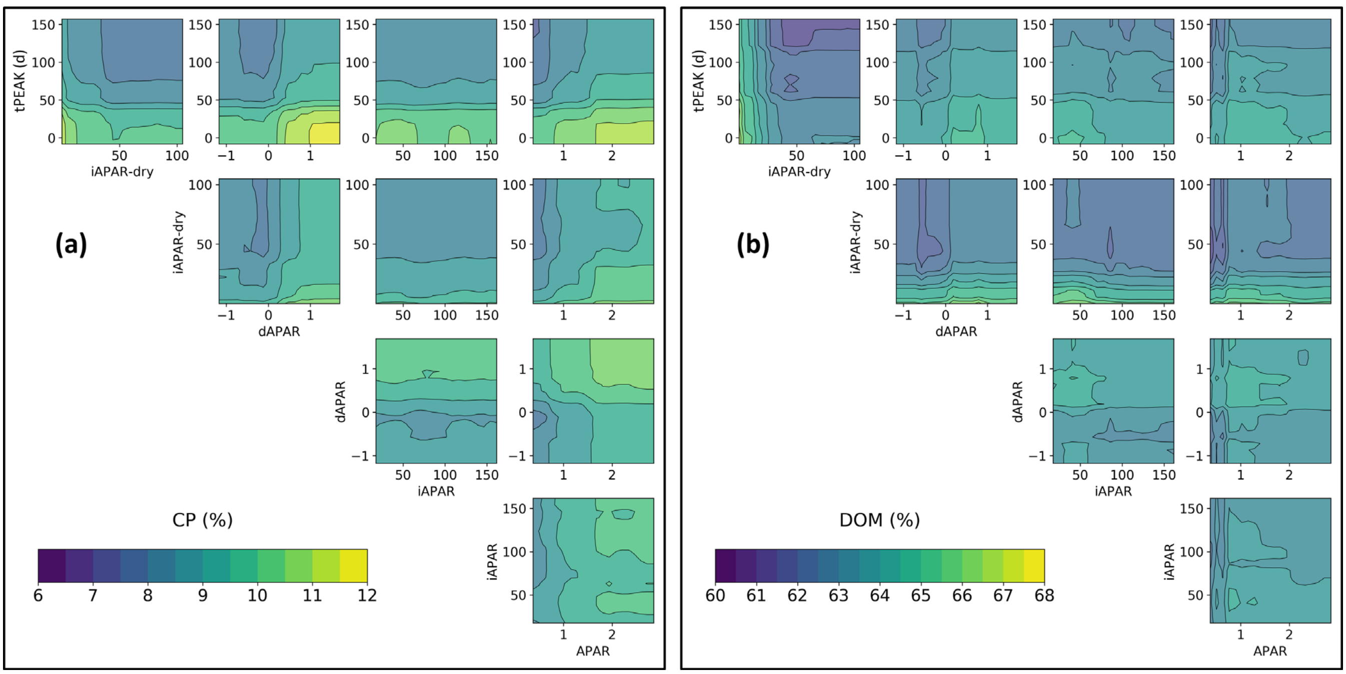

FIGURE 3 Two-way partial dependence plots for each pair of phenological metrics used in random forest models predicting (a) percent crude protein (CP) and (b) percent digestible organic matter (DOM). For each two-way plot, predictions are averaged over all possible values of the metrics not included in that plot

coefficients). The R^2-CV was 0.62 and the RMSE-CV was 0.30 kg·head^{-1}·d^{-1} (SD = 0.04 kg), equivalent to 34% of the mean observed monthly ADG. All coefficients were significantly different from zero ($p < 0.05$) except the interactions between AU and ANHP, and between AU and CP (Appendix S1: Table S2). In general, the model fit a nonlinear relationship between ADG and ANHP; ADG increased with increasing ANHP up to a point, then decreased, especially when diet quality was low (Figure 5). High diet quality was only observed when ANHP was less than ~2000 kg/ha. As stocking density increased, ADG became more sensitive to changes in diet quality and ANHP.

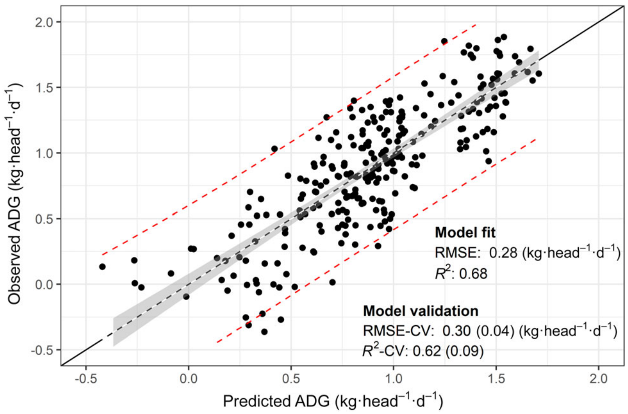

FIGURE 4 Predicted vs. observed average daily gain (ADG) of monthly cattle mass. The solid black line indicates the 1:1 fit. The dashed white line with shading indicates the fit and standard error of fit, respectively. The dashed red lines indicate the 95% confidence interval of predictions. Model validation values are the mean and standard deviation calculated using cross validation

Monthly ADG showed a clear segmented relationship with CP and DOM (Appendix S1: Figure S2). Mass gains declined more sharply below about 7.5% and 62.0% satellite-derived CP and DOM, respectively, and mass loss was only observed when CP was less than 8.0% and DOM was less than 61.5%. Once interactions were included in the final model, the segmented relationship was less pronounced and slopes were similar below and above the breakpoints for both CP and DOM (Appendix S1: Table S2).

Season-long cattle mass gain

When we applied the monthly ADG model to estimate ADG at a pseudo-daily time step (e.g., Figure 6), we obtained season-long ADG predictions that were strongly correlated with observed ADG (Pearson's r = 0.76; $P < 0.01$). The mean average error (MAE) for ADG was 0.08 kg·head^{-1}·d^{-1}, equivalent to 8.9% of the mean observed season-long ADG. Overall, predicted ADG showed a slight bias toward overprediction (mean percent error,

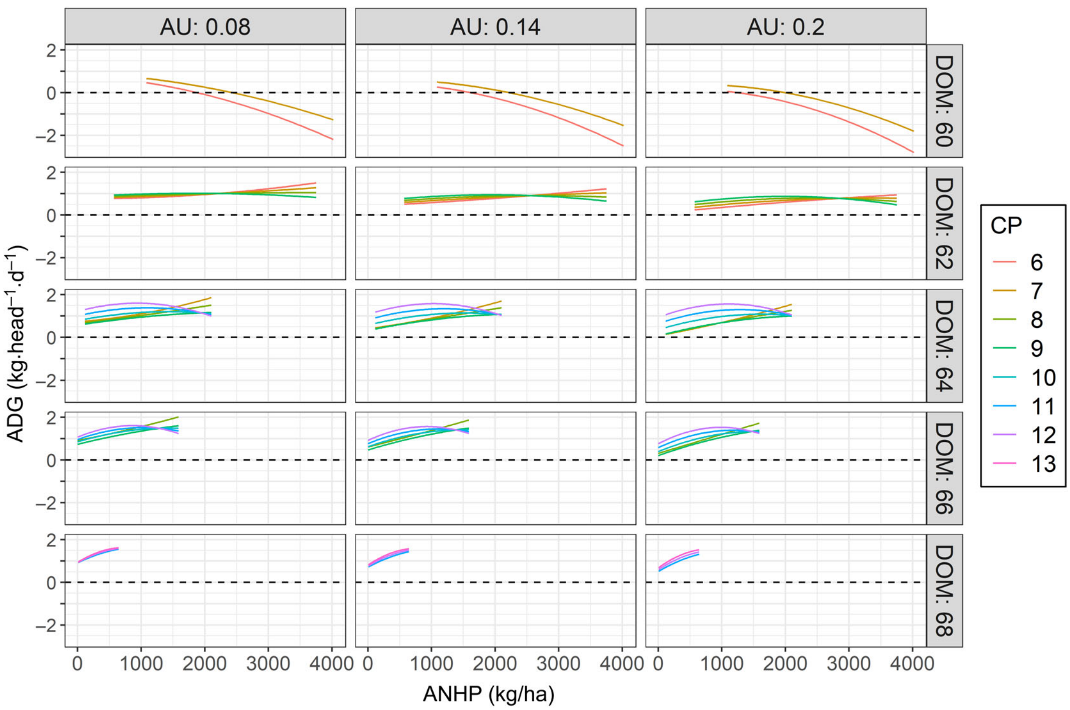

FIGURE 5 Marginal effects on average daily cattle mass gain (ADG; *y*-axis) of digestible organic matter (DOM, %; rows), stocking density (animal units [AU] per ha; columns), and crude protein (CP, %; colors) across the range of forage production (ANHP; *x*-axis). Lines in each panel show only the range of observed CP and ANHP associated with corresponding DOM (±1%) for that row

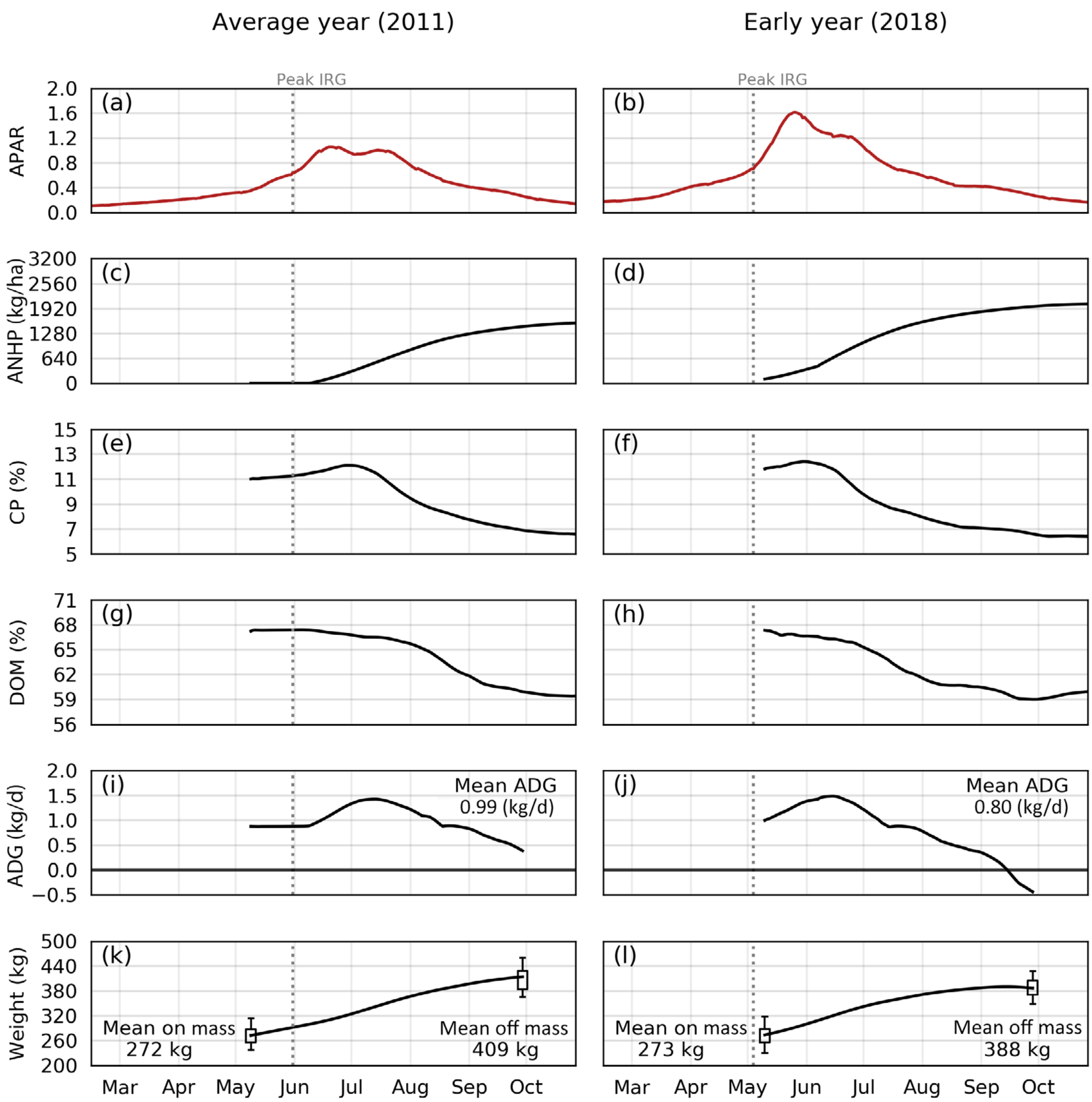

FIGURE 6 Example from paddock 31E of (a, b) satellite-derived APAR, (c, d) predicted forage quantity (ANHP), (e–h) diet quality (CP and DOM), (i, j) pseudo-daily mass gain (ADG), and (k, l) cattle mass during the grazing season for a typical "average" year (2011) and an "early" year with earlier-than-average forage green-up. Box plots in panels k and l show the observed on and off mass for all cattle in that paddock

MPE = 2.7%), which was most pronounced when observed ADG was above ~0.9 kg·head^{-1}·d^{-1} (Figure 7). For final cattle off-masses, MAE was 11.95 kg, or 2.9% of the mean observed off-mass.

Observed season-long cattle mass gains varied more over time than over space (Figure 7) and predictions were less strongly correlated with observations when evaluated spatially (Appendix S1: Tables S3 and S4). When we evaluated season-long predictions spatially within each of the nine years with available data, we found an average correlation coefficient between predicted and observed ADG of 0.43 (SD = 0.35) and significant correlations in six of the nine years (Figure 7a, Appendix S1: Table S3). The three years with the lowest and nonsignificant correlations where the three years with highest productivity (Appendix S1: Figure S3a). On average, the MPE was +2.3% (SD = 8.5%), indicating a slight bias toward over-predicting ADG across years. Predictions were less biased in years with average biomass production (ANHP ~1,000–2,500 kg/ha), whereas the model was more likely to overpredict ADG in years with very high productivity (Figure 7b, Appendix S1: Figure S3b).

When we evaluated the season-long predictions temporally (i.e., across paddocks with four or more years of data), we found an average correlation coefficient between predicted and observed ADG of 0.79 (SD = 0.19) and significant correlations in 8 of 10 pastures. On average, MPE was +2.0% (SD = 5.2%), again indicating a slight bias

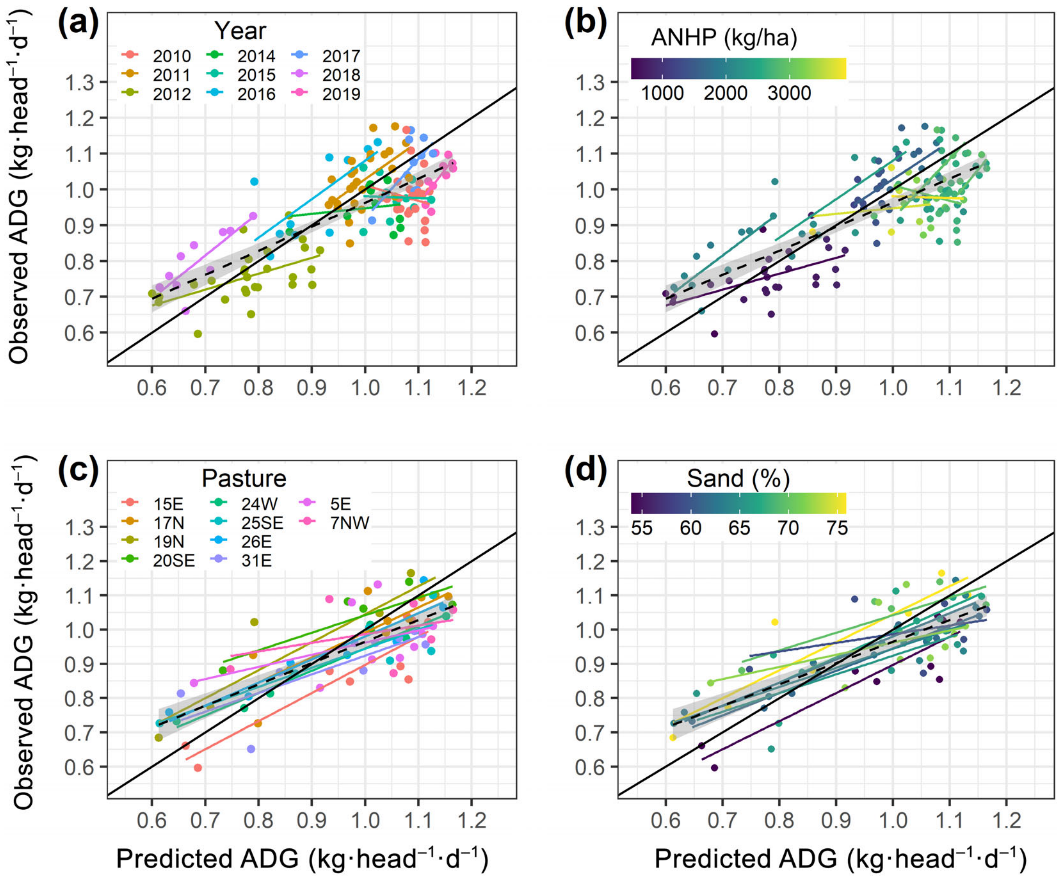

FIGURE 7 Predicted vs. observed season-long average daily cattle mass gain (ADG). (a, b) The spatial fit of the model within each year (a) and by the season-long productivity for each year (b). (c, d) The temporal fit of the model within individual paddocks (c) and by the sand content of each paddock (d). The solid black line in each panel shows the 1:1 fit and the dashed line with shading shows the overall linear fit (and its standard error) between predicted and observed ADG across all years and paddocks (Pearson's correlation coefficient = 0.76; $P < 0.01$)

toward over-prediction (Figure 7c, Appendix S1: Table S4). Correlations between predicted and observed ADG did not appear to be related to sand content (Appendix S1: Figure S3c). However, predictions tended to be less biased in paddocks with intermediate to high soil sand content (~60%–70%), whereas the model overpredicted ADG in the paddock with the lowest sand content and underpredicted in the paddock with the highest sand content (Appendix S1: Figures 7d and S3d).

DISCUSSION

Predicting diet quality and large herbivore performance from satellite data

Using five remotely sensed metrics, we were able to explain over 90% of the variation in field-based measurements of diet quality (CP and DOM). Previous work, mostly with migrating wild ungulates, focused on the timing and rate of spring green-up (i.e., IRG) as a key predictor of habitat selection, diet quality, and animal performance (Bischof et al., 2012; Garel et al., 2011; Hamel et al., 2009; Middleton et al., 2018). Time since peak IRG (tPEAK) was important in our models as well, particularly for predicting CP. However, we had the unique ability to explore the impacts of lower diet quality because cattle confined to paddocks are not able to "surf the green wave" (Bischof et al., 2012; Merkle et al., 2016; Middleton et al., 2018). Instead, they must respond to season-long shifts in forage quality. In both CP and DOM models, iAPAR-dry (an indicator of accumulated senesced forage) was an important predictor, emphasizing the contribution of vegetation senescence as a driver of diet quality, especially later in the growing season. Another important parameter, dAPAR, allowed us to capture secondary green-up or drydown events occurring later in the season, which were not captured by tPEAK. These results may be applicable to other grazing systems where herbivores are forced to graze on senesced vegetation, including wildlife experiencing regional drought that leads to widespread forage senescence, or animals constrained by reduced mobility due to habitat fragmentation (e.g., from roads, fencing, and settlements).

Compared to the three metrics derived from the slope and shape of the APAR curve, raw APAR and integrated APAR were weak predictors of diet quality. This finding underscores that raw NDVI levels, or predictions of accumulated forage biomass, are insufficient for predicting diet quality, and ultimately, animal performance. The high variable importance of iAPAR-dry for predicting DOM in this study demonstrates the value of using satellite time-series metrics that seek to represent known phenological drivers of diet quality such as shifts in cell structure, lignin content, and C:N ratio. Our monthly mass gain model further emphasizes the role that senesced forage biomass plays in herbivore performance. For monthly gains, we observed a complex relationship between ANHP and diet quality; when diet quality was low, higher biomass led to lower mass gains. Cattle in this situation likely ate a higher proportion of vegetation components with lower nutritional quality (e.g., stems rather than leaves; Kloppenburg et al., 1995). This concept of "rank grass" suppressing diet quality is widely recognized in productive, mesic grasslands (e.g., Craine et al., 2013) and has led to the incorporation of various prescribed burning techniques to enhance forage quality (e.g., Allred et al., 2011). Here we show that these same principles apply for cattle in shortgrass steppe where biomass levels are relatively low. Even in this low-biomass system, cattle shift their grazing distribution in space and time in response to known drivers of forage quality such as topographic variation (Gersie et al., 2019) and prescribed burns (Augustine & Derner, 2014).

It is important to reiterate that the model used to estimate forage quantity here was developed to predict ANHP (Gaffney et al., 2018), and does not account for biomass lost during the season (e.g., via trampling, transfer to the litter layer, and consumption). Additionally, Gaffney et al. (2018) showed that ANHP models that account for spatial variation in vegetation structure performed better than a single model, suggesting our estimation of ANHP includes spatial error that cannot be corrected without spatially explicit information on vegetation structure. This may partly explain why our final mass gain model performed better over time than over space (Figure 7, Appendix S1: Tables S3 and S4). Models that accurately predict standing biomass across a range of sites at a given point in time may better reveal when cattle mass gains are limited by forage quantity rather than quality.

Our efforts to scale models up to predict season-long mass gains revealed both strengths and limitations of this approach. Our model-predicted, season-long mass gains showed strong correlations with observed mass gains using few input variables, and we were able to predict final cattle off-masses with just 3.0% error (corresponding to average off-mass errors of ~12 kg per steer). However, predictive ability varied across years and paddocks. The model performed better over time than across space and tended to predict better and with less bias in years with average forage productivity and in paddocks with sandier soils (Figure 7). These results emphasize the importance of spatial heterogeneity as a driver of forage conditions and large herbivore performance in semiarid rangelands. We were limited in our ability to capture spatial dynamics since most monthly mass gain data were collected from paddocks containing loamy soils with gently undulating topography, and all data were from a single experimental range (6,270 ha) and only available at the scale of individual paddocks. Our predictions would likely be improved if data covered a wider range of soil types and topographic conditions and better accounted for within-paddock heterogeneity.

Another limitation of our model was the weaker and more biased (tendency for overprediction) performance when predicting cattle mass gain in years with high forage production. Given that our modeling approach (1) allowed for a nonlinear relationship between forage quantity and cattle gains and (2) accounted for the role of diet quality, we expected the model to account for factors that can suppress mass gains in productive years. One possible explanation for why this wasn't always the case is that any spatial estimation error from the simple linear regression model used to estimate ANHP from iAPAR is likely exacerbated in years with high forage production. Furthermore, paddocks used to train the model were dominated by C_4 short grasses, which have only minor negative feedback of grass stem growth in highly productive years. In contrast, paddocks where short grasses are less dominant may have stronger negative feedbacks to mass gains in years of high forage production with more grass stem growth (Derner & Hart, 2007).

Applications

One major advantage of our approach is the use of a Landsat-MODIS fusion product (Gao et al., 2015), enabling the combination of ground data collected at different temporal frequencies to predict forage conditions and cattle mass gains at a daily time step. This allows us to evaluate how temporal mismatches between forage phenology and the timing of grazing affect animal performance. For example, in years where IRG peaked before cattle started grazing, cattle lost mass at the end of the season and season-long ADG was below average, despite above-average ANHP (Figure 6). These evaluations provide valuable insight for adapting to predicted changes in forage phenology, such as earlier green-up in temperate grasslands due to invasion by exotic plant species and climate change (Wilsey et al., 2018). This pseudo-daily approach could be operationalized to generate near-real-time estimates of diet quality and mass gains, which could inform triggers used to move livestock among paddocks, or to predict wildlife herd health and reproduction (Middleton et al., 2018).

Our work emphasizes that diet quality, rather than forage quantity, may be the primary driver of cattle performance in semiarid rangelands in most years. This reinforces findings from previous studies of wild ungulates (Garel et al., 2011; Middleton et al., 2018) and bison (Craine et al., 2013), and supports the forage maturation and green wave hypotheses that herbivores migrate to track high-quality forage at intermediate biomass (Bischof et al., 2012; Merkle et al., 2016). The impact of diet quality on mass gains may become even more important to consider in the context of climate change. Warming temperatures are expected to lower forage quality and cause it to peak earlier, especially if coupled with decreased precipitation (Craine et al., 2010). Increased CO_2 concentrations may also reduce forage quality in the shortgrass steppe, regardless of warming (Augustine et al., 2018). Our findings suggest that such reductions in forage quality will suppress large herbivore performance even if forage production remains high. On the other hand, increasingly intense "deluge" precipitation events may lead to late-season vegetation growth that enhances forage quality without changing total production (Post & Knapp, 2019), which could improve animal performance.

Linking vegetation dynamics with large herbivore performance has always been challenging in rangelands and other extensive landscapes; the impetus to do so is urgent given changing climatic conditions. The satellite-based pseudo-daily approach presented here offers new capabilities to understand these links, recognize the ways in which they are changing, and evaluate the options available for adaptive management.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Sean P. Kearney, Lauren M. Porensky, and David J. Augustine conceived the ideas and designed methodology; Feng Gao, Lauren M. Porensky, David J. Augustine, and Justin D. Derner collected data; Sean P. Kearney and Feng Gao analyzed data; Sean P. Kearney, Lauren M. Porensky, David J. Augustine, and Justin D. Derner led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All tabular data (Kearney et al., 2021) are available through Ag Data Commons at http://doi.org/10.15482/USDA.ADC/1522609. Landsat and MODIS satellite imagery are publicly hosted by NASA and can be accessed at https://search.earthdata.nasa.gov/search. The STARFM algorithm (Gao, 2019) used to produce the Landsat-MODIS fusion product is available through the Ag Data Commons at https://data.nal.usda.gov/dataset/starfm.

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