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Large-scale and local climatic controls on large herbivore productivity: implications for adaptive rangeland management

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Abstract. Rangeland ecosystems worldwide are characterized by a high degree of uncertainty in precipitation, both within and across years. Such uncertainty creates challenges for livestock managers seeking to match herbivore numbers with forage availability to prevent vegetation degradation and optimize livestock production. Here, we assess variation in annual large herbivore production (LHP, kg/ha) across multiple herbivore densities over a 78-yr period (1940–2018) in a semiarid rangeland ecosystem (shortgrass steppe of eastern Colorado, USA) that has experienced several phase changes in global-level sea surface temperature (SST) anomalies, as measured by the Pacific Decadal Oscillation (PDO) and the El Niño–Southern Oscillation (ENSO). We examined the influence of prevailing PDO phase, magnitude of late winter (February–April) ENSO, prior growing-season precipitation (prior April to prior September) and precipitation during the six months (prior October to current April) preceding the growing season on LHP. All of these are known prior to the start of the growing season in the shortgrass steppe and could potentially be used by livestock managers to adjust herbivore densities. Annual LHP was greater during warm PDO irrespective of herbivore density, while variance in LHP increased by 69% (moderate density) and 91% (high density) under cold-phase compared to warm-phase PDO. No differences in LHP attributed to PDO phase were observed with low herbivore density. ENSO effects on LHP, specifically La Niña, were more pronounced during cold-phase PDO years. High herbivore density increased LHP at a greater rate than at moderate and low densities with increasing fall and winter precipitation. Differential gain, a weighted measure of LHP under higher relative to lower herbivore densities, was sensitive to prevailing PDO phase, ENSO magnitude, and precipitation amounts from the prior growing season and current fall–winter season. Temporal hierarchical approaches using PDO, ENSO, and local-scale precipitation can enhance decision-making for flexible herbivore densities. Herbivore densities could be increased above recommended levels with lowered risk of negative returns for managers during warm-phase PDO to result in greater LHP and less variability. Conversely, during cold-phase PDO, managers should be cognizant of the additional influences of ENSO and prior fall–winter precipitation, which can help predict when to reduce herbivore densities and minimize risk of forage shortages.

Key words: adaptive management; climate adaption; climate variability; El Niño-Southern Oscillation; herbivore density; large herbivore production; livestock grazing; net secondary production; Pacific Decadal Oscillation; semiarid rangelands; shortgrass steppe.

Introduction

Understanding the effect of climate variability on large herbivore production (LHP) is central to sustainable and effective rangeland management and planning (McKeon et al. 1990, O'Reagain et al. 2009, Derner et al. 2018, Shrum et al. 2018). Rangeland ecosystems worldwide are characterized by high precipitation variability, which creates management challenges for livestock producers seeking to match forage production with livestock demand in a proactive manner to prevent resource degradation and optimize livestock production (O'Reagain et al. 2009, Derner and Augustine 2016). Because precipitation variability is particularly pronounced in rangeland ecosystems and occurs at monthly, annual, decadal, generational, and longer time scales (McKeon et al. 1990, Augustine 2010), a lack of appreciation for such variability presents a challenge to sustainable management. For example, in Australian rangelands, resource degradation results from a typical

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pattern: a period of high commodity prices and consecutive wet years leads to high large herbivore stocking densities, followed by drought with ensuing low commodity prices and concomitant over-grazing (McKeon et al. 2004). Such problems stem from poor recognition of temporal variability in precipitation, its predictability, and oversight to manage accordingly (O'Reagain and Scanlan 2013). To date, research efforts have primarily addressed relationships between precipitation and forage production (Le Houérou and Hoste 1977, Milchunas et al. 1994, O'Connor et al. 2001, Derner and Hart 2007), with less emphasis on how these relationships extend to LHP (Derner et al. 2008, Reeves et al. 2013, 2014). To enhance decision-making for livestock producers, the incorporation of knowledge of the large-scale climate controls, including global-scale sea surface temperature (SST) anomalies like Pacific Decadal Oscillation (PDO; Mantua and Hare 2002) and El Niño-Southern Oscillation (ENSO; Trenberth 1997) is needed. The reliable, predictive nature of the phases of these anomalies (Derner and Augustine 2016) has been examined relative to vegetation growth (e.g., Chen et al. 2017), but not livestock productivity. Further, possible long-term changes in these large-scale climate anomalies are an essential component of future climate projection scenarios (Pachauri et al. 2014, Cai et al. 2015).

Sea surface temperature variability is reflected in different phases of PDO (warm, cold) and ENSO (La Niña to neutral to El Niño) at large spatial scales, which affect local weather (McCabe et al. 2012), with most efforts focused on how this relates to drought (White et al. 2004, Edossa et al. 2014). Despite broad similarities in the teleconnection patterns of PDO and ENSO across the western United States, there are significant disparities in the spatial and temporal dynamics between these two oscillations. The spatial signature of PDO is most evident in the North Pacific, whereas the equatorial region is the primary spatial signature for ENSO. Temporally, PDO phases cycle between warm (positive) and cool (negative) phases every 15–30 yr (Mantua et al. 1997, Mantua and Hare 2002). In contrast, ENSO is characterized by temporal variability with a 2–4 yr cycle between warm (El Niño) and cool (La Niña) phases (Hu and Huang 2009). The various combinations of PDO and ENSO can result in either in-phase (warm PDO and El Niño; cold PDO and La Niña), or out-of-phase conditions (warm PDO and La Niña; cold PDO and El Niño; Hu and Huang 2009). During in-phase conditions, warm and moist air flows from both the southwestern and northwestern United States across the Great Plains, whereas dry conditions occur in the western United States when both climate modes are in cold phases (Hu and Huang 2009). During out-of-phase teleconnections, neutral effects on Great Plains ecosystems are common (Hu and Huang 2009, Flanagan and Adkinson 2011). Furthermore, in the western United States, when ENSO is weak or neutral (e.g., −0.5 to 0.5°C Niño-3.4 SST anomalies), seasonal precipitation patterns are similar to those during years of La Niña–cold PDO and, to a lesser extent, years of El Niño-warm PDO (Goodrich 2007).

Teleconnections of SST anomalies in the northern hemisphere influence abiotic processes (e.g., wildland fire; Duffy et al. 2005) and conditions (e.g., precipitation and soil wetness; Kittel 1990, Hu and Huang 2009, Flanagan and Adkinson 2011). Several studies have examined the role of these large-scale climate regime variations in modulating consumer population dynamics in terrestrial systems (Post et al. 1999, Wang and Schimel 2003, Hallett et al. 2004, Wiederholt and Post 2011). Few investigations, however, have assessed relationships between large-scale climate regimes and trophic processes (Wang and Schimel 2003), such as individual herbivore performance or mass gain (but see Stige et al. 2006). Such work could have important implications for rangeland management, particularly in rural communities, where rural sustainability is highly dependent on income from livestock production (Reid et al. 2014).

Because climate anomalies vary on annual to multi-decadal timescales, long-term records of climate and livestock production are required to fully understand the complex relationships between teleconnections, local climate, and LHP. To date, many studies examining the impact of precipitation variability on net primary production in rangelands have used short-term (~2–3 yr) experiments manipulating precipitation (e.g., changes in amount or pattern; Heisler-White et al. 2009, Wilcox et al. 2017), or remote sensing to examine biogeochemical and vegetation responses to local weather and climate variability (Zhang et al. 2011, Moran et al. 2014). Statistical or simulation models, using findings from short-term studies, can be used to predict longer-term ecological responses to scenarios of climate change (e.g., Reeves et al. 2017). Although experiments are increasing in scope and scale, and remote sensing advancements continue, short-term observations and their model-based extensions have limited capacity to predict long-term events and processes (Vaughan et al. 2016, Shrum et al. 2018), such as LHP, during periods of above- or below-average rainfall years with different phases of PDO and ENSO.

Semiarid ecosystems are characterized by a high degree of interannual variability and uncertainty in precipitation patterns and amounts (Shrum et al. 2018), creating a challenging environment for livestock managers to match animal demand with forage availability in these ecosystems worldwide (Illius et al. 1998, Reid et al. 2014). This challenge is especially evident on the shortgrass steppe of central North America, where <30% of the annual precipitation occurs during the fall–winter preceding a growing season (Pielke and Doesken 2008), and livestock producers make herbivore density decisions during late winter/early spring without robust and accurate forecasts of impending growing-season conditions. Although reasonable predictions of growing-season forage production are possible with accurate knowledge of April–June precipitation (Dunn et al. 2013), herbivore density adjustments are difficult to make as the growing season progresses. One- and three-month precipitation forecast maps (NOAA 2019) and GrassCast (Peck et al. 2019; *available online*)[5] are tools available to assist decision-making for livestock producers in North America, but these forecasts still have high uncertainty prior to the start of the growing-season (e.g., in April). In Australia, more robust atmospheric teleconnections between rainfall and the Southern Oscillation Index (SOI) provide forecasting tools with considerable promise in assisting managers with herbivore density adjustments further in advance (several months) of the next growing season (Ash et al. 2002, O'Reagain and Scanlan 2013). Collectively, these observations suggest uncertainty in mass gain outcomes for variable large herbivore densities can be reduced by integrating prevailing large-scale climate modes as well as local-scale precipitation amounts into current grazing-season planning.

Here, we assess the variation in annual LHP across multiple herbivore densities (low, moderate, and high) over 78 yr (1940–2018) in a semiarid rangeland ecosystem that has experienced several phase changes in PDO and ENSO. We examined the influence of the prevailing PDO phase, the magnitude of late winter (February–April) ENSO, prior growing-season precipitation (prior April to prior September), and precipitation received (local-scale) during the six months (prior October to current April) preceding a given growing season on LHP. We also assessed the effect of prior growing-season precipitation (prior April to prior September) for one and two previous years on annual LHP because net primary production is positively related with previous-year precipitation (Oesterheld et al. 2001, Petrie et al. 2018). In our study region, April precipitation is key to initiating plant growth and establishing early-season estimates of available forage (Dunn et al. 2013). Furthermore, if there is a precipitation deficit by the end of April, then it is likely that precipitation in later months will fail to fill the gap (Smith 2007, Dunn et al. 2013); therefore, April represents a key decision time for livestock producers regarding herbivore densities. In addition to the magnitude of LHP responses to climatic conditions, we evaluated the sensitivity of LHP to herbivore density and the hierarchical temporal climatic controls. We use a model selection approach to evaluate the degree to which PDO, ENSO, and recent local-scale precipitation (October–April preceding the growing season) can be used to predict LHP at varying densities in the shortgrass steppe of eastern Colorado.

Materials and Methods

Site description

The USDA-Agricultural Research Service Central Plains Experimental Range (CPER) is a Long-Term Agroecosystem Research (LTAR) network site located ~20 km northeast of Nunn, in north-central Colorado, USA (40°50′ N, 104°43′ W, 1645 m above sea level). Mean annual precipitation (1939–2018) is 340 mm, with 43% of this occurring from April through June and 37% from July through September. Major soils on the study pastures were Ascalon fine sandy loam (fine-loamy mixed mesic Aridic Argiustoll), and Renohill fine sandy loam (fine montmorillonitic mesic Ustollic Haplargid). The main ecological site in the study pastures is Loamy Plains (Site ID: R067BY002CO; data *available online*).[6] The perennial C_4 shortgrass blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag ex Griffiths) is the dominant species and increases as grazing intensity increases, as does the perennial C_4 shortgrass buffalograss (*B. dactyloides* [Nutt.] J.T. Columbus). Conversely, the perennial C_3 mid-height grasses western wheatgrass (*Pascopyrum smithii* [Rydb] A. Love) and needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth ssp. *comata*) decrease with increasing grazing intensity (Hart and Ashby 1998, Porensky et al. 2017). Needleleaf sedge (*Carex duriuscula* C.A. Mey) is another important perennial C_3 graminoid. Scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) is the primary forb, and plains pricklypear cactus (*Opuntia polyacantha* Haw) is common.

Experiment description

In 1939, three 129.5-ha pastures were randomly assigned to one of three herbivore density treatments with one replicate per treatment (Hart and Ashby 1998). Treatments included light grazing (9.3 Animal Unit Days (AUD)/ha, targeted for 20% utilization of peak growing-season biomass), moderate grazing (12.5 AUD/ha, 40% utilization), and heavy grazing (18.6 AUD/ha, 60% utilization; Irisarri et al. 2016, Porensky et al. 2017). British-breed yearling cattle were used throughout the study, with similar herbivore densities (yearlings/ha) maintained for each density treatment in each pasture over the years. The grazing season typically began in May and ended in October but was shorter in some years when the yearlings were adaptively removed from pastures prior to the end of the grazing season, either because threshold triggers of desired use were met (1939–1964) or forage was inadequate (1965–2018). Yearlings were weighed prior to and following the grazing season, after being held overnight without feed or water. Large herbivore production (LHP, kg/ha) was calculated by multiplying seasonal animal mass gain (kg/head) by the number of yearlings in the respective herbivore density treatment and dividing the product by the pasture area. Livestock data from 1954, 1955, 1957, 1962–64, 1969, and 1982 were removed as the cattle were rotated among treatments across months in those years rather than remaining on the same treatment pasture for

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[5] http://grasscast.agsci.colostate.edu/

[6] https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY002CO

the entire grazing season (1957, 1962–1964, 1969) or were not stocked in each herbivore density treatment (1954, 1955, 1982) (Appendix S1: Table S1); totaling 71 yr for analyses.

Large-scale climate mode and local precipitation data

The PDO time-series was provided by University of Washington, College of the Environment, JISAO (2018). The PDO time-series is computed after Mantua et al. (1997) as the leading empirical orthogonal function of North Pacific (20°–70° N) monthly averaged SST anomalies after removing the global mean. The specific time-series is calculated from 1940 to 2018 based on the Reynolds OI SST V2 data set (Reynolds et al. 2007). The NINO-3 time series was determined from data published by the Physical Sciences Division (2019). The NINO-3 time series is calculated as the area-weighted average SST anomaly over the central equatorial Pacific (5° S to 5° N, 150° W to 90° W) with the anomaly calculated using a base period of 1951–2000. The specific time-series used is the PSD WG-SP time-series calculated from 1870 to present based on the HADISST 1 data set (Rayner et al. 2003).We used monthly precipitation data collected from 1939 to 2018 at USDA-ARS headquarters at CPER (Rangeland Resources and Systems Research Unit 2018).

Statistical analyses

Model selection procedure for predicting large herbivore production.—The influence of seasonal variation in local precipitation, atmospheric circulation regime (PDO and ENSO), and herbivore density on our LHP data was evaluated using a hierarchical model selection procedure using Akaike's Information Criterion corrected for sample size (AIC_c) to infer support for models (Burnham and Anderson 2002). Our approach sought to identify the most parsimonious model that could provide utility for decision support tools (Derner et al. 2012, 2017), and hence we aggregated climatic data to parallel the seasonal weather and atmospheric circulation regime forecasts available from the National Atmospheric and Oceanic Administration (NOAA) and NOAA Climate Prediction Center (*available online*).[7,8]

To isolate local precipitation influences on LHP, we examined the relative performance of models that tested dormant-season precipitation only and dormant-season precipitation and lagged effects of precipitation on annual LHP (Appendix S1: Table S2). Through this evaluation, we addressed the possibility that previous growing-season conditions impact annual LHP. In our study area, Oesterheld et al. (2001) showed variation in current-year ANPP was not only explained by annual precipitation but was also influenced by previous-year precipitation with precipitation amount during the first previous year being the strongest driver of lagged precipitation effects on ANPP. In addition, we assessed the support of an herbivore density × dormant-season precipitation interaction because we expected that increasing rainfall can reduce herbivore density limitations on annual LHP. We then chose the most parsimonious model representing local precipitation variables and herbivore density as a base model. This hierarchical approach allowed us to reduce the overall number of models while identifying variables that best contributed to model fit.

Our evaluation of prior-year precipitation effects on LHP indicated the inclusion of an additional previous year of precipitation did not improve model fit for LHP. Although a model containing a previous two-year lag effect term was reasonable (Appendix S1: Table S2), again model fit was not improved, and the model was not the most parsimonious. Therefore, we proceeded by including a term representing a single year lag effect of prior-year growing-season precipitation.

Using the base model, we evaluated the influence of large-scale climate regime variables on annual LHP, where new independent variables were the sole large-scale climate regime predictor (PDO or ENSO), the two large-scale climate regimes (PDO and ENSO), and their interaction. We expected that local-scale precipitation amounts may exacerbate or ameliorate larger-scale climatic influences on LHP when atmospheric teleconnections are out of phase, thus we tested a three-way interaction between dormant-season precipitation, PDO, and ENSO. We included the following covariates to explain LHP: (1) dormant-season precipitation (prior October to current April), (2) prior growing-season precipitation (prior April to prior September), (3) herbivore density (AUD/ha), (4) current ENSO magnitude (annual average February to April NIÑO-3 SST °C anomaly), and (5) prevailing average February to April PDO phase (cold or warm). The final candidate set contained a set of models comprising covariates of the most parsimonious models from the local-scale climate assessments, a set of the same models that included the interaction between herbivore density and dormant-season precipitation, and a model including a three-way interaction between dormant-season precipitation, prevailing PDO phase (cold or warm), and ENSO magnitude (SST °C anomaly). Models examining potential interactions between prior growing-season precipitation and local and large-scale atmospheric circulation variables were not considered, as we had no mechanistic hypothesis for how these interactions would operate. Entry masses of yearlings at the start of the grazing season increased over the seven-decade time period (Appendix S1: Fig. S1), so we accounted for this trend by including average j masses at the start of each grazing season (entry mass) in the LHP models following Reeves et al. (2014).

We used linear mixed models in our model selection procedure to evaluate the effects of local precipitation and large-scale climate modes on LHP. To account for

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[7] http://www.nws.noaa.gov/predictions.php

[8] https://www.cpc.ncep.noaa.gov/

repeated measurements within the same pasture, we included pasture as a random intercept and used a continuous autoregressive moving average covariance structure specifying a time covariate (i.e., year) and a grouping factor of pasture, so the correlation structure only applies to observations in the same pasture. For each model, we calculated $\mathrm{AIC_c}$, $\Delta\mathrm{AIC_c}$ (relative to the model with the lowest $\mathrm{AIC_c}$), and the model's Akaike weight relative to the overall model set. This model selection analysis was carried out using the MuMIn package (Bartoń 2016), and linear mixed models were constructed using package nlme in R 3.5.1 (R Development Core Team 2019). We calculated standardized coefficient estimates (subtracting the mean and dividing by the standard deviation using the scale function in R) to permit direct comparisons of independent variables as herbivore density, precipitation (mm), and ENSO NIÑO 3.4 SST °C values are on different scales. We report exact P values to allow readers to distinguish between significant effects ($P < 0.05$) and marginally significant effects that may still warrant attention ($0.05 < P < 0.10$).

Differential gain under precipitation variability.—To assess responses of LHP in relation to differences among treatments in the number of individual herbivores, we calculated differential gain in LHP as the magnitude of response relative to the herbivore density change:

$$\mathrm{LHP}_{\text{differential gain}} = \frac{\bar{X}_c - \bar{X}_t}{\text{Individuals}_c - \text{Individuals}_t}$$

where $\bar{X}_c$ and $\bar{X}_t$ are the livestock mass gain (productivity) means of control and treatment herbivore densities, respectively, and Individuals_c and Individuals_t are the number of individual yearlings in control and treatment herbivore densities, respectively. This metric represents the net increase in livestock mass gain changing from one herbivore density (control) to a higher density (treatment), expressed relative to the change in number of animals added. To determine whether differential gains differed from zero (i.e., no difference in mass gain between the two densities), we performed one-sample t tests for differential gain under moderate-to-high herbivore density increases and low-to-moderate herbivore density increases. Next, we tested for climatic drivers of differential gain under moderate-to-high herbivore density increases and low-to-moderate herbivore density increases. We evaluated several candidate models built to include the following: a full model (differential gain = prior growing-season precipitation + dormant-season precipitation + ENSO magnitude + PDO phase), a null model (mean entry mass without environmental variables), a model for each individual covariate, and a set of models comprising multiple combinations of two covariates, which revealed several competing models with $\Delta\mathrm{AIC_c} < 2$. Thus, we considered variables in these models with $\Delta\mathrm{AIC_c} \leq 2.0$ to be important drivers of differential gain under each herbivore density manipulation. Because our goal was to provide inferences that reduce management decision risk of negative monetary returns under different large-scale atmospheric circulation regimes, we illustrated differential gain from our predictive models. These depictions show the 95% confidence interval to provide a measure of accuracy in our estimation of differential gain based on ENSO magnitude and 95% prediction intervals to provide an impression of the variability of differential gain given the three-month average of ENSO magnitude (February to April) leading up to the growing-season. This period coincides with two critical aspects of range management: (1) when final pre-grazing-season management decisions (i.e., setting herbivore density) are made and (2) provides a measure of certainty as to whether growing-season local weather will be modulated by ENSO. The relationship between PDO-ENSO correlation and local weather anomalies in the Great Plains is strongest during this time period (Hu and Huang 2009); thus, we chose this three-month period to demonstrate when decision-making in regard to increasing herbivore density correlates with the highest relative gain and may alleviate any potential risk with density increases and underlying local precipitation large-scale climate mode relationships.

RESULTS

Entry masses of yearlings

Entry masses increased from approximately 175 kg/animal in the early 1940s to near 250 kg/animal by the mid-1980s (Appendix S1: Fig. S1). Entry masses have averaged 285 kg/animal over the last decade. As noted above, due to the increase in entry masses over the course of this seven-decade study, we included entry mass as a covariate in all models.

Local weather determinants

Prior growing-season (prior April to prior September) and dormant-season (prior October to current April) seasonal precipitation amounts varied widely over the seven decades of this study (Appendix S1: Table S1). In 1940, prior growing-season precipitation (mean 271 mm) was the lowest (88 mm) and, in 2000, it was the highest (513 mm). Dormant-season precipitation (mean 102 mm) was lowest in 1966 (33 mm) and highest in 1999 (237 mm).

Atmospheric circulation regimes

Our seven-decade investigation encapsulated five phase changes of the PDO (Fig. 1a) and substantial variability in ENSO (Fig. 1b). The data show 15- to 30-yr periods with either above-normal or below-normal SST anomalies for PDOs, which include two cold phases (1945–1977 and 1999–2013) and three warm phases (1940–1944, 1978–1998, and 2014–2018). The NIÑO-3.4 (ENSO SST °C patterns) sea surface anomalies vary

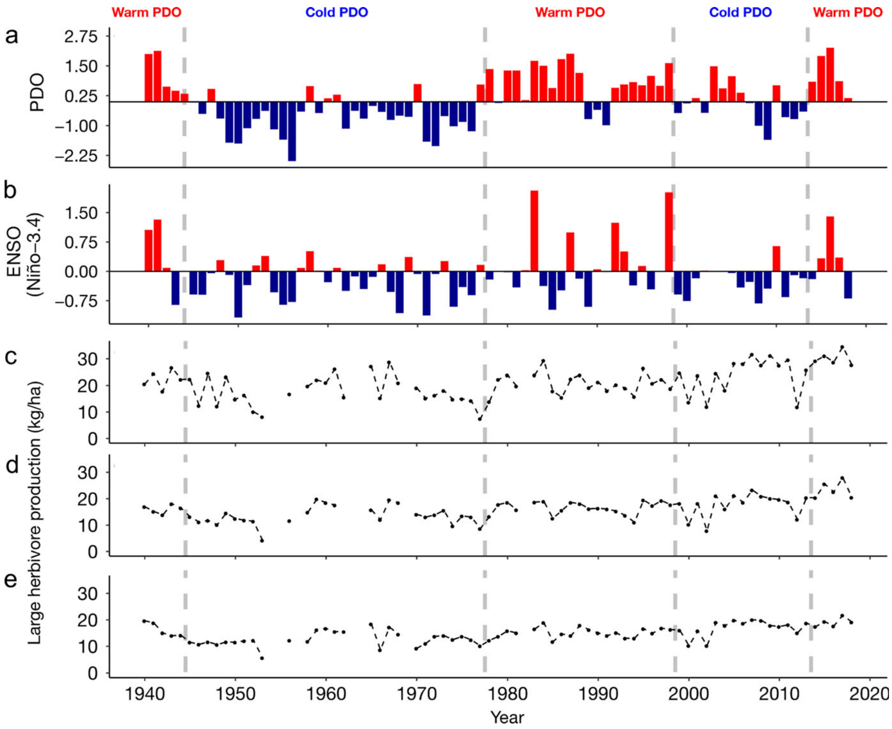

Fig. 1. Average February to April (a) Pacific Decadal Oscillation (PDO), (b) NIÑO-3.4 sea surface temperature anomalies, and mean annual large herbivore production under (c) high, (d) moderate, and (e) low herbivore densities from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA.

with a much higher frequency (2–4 yr pattern), and NIÑO-3.4 has a weak positive correlation to PDO ($R^2 = 0.22$, $P < 0.0001$). A relatively dry period (based on water-year, October to September, anomalies) in the 1950s to late 1970s coincided with a cold PDO period and frequent La Niña events (ENSO ≤ 0.5 SST °C).

Large herbivore production

Across the entire study period, mean annual LHP in the high herbivore density treatment (mean ± SD: 19.3 ± 6.52 kg/ha; Fig. 1c) was 23% and 51% greater than the moderate (15.4 ± 4.48 kg/ha; Fig. 1d) and low (11.7 ± 3.66 kg/ha; Fig. 1e) herbivore density treatments, respectively. However, interannual variance in LHP increased monotonically with increasing herbivore density, from $\sigma^2 = 13.4$ under low, to 20.0 under moderate, and 42.5 under high. Most notably, we identified substantial disparity in LHP variance between PDO phases, with 69% and 91% increases in mean sample variance for moderate and high herbivore density treatments, respectively, under cold relative to warm PDO regimes (Fig. 2). Negligible differences (3%) in LHP variance were observed for the low herbivore density treatment.

Models with climatic (both local- and large-scale) and management variables for LHP performed considerably better than the null model (mean entry mass; Table 1). Evidence ratios to assess the relative strength of candidate models indicated our top model was 1.5 times more likely to be the best-approximating model than our second most parsimonious model without a herbivore density × dormant-season precipitation interaction and 28 times more likely than the third most parsimonious model without an interaction between PDO phase, ENSO magnitude, and dormant-season precipitation. Collectively, 72% of the variability in annual LHP was explained by the top model containing an herbivore density × dormant-season precipitation interaction and a three-way interaction among PDO phase, ENSO magnitude, and dormant-season precipitation (Table 2). A marginally significant interaction between herbivore density and dormant-season precipitation revealed that LHP under high herbivore density increased at a greater rate than under low and moderate herbivore density with increasing dormant-season precipitation (Fig. 3). A three-way interaction among PDO phase, ENSO magnitude, and dormant-season precipitation suggested LHP increased with increasing ENSO magnitude and dormant-season precipitation during warm PDO phases (Fig. 4a), while, in cold PDO phases, increasing ENSO magnitude reduced LHP if cumulative precipitation from the prior October to current April was low (Fig. 4b).

Differential gain in large herbivore production

Across all years, mean differential gain of LHP was greater than zero when calculated both for the change from moderate-to-high herbivore density (LHP_{mh},

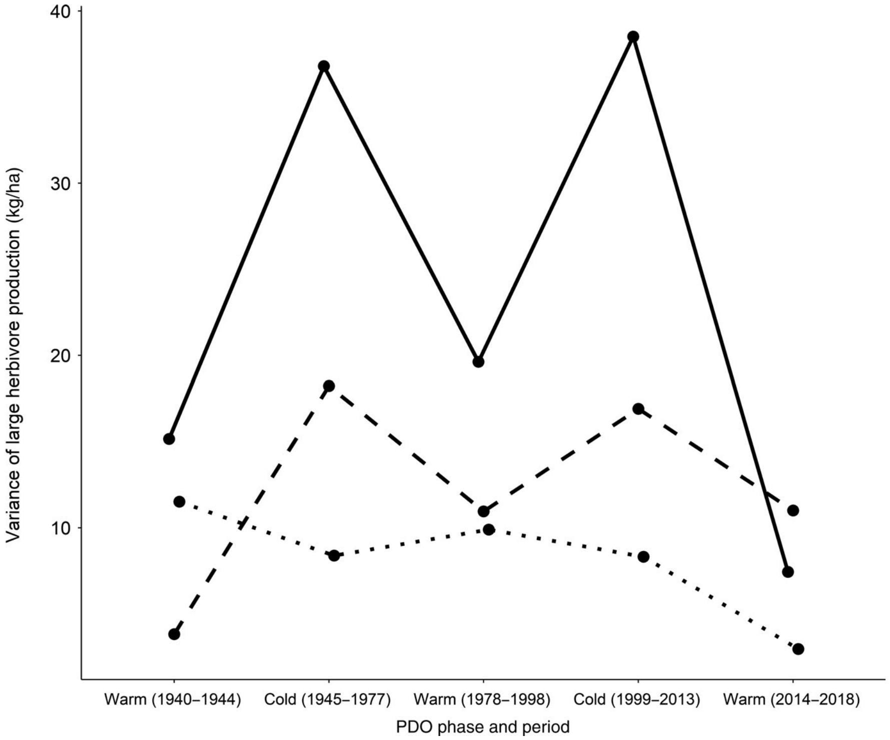

FIG. 2. Sample variance (σ) for large herbivore production under different herbivore densities: low, dotted line; moderate, dashed line; and high, solid line; binned by cold or warm PDO regimes from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA.

TABLE 1. Model selection table for linear mixed models explaining large herbivore production (kg/ha) as a function of local weather, atmospheric circulation regime, and herbivore density from 1940 to 2018, at Central Plains Experimental Range, Nunn, Colorado, USA.

Model	K	logLik	AIC$_c$	Δ AIC$_c$	w$_i$	Adj. R^2
I + EW + HD + DS + HD × DS + PG − 1 + ENSO + PDO + DS × ENSO + DS × PDO + ENSO × PDO + DS × PDO × ENSO	15	−535.01	1102.45	0.00	0.58	0.72
I + EW + HD + DS + PG − 1 + PDO + ENSO + DS × PDO + DS × ENSO + PDO × ENSO + DS × PDO × ENSO	14	−536.55	1103.22	0.77	0.39	0.71
I + EW + HD + DS + HD × DS + PG − 1 + PDO + ENSO + PDO × ENSO	12	−541.78	1109.13	6.68	0.02	0.69
I + EW + HD + DS + HD × DS + PG − 1 + PDO + ENSO	11	−544.24	1111.79	9.34	0.01	0.68
I + EW + HD + DS + HD × DS + PG − 1 + PDO	10	−545.59	1112.27	9.82	0.00	0.68
I + EW + HD + DS + PG − 1 + PDO + ENSO	10	−546.57	1114.22	11.77	0.00	0.68
I + EW + HD + DS + PG − 1 + PDO	9	−547.73	1114.34	11.89	0.00	0.67
I + EW + HD + DS + HD × DS + PG − 1	9	−551.06	1121.01	18.57	0.00	0.66
I + EW + HD + DS + PG − 1	8	−552.91	1122.52	20.07	0.00	0.66
I + EW + HD + DS + HD × DS + PG − 1 + ENSO	10	−550.76	1122.61	20.16	0.00	0.66
I + EW + HD + DS + PG − 1 + ENSO	9	−552.67	1124.23	21.78	0.00	0.65
I + EW + HD + PDO + ENSO	8	−572.24	1161.18	58.74	0.00	0.61
I + EW + HD + PDO × ENSO	9	−571.35	1161.60	59.15	0.00	0.61
I + EW	5	−613.84	1238.00	135.52	0.00	0.42

Notes: DS, Dormant-season precipitation (prior October to current April); ENSO, El Niño-Southern Oscillation; EW, entry mass; HD, herbivore density; I, intercept; PDO, Pacific Decadal Oscillation; PG-1, prior growing-season precipitation (prior May to prior September); LogLik, log-likelihood; AIC$_c$, Akaike information criterion corrected for sample size; ΔAIC$_c$, difference in AIC$_c$ attributed to the model; w_i, Akaike weight; Adj., adjusted.

TABLE 2. Model coefficient estimates for the selected linear mixed-model predicting large herbivore production (kg/ha) from 1940 to 2018 in shortgrass rangeland at the USDA-ARS Central Plains Experimental Range, northeastern Colorado, USA.

Variable	β	SE
(Intercept)	15.52	0.53
Entry mass	1.22	0.29
Herbivore density	3.53	0.31
Dormant-season precipitation	1.55	0.28
Prior growing-season precipitation	−1.36	0.26
PDO phase (Warm)	2.26	0.60
ENSO	−1.06	0.40
Herbivore density × dormant-season precipitation	0.40	0.23
Dormant-season precipitation × PDO phase (Warm)	−0.47	0.51
Dormant-season precipitation × ENSO	1.17	0.34
PDO phase (Warm) × ENSO	1.20	0.109
Dormant-season precipitation × PDO × ENSO	−1.45	0.44

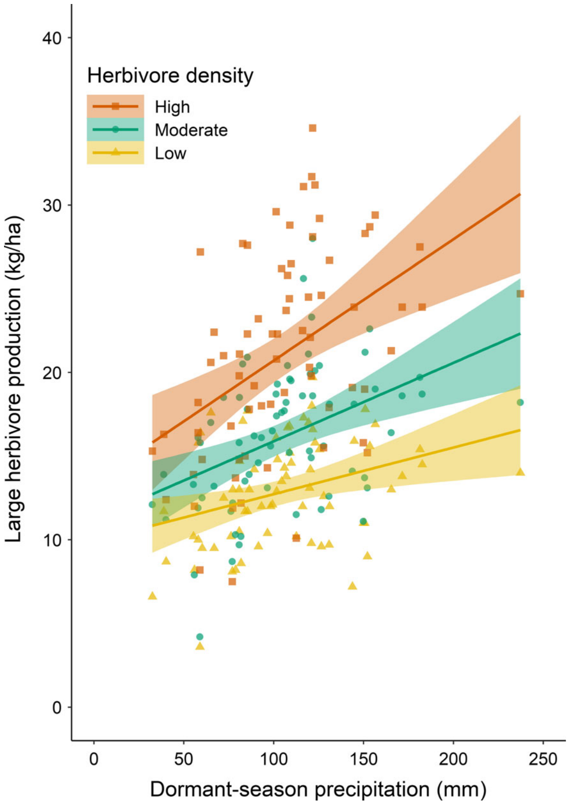

FIG. 3. Relationship between dormant-season precipitation (prior October to current April) and large herbivore production (kg/ha) under three herbivore densities from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA. Shading is 95% confidence interval.

$t_{1,71}$ = 7.60, $P < 0.0001$) and from low-to-moderate herbivore density (LHP$_{\text{lm}}$, $t_{1,71}$ = 17.60, $P < 0.0001$). We found no evidence for interactions among PDO phase, ENSO magnitude, and dormant-season precipitation for either increase in herbivore density (moderate-to-high, $F_{1,62}$ = 0.14, P = 0.71; low-to-moderate, $F_{1,62}$ = 0.42, P = 0.52). This indicates that differential gain under either density increase was not substantially dependent on a specific PDO phase or ENSO magnitude. Next, we evaluated all possible models containing combinations of the main effects of PDO phase, ENSO magnitude, prior growing-season precipitation, and dormant-season precipitation on LHP$_{\text{mh}}$ (Appendix S2: Table S1). This analysis identified four models with $\Delta\text{AIC}_\text{c} \leq 2.0$, with the greatest strength of evidence for a model based on dormant-season precipitation, PDO phase, and ENSO magnitude. All four top models included dormant-season precipitation but differed in terms of inclusion of prior year growing-season precipitation, PDO phase, and ENSO magnitude (Appendix S2: Table S1). We therefore estimated coefficients based on model averaging of these top four models. Based on this model averaging approach, dormant-season precipitation was a robust estimator of differential gain from moderate-to-high herbivore density (LHP$_{\text{mh}}$; β ± SE; 0.45 ± 0.12). Although PDO phase (−0.20 ± 0.24), ENSO magnitude (−0.19 ± 0.12), and prior growing-season precipitation (0.05 ± 0.11) ranked in the top models, their estimates were not robust.

For differential gain, when herbivore density increased from low density to moderate density (LHP$_{\text{lm}}$), prior growing-season precipitation, dormant-season precipitation, and ENSO magnitude were included in the four models with $\Delta\text{AIC}_\text{c} \leq 2.0$ (Appendix S2: Table S2). As with the moderate-to-high herbivore density increase (LHP$_{\text{mh}}$), model-averaged coefficients indicated that dormant-season precipitation was an influential estimator of differential gain from light-to-moderate herbivore density (LHP$_{\text{lm}}$) (0.23 ± 0.12). Prior growing-season precipitation (−0.16 ± 0.12) and ENSO magnitude (0.11 ± 0.12) were not robust.

During years of warm PDO, when dormant-season and prior growing-season precipitation was at least average, the risk of reduced livestock gain under high density relative to moderate herbivore density was unrelated to ENSO magnitude (Fig. 5a). When a cold PDO phase

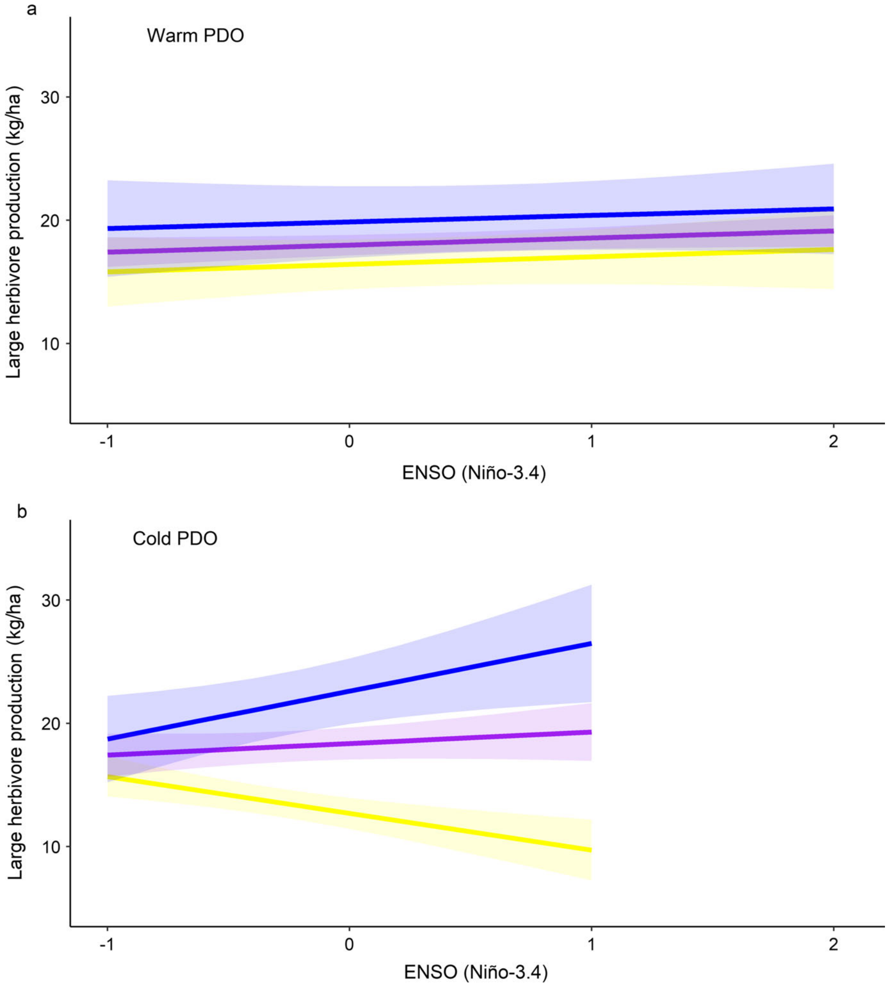

FIG. 4. Mean large herbivore production (kg/ha) across herbivore density treatments at low (yellow line), moderate (purple line), and high (blue line) dormant-season precipitation levels (prior October to current April) from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA as a function of average February to April ENSO (Niño 3.4) SST °C anomaly in years of (a) warm, (b) and cold PDO regimes. Shading is a 95% confidence interval.

was in place, the risk of reduced livestock gains under high relative to moderate herbivore density was more evident as predictions bands were ~0.5 kg/ha per added individual wider than for warm PDO years (Fig. 5b). Under different levels of ENSO during a cold PDO phase, a slight increase in the negative slope with increasing ENSO magnitude when compared to warm PDO years was evident, suggesting greater potential risk under high herbivore densities as ENSO approaches neutral or El Niño conditions (Fig. 5b). In general, the values of differential gain for moderate vs. high herbivore density increasingly deviated from zero across qualitative PDO–ENSO regimes (Fig. 5c). In most cases, the values of differential gain were greater than zero, indicating that increased herbivore density resulted in higher mass gain than the moderate herbivore density. However, there were also some cases of negative differential gain, indicating density increases did not always result in greater herbivore production. Negative values of differential gain were most frequent (31%) in cold PDO phase years experiencing positive ENSO conditions (i.e., El Niño) in February–April (Fig. 5c). When ENSO and PDO were in phase, the proportion of positive differential gain values was >89%.

Differential gain for low-to-moderate herbivore density comparisons was more certain than gains for the moderate-to-high comparison. Regardless of PDO phase, differential gain was consistently above zero except for three years under neutral ENSO (Fig. 6a), indicating moderate herbivore densities realized greater production relative to low densities under strong ENSO events. The proportion of negative values of differential gain in moderate-to-high density increases was generally greater than that of low-to-moderate density increases across PDO–ENSO regimes

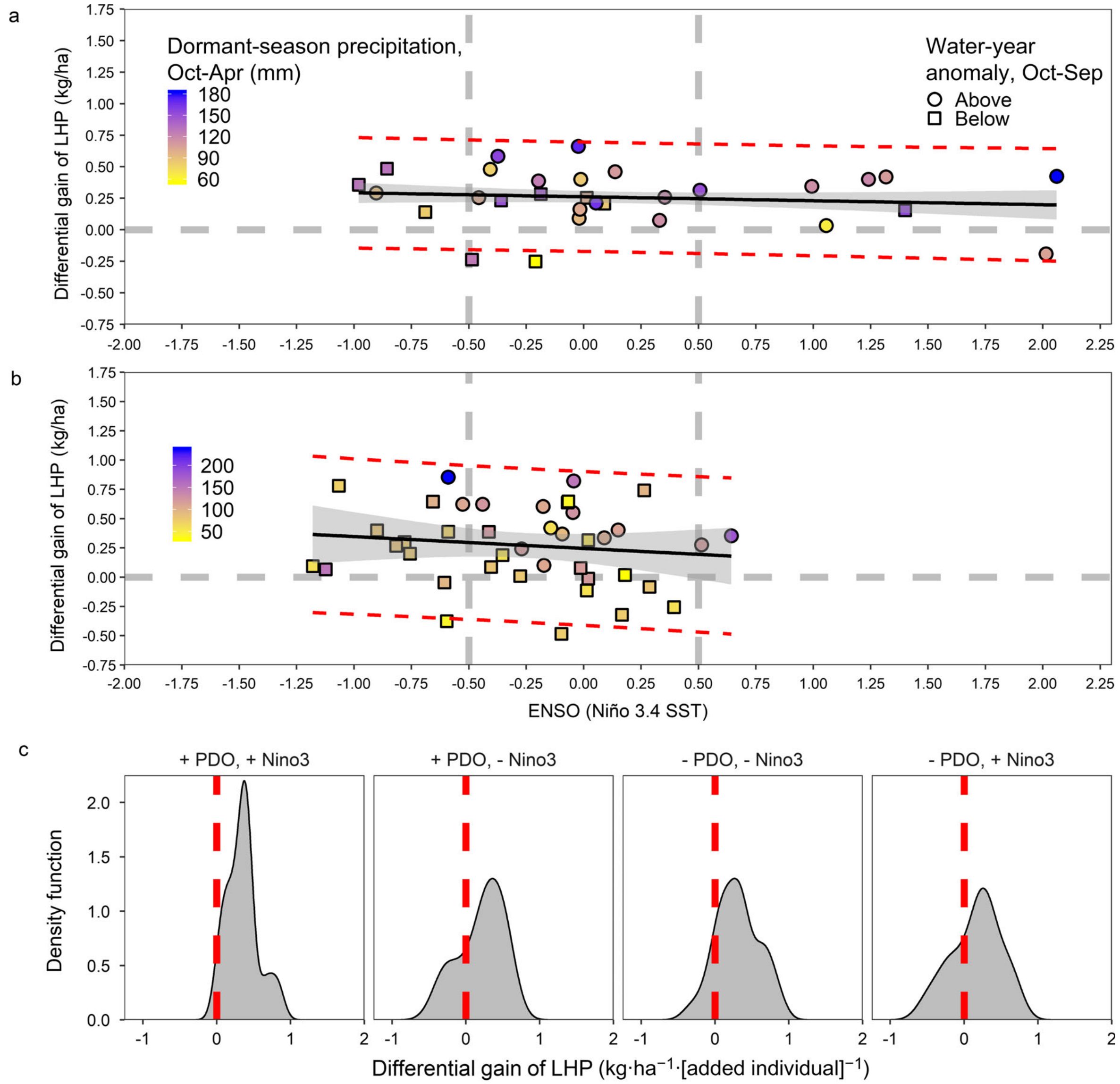

FIG. 5. Differential gain (kg·ha^{-1}·[added individual]$^{-1}$) relationship with ENSO (average February–April ENSO SST °C anomaly) for (a) a warm PDO regime and (b) a cold PDO regime under moderate-to-high herbivore density increases from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA. Dashed red line denotes 95% prediction interval bands, gray shading indicates 95% confidence interval, dashed gray line at *y*-intercept denotes equal mass gain between herbivore densities, and space between dashed gray vertical lines at −0.5 to 0.5 ENSO SST °C indicates general range of neutral ENSO, while below and above 0.5°C are general minimums for La Niña and El Niño events, respectively. LHP, large herbivore production. (c) Distribution of differential gain (kg/ha per added individual) under moderate-to-high herbivore density increases.

(Fig. 6b), suggesting greater risk for lower production under high herbivore density.

DISCUSSION

In this seven-decade study, we quantified relationships among herbivore density, precipitation variability, teleconnections, and LHP for one of the major livestock-producing grasslands in North America. Results illustrated that increasing ENSO magnitude interactively controlled annual LHP as a function of prior October to current April precipitation and PDO phase. This could have significant impacts on rangeland management in the shortgrass steppe given that all this information is available prior to the growing season (i.e., by April). Furthermore, our exploration of differential gain between herbivore densities suggested that the degree to which increased herbivore density improved LHP relative to moderate herbivore densities (LHP_{mh}) was related to PDO phase, ENSO magnitude, prior growing-

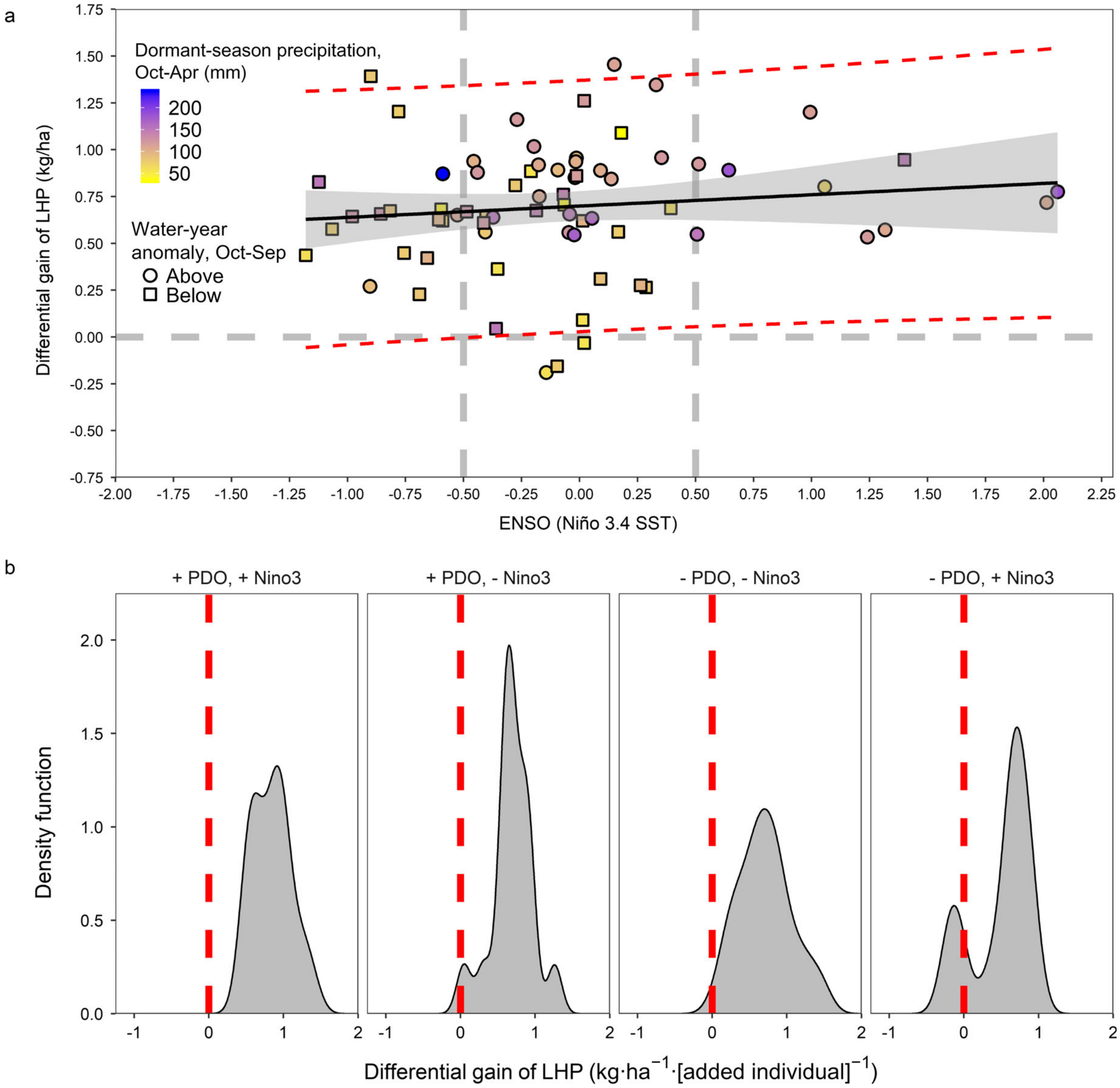

FIG. 6. (a) Differential gain (kg·ha^{-1}·[added individual]$^{-1}$) relationship with ENSO (February–April) under low-to-moderate density increases from 1940 to 2018 at the Central Plains Experimental Range, northeastern Colorado, USA. Dashed red line indicates equal mass gain between herbivore densities. Dashed red line denotes 95% prediction interval bands, gray shading indicates 95% confidence interval, dashed gray line at *y*-intercept denotes equal mass gain between herbivore densities, and space between dashed gray vertical lines at −0.5 to 0.5 ENSO SST °C indicates general range of neutral ENSO, while below and above 0.5°C are general minimums for La Niña and El Niño events, respectively. (b) Distribution of differential gain under low-to-moderate herbivore density increases.

season precipitation, and dormant-season precipitation, while PDO phase did not impact LHP$_{\mathrm{lm}}$ sensitivity. This finding emphasizes two points: (1) relationships between prevailing climate modes and LHP are sensitive to non-growing-season precipitation and (2) the magnitude of larger-scale ENSO magnitude and PDO phase effects on precipitation–LHP relationships is contingent on herbivore density. These findings suggest that including knowledge of recent local weather with atmospheric climate modes has the potential to enhance flexibility in matching animal demand to variable forage production in this semiarid rangeland ecosystem. Based on these results, we developed a key to reducing the risk associated with herbivore density adjustments under broad- to local-scale precipitation drivers in our semiarid ecosystem (Fig. 7). By focusing on a temporal hierarchy of climate controls on rangeland production, herbivore-density-based risk for suboptimal LHP can be alleviated through cognizance of (1) decadal-scale climate modes (PDO: warm or cold) that modulate how (2) ENSO (roughly 2–4 yr cycle) moderates (3) local-scale precipitation at a finer, monthly resolution (Fig. 7). For

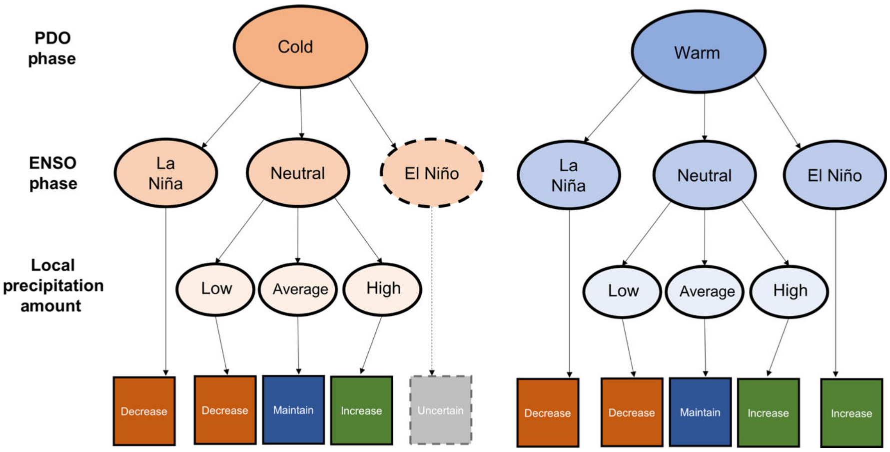

FIG. 7. Graphical representation of temporal hierarchical controls addressing suggested herbivore density adjustment (boxes) for large herbivore production (kg/ha) based on climatic knowledge available by April in the shortgrass steppe. Largest ovals represent prevailing Pacific Decadal Oscillation (PDO) regime, moderate-sized ovals denote El Niño-Southern Oscillation (ENSO) regime average from February to April, and small ovals indicate local precipitation level from prior October to current April before summer grazing season. Inadequate number of El Niño events during cold PDO regimes prohibit prediction for suggested herbivore density adjustment.

example, our temporal hierarchical control key illustrates herbivore density reductions benefit LHP when PDO phase is cold, ENSO is neutral or at the La Niña-level, and local precipitation during the winter and early spring has been below average.

Our prediction that variance in LHP would be enhanced under cold-phase PDO and increase monotonically with additional herbivore density was met, and this finding aligns with forage production (ANPP) response to forcing during cold-phase PDO (Chen et al. 2017). Substantial disparity between multiyear PDO phases and LHP variability among herbivore densities was evident with stark contrasts in the relationship between herbivore density and LHP variability during cold vs. warm PDO phases (i.e., 90% higher LHP variability under cold PDO phases than warm PDO phases with high herbivore density). Because variability in LHP is inherent to cold PDO phases for our semiarid study system, we provide empirical evidence to bolster dynamic optimization modeling results of Torell et al. (2010), which showed that, as forage production variability increased, so too did the value of adjusting herbivore densities. Moreover, a recent study from this site showcased that increasing herbivore density results in greater LHP variance (Irisarri et al. 2019). Thus, adaptive management strategies that incorporate knowledge of the PDO phase, ENSO magnitude, and recent precipitation to manage herd size could be implemented by livestock producers to better match herbivore numbers with forage availability and provide a buffer against the negative impacts of dry years.

Through our analyses of large-scale climate modes, local precipitation, and LHP, key differences emerged between cold- and warm-phase PDO years in how herbivore density affects LHP in response to ENSO magnitude. The number of years when LHP was greater in moderate compared to high herbivore density was two-fold greater during cold PDO phases (8 of 41 yr, or 20%) vs. during warm PDO phases (3 of 30, or 10%; Fig. 5). During these eight cold-phase PDO years, LHP was greater under moderate herbivore density than high herbivore density when the February to April ENSO anomaly was near zero (neutral) for each year and dormant-season precipitation (prior October – current April) was minimal for at least six of those years (Fig. 5b). Thus, when prevailing climate modes and dormant-season cumulative precipitation levels are not conducive to LHP, reducing herbivore densities to moderate levels can enhance LHP, with concomitant economic benefits for producers (Hart and Ashby 1998). Moreover, each year that LHP was maximal under moderate herbivore density was a below-average rainfall year based on the water-year (October–September) precipitation anomaly (Fig. 5b). This finding suggests the decision to increase herbivore density above the moderate level could have been averted for six of the eight years if poor non-growing-season conditions (cold PDO, negative or neutral ENSO, and low cumulative precipitation) were known by April. Changing management from high to moderate herbivore density when optimal conditions are present before May could have substantially larger benefits in terms of LHP response to variable precipitation in cold vs. warm PDO years.

Comparisons of LHP under moderate vs. low herbivore density demonstrated mass gains with low herbivore density were less sensitive to prevailing PDO phase. As herbivore density increased from low to moderate, PDO phase was not an important factor based on our model selection results for LHP_{lm}, whereas cumulative prior fall–winter precipitation up to current April and

ENSO magnitude during February to April remained important. The three years when LHP was greater at low than at moderate herbivore density (1965, 2002, and 2012) were all within suboptimal, non-growing-season conditions for mass gain (cold PDO, negative or neutral ENSO, and low cumulative precipitation up to April). These results suggest cognizance of these prevailing climatic conditions before the grazing season could have limited the widespread impact of the 2012 Great Plains drought on the region's cattle industry (Shrum et al. 2018). Although reducing herbivore density has significant economic costs for producers (Hart and Ashby 1998), such a reduction could enhance other ecosystem services including carbon sequestration (Irisarri et al. 2016) and provisioning wildlife habitat through enhanced vegetation heterogeneity (Derner et al. 2009).

Prior growing-season precipitation can promote ANPP in the current year at our study site (Oesterheld et al. 2001, Moran et al. 2014). In contrast to this finding, LHP was negatively impacted by prior growing-season precipitation, suggesting a decoupling of ANPP and LHP with respect to legacy influences (Reeves et al. 2013). Increased ANPP in the prior year is manifest as standing dead forage in the current year and senescent stems of bunchgrasses such as *H. comata* contain high lignin (Milchunas et al. 2005), which reduces forage quality on offer to grazing animals and inhibits livestock performance in our study system (Vavra et al. 1973). Understanding that the current warm PDO phase is likely to promote higher mean ANPP for the next decade or longer (Chen et al. 2017), opportunistic experimental efforts may further clarify the role of forage carry-over effects on LHP.

Conclusion

Understanding how hierarchical climatic (PDO, ENSO, prior growing-season and dormant-season precipitation amounts) and management determinants (herbivore density) influence net secondary production in grazing lands is critical to the long-term sustainability of these agroecosystems (Godde et al. 2018). Current decision-making relies primarily on local-scale current precipitation amounts to adjust herbivore density rather than forecasts of future conditions (Shrum et al. 2018), so uncertainty is high for livestock producers, and risk is reduced by the traditional use of set conservative (moderate) stocking densities. Inclusion of longer-term SST anomalies like PDO and ENSO in decision-making for herbivore density levels could reduce enterprise risk by translating short-term (months) climate outlooks into more applicable grazing-season forage outlooks (Ritten et al. 2010, Derner et al. 2012, 2018, Derner and Augustine 2016, Chen et al. 2017, Peck et al. 2019). The cross-scale relationships between decadal (PDO) to multiyear (ENSO) atmospheric-circulation modes and local weather provide plausible biophysical mechanisms for teleconnections to influence net secondary production (LHP) in the western Great Plains of North America and benefit the adaptive capacity and climate risk management for livestock systems. Hierarchical temporal approaches using PDO, ENSO, and local-scale precipitation may increase the robustness of decision-making for flexible herbivore densities. Our long-term data suggest that herbivore densities could be increased above recommended levels with lowered risk for managers during warm-phase PDO to result in greater LHP and less variability (Fig. 7). Conversely, during cold-phase PDO, managers need to be more cognizant of the additional influences of ENSO (specifically La Niña) and dormant-season precipitation as herbivore densities will likely need to be reduced to accommodate less forage availability that results in lower mean LHP with higher variability.

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Supporting Information

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