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Multidecadal directional shift in shortgrass stocking rates ☆

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ABSTRACT

Bement (1969) developed a stocking rate (SR) guide for yearling cattle grazing shortgrass steppe based on relationships among average daily weight gain (ADG, $kg \cdot d^{-1}$), beef production per hectare (BP, $kg \cdot ha^{-1}$), and stocking rate (animal unit days, $AUD \cdot ha^{-1}$) measured in long-term grazing experiments conducted from 1940 to 1963. These analyses identified an optimal biophysical SR of 13.5 $AUD \cdot ha^{-1}$. Here, we 1) examine modern era (2000–2018) SR results from these same long-term grazing experiments to determine if there has been a shift in the optimal biophysical SR and 2) assess the influence of drought (< 75% of normal precipitation) on the optimal biophysical SR. For all years in the modern era, the optimal SR occurred at 23.2 $AUD \cdot ha^{-1}$, 72% higher than the value reported by Bement (1969). For the 3 drought yr, the optimum SR was 14.2 $AUD \cdot ha^{-1}$, which still exceeded the optimal SR by Bement (1969). Our results show the capacity of this shortgrass steppe rangeland to produce livestock weight gains has increased substantially between the Bement and modern eras. This multidecadal directional shift to a higher optimum biophysical SR is likely driven by two nonmutually exclusive factors. First, the plant community changed from dominance by a C_4 shortgrass *(Bouteloua gracilis)* in the Bement era to codominance with a more productive C_3 midgrass *(Pascopyrum smithii)* in the modern era. This change has resulted in pasture-level forage production increasing notably between the two eras. Second, the entry weights and genetic growth potential of yearling steers increased over the 8 decades and may have influenced the efficiency of weight gain for a given amount of forage consumed. Our findings provide guidance for incorporating flexible optimum SR in nondrought and drought years for adaptive grazing management strategies.

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Introduction

Carrying capacity is an overarching concept of rangeland science and management that needs to be expressed quantitatively for use in practical settings. Although this concept has been considered vague in the past and difficult to define (Dhondt 1988; Scarnecchia 1990), carrying capacity defines the boundaries of acceptable practice, commonly expressed in terms of a maximum or a minimum (Holechek et al. 1998). Such boundaries of acceptable practice can be examined from quite different perspectives (Allen et al. 2011), the most clear difference being that between concern for the vegetation and concern for the animal (Scarnecchia 1990).

In rangelands worldwide, carrying capacity has often been viewed from the resource perspective, with the resource being a functioning soil/plant complex, as measured by primary production potential, botanical composition, and soil health. The central question of the resource perspective is: What is the level of utilization that can be imposed on the resource without causing long-term declines in forage production and overall degradation of the resource? Location-specific answers to this question have enabled the development of “rules of thumb” on what is considered acceptable range management (e.g., “take half, leave half”; Frost et al. 1994). For example, across multiple rangeland types in central North America, sustainable, moderate stocking rates are generally associated with livestock directly consuming ~25% of forage production. At the same time, more intense grazing of up to 50% direct consumption of forage production during the growing season can, in some cases—particularly in grasslands with a long evolutionary

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history of grazing—be associated with sustainable rates of grassland growth and regrowth (e.g., Frank et al. 2016; McNaughton 1985). In addition, it is possible for grazers to induce changes to the vegetation in terms of composition and/or productivity without reducing the capacity of that system to support livestock production (Fynn and O'Connor 2000; Wilson and MacLeod 1991), such that defining or measuring a point at which the soil/plant complex has been degraded can be difficult.

Another way to examine carrying capacity is through the lens of animal productivity. As the density of animals grazing a given area increases, the rate at which individual animals gain weight declines, typically in a linear manner (Jones and Sandland 1974; Wilson and McLeod 1991). The slope of this linear relationship then defines the shape of the quadratic relationship between total animal weight gain per unit area (i.e., total production of the entire livestock herd sustained in a defined area) and stocking rate. In addition, long-term shifts in the slope of this relationship (i.e., increasingly negative values of the slope) are one clear quantitative indicator of rangeland degradation over time (Wilson and McLeod 1991). Studies that quantify how weight gain per individual and total weight gain per unit land area change as a function of animal density can also be used to identify an optimal density that balances the tradeoff between these two factors (e.g., Bement 1969; Wilson and MacLeod 1991). However, in extensive rangeland landscapes with variable precipitation and forage production, long-term studies conducted at multiple stocking rates are needed to assess these relationships in a manner that accounts for such interannual variability (Andales et al. 2005; Beck et al. 2020; Del Monte-Luna et al. 2004; Jones and Sandland 1974). Such long-term studies on rangeland beef cattle production under sustained stocking rate (SR, defined here as animal unit days per hectare, $\mathrm{AUD \cdot ha^{-1}}$) treatments are rare (see Sanderson et al. 2015; Ungar 2019). These controlled experiments provide unique data for determining biophysical consequences of environmental variation and SR decisions for livestock production (Ash and Smith 1996; Fynn and O'Connor 2000; Smart et al. 2010; Wilson and MacLeod 1991).

Research at the Central Plains Experimental Range (CPER) in the shortgrass steppe of northeastern Colorado has been examining the effects of SR decisions on vegetation dynamics and beef production since 1939 (Bement 1969; Hart and Ashby 1998; Klipple and Costello 1960). On the basis of measurements during the 1940s through the early 1960s, Bement (1969) determined that light SR resulted in high average daily weight gains (ADG, $\mathrm{kg \cdot d^{-1}}$) per animal but low beef production (BP, $\mathrm{kg \cdot ha^{-1}}$) per unit area. In contrast, moderate-to-heavy SR resulted in lower ADG but higher BP. By graphing the relationships between ADG and BP in a manner that matched the scale of each relationship to its peak, Bement (1969) estimated that the optimal balance between maximizing both ADG and BP occurred at an SR (expressed in nonmetric units) of 2.9 $\mathrm{acres \cdot yearling^{-1} \cdot mo^{-1}}$. Given that yearlings used in these early years of the experiment averaged 241 kg (Derner et al. 2020), the Bement (1969) SR equates to 13.5 $\mathrm{AUD \cdot ha^{-1}}$.

Bement (1969) extended his SR guide on blue-grama *(Bouteloua gracilis)* rangeland to economic returns using economic data from average-to-wet precipitation years (1965−1967). Lacking, however, was the consideration of economic data from drought years and over a longer time period. Analyses with SR that explicitly addresses variability among years in precipitation and cattle weight gains (e.g., Fynn and O'Connor 2000) may provide rangeland managers with a more effective means to adjust SR across years of variable forage production and potentially reduce the impact of drought on animal production and economic returns (Torell et al. 1991). Economic returns are dependent upon the market conditions in any given year, fluctuate widely over time (Komarek et al. 2020; Pacín and Oesterheld 2014), and therefore represent a primary source of uncertainty for livestock producers (Irisarri et al. 2019).

As causal biophysical mechanisms behind the consequences of increasing climatic variability on beef production from rangelands continue to be studied (e.g., Augustine et al. 2018; Irisarri et al. 2019), an emphasis is growing on the importance of informing strategic agribusiness decisions and long-term financial strategies for climate adaptation planning (Shrum et al. 2018; Wilmer et al. 2016). Unlike cropping systems (Hatfield et al. 2018), the potential value of adaptation strategies for rangelands under various climate prediction scenarios has not been adequately developed (see Derner et al. 2018) and the potential economic losses to climate variability or the benefits of climate adaptation strategies have not been clearly defined in rangeland beef cattle systems (Briske et al. 2015; Klemm and Briske in press). Insights from long-term investigations provide contextual foundations for management influences on livestock production (Houghton et al. 1990).

Here, we 1) compare levels of forage production between the Bement era (1940−1963) versus the modern era (2000−2018) in the same study pastures, 2) examine the modern era relationships among SR, ADG, and BP to determine if a shift has occurred from the Bement (1969) value for the biophysical optimum SR, and 3) determine the differences in relationships among SR, ADG, and BP between drought and nondrought years in the modern era. To provide broader comparisons of our results to other rangeland systems, we also express our SR specific to the shortgrass steppe in terms of the grazing pressure index (GPI), which is a measure of animal density per unit of available forage biomass rather than land area (Smart et al. 2010).

Methods

Site description

The US Department of Agriculture−Agricultural Research Service CPER is a Long-Term Agroecosystem Research (LTAR) network site located 12 km northeast of Nunn, in north-central Colorado (40°50′N, 104°43′W, 1 645 m above sea level). Mean annual precipitation (1939–2018) is 340 mm, with 43% 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). In 1939, a long-term grazing intensity study was initiated with yearling British breed cattle *(Bos taurus)* stocked on three, 129.5-ha pastures at three SR levels: light, moderate, and heavy (Bement 1969). Yearlings have been sourced from neighboring beef cattle operations since the start of this long-term study. The main ecological site in these three study pastures is Loamy Plains (Site ID: R067BY002CO).

Beginning in 2004, a 65-ha pasture with a 20-yr prior history of moderate stocking was stocked at a very heavy level (30−36 $\mathrm{AUD \cdot ha^{-1}}$) annually through 2012 (Augustine et al. 2012). The dominant soils in this pasture were also represented by the Loamy Plains ecological site. To reduce the potential impact of legacy effects from its history of moderate stocking on our inference, we excluded the first 2 yr of livestock weight gain data from this pasture from our analyses.

Forage production analyses

We estimated forage production as the peak growing season biomass harvested from 12–15, 1.5-m^2 temporary exclosures (moved each year a random distance and cardinal direction from established transects before the grazing season) for each pasture in the long-term grazing intensity study. Within each temporary exclosure, biomass was hand-clipped to ground level from one 0.10-

m^2 quadrat in late July or early August each yr from 1940 to 1962 for the Bement era and 2000 to 2018 for the modern era. In 1954, operations ceased at the research station due to extreme drought and forage production data were not collected; therefore this year was excluded from analysis.

We used linear mixed models to evaluate the effects of study era, SR, and spring precipitation on perennial C_3 cool-season graminoids and perennial C_4 warm-season grasses. We chose to focus our attention on this vegetation component because biomass data for annual grasses, forbs, and subshrubs was incomplete for the Bement era. In Colorado, grass species dominate cattle diet composition (~70%; Scasta et al. 2015). Standing dead biomass from the prior yr was also excluded. For precipitation, we compared models that included either annual precipitation or spring precipitation (April–June). In all cases, spring precipitation performed better (higher R^2) than annual precipitation; therefore we only evaluated the role of spring precipitation on forage production. Fixed effects included study era (Bement or modern), SR (as a continuous variable), spring precipitation (April to June), and all two- and three-way interactions. We included pasture ($n = 3$; one pasture for each SR in each study era) as a random intercept and used a compound symmetry covariance structure to address the nonindependence of repeated annual measurements within the same pasture. Since biomass did not have a normal distribution, we square-root-transformed values before analysis. Linear mixed models were constructed using package *"lme4"* (Bates et al. 2015) in R 4.0.1 (R Development Core Team 2020).

Stocking rate analyses

We assessed relationships among ADG, BP, and SR during 2000–2018 (modern era). This is a period in which 1) genetic changes in British breed beef cattle have resulted in significantly larger body size of yearling steers (Derner et al. 2020), and 2) substantial variation in annual rainfall occurred (Petrie et al. 2018). Our analyses are based on 19 yr of measurements for each of the three SR levels (light, moderate, heavy) implemented in this long-term experiment (totaling 57 SR by yr measurements) and 7 yr (2006–2012) of measurements at a very heavy SR, giving a total dataset of 64 SR by yr measurements to assess variation in ADG and BP. Yearlings were weighed before and following the grazing season (mid-May to 1 October), after being held overnight without feed or water.

We followed the approach of Bement (1969), as described in greater detail by Wilson and MacLeod (1991) and Ash and Smith (1996), to examine how ADG and BP were related to SR. First, we plotted ADG versus SR for each of the 64 unique SR by yr combinations. On the basis of theory (Ash and Smith 1996), we expected ADG to either 1) decline linearly over the entire range of SR evaluated (hereafter, the negative linear model) or 2) remain constant over a range of low SR (slope = 0 at constant intercept) and then decline linearly above a certain SR (hereafter, the broken stick model). To identify the breakpoint for ADG with increasing SR, we used the *segmented* package (Muggeo and Muggeo 2017) in program R (R Development Core Team 2020). We defined the breakpoint in the broken stick model as the SR at which the fitted line to the left of the breakpoint had a slope of zero. We fitted both potential models and selected the one that minimized the root mean square error. We then used the slope and intercept of the negatively sloping portion of the model to predict BP as a quadratic function of SR, as follows:

$$\mathrm{ADG} = \mathrm{a} - \mathrm{b} \times \mathrm{SR} \quad (1)$$

where a = y-intercept and b = slope for the negatively sloping portion of the model and

$$\mathrm{BP} = \mathrm{SR} \times (\mathrm{ADG}) = \mathrm{a\,SR} - \mathrm{b\,SR}^2 \quad (2)$$

We then plotted the actual measured values of BP for each of the 64 SR by yr combinations and confirmed that the predicted quadratic BP curve fit these values. Bement (1969) reported that yearlings started the grazing season at an average initial weight of 182 kg and ended at an average of 300 kg; hence we used the midpoint of 241 kg to estimate that a yearling during the Bement era was 0.53 animal unit (AU). For the modern era, we calculated AU for yearlings annually using the midpoint of the start and end weights of all yearlings. The AU values varied from a low of 0.68 in 2000 to a high of 0.83 in 2015 for the modern era. We overlaid plots of ADG versus SR and BP versus SR, where the y-axes for ADG and BP were scaled such that the maximum predicted value for ADG was equivalent to the maximum predicted value for BP.

To examine the influence of droughts on the intersection of ADG and BP curves, we classified each year as either drought or nondrought on the basis of the 1940–2018 long-term precipitation for October-September mean water year (MWY). We defined drought years as those in which rainfall was $<$ 75% of MWY ($n = 3$ yr: 2002, 2004, and 2012) and nondrought years as those with $>$ 75% of MWY ($n = 16$ yr) (Augustine 2010). We then analyzed the relationships between ADG and BP for SR in the same manner as described previously for the drought and nondrought years.

In an effort to offer a more universal understanding of the relationship among climate variability, stocking, and forage production, we illustrate the GPI ($\mathrm{AUD} \cdot \mathrm{Mg}^{-1}$) for a given stocking rate ($\mathrm{AUD} \cdot \mathrm{ha}^{-1}$) in drought and nondrought years, as well as all 19 yr of the modern era (2000–2018). GPI provides a means to reduce the ambiguity associated with qualitative terms of heavy, moderate, or light SR (Smart et al. 2010). Forage production used in our GPI calculation was the sum of peak growing season biomass (late July–early August) clippings as described earlier. We excluded prickly pear cactus *(Opuntia polyacantha)* and subshrub species from our measure of forage production.

Economic analyses

Annual purchase costs and sale revenues of yearlings were determined by multiplying mean entry (mid-May) and exit (early October) weights from each SR by the market prices reported for the week in which weights were obtained. Livestock prices were obtained from the Livestock Marketing Information Center (LMIC), which relies on data compiled by the USDA Agricultural Marketing Service, in the Colorado Auction Feeder Cattle Summary report (AMS report GL_LS795). Forage leasing costs ($\$ \cdot$ animal unit month^{-1}, AUM) were estimated annually using the 11 US western states lease rates (Wyoming Agricultural Statistics Service, WASS; Internet site: https://www.nass.usda.gov/Statistics_by_State/Wyoming/index.php). Net revenue was determined annually for each SR by subtracting purchase costs and forage leasing costs from sale revenues. All monetary variables were normalized to 2019 using the Producer Price Index. We used the average purchase and sale weights of steers across the 19 yr, with values adjusted to 2019 US dollars. We assumed interest was 8%.

Results

Water year (October to September) annual precipitation was similar during the Bement (1940–1963; mean ± standard deviation [SD]; 312 ± 84 mm) and modern eras (2000–2018; 330 ± 55 mm), but the range in values was twofold greater during the Bement era (362, 127–489 mm) compared with the modern era (175, 231–406 mm; Fig. 1). The very heavy SR pasture experienced the same range of water year precipitation levels as the light, moderate, heavy SR pastures because the highest and lowest precipitation levels, 2009 and 2012, respectively, also occurred within the 7-yr

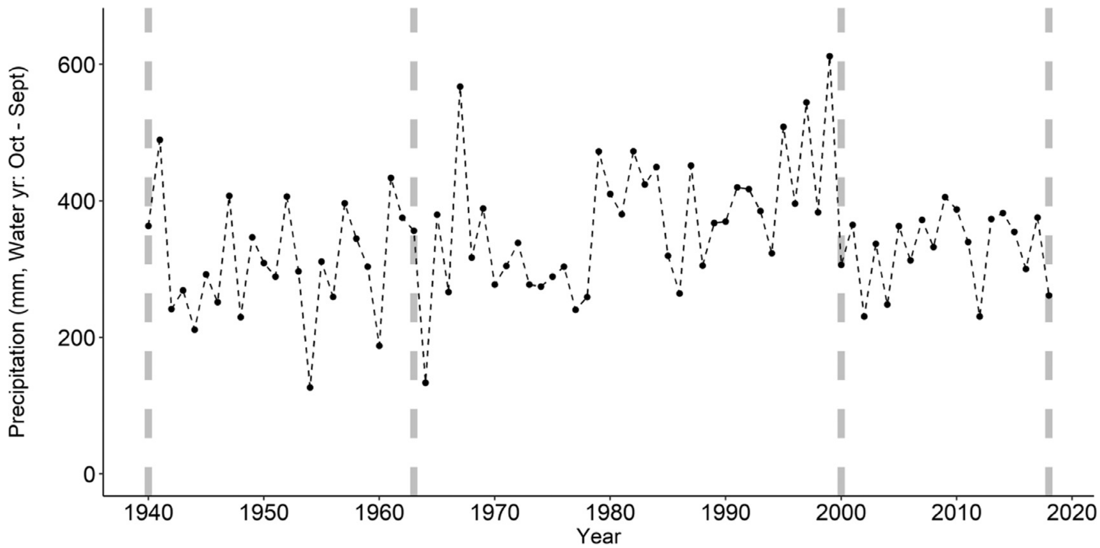

Fig. 1. Water year (October–September) annual precipitation (mm) from 1940 to 2018 at the US Department of Agriculture–Agricultural Research Service Central Plains Experimental Range. *Vertical dashed lines* illustrate annual precipitation variability during the Bement (1940–1963) and modern eras (2000–2018).

Table 1
Linear mixed model results for predicting perennial grass production relative to study era, spring precipitation, and stocking rate.

Factor	β (SE)	F	P
Intercept	57.976 (3.759)	34.463	< 0.0001
Era	24.628 (5.261)	4.500	< 0.0001
Stocking rate	−7.520 (3.734)	−2.130	0.032
Spring precipitation	6.987 (4.152)	2.071	0.043
Era × Spring precipitation	11.652 (5.380)	1.652	0.101
Era × Stocking rate	6.251 (5.276)	1.513	0.134
Stocking rate × Spring precipitation	−0.177 (4.161)	−0.001	0.991
Era × Stocking rate × Spring precipitation	−2.692 (5.416)	−0.319	0.752

time span (2006–2012). Additionally, this 7-yr time span experienced similar mean water year precipitation (340 ± 58 mm) with a similar coefficient of variation (very heavy: 0.171, light, moderate, heavy: 0.165).

Forage production of C_3 graminoids and C_4 grasses for each SR in both study eras are presented in Figure 2a. Perennial forage production (C_3 graminoids and C_4 grasses combined) was 36% greater in the modern era (mean ± SD; 803 ± 403 kg · ha^{-1}) than the Bement era (585 ± 180 kg · ha^{-1}) (Table 1). Within each study era, forage production declined linearly with increasing SR (see Table 1). Perennial grass biomass responded positively to spring precipitation (see Table 1, Fig. 2b) with this response stronger during the modern era than the Bement era based on a marginally significant interaction between spring precipitation and study era. SR did not significantly affect the relationship between forage production and spring precipitation, and relationships among forage production, SR, and spring precipitation did not vary significantly by study era (nonsignificant three-way interaction, see Table 1).

Bement (1969) reported that ADG of yearling beef cattle followed a broken stick model, where ADG averaged 1.27 kg · AUD^{-1} for SR < 11 AUD · ha^{-1} and then declined approximately linearly as SR increased from 11 to 27 AUD · ha^{-1}, with a slope of −0.0551 (Fig. 3a). Estimates of ADG for SR > 27 AUD · ha^{-1} were not reported. For the modern era, when SR > 27 AUD · ha^{-1}, substantial variation in ADG occurred with values ranging from −0.23 kg to 1.33 kg · AUD^{-1} (see Fig. 3b). For all years in the modern era combined, we found that a broken stick model explained more variation in ADG relative to SR than a simple linear model; ADG averaged 1.28 kg · AUD^{-1} for all SRs < 15.5 AUD · ha^{-1} and then declined linearly with a slope of −0.021 (see Table 1, Fig. 3b). At low SR in both eras, ADG was nearly identical (1.27 vs. 1.28 kg · AUD^{-1}). However, ADG declined much less rapidly with increasing SR in the modern era relative to the Bement era.

The model fit for ADG based on all modern era years combined ($r^2 = 0.168$, see Table 1) was poor; thus, we examined models for drought years separately from nondrought years. For nondrought years, we found that a broken stick model explained more variation in ADG relative to SR than a simple linear model; ADG averaged 1.30 kg · AUD^{-1} for all SR < 13.6 AUD · ha^{-1} and then declined linearly with a slope of −0.016 (see Table 1; Fig. 3c). In all years combined and nondrought years of the modern era, ADG was nearly identical (1.28 vs. 1.30 kg · AUD^{-1}) at low SR, whereas the linear decline in ADG with increasing SR was less abrupt in the nondrought years (slope: −0.021 vs. −0.016), which was expected as dry years were removed. In contrast, ADG and BP were markedly reduced in the 3 drought yr, with ADG averaging 1.09 kg · AUD^{-1} for SR < 14.2 AUD · ha^{-1}, and then declining more rapidly with increasing SR, with a slope of −0.073 (see Table 1; Fig. 3d). Model fit for ADG in drought years was relatively high ($r^2 = 0.82$) but still low for nondrought years ($r^2 = 0.23$). Visual inspection of the latter relationship shows a notable outlier well below the fitted ADG model at 31 AUD · ha^{-1} (see Fig. 3c). This outlier occurred in 2006 when mean annual precipitation was 313 mm, or 92% of the long-term average (Table 2).

Bement (1969) projected BP as a function of SR, graphed this relationship in a manner that scaled maximum BP equivalently to maximum ADG (see Fig. 3a), and thereby identified 13.5 AUD · ha^{-1} as the optimal SR to balance maximization of individual weight gain and gain per unit area. Following the same approach, we used the fitted broken stick models to graph predicted BP as a function of SR and then identified the optimal SR to balance maximization of individual weight gain and gain per unit land area in the modern era. For all modern era years combined, this optimum occurred at 23.2 AUD · ha^{-1} (see Fig. 3b), which is 72% higher than the Bement (1969) value. Removal of the 3 drought yr increased the optimum SR for the modern era to 25.6 AUD · ha^{-1} (see Fig. 3c). For the 3 drought yr in the modern era, the optimum SR declined to 14.2 AUD · ha^{-1} (see Fig. 3d), which was still 5% higher than the Bement (1969) value.

Using the SR of 13.5 AUD · ha^{-1} from Bement (1969) during the modern era of 2000–2018 would have generated a mean annual

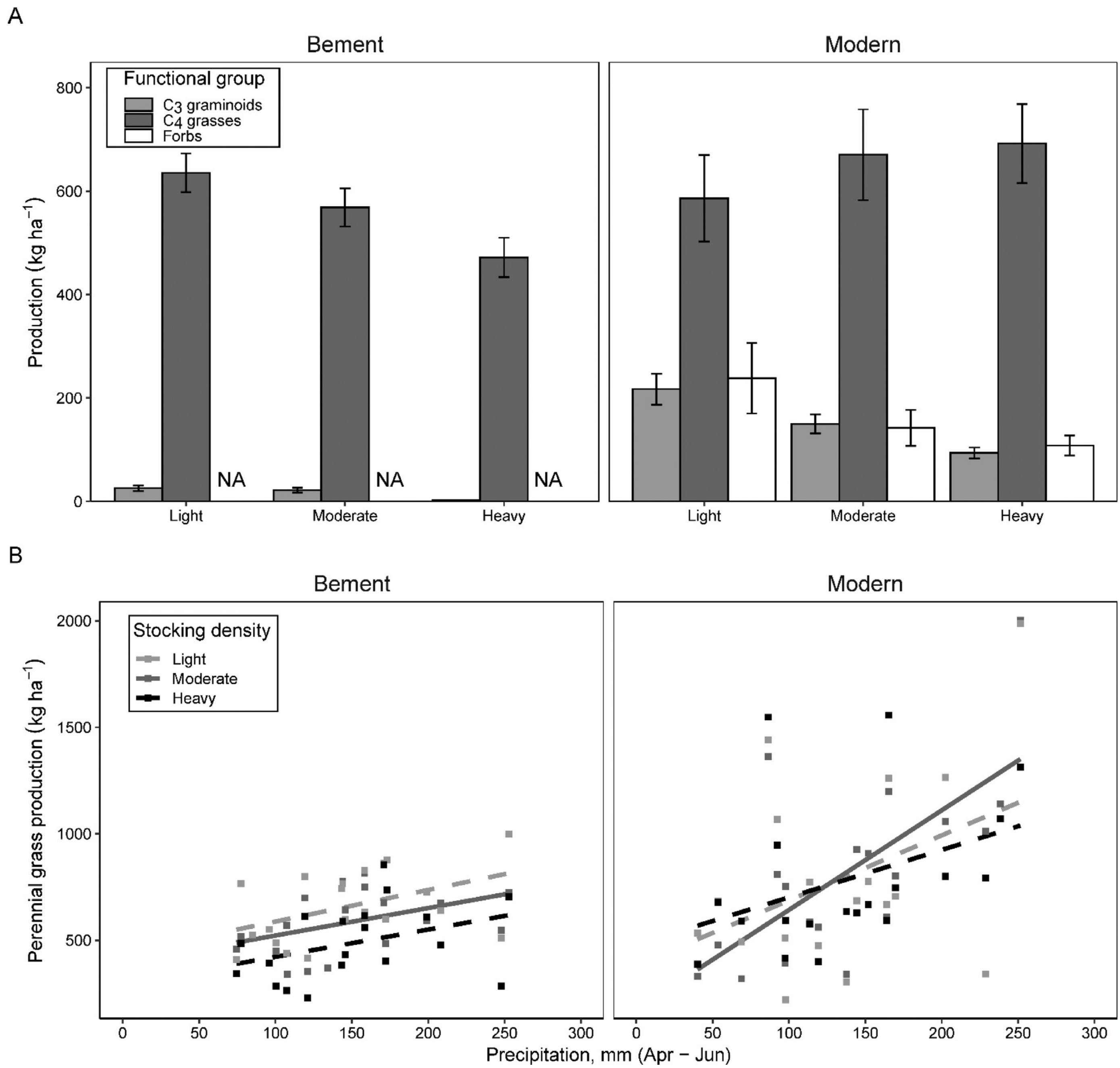

Fig. 2. Panel A shows mean production (±SE) of C_3 graminoids, C_4 grasses, and forbs for each stocking rate in the Bement (1940–1963) and modern (2000–2018) eras. Forb data in the Bement era were not available. Panel B shows relationship between perennial grass production and spring precipitation (mm, sum of April–June). Points are raw data and lines show the linear regression between forage production and spring precipitation for each stocking rate and study era.

Table 2
Comparisons of regression models for the relationship between average daily gain (ADG, kg · AUD^{-1}) and stocking rate (SR, AUD · ha^{-1}) for all 19 yr (2000–2018) in the modern era, for a subset of 3 drought yr (2002, 2004, 2012), and for the remaining 16 nondrought yr for shortgrass rangeland grazed by yearling cattle in northeastern Colorado.

Data set	Model type	Equation	R^2
All 19 yr	Negative linear	ADG = 1.4386 – 0.01585 (SR)	0.156
All 19 yr	Broken stick	If SR < 15.5, ADG = 1.283; else ADG = 1.559 – 0.0207 (SR)	0.168
Nondrought yr	Negative linear	ADG = 1.439 – 0.0159 (SR)	0.223
Nondrought yr	Broken stick	If SR < 13.6, ADG = 1.297; else ADG = 1.512 – 0.0158 (SR)	0.229
Drought yr	Negative linear	ADG = 1.653 – 0.0516 (SR)	0.734
Drought yr	Broken stick	If SR < 14.2, ADG = 1.095; else ADG = 2.132 – 0.073 (SR)	0.815

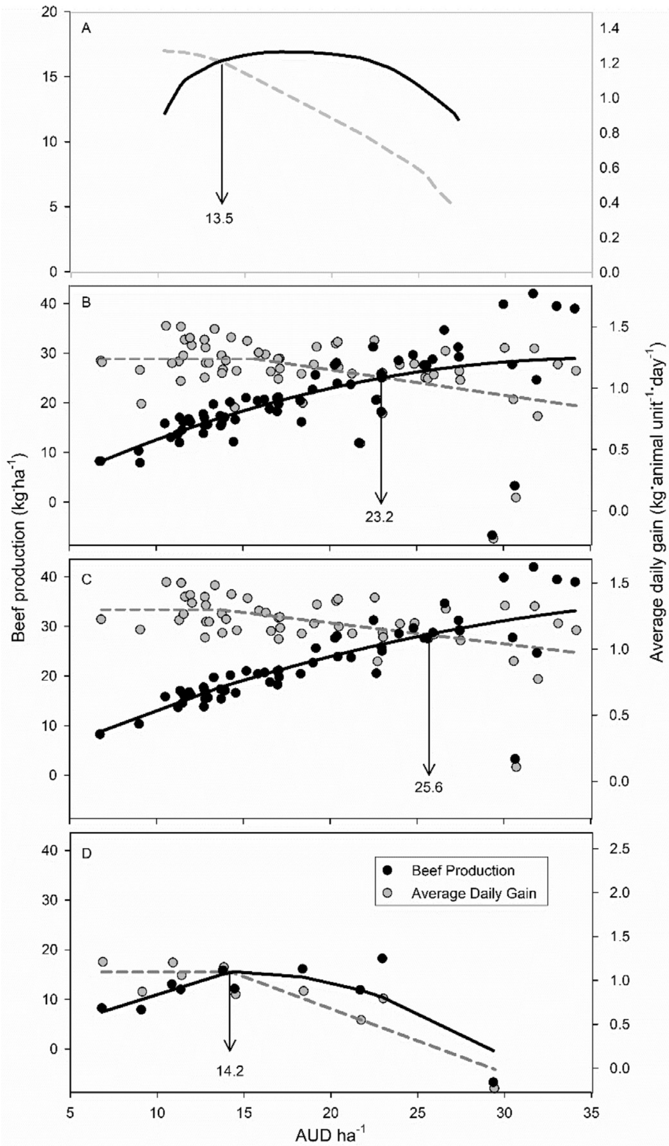

Fig. 3. Relationships between average daily weight gain (gray circles, ADG, kg AUD^{-1}) and beef production (black circles, BP, kg ha^{-1}) for yearling cattle grazing shortgrass steppe of northeastern Colorado across a range of stocking rates (animal unit days [AUD] ha^{-1}). In all panels, the *dashed line* shows the relationship for ADG with stocking rate (SR), and the *solid line* shows the relationship for BP with SR. A, Relationships published by Bement (1969) for the study yr 1940–1963, after conversion to metric units. B, Relationships for all 19 modern era yr (2000–2018). C, Same relationships for nondrought yr ($n = 16$) during the modern era. D, Relationships for 3 drought (< 75% annual precipitation) yr (2002, 2004, and 2012). For each panel, y-axes are scaled so that the maximum values of the fitted curve for ADG and BP are set at the same level. Predicted curves for BP are the product of SR and the equation for the fitted relationship between ADG and SR. The intersection of the two curves indicates the optimal SR value as depicted by the *arrow line* and associated number.

BP rate of 16.7 kg · ha^{-1}. In contrast, applying the optimal SR across all years from the modern era (23.2 AUD · ha^{-1}; see Fig. 3b) each year would lead to a mean annual BP of 25.2 kg · ha^{-1}, an increase of 51%. However, applying this SR during the 3 drought yr would have resulted in an average BP of only 10.2 kg · ha^{-1} across those years. Further, if SR was > 23.2 AUD · ha^{-1} during the 3 drought yr, a precipitous decline in BP would be expected (see Fig. 3d). Assuming perfect prior knowledge of which years would be droughts, increasing SR to the biophysical optimum of 25.6 AUD · ha^{-1} in the nondrought years would yield an average BP of 28.4 kg · ha^{-1} during those 16 yr, and reducing SR to 14.2 AUD · ha^{-1} in the 3 drought yr would have yielded an average of 15.6 kg · ha^{-1} during those 3 yr. Cumulatively, this would have yielded an overall 19-yr BP average of 26.3 kg · ha^{-1}, or a 4.4% increase over the average 19-yr BP at constant SR of 23.2 AUD · ha^{-1}.

Grazing pressure index increased linearly with stocking rate in drought, nondrought, and all 19 yr of the modern era (Fig. 4). In drought years, GPI showed a higher relative increase in response to SR than nondrought years (1.6 × more positive slope coefficient: 2.56 vs. 1.57 AUD · Mg^{-1}; see Fig. 4). During drought years, a GPI of 25.5 AUD · Mg^{-1} corresponded with the optimal biophysical SR of 14.2 AUD · ha^{-1}, while 18.2 AUD · Mg^{-1} equated to the nondrought year SR optima of 25.6 AUD · ha^{-1}. Across all 19 modern era yr in this study, GPI at optimal biophysical SR, 23.2 AUD · ha^{-1}, was 36.5 AUD · Mg^{-1}.

Table 3
Economic returns for a range of stocking rates from light to very heavy, using average purchase and sale weights of steers across the 19 yr in the modern era (2000–2018) and the 7 yr for very heavy stocking rate (2006–2012). Economic values adjusted to 2019 dollars.

Item	Unit	Stocking rate (AUD · ha^{-1})			
		12.3	16.7	23.1	33.8
Yearlings · 129.5 ha^{-1}	Number	15	20	30	40
Entry weight · yearling^{-1}	kg	286.00	285.30	285.20	266.20
Entry value · kg^{-1}	$	3.31	3.29	3.29	3.01
Entry value · yearling^{-1}	$	946.66	938.64	938.31	801.26
Exit weight · yearling^{-1}	kg	419.10	405.40	398.60	350.00
Exit value · kg^{-1}	$	2.92	2.95	2.97	2.73
Exit value · yearling^{-1}	$	1 223.77	1 195.93	1 183.84	955.50
Gross return · yearling^{-1}	$	277.11	257.29	245.53	154.24
Gross return · ha^{-1}	$	32.42	39.63	56.45	48.49
Interest @ 8% for 6 mo · ha^{-1}	$	4.44	5.80	8.67	10.03
Misc. costs (salt, taxes) · ha^{-1}	$	1.40	1.60	2.03	2.48
Net return · ha^{-1}	$	26.58	32.23	45.75	35.98

Economic results

Economic outcomes were calculated for four SR levels used in the modern era, representing a range from light to very heavy SR (Table 3). Net returns increased from $26.58 to $32.23 · ha^{-1} as SR increased from 12.3 (light) to 16.1 (moderate) AUD · ha^{-1}. Increasing SR to heavy at 23.1 AUD · ha^{-1} further increased average net annual returns to $45.75 · ha^{-1}, or a 42% greater average return compared with moderate stocking.

Discussion

Our revisitation of the Bement (1969) SR rate guide for the modern era (2000–2018) revealed two key findings. First, the multidecadal directional shift in optimal SR, from the Bement era (1940–1963) value of 13.5 AUD · ha^{-1} to 23.2 AUD · ha^{-1} in the modern era, showcases that the capacity of this semiarid rangeland to produce livestock weight gains has increased substantially over the past 8 decades. Second, the slope of the relationship between SR and ADG was 2.6 × more negative during the Bement era (slope coefficient of −0.0551) than the modern era (slope coefficient of −0.0207). This change in slope is exactly opposite of the expected shift over time if grazing was inducing degradation in this rangeland ecosystem (Wilson and MacLeod 1991) and provides clear evidence that the productivity of this semiarid rangeland system has increased. Our observed directional shift in the ADG/BP curve intersection to a higher SR in the modern era is likely driven by two non−mutually exclusive factors: 1) changing plant communities in the study pastures (Porensky et al 2017) and 2) an increase in the entry weights and genetic potential of study animals over the 8 decades (Derner et al. 2020). Plant communities in moderately

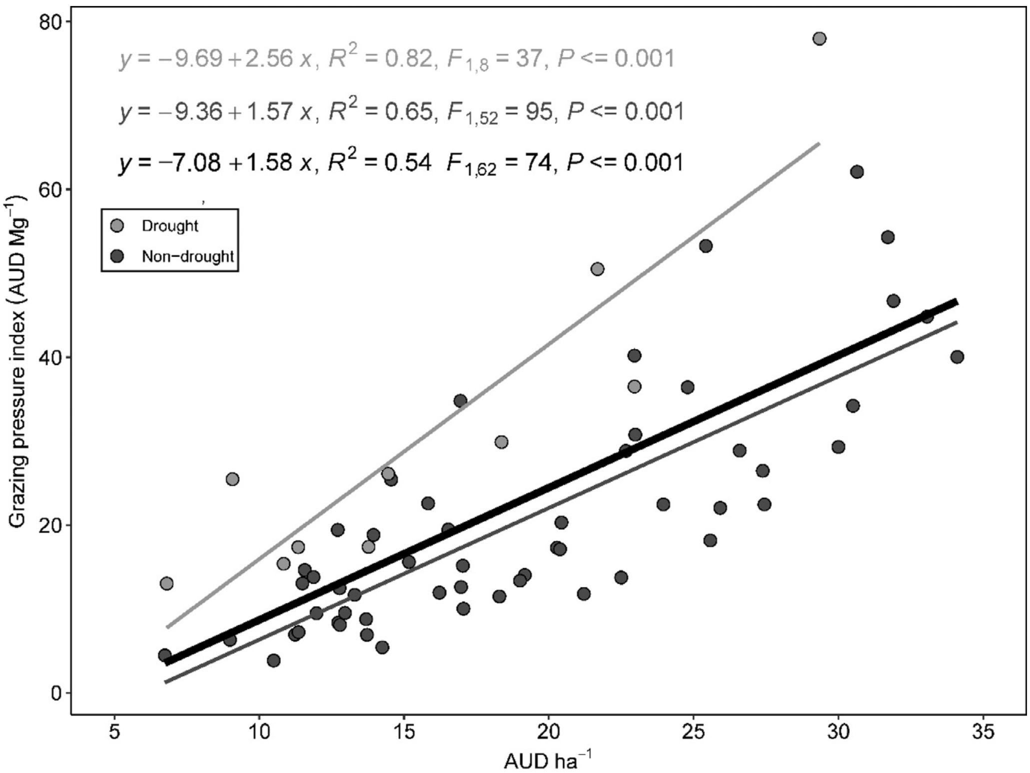

Fig. 4. Grazing pressure index (GPI; animal unit days [AUD] $\cdot$ Mg^{-1}) in relation to stocking rate (SR) (AUD $\cdot$ ha^{-1}) for yearling cattle grazing shortgrass steppe of northeastern Colorado during the modern study era (2000–2018). We show linear regression equations, R^2s, F statistics, and P values for GPI-SR relationships during drought years, nondrought years, and all 19 yr of the modern era.

stocked pastures at this study site have moved from dominance by a C_4 shortgrass *(Bouteloua gracilis)* in the 1940s to codominance with a more productive C_3 mid-grass *(Pascopyrum smithii)* in the modern era, as a fivefold increase in basal cover of C_3 perennial grasses has been observed (Augustine et al. 2017). Most of this increase in C_3 perennial grasses has occurred over the past 30 yr (Porensky et al. 2017). This shift in plant community composition has resulted in increased forage productivity (Irisarri et al. 2016; this study).

Possible explanations for the observed increase in C_3 perennial grasses are 1) a low abundance early on at this study site (Costello 1944; Klipple and Costello 1960) resulted from the plant functional group being in an initial state of recovery following the extreme drought conditions, dust storms, and soil movement during the 1930s Dust Bowl; 2) a response to increasing atmospheric concentration of carbon dioxide (CO_2; Morgan et al. 2007); and 3) to a lesser extent, increasing atmospheric nitrogen deposition (Burke et al. 2008). Concurrent with this increase in vegetation productivity resulting from the C_3 perennial grasses is the > 50% increase in entry weights of yearlings in this experiment over time (Derner et al. 2020). This increase may be attributable to an emphasis in genetic selection for larger mature cow size and more rapid growth potential in the beef cattle industry; unclear is whether or not this selection emphasis has also increased the efficiency with which livestock grow per unit amount of forage. Additionally, advances in vaccination protocols for improvements in animal health from the Bement to the modern era may have also impacted observed animal gains during this long-term evaluation.

Precipitation variability is an intrinsic and defining feature of semiarid rangelands, where average annual rainfall is low but interannual variation is high, relative to mesic systems (Knapp and Smith 2001). Thus, managing these semiarid rangelands for beef production involves substantial challenges matching animal demand and forage supply in the face of inherent interannual weather variability. Whereas a vast majority of yearling livestock purchases in the shortgrass steppe are made before April for the upcoming grazing season (Bement 1969; Hart et al. 1988), > 70% of the annual precipitation falls after this period (i.e., between April and September; Pielke and Doesken 2008). Therefore, even for yearling livestock producers, who have substantially greater ability to vary SR from year to year compared with cow-calf operations (Kachergis et al. 2014), uncertainty in late spring and summer rainfall is a major challenge for setting SR.

Rather than use the same SR each year, applying flexible SR (Derner et al. 2018; Derner and Augustine 2016; Espeland et al. 2020) annually could provide a strategy to blend precision environmental data with precision livestock management. We estimated that if prior knowledge of drought conditions was absolute in advance, a 4.4% increase in BP could be expected with employing the optimal SR in nondrought years of the modern era (see Fig. 2c) and the optimal drought SR in drought years (see Fig. 2d) compared with applying a constant SR (see Fig 2b). This is consistent with findings from other rangelands of Australia and North America, where a tight coupling of SR with predicted forage supply increases BP, as well as revenue, relative to constant stocking (Ash et al. 2000; Ritten et al. 2010; Torell et al. 2010).

To date the only long-term empirical test of the relative performance of variable SR using pre–grazing-season weather predictions relative to constant moderate stocking is that by O'Reagain et al. (2009; 2011) in Australia. They varied SR in ~100 ha pastures using dormant season pasture conditions and upcoming wet season forecasts from the Southern Oscillation Index. Higher long-term profitability of flexible stocking relative to constant moderate stocking occurred, but flexible stocking exhibited more interannual variability in profitability (O'Reagain et al. 2009; O'Reagain et al. 2011), which is challenging to the economic sustainability of individual operations (Hart and Ashby 1998). Modeling of the economic outcomes of varying SR based on emerging weather forecasting approaches (Peck et al. 2019; Raynor et al. 2020) is needed to provide foundational knowledge for evaluating enterprise risks associated with flexible stocking.

Conclusions and implications

Our modern era (2000–2018) analyses of determining optimal SR rates in this semiarid, shortgrass steppe from the intersection of response curves of ADG and BP revealed that use of the Bement (1969) optimum SR would have led to substantial understocking (13.5 vs. 23.2 AUD $\cdot$ ha^{-1}) and associated reduced BP over these 19 yr. Ranchers and managers employing the modern era optimal SR still need to be cognizant of matching forage availability to animal demand and that our SR analysis only applies to shortgrass steppe, which is dominated by grazing-tolerant grasses (Milchunas et al. 1988). Because interannual variability of economic revenue increases as SR (Irisarri et al. 2019) and seasonal precipitation variation increases (Hamilton et al. 2016), ranching enterprises attempting to reduce economic risk associated with weather/climatic variability will need to dynamically manage animal demand through SR adjustments (i.e., flexible stocking; Derner et al. 2018; Derner and Augustine 2016; Espeland et al. 2020). Decision making to adjust SR should take into account not only biophysical and ecological factors but also economic considerations that underlie long-term sustainability of ranching enterprises (Shrum et al. 2018). A fundamental understanding of how SR influences both livestock production and economic outcomes, as well as how climatic, biophysical, and market factors mediate these outcomes, is paramount to prioritizing adaptive management actions within these complex social-ecological systems.

Declaration of Competing Interest

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

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