# Prairie Dog (*Cynomys ludovicianus*) Influence on Forage Quantity and Quality in a Grazed Grassland-Shrubland Ecotone ☆

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## ARTICLE INFO

## ABSTRACT

Black-tailed prairie dogs (*Cynomys ludovicianus*) have high dietary overlap with livestock, which can cause forage-centric conflicts between agriculture and conservation. Research suggests prairie dogs can enhance forage quality, but trade-offs between quality and quantity throughout the growing season remain unclear, as well as the degree to which increased forage quality is caused by altered species composition versus altered plant physiology. To assess the effects of prairie dog herbivory on forage in a northern mixed-grass prairie, we collected samples on prairie dog colonies and at sites without prairie dogs during June, July, and August 2016 - 2017 for forage quality, and August 2015 - 2017 for herbaceous biomass. To isolate mechanisms affecting forage quality, we collected both composite samples of all herbaceous species and samples of western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve). Across years and plant sample types, crude protein, phosphorus, and fat were 12-44% greater and neutral detergent fiber was 6-10% lower on prairie dog colonies than at sites without prairie dogs. The effects of prairie dogs on forage quality persisted throughout the season for western wheatgrass samples (all treatment*time p-values ≥ 0.4). Across years, aboveground herbaceous biomass did not differ significantly between prairie dog colonies and sites without prairie dogs (on-colony: 933 ± 156 kg/ha, off-colony: 982 ± 117 kg/ha). The effects of prairie dogs on herbaceous biomass were significantly influenced by spring precipitation. In years with dry springs, herbaceous biomass was lower on colonies than sites without prairie dogs and this pattern was reversed in years with wet springs. Our results demonstrate season-long enhanced forage quality on prairie dog colonies, indicating that multiple mechanisms are shaping forage quality in this system, including altered species composition, phenological growth stage, and soil condition. Across years, enhanced forage quality may help to offset reductions in forage quantity for agricultural producers.

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## Introduction

Free-roaming herbivores have historically been major drivers of structural and evolutionary patterns and processes in rangeland ecosystems (Frank et al., 1998; Sankaran et al., 2005). In the western United States, rangelands have evolved under grazing and browsing pressure from herds of native free-roaming ungulates that interacted with small mammal assemblages (Stebbins, 1981). Before European settlement, wild ungulate herbivores included species from the Cervidae (deer and elk), Antilocapridae (American pronghorn), and Bovidae (bison) families (Danell et al., 2006). In the absence or reduction of these large native grazers, domestic livestock now serve as the dominant large herbivore interacting with small mammals on North American rangelands. Contemporary livestock management on rangelands influences animal distribution and competition for forage, creating a unique anthropogenic interaction between large ungulates and small mammals where both agricultural production and the conservation of biodiversity are of concern (Heitschmidt and Stuth, 1991).

In the northern mixed-grass prairie of the United States, black-tailed prairie dogs *(Cynomys ludovicianus)* co-occur with domestic livestock, particularly beef cattle (Koford, 1958). The sympatric distribution of beef cattle and prairie dogs was historically viewed as competitive for forage due to their dietary overlap (~75%) and shared preference for graminoids (Koford, 1958; Summers and Linder, 1978; Uresk, 1984; Miller et al., 2007). Potential competition for perennial grasses between

cattle and prairie dogs can be heightened when forage attains peak quality and quantity during the growing season of spring and summer, a time when cattle rely solely on pasture forage for sustenance and prairie dogs consume greater quantities of graminoids (Fagerstone et al., 1981; Vermeire et al., 2004; Scasta et al., 2016a; Scasta, 2017). The preferential selection for graminoid forage changes in the fall and winter, when prairie dogs consume greater amounts of forbs, shrubs, seeds, roots, and cacti (Fagerstone et al., 1981) and cattle are typically moved to winter pastures where their diets are supplemented with harvested feed. Thus, dietary overlap and potential competition between beef cattle and prairie dogs are highest in spring and summer.

Competition for shared and limited resources dictates occupancy, distribution, and spatiotemporal use in free-roaming animals on rangelands. Direct competition occurs when a limited resource is exploited to the benefit of one individual or species, rendering the remaining resource insufficient for another species or individual (Gause, 1934). Animals may mitigate interspecific competition by avoiding overlapping resource use in time or space (Rosenzweig, 1995) or by capitalizing on phenologic growth whereby the first herbivory event causes palatable, nutritious regrowth and thus mitigates competition for the second herbivory event. However, modern grazing management practices alter the evolutionary ungulate — prairie dog interaction by imposing artificial restrictions on livestock movement (i.e., fences), which may limit the ability of livestock to mitigate interspecific competition with relatively sedentary small mammals such as prairie dogs.

For perspective, an individual prairie dog consumes the same relative forage as ~0.003 animal units (AUs), or 335 prairie dogs consume the same forage as a 454-kg (1 000-lb) cow with a calf, which is the basis for the AU concept in rangeland grazing management (Koford, 1958). However, the subsequent reduction of herbaceous forage biomass on rangeland landscapes by prairie dogs is also influenced by prairie dog density, which can be highly variable, ranging from 2 to 36 individuals per hectare (Powell et al., 1994; Severson and Plumb, 1998; Johnson and Collinge, 2004; Derner et al., 2006; Eads and Biggins, 2012). In addition, prairie dogs may further deplete aboveground biomass by clipping, but not consuming, standing forage as a vigilance strategy to enhance their ability to see predators (Hoogland, 2006). In both mixed-grass and shortgrass prairies, prairie dogs are capable of decreasing graminoid biomass by half (Fahnestock and Detling, 2002) and causing morphological variation of native graminoids in the form of reduced height and greater prostrate form (Painter et al., 1993). These effects may be exacerbated in low-production grasslands (Derner et al., 2006; Lauenroth and Burke, 2008) or mitigated by spring precipitation and colony characteristics such as occupancy and colony age (Augustine and Springer, 2013).

Prairie dogs have the ability to negatively affect cattle weight gains, but the magnitude of such an effect is highly dependent on colony scale, spatial overlap of colonies with livestock pastures, instantaneous intake rate of the ruminant, site-specific grass species, soil type, and spring precipitation (Derner et al., 2006; Augustine and Springer, 2013). Indeed, these results alone suggest that prairie dogs are in direct competition with cattle for forage. However, effects of prairie dogs on livestock may be mitigated by enhanced forage quality found on prairie dog colonies, where grass regrowth following defoliation is tender and highly nutritious (Chipault and Detling, 2013).

Currently, few studies are available that directly examined the tradeoffs between prairie dog effects on forage quantity (likely negative) and their effects on forage quality (likely neutral to positive). Augustine and Springer (2013) found prairie dogs in northern mixed-grass prairie sites reduced herbaceous biomass of commonly grazed species by 63–94%, but in the shortgrass prairie there was little to no significant reduction in herbaceous biomass at one site and substantial reductions at another. Under dry conditions, reductions of forage biomass were substantial but effects on forage digestibility were nonexistent or very small. Under wet conditions, forage biomass was not reduced at one shortgrass prairie

site but was reduced at a northern mixed-grass prairie site, and both sites had enhanced forage digestibility and nitrogen content. The authors of this study concluded that the interactive effects of prairie dogs on forage quantity and quality were highly variable across space and time, and competition between cattle and prairie dogs may be evident under dry conditions but offset under wet conditions (Augustine and Springer, 2013).

To better understand the potential for forage-centric competition between livestock and prairie dogs, we investigated the effects of prairie dog herbivory on aboveground herbaceous biomass and forage quality in the northern mixed-grass prairie and sagebrush steppe ecotone in northeastern Wyoming. Specifically, we assessed how prairie dog herbivory, across variable colony characteristics, livestock stocking rates, and interannual precipitation, influenced forage biomass and quality throughout the growing season and across years. In order to distinguish between prairie dog effects on plant phenology and plant species composition, we examined forage quality of composite herbaceous samples and the dominant, palatable perennial grass species in this ecosystem.

## Methods

### Study Area

Our study occurred in the Thunder Basin National Grassland (Thunder Basin), a 6 880-km$^2$ northern mixed-grass prairie and sagebrush steppe ecotone in northeastern Wyoming (497013.101, 4830298.439 m, UTM Zone 13; Fig. 1). Long-term mean annual precipitation (1981 − 2010) was 320 mm (PRISM Climate Group, 2017), and long-term mean growing-season precipitation was 177 mm (April–June 1981–2010; Derner and Hart, 2007; WRCC, 2016). Mean growing-season precipitation at our sampling sites during the study period was above average in 2015, below average in 2016, and very close to average in 2017 (308 mm, 125 mm, and 171 mm, respectively; PRISM Climate Group, 2017). Sampling sites were constrained to loamy soils, which dominate 33% of the landscape (Ecological Site R058BY122WY, USDA-NRCS), and elevation ranged from 1 328 to 1 511 m (PRISM Climate Group, 2017). Sampling sites were located on both private land and public land managed by the US Forest Service.

Vegetation was dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *Wyomingensis* [Beetle & Young]), and common perennial grasses included blue grama (*Bouteloua gracilis* [H.B.K.] Lag. Ex Griffiths), western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve), prairie junegrass (*Koeleria macrantha* [Ledeb.] Schult.), threadleaf sedge (*Carex filifolia* Nutt.), Sandberg bluegrass (*Poa secunda* J. Presl), and needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth). Annual grasses included exotic bromes (*Bromus arvensis* and *B. tectorum* [L.]) and the native sixweeks fescue (*Vulpia octoflora* (Walter) Rydb) (Porensky and Blumenthal, 2016). Plains pricklypear cactus (*Opuntia polyacantha* [Haw.]) was also common throughout the landscape.

### Study Design

We randomly selected four 16-km$^2$ sites in Thunder Basin (see Fig. 1). Each site was selected a priori as part of a larger study to encompass three types of disturbance history: a black-tailed prairie dog colony, a historic wildfire (results presented in a separate manuscript; Connell et al., 2018), and an adjacent undisturbed control (hereafter: sites without prairie dogs). The experiment had a blocked design with each of the three disturbances present in each of the four sites ($n = 12$). Within each site, large candidate areas were selected within each disturbance so that sampling areas were matched in terms of soil type, slope, aspect, and topographic wetness index (an indicator of landscape
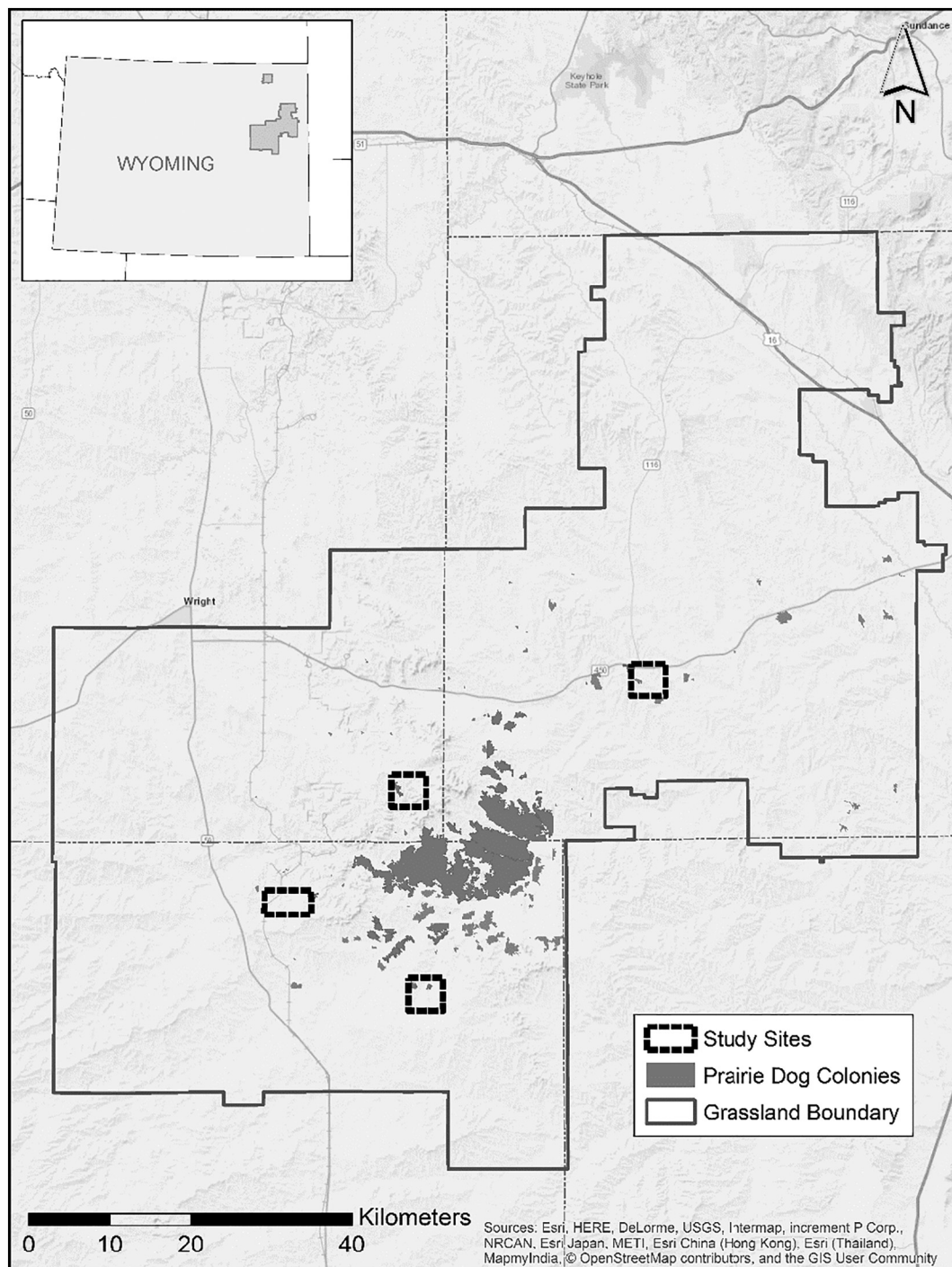
**Figure 1.** We established four study sites in Thunder Basin National Grassland, Wyoming. Each study site contained 1) a black-tailed prairie dog colony, 2) a historical wildfire (not pictured; data represented in a separate manuscript), and 3) an undisturbed site without prairie dogs or fires (control). Study sites were located on public land managed by the US Forest Service and privately owned property.

position). At each site, we permanently established paired 20-m monitoring stations (transects) randomly located within the prairie dog colony or sites without prairie dogs (≥ 280 m from colony edge; $n = 4$ paired stations across sites). Monitoring stations were fully accessible to livestock, wild ungulate, and small mammal grazing. Livestock grazing, which included cow-calves, cows, bulls, yearling steers, ewes-lambs, and ewes, was variable between pastures and years. Across livestock class, grazing ranged from 0.1 to 0.4 AU mo·• ha$^{-1}$ • yr throughout the study period, with a median of 0.2 (Table 1; see Appendix A for greater detail). Prairie dog colonies at our sites ranged in time since

settlement (9–20 + yr), size (48–69 ha), and occupied density (7–25 individuals • ha$^{-1}$; Table 1; see Data Collection for methodology).

*Data Collection*

To determine how soil nutrients differed between prairie dog colonies and sites without prairie dogs, we collected soil samples in June 2015 along one side of each monitoring station at distances of 5, 10, 15, and 20 m with a 7-cm diameter soil auger. At each sampling station, we collected soil at two depths (0–10 cm and 10–30 cm) and pooled soil

**Table 1**

Characteristics of black-tailed prairie dog colonies at study sites in Thunder Basin National Grassland, Wyoming. Colony age (total and continuous years), size, and year of colony size were derived maps of colony boundaries created annually by the US Department of Agriculture Forest Service. Active prairie dog burrows were estimated at each site in 2017. Livestock grazing information provided by the Thunder Basin Grazing Association.

| Location | Colony age (total yr)[1] | Active burrows / ha | Prairie dogs / ha | Colony size (ha)[2] | Yr of colony size | Avg. animal unit mo • ha$^{-1}$ (yr)[3] | Site description |
|---|---|---|---|---|---|---|---|
| Site 1 | 9 | 142 | 25 | 47.63 | 2016 | 0.2 (2015)<br>0.4 (2016)<br>0.1 (2017) | Prairie dog colony |
| | — | — | — | — | — | 0.1 (2015)<br>0.2 (2016)<br>0.3 (2017) | Site without prairie dog colony |
| Site 2 | 15 | 67 | 12 | 20.31 | 2016 | 0.2 (2015)<br>0.1 (2016)<br>0.2 (2017) | [4]Pasture contains prairie dog colony and site without prairie dogs |
| Site 3 | 20 | 133 | 24 | 68.63 | 2016 | 0.1 (2015)<br>0.1 (2016)<br>0.1 (2017) | [4]Pasture contains prairie dog colony and site without prairie dogs |
| Site 4[5] | 11 | 42 | 7 | 34.72 | 2014 | 0.2 (2015)<br>0.2 (2016)<br>0.3 (2017) | [4]Pasture contains prairie dog colony and site without prairie dogs |

[1] Colony age was determined by colony mapping conducted by the US Forest Service beginning in 1997. The colony at Site 3 was present at this time and therefore this colony may be older.

[2] Estimate of colony limited to areas contained on public land. Values represent a conservative estimate of colony size.

[3] See Appendix A for greater detail of livestock grazing type and animal unit months by pasture size and site.

[4] Pastures containing both prairie dog colonies and site without prairie dogs were large (≥ 1 137 ha) and sampling stations were spatially distinct (sites without prairie dogs were ≥ 280 m from colony edge).

[5] Colony last mapped in 2014 and does not reflect growth experienced 2015-2016. Values represent a conservative estimate of colony size.

samples across sampling distances to generate two composite soil samples per monitoring station (one per depth by station combination). Soil samples were passed through a 2-mm sieve and then analyzed for total C and N (Matejovic, 1997). Organic carbon (%) was determined with a modified pressure-calcimeter method (Sherrod et al., 2002).

To determine how forage quantity differed between prairie dog colonies and sites without prairie dogs, we clipped peak standing herbaceous biomass at each monitoring station according to peak plant maturity each year (the first week of August in 2015, 2016, and during the third week of July in 2017). We collected three subsamples at each monitoring station by randomly locating a 0.5-m$^2$ hoop within 20 m of the monitoring station and clipping all herbaceous vegetation rooted within the hoop to ground level ($n = 24$ per yr). Samples were oven-dried at 60°C for 48 hr before weighing and averaged by sampling event and monitoring station prior to analysis ($n = 8$ per sampling event; Elgersma et al., 2014).

We collected forage quality samples at each monitoring station during the first week of June, July, and August in 2016 and 2017. For each sampling event, we collected two forage quality sample types: 1) a composite of all herbaceous vegetation (i.e., COMP) obtained by randomly tossing and clipping vegetation inside a 0.5-m$^2$ hoop and 2) a sample of western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) (i.e., PASM), a palatable C3 perennial grass, obtained by collecting $30 - 50$ individual plants as close to the random hoop position as possible. We collected three subsamples of each forage sample type, within a 100-m$^2$ area surrounding each monitoring station. We chose to collect these two sample types to isolate the mechanisms driving forage quality, which could be caused by species composition, the presence or absence of standing dead material, or phenological growth stage. We clipped samples to the soil surface and excluded ground litter while including standing-dead vegetation that was intermingled with live material at the bite scale.

Samples were stored in paper bags and oven-dried at 60°C for 48 hr and analyzed at Ward Laboratories, Kearney, Nebraska, a facility certified by the National Forage Testing Association. Samples were evaluated with near infrared reflectance spectrometry (NIRS) using a Foss 2500 at 850- and 2 500-nm wavelengths to quantify presence of key forage quality factors (Marten et al., 1989; Schutte and Lauriault, 2015). We assessed forage quality by evaluating specific quality metrics within 3 general categories of quality, which are typically evaluated by producers to determine supplementation needs: 1) protein, energy, and fat (crude protein [CP], total digestible nutrients [TDN], and crude fat); 2) digestibility (acid detergent fiber [ADF], *in-vitro* true dry matter digestibility [IVTMD 48-hr], neutral detergent fiber [NDF], and percent lignin), and 3) minerals (ash, calcium [Ca], magnesium [Mg], phosphorous [P], and potassium [K]). Samples were passed through a 1-mm sieve by Ward Laboratories before analysis and results are reported on a dry matter basis.

We estimated prairie dog densities in July 2017 by counting the density of prairie dog burrow entrances as a surrogate for estimating prairie dog populations (see Table 1; Biggins et al. *in* Fish and Wildlife Service, 1993). At each site, we conducted surveys within a 20 × 20 m area at three randomly and permanently established survey points for a total survey area of 1 200 m$^2$ and reported mean burrow density by site. We assessed burrow entrance activity based on signs of activity during the growing season, as this represents their peak population and colony density before a collapse from plague in midsummer 2017. Signs of active burrows include fresh scat, vegetation clipping near burrow, and pathways worn in vegetation, while signs of inactive burrows include multiple layers of spider webs and vegetation overgrowth near burrow entrance (Andelt and Hopper, 2016).

*Statistical Analyses*

We evaluated the effects of prairie dog herbivory on herbaceous biomass across and within years using linear mixed effects models (LMMs). Our response variable was mean herbaceous biomass pooled by site and treatment, and our fixed effect was prairie dog presence (prairie dog colonies vs. sites without prairie dogs; henceforth "Site Type"). We included site, monitoring station nested within site, and spring precipitation and year (when examining effects across years) as random effects to account for site-specific variation and repeated measurements across years.

To better understand how environmental variation modulates prairie dog effects, we used an LMM to determine whether spring precipitation altered the relationship between prairie dog presence and herbaceous biomass. Our response variable was mean herbaceous biomass pooled by site and treatment. We estimated spring precipitation, received 1 April–30 June, by averaging the total monthly precipitation received at the four corners of each site (Derner and Hart, 2007; PRISM Climate Group). We included spring precipitation of each site and year as a fixed effect, as well as prairie dog presence, and the prairie

dog × precipitation interaction. We included site, monitoring station nested within site, and year as random effects to account for site-specific variation and repeated measurements across years, and to identify robust patterns that could be generalized across spatial and temporal variability.

We used multiple LMMs to determine whether prairie dog presence affected the forage quality of composite and western wheatgrass samples. Forage-quality response metrics were evaluated separately and included 1) protein, energy, and fat metrics (crude protein [CP], total digestible nutrients [TDN], and fat); 2) digestibility metrics (acid detergent fiber [ADF], *in-vitro* true dry matter digestibility [IVTMD 48-hr], neutral detergent fiber [NDF], and percent lignin); and 3) mineral metrics (ash, calcium [Ca], magnesium [Mg], phosphorous [P], and potassium [K]). All nutrients were evaluated as percent dry matter content. Our fixed effects included prairie dog presence, month (treated as a categorical variable with three levels to account for potentially

nonlinear responses through the growing season), and the interaction of prairie dog presence by month. We included site, monitoring station nested within site, and year as random effects to account for site-specific variation and repeated measurements across years. When evaluating the composite sample for *in-vitro* true dry matter digestibility, we included year as a fixed effect to assist in model convergence.

To further understand the potential tradeoff between forage quantity and quality, as well as to directly relate the two, we calculated kg $CP \cdot ha^{-1}$ by multiplying peak-season herbaceous biomass by the corresponding percent CP from the composite sample (data collected in August $2016-2017$). We then evaluated the effects of prairie dogs on kg $CP \cdot ha^{-1}$ across and within years by using LMMs. Our response variable was kg $CP \cdot ha^{-1}$, and prairie dog presence was our fixed model effect. We included site, monitoring station nested within site, and year (when analyzing trends across years) as random effects. All linear mixed effects models were executed in JMP (JMP, Cary, NC,
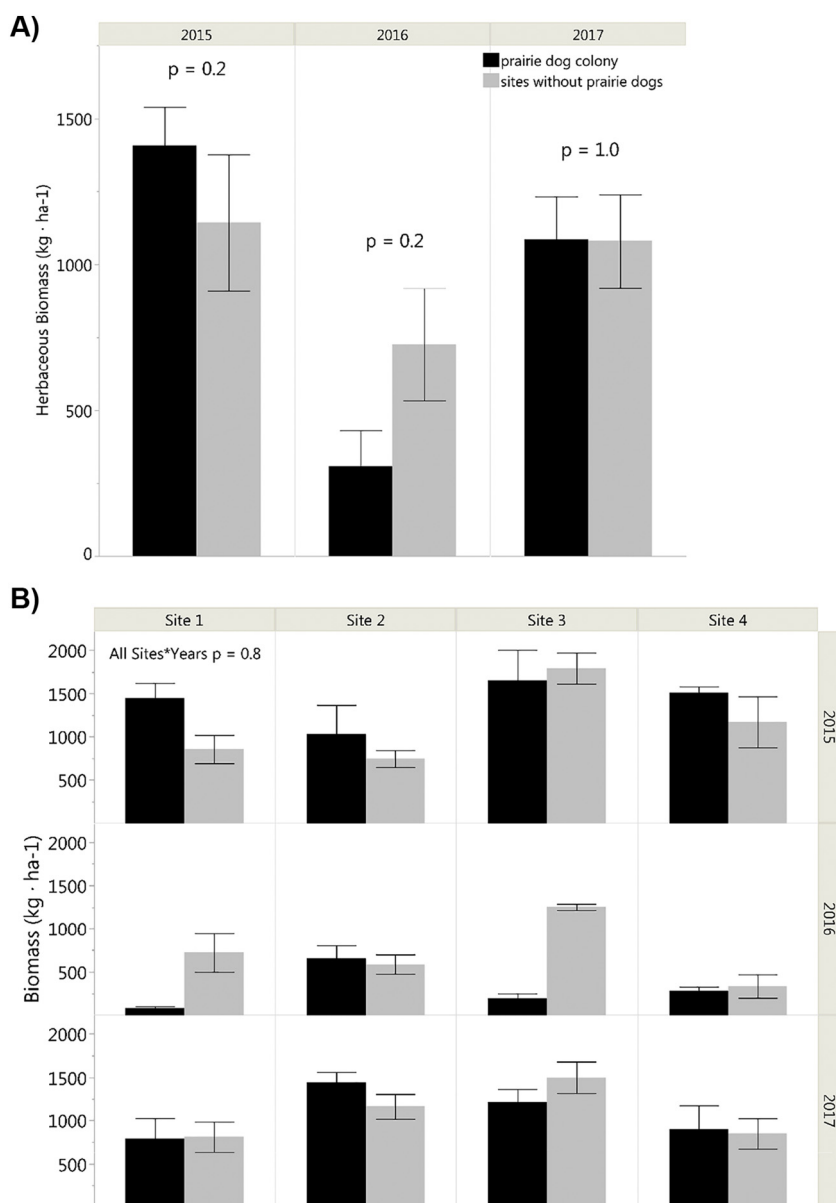


**Figure 2.** Effects of black-tailed prairie dogs on herbaceous biomass in Thunder Basin National Grassland, Wyoming. Biomass was measured during peak growing season (17 July–10 August). Results reflect effects of prairie dogs on (**A**) herbaceous biomass across four sites, over 3 yr (error bars in Panel A are ± SE from means across sites) and (**B**) herbaceous biomass at four sites, over 2 yr (error bars in Panel A are ± SE from subsamples).
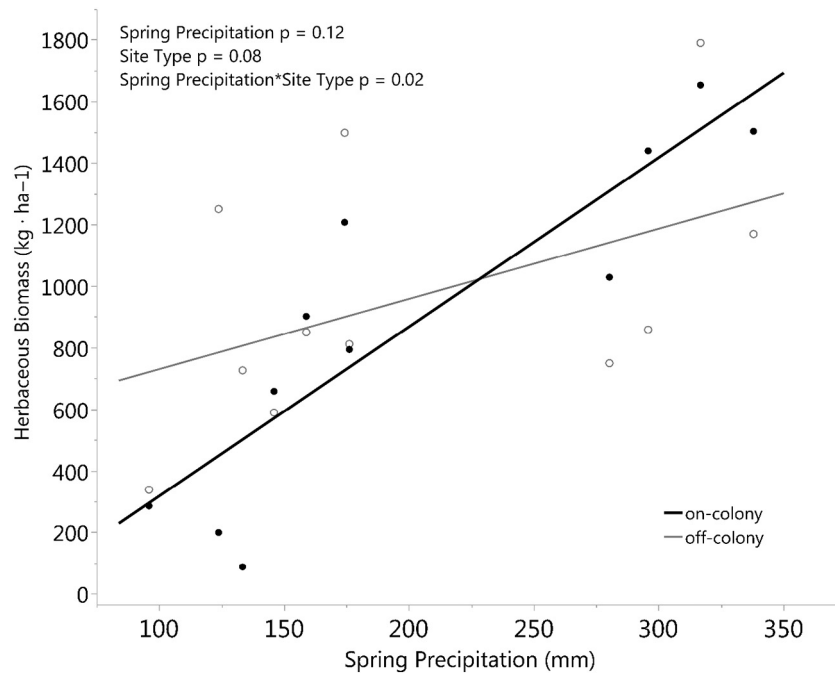
**Figure 3.** Herbaceous biomass response to spring precipitation, across four study sites and 3 yr, in Thunder Basin National Grassland, Wyoming. *Closed circles* and *black lines* represent data from sites on prairie dog colonies while open circles and gray lines represent data from sites without prairie dogs.

version 12.0.1). Data were transformed when necessary to meet model assumptions of normality and homoscedasticity, and results are presented as means $\pm$ SE.

We used a constrained form of principal components analysis—a partially constrained redundancy analysis (RDA) to further understand the complexity of forage quality composition and the influence of abiotic factors and seasonality on multiple aspects of forage quality. We chose this method because it allows for comparison of response variables of differing units and is ideal for short-term studies where treatments are the explanatory variables (Šmilauer and Lepš, 2014; Ordination Methods for Ecologists). This ordination technique is a direct gradient ordination of forage quality response metrics and was constrained by abiotic and temporal factors. Ordination variables in our partially constrained RDA included soil nutrients (% nitrogen and % organic carbon) at variable depths ($0-10$ cm and $10-30$ cm), metrics of forage quality (previously described), site, month, and sample type. Year was a covariate of the RDA to account for interannual variation in forage quality. All constrained axes were tested for significance ($P \leq 0.05$) using a permutation test with 999 iterations and random seed number generator. Ordination analyses were conducted in CANOCO 5 version 5.04 (ter Braak and Šmilauer, 2012). To examine and account for forage quality as it relates to peak-season herbaceous biomass, we performed a second partially constrained RDA on herbaceous biomass coupled with August forage quality data. This second analysis used the same constraints and covariates as described earlier, with the additional metric of kg CP $\cdot$ ha$^{-1}$.

## Results

### Aboveground Herbaceous Biomass

Aboveground herbaceous biomass did not differ between prairie dog colonies and sites without prairie dogs across three growing seasons (prairie dog colonies: $933 \pm 156$ kg $\cdot$ ha$^{-1}$, sites without prairie dogs: $982 \pm 117$ kg $\cdot$ ha$^{-1}$, $P = 0.8$; Fig. 2A). Results were similar when each year was analyzed individually (prairie dog presence by year, all $P$ values $\geq 0.2$; see Fig. 2A). Effects of prairie dog presence on

herbaceous biomass differed among colonies and years (Fig. 2B) and were contingent on spring precipitation (prairie dog presence $\times$ precipitation $F_{1,12} = 7.72$, $P = 0.02$; Fig. 3). For years and sites with dry spring seasons, herbaceous biomass tended to be lower on colonies than at sites without prairie dogs. However, this pattern was reversed for years and sites with wet spring seasons (see Fig. 3).

### Forage Quality: Protein, Energy, and Fat

Crude protein (CP) was 1.4$\times$ higher on prairie dog colonies ($12.33 \pm 0.81$) than sites without prairie dogs ($8.7 \pm 0.38$; $P = 0.04$) across years for composite samples (Fig. 4A; Table 2), but the strength of this effect varied by month (Month $\times$ Site Type $P = 0.009$). In June, CP of composite samples was significantly greater on prairie dog colonies than on sites without prairie dogs, but in July and August, CP did not differ significantly between sites with prairie dogs and sites without prairie dogs (see Fig. 4A). For both site types, CP was significantly higher in June than July or August (see Fig. 4A). Western wheatgrass samples contained 1.4$\times$ higher CP on prairie dog colonies ($12.66 \pm 0.72$) than sites without prairie dogs ($8.79 \pm 0.61$; $P = 0.008$; see Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.4$). CP in western wheatgrass samples was higher in June than July or August (Month $P < 0.0001$; see Fig. 4A).
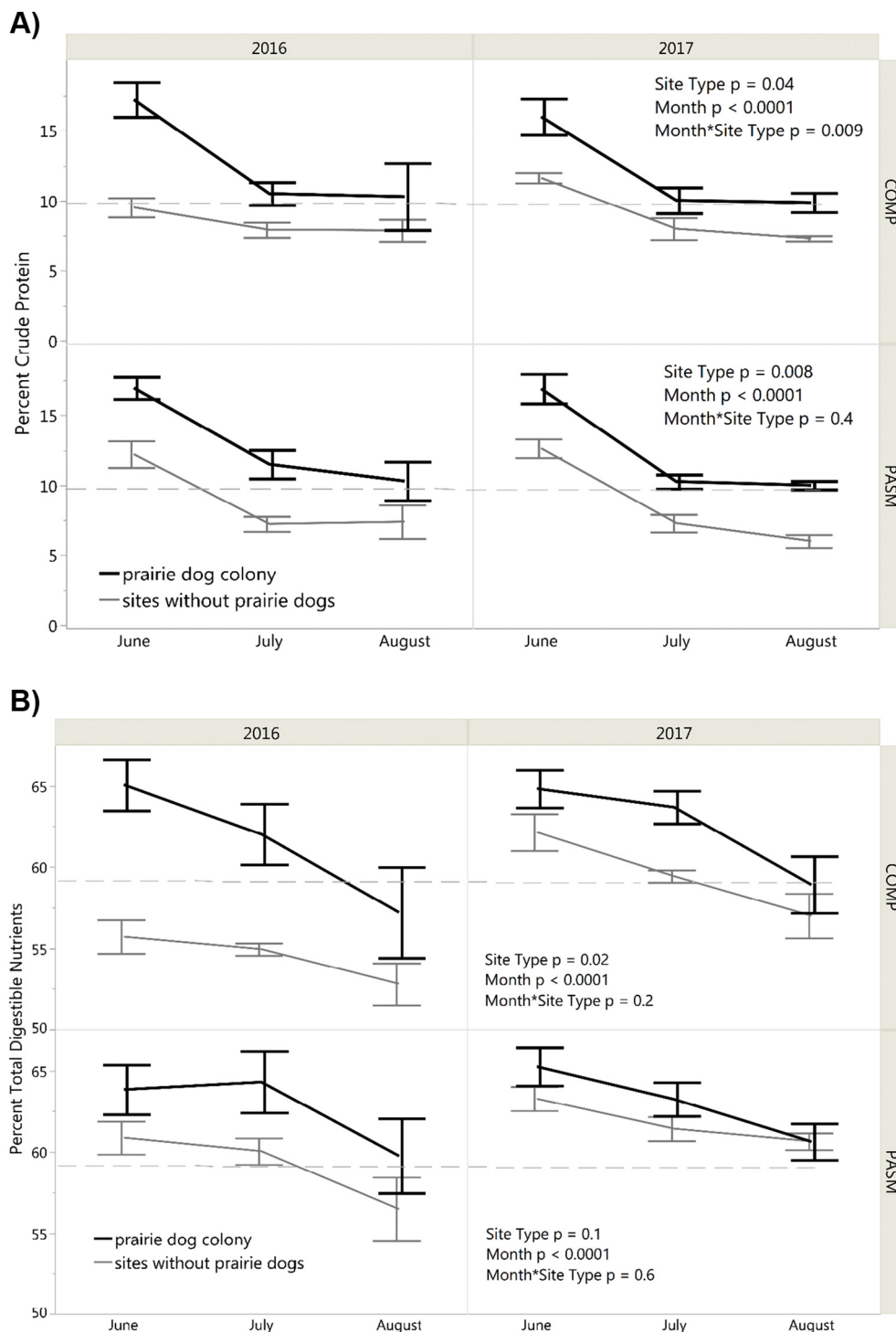
Total digestible nutrients (TDN) was 1.1$\times$ higher on prairie dog colonies ($61.95 \pm 0.90$) than sites without prairie dogs ($57.0 \pm 0.74$; $P = 0.02$) for composite samples (see Fig. 4B and Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.2$). TDN of composite samples was lower in August than June or July across both site types (Month $P < 0.0001$). In contrast, TDN of western wheatgrass samples was not significantly different between prairie dog colonies ($62.84 \pm 0.70$) and sites without prairie dogs ($60.46 \pm 0.58$; Site Type $P = 0.1$; Month $\times$ Site Type $P = 0.6$; see Fig. 4B). TDN was lower in August than June or July (Month $P < 0.0001$).

Fat content (%) was 1.3$\times$ higher on prairie dog colonies ($3.14 \pm 0.15$) than sites without prairie dogs ($2.44 \pm 0.09$; $P = 0.04$) across years for composite samples (see Fig. 4C and Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.2$). Fat content

of composite samples was significantly higher in July than in June, likely due to peak seed production of forbs and graminoids midseason, while August had intermediate values (Month $P < 0.001$). Similarly, western wheatgrass samples contained $1.1\times$ higher fat content on prairie dog colonies ($3.53 \pm 0.16$) than sites without prairie dogs ($3.15 \pm 0.13$; $P = 0.02$; see Table 2), and this difference was maintained across all 3 mo (Month × Site Type $P = 0.4$). Fat content was significantly higher in July than August and June (Month $P < 0.0001$; see Fig 4C).

*Forage Quality: Digestibility*

Neutral detergent fiber (NDF) was 9% lower on prairie dog colonies ($62.36 \pm 1.15$) than sites without prairie dogs ($68.88 \pm 1.04$) and marginally significant ($P = 0.07$) for composite samples. Differences were not affected by the month × site type interaction (Month × Site Type $P = 0.2$; Fig. 5; see Table 2). NDF was significantly higher in August than July and significantly higher in July than June (Month $P < 0.0001$).



**Figure 4.** Effects of black-tailed prairie dog herbivory on metrics of (**A**) crude protein (CP, % dry matter), (**B**) energy (total digestible nutrients [TDN] % dry matter), and (**C**) fat (% dry matter) across four sites in Thunder Basin National Grassland, Wyoming. Prairie dog colonies and sites without prairie dogs are denoted in model results by "Disturbance Type." *Dashed line* indicates the CP and TDN requirements for an average lactating beef cow of moderate size, $3-4$ months postpartum. Error bars show $\pm$ SE.
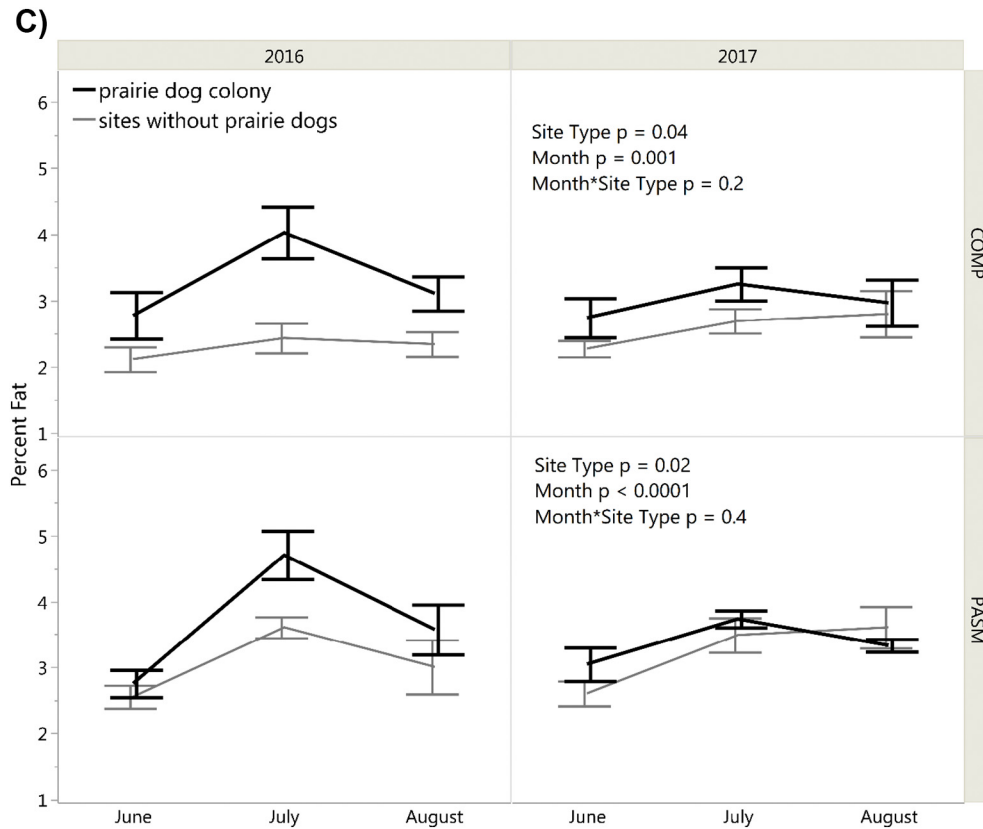
C)



**Figure 4** (continued).

Western wheatgrass samples contained 6% less NDF on prairie dog colonies ($64.01 \pm 0.82$) than sites without prairie dogs ($67.80 \pm 0.84$; $P = 0.006$), and this difference was maintained across all 3 mo (Month × Site Type $P = 0.5$). NDF was higher in August than June or July (Month $P = 0.001$; see Fig. 5).

Acid detergent fiber (ADF) was 11% lower on prairie dog colonies ($35.61 \pm 0.78$) when compared with sites without prairie dogs ($39.95 \pm 0.64$; $P = 0.02$) across years for composite samples, and these differences were maintained throughout the season (Month ×

Site Type $P = 0.2$; see Table 2). ADF was higher in August than June or July (Month $P < 0.0001$). However, western wheatgrass samples contained similar ADF on prairie dog colonies ($34.83 \pm 0.62$) as sites without prairie dogs ($36.92 \pm 0.50$; Site Type $P = 0.1$; Month × Site Type $P = 0.6$). For western wheatgrass samples, ADF was higher in August than June or July (Month $P < 0.0001$).

*In-vitro* true dry matter digestibility (IVTDMD) was $1.03\times$ higher on prairie dog colonies ($70.93 \pm 1.20$) than sites without prairie dogs ($68.29 \pm 0.65$; $P = 0.004$) across years for composite samples, but the

**Table 2**
Select summary of forage quality nutrients at paired sites (with and without prairie dogs) across month (June, July, and August) and yr (2016–2017) in northeastern Wyoming. Statistically significant values ($P < 0.05$) are denoted in bold print. All month effects were significant ($P \leq 0.003$).

| % Nutrient from dry matter | Composite forage samples | | | | Western wheatgrass forage samples | | | |
|---|---|---|---|---|---|---|---|---|
| | On-colony (mean ± SE) | Off-colony (mean ± SE) | Site type[2] P value | Month x Site type P value | On-colony (mean ± SE) | Off-colony (mean ± SE) | Site type[2] P value | Month x Site type P value |
| *Metrics of protein, energy, and fat* | | | | | | | | |
| Crude protein | 12.33 ± 0.81 | 8.7 ± 0.38 | **0.041** | **0.009** | 12.66 ± 0.72 | 8.79 ± 0.61 | **0.008** | 0.409 |
| Kilograms of crude protein per hectare[1] | 73.93 ± 13.20 | 61.34 ± 5.14 | 0.5 | n/a | | | | |
| Total digestible nutrients | 61.95 ± 0.90 | 57 ± 0.74 | **0.017** | 0.161 | 62.83 ± 0.70 | 60.46 ± 0.58 | 0.119 | 0.600 |
| Fat | 3.14 ± 0.15 | 2.44 ± 0.09 | **0.037** | 0.182 | 3.53 ± 0.16 | 3.15 ± 0.13 | **0.022** | 0.380 |
| *Metrics of digestibility* | | | | | | | | |
| Acid detergent fiber | 35.61 ± 0.78 | 39.95 ± 0.64 | **0.017** | 0.164 | 34.84 ± 0.62 | 36.92 ± 0.50 | 0.120 | 0.603 |
| *In-vitro* true dry matter digestibility | 70.93 ± 1.2 | 68.29 ± 0.65 | **0.004** | **0.016** | 71.77 ± 0.78 | 69.4 ± 0.66 | 0.163 | 0.437 |
| Neutral detergent fiber | 62.36 ± 1.15 | 68.88 ± 1.04 | 0.068 | 0.213 | 64.01 ± 0.82 | 67.8 ± 0.84 | **0.006** | 0.478 |
| Neutral detergent fiber digestibility | 49.75 ± 2.21 | 51.79 ± 1.00 | 0.284 | 0.068 | 55.57 ± 1.31 | 54.69 ± 1.24 | 0.646 | 0.863 |
| Lignin | 4.12 ± 0.27 | 4.01 ± 0.12 | 0.969 | 0.350 | 3.3 ± 0.12 | 3.36 ± 0.11 | 0.702 | **0.041** |
| *Metrics of minerals* | | | | | | | | |
| Ash | 8.06 ± 0.70 | 6.47 ± 0.42 | 0.379 | 0.685 | 6.9 ± 0.43 | 4.84 ± 0.36 | 0.151 | 0.568 |
| Calcium | 0.56 ± 0.04 | 0.41 ± 0.03 | 0.358 | 0.747 | 0.4 ± 0.02 | 0.3 ± 0.02 | **0.034** | 0.474 |
| Magnesium | 0.2 ± 0.01 | 0.11 ± 0.01 | **0.031** | 0.243 | 0.18 ± 0.01 | 0.15 ± 0.01 | 0.148 | 0.995 |
| Phosphorus | 0.2 ± 0.01 | 0.14 ± 0.01 | **0.006** | 0.074 | 0.23 ± 0.01 | 0.19 ± 0.01 | **0.049** | 0.740 |
| Potassium | 1.32 ± 0.13 | 0.9 ± 0.07 | 0.090 | 0.090 | 1.55 ± 0.12 | 1.28 ± 0.10 | 0.094 | 0.315 |

[1] Kilograms of crude protein • ha$^{-1}$ was estimated for composite samples only to reflect field conditions of species composition in our study sites.
[2] Site type indicates sites with prairie dogs versus sites without prairie dogs.
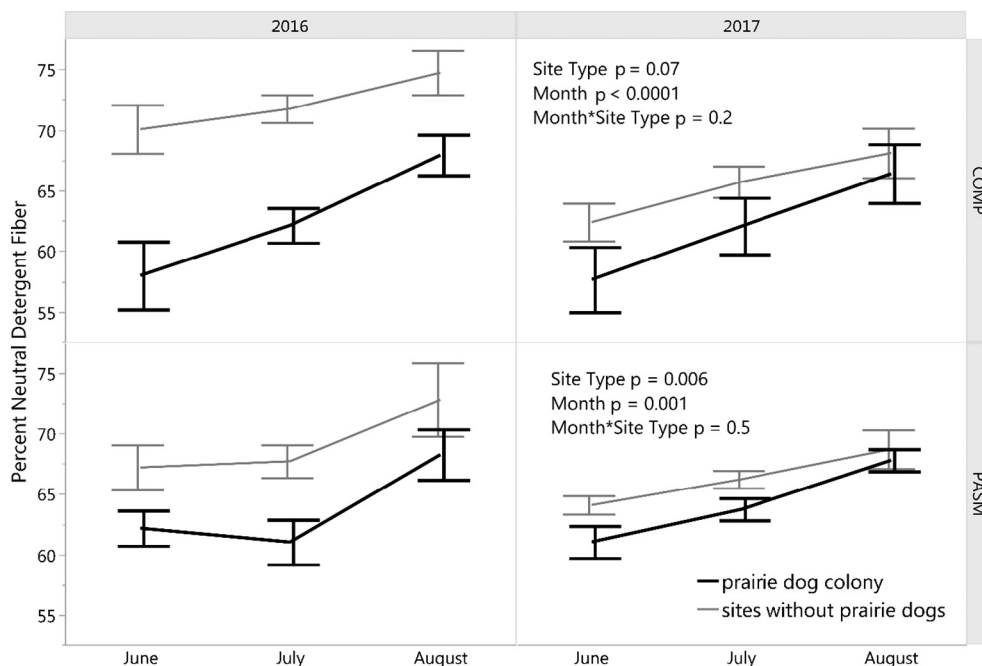
**Figure 5.** Effects of black-tailed prairie dog herbivory on neutral detergent fiber (NDF; % dry matter), across four sites and 2 yr, in Thunder Basin National Grassland, Wyoming. Prairie dog colonies and sites without prairie dogs are denoted in model results by "Disturbance Type." Error bars show ± SE.

strength of this effect varied by month (Month × Site Type $P = 0.02$; see Table 2). In June, IVTDMD of composite samples was significantly greater on prairie dog colonies than on sites without prairie dogs, but in July and August, IVTDMD did not differ significantly between sites with prairie dogs and sites without prairie dogs. For both site types, IVTDMD was significantly higher in June than July or August. Across years, western wheatgrass samples contained similar IVTDMD on prairie dog colonies ($71.77 \pm 0.78$) as sites without prairie dogs ($69.40 \pm 0.66$; Site Type $P = 0.2$; Month × Site Type $P = 0.4$).

IVTDMD in western wheatgrass samples was significantly higher in June than July and significantly higher in July than August (Month $P < 0.0001$).

For composite samples, lignin was not different between prairie dog colonies ($4.12 \pm 0.27$) and sites without prairie dogs ($4.01 \pm 0.12$; Site Type $P = 1.0$; Month × Site Type $P = 0.4$; see Table 2). Lignin in composite samples was significantly higher in July than June, while August had intermediate values (Month $P < 0.003$). Western wheatgrass samples contained similar amounts of lignin on prairie dog colonies ($3.30 \pm$


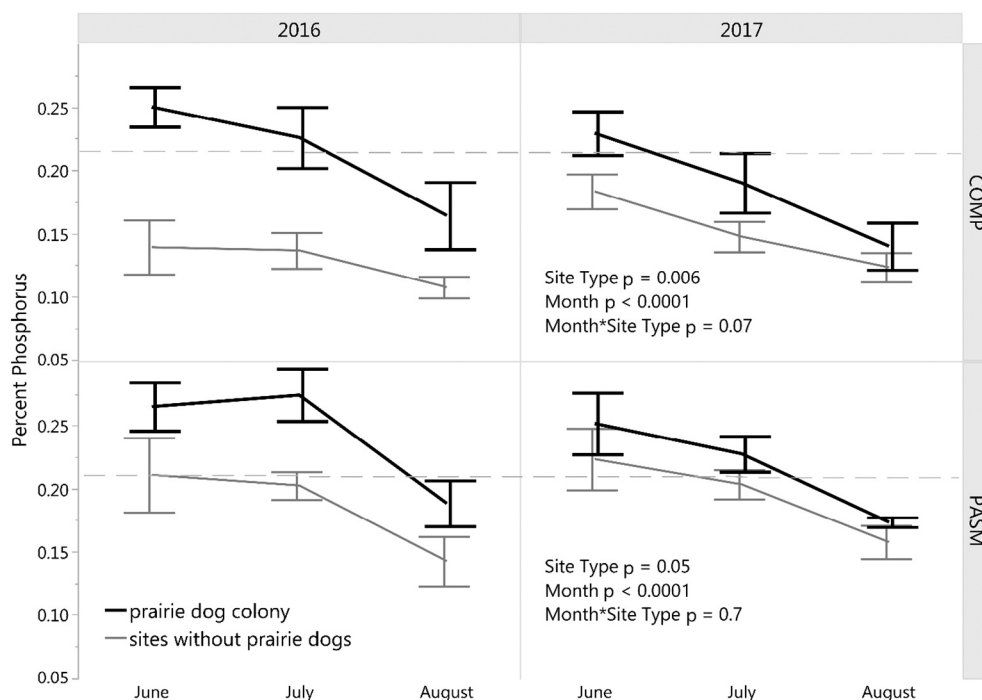
**Figure 6.** Effects of black-tailed prairie dog herbivory on phosphorus (P; % dry matter), across four sites and 2 yr, in Thunder Basin National Grassland, Wyoming. *Dashed line* indicates the phosphorus requirements for an average milking beef cow of moderate size, $3-4$ mo postpartum. Error bars ± SE.
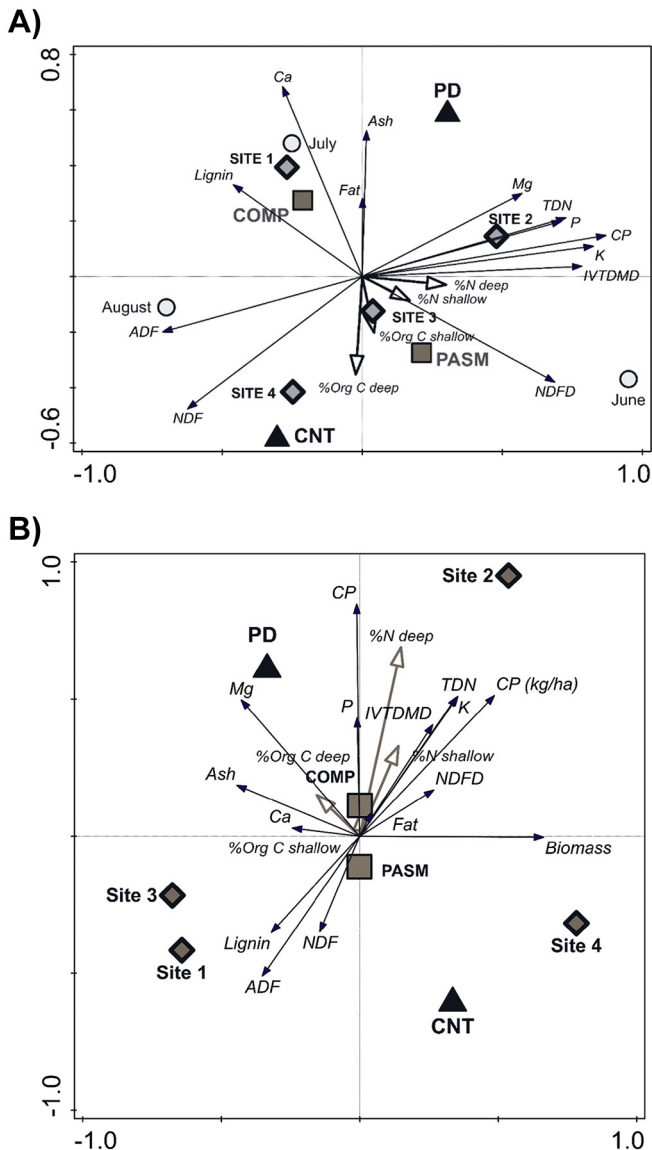
**Figure 7.** (**A**) Partially constrained RDA ordination of all forage quality metrics collected June − August 2016 − 2017 and soil nutrient content collected June 2015. Axis 1 explained 73.22% of the fitted variation, and Axis 2 explained 17.9% of the fitted variation. Triangles indicate site type; "PD" stands for prairie dog colonies and "CNT" stands for control (sites without prairie dogs). "%Org C" and "%N" represent percent organic soil carbon and percent soil nitrogen, respectively; "shallow" represents samples from 0 to 10 cm, and "deep" indicates soils from 10 to 30 cm. (**B**) Partially constrained RDA ordination of biomass and forage quality metrics collected August 2016 − 2017 and soil nutrient content collected June 2015. Axis 1 explained 99.41% of the fitted variation. Axis 2 explained an additional 0.54% of the fitted variation. Triangles indicate site type; "PD" stands for prairie dog colonies, and "CNT" stands for control (sites without prairie dogs). "%Org C" and "%N" represent percent organic soil carbon and percent soil nitrogen, respectively; "shallow" represents samples from 0 to 10 cm and "deep" indicates soils from 10 to 30 cm.

0.12) as sites without prairie dogs (3.36 ± 0.11; $P = 0.7$), but seasonal patterns varied between site types (Month × Site Type $P = 0.04$). On sites without prairie dogs, lignin values were significantly lower in June than July or August, but lignin values on prairie dog colonies did not differ significantly across months.

*Forage Quality: Minerals*

Phosphorous was 1.4× higher on prairie dog colonies (0.20 ± 0.01) than sites without prairie dogs (0.14 ± 0.01; $P = 0.006$) across years for composite samples, though the strength of this effect varied marginally by month (Month × Site Type $P = 0.07$; Fig. 6, see Table 2). Across site types, phosphorous was higher in June than July and higher in July than August (Month $P < 0.0001$). Western wheatgrass samples contained 1.2× greater phosphorous on prairie dog colonies (0.23 ± 0.01) than sites without prairie dogs (0.19 ± 0.01; $P = 0.05$; see Table 2), and this difference was maintained across all 3 mo (Month × Site Type $P = 0.7$). For western wheatgrass samples, phosphorous was lower in August than June or July (Month $P < 0.0001$; see Fig. 6).

Calcium did not differ between prairie dog colonies (0.56 ± 0.04) and sites without prairie dogs (0.41 ± 0.03; Site Type $P = 0.4$; Month × Site Type $P = 0.7$; see Table 2) across years for composite samples. Calcium in composite samples was significantly higher in July than June, while August had intermediate values (Month $P < 0.006$). In contrast, western wheatgrass samples contained 1.3× higher Calcium on prairie dog colonies (0.40 ± 0.02) than sites without prairie dogs (0.30 ± 0.02; $P = 0.03$), and this difference was maintained across all 3 mo (Month × Site Type $P = 0.5$). Calcium in western wheatgrass samples was lower in June than July or August (Month $P < 0.0001$).

Magnesium was 1.8× higher on prairie dog colonies (0.20 ± 0.01) than sites without prairie dogs (0.11 ± 0.01; $P = 0.03$) across years for composite samples, and these differences were maintained across all 3 mo (Month × Site Type $P = 0.2$; see Table 2). Magnesium in composite samples was higher in June than July or August (Month $P < 0.0001$). In contrast, western wheatgrass samples contained similar amounts of Mg on prairie dog colonies (0.18 ± 0.01) and sites without prairie dogs (0.15 ± 0.01; $P = 0.1$; Month × Site Type $P = 1.0$). Magnesium values in western wheatgrass samples were higher in June than July or August (Month $P < 0.0001$).

*Available Crude Protein (kg • $ha^{-1}$)*

In 2016, a drier than average year, kg CP • $ha^{-1}$ on prairie dog colonies (38.0 ± 14.3) did not differ from sites without prairie dogs (52.1 ± 6.8; $P = 0.3$; see Table 2). In contrast, in 2017, an average precipitation year, kg CP • $ha^{-1}$ was 1.5× greater on prairie dog colonies (109.8 ± 13.2) than sites without prairie dogs (70.6 ± 6.5; $P = 0.04$). Across years, kg CP • $ha^{-1}$ did not differ between prairie dog colonies (73.9 ± 13.2) and sites without prairie dogs (61.3 ± 5.1; $P = 0.5$; see Table 2). The variances in available crude protein are likely due to high variability in herbaceous biomass among sites.

*Forage Quality Composition Relative to Site, Seasonality, and Biotic/Abiotic Factors*

Our partially constrained RDA of forage quality composition for June − August in 2016 and 2017 revealed Axis 1 explained 73.22% of the fitted variation and was associated with growing season, site type, and sample type. Minerals and digestibility were associated with early growing season (June) samples, prairie dog colony samples, and western wheatgrass samples on the right side of the ordination diagram, while metrics associated with plant maturity were associated with later growing season (August) samples, composite samples, and samples from sites without prairie dogs on the left side of the ordination diagram (Fig. 7a). Forage quality response variables associated with early plant growth stage, prairie dog colonies, and western wheatgrass include IVDMD and CP, whereas NDF and ADF were associated with increasing plant maturity, sites without prairie dogs, and composite samples. Abiotic response variables associated with Axis 1 included % N (0 − 10 cm and 10 − 30 cm). The second axis was largely a function of site and sample type, with fat, ash, Ca, Mg, TDN, and P associated with prairie dog colonies

and composite samples, whereas % organic C $(0-10$ and $10-30$ cm), ADF, and NDF were associated with western wheatgrass samples and sites without prairie dogs. The permutation test for significance of all constrained axis was significant (pseudo-F 18.5; $P = 0.001$), suggesting growing season, site type (prairie dog colonies vs. sites without prairie dogs), and sample type explained a significant amount of variation in our forage quality metrics. Overall, our data show strong differences in site type (prairie dog colony vs. sites without prairie dogs) and sample type (composite vs. western wheatgrass) and reinforce the unique characteristics associated with these features.

In our partially constrained RDA for herbaceous biomass and forage quality composition during peak-seasonal biomass (August) of 2016 and 2017, Axis 1 explained 99.41% of the fitted variation and was a function of August peak standing herbaceous biomass, site variation, and site type (see Fig. 7b). Sites without prairie dogs were associated with higher herbaceous biomass and lower mineral content compared with prairie dog colonies. The second axis explained 0.54% of the remaining fitted variation for a total of 99.95% of the fitted variation explained by Axis 1 and 2. The second axis was largely a function of site type, with metrics of nutrition and digestibility (CP, P, Mg, TDN, and K) more strongly associated with prairie dog colonies, whereas metrics of plant maturity and nondigestibility (NDF, ADF, and lignin) were more closely associated with sites without prairie dogs. Forage quality was not strongly influenced by sample type (western wheatgrass vs. herbaceous composite) in August (as indicated by proximity in ordination space in Fig. 7b). The permutation test for significance of all constrained axis was significant (pseudo-F 11.3; $P = 0.001$), suggesting site variability and site type (prairie dog colonies vs. sites without prairie dogs) explained the majority of variation in our herbaceous biomass data.

## Discussion

We used a replicated, paired design to compare herbaceous forage quality and quantity on prairie dog colonies and sites without prairie dogs across three growing seasons. We found that during the spring and summer, when livestock diets are most heavily dependent on grasses, forage produced on prairie dog colonies was consistently higher in nutrition for many metrics associated with livestock and native ungulate growth and weight gain (see Table 2). For composite samples in our study site, the average lactating beef cow, which produces 5 kg of milk $\cdot$ day$^{-1}$ at $3-4$ mo postpartum and weighs 450 kg, could potentially meet their nutritional requirements of TDN, CP, Ca, and P for part or all of the growing season on prairie dog colonies (Figs. 4, 5; The National Research Council, 2000). Similarly, Ca requirements could be met on prairie dog colonies throughout most months and years, and P requirements could be met for an additional month on colonies (although, we note a deficiency for the composite sample in 2017; Fig. 6). Access to enhanced fat via foraging on prairie dog colonies is advantageous to maintain body condition and reproductive status (Scasta et al., 2016b). Finally, the role of dormant plant material and neutral detergent fiber (NDF) has implications for animal intake rates because NDF, a metric of forage bulk, limits maximum forage dry matter intake rate to 1.1% of a cow's body weight (Belyea et al., 1993). Although clipping methods may not be analogous to animal foraging decisions at multiple scales within a pasture, our study clearly demonstrates that forage resources available to grazing animals at the bite scale differ between sites occupied and unoccupied by prairie dogs.

In northern mixed-grass prairies, vegetation community composition and cover change within $3-4$ yr following prairie dog colonization, whereby graminoids become displaced by annual forbs (Coppock et al., 1983; Archer et al., 1987). Our composite samples included a diverse assemblage of plant functional groups that were capable of mechanistically structuring nutritional composition. For example, nutritional content at different times during the growing season may be influenced by the relative abundance of warm- versus cool-season grasses. The warm-season species blue grama, which was present in our composite samples, can contain lower CP than western wheatgrass early in the growing season but greater CP later in the growing season and generally has greater digestibility most of the year (Scasta, 2017). Foliar cover of warm-season grasses was greater on sites without prairie dogs in $2015-2016$ and did not differ strongly between site types in 2017 (Fig. S1, available online at https://doi.org/10.1016/j.rama.2018.10.004). Forb abundance could also drive compositionally induced quality differences depending on the timing of sampling. Foliar cover of short-lived forbs, which typically reach peak performance and nutritional quality in June, was higher on prairie dog colonies than sites without prairie dogs (see Fig. S1). Despite these compositional considerations, we observed differences in metrics of forage quality on prairie dog colonies in both our composite (multispecies) and western wheatgrass (single-species) samples. Repeated herbivory by prairie dogs causes plants to regrow new, tender leaves that are more nutritious and palatable (Detling and Painter, 1983). By isolating western wheatgrass, we removed the confounding influence of variable species composition and isolated a smaller subset of potential mechanisms contributing to increased forage quality on prairie dog colonies. Western wheatgrass results suggest that repeated herbivory by prairie dogs can maintain higher forage quality within a single species by reducing standing dead material at the bite scale or by maintaining plants in an earlier phenological growth stage due to compensatory regrowth. Forage quality often differed between our composite and western wheatgrass samples, indicating that multiple mechanisms are shaping forage quality in this system (e.g., species composition, phenological growth stage, or soil condition changes). Moreover, both composite and western wheatgrass samples contained standing dead material, which is $2-4\times$ lower on prairie dog colonies (Whicker and Detling, 1988). The removal of standing dead material is another important mechanism through which prairie dogs may directly enhance forage quality on colonies.

Surprisingly, the expected effect of prairie dog herbivory on herbaceous biomass was not statistically different between sites with and without prairie dogs and remained highly variable throughout our study period due to site and precipitation variability. Our experiment assessed forage characteristics within the context of working landscapes where prairie dogs, other wildlife, and livestock are fully interacting. We compared forage characteristics on sites with and without prairie dogs in the presence of wildlife and livestock grazing, and variability in stocking rates and season of use may have contributed to observed results (see Table 1). Each year, we documented greater herbaceous biomass on one or more sites with prairie dog colonies than sites without prairie dogs. This increase in herbaceous biomass on prairie dog colonies may be an inherent site characteristic of prairie dogs, as they are known to select habitat generally free of shrubs (Hoogland, 1995); thus, herbaceous forage on colonies experiences decreased competition (Lett and Knapp, 2003). However, the influential role of precipitation and interactions of precipitation and prairie dog herbivory at the local site scale may also explain the variable effects prairie dogs can have on herbaceous biomass (Augustine and Springer, 2013).

Our regression of aboveground herbaceous biomass response to spring precipitation illustrates the influential role of spring precipitation on the effect of prairie dog herbivory. For example, in 2015 when herbaceous biomass was 23% higher on prairie dog colonies than undisturbed sites, our study sites received spring precipitation (April–June) 13.1 cm greater than the average long-term spring precipitation. In contrast, herbaceous aboveground biomass was reduced by 58% in 2016, when our study sites received spring precipitation 5.2 cm below the long-term average. Livestock and native ungulates may also contribute to observed biomass reductions during dry periods via potentially increased utilization of higher-quality forage on prairie dog colonies. Following this trend, herbaceous biomass was similar at sites with versus without prairie dogs in 2017, when spring precipitation nearly matched the long-term average (0.6 cm below long-term average).

Thus, the interaction of prairie dog herbivory with the spatiotemporal distribution of precipitation across the landscape and the subsequent effect on herbaceous biomass are more informative than the overly simplistic view that prairie dogs always are antagonistic to livestock production (see also Augustine, 2010; Augustine and Springer, 2013).

Complex trade-offs between forage quality and quantity were further illustrated by the interactive effects of prairie dog herbivory and spring precipitation on kg CP • ha$^{-1}$, a metric that accounts for both biomass and forage quality simultaneously. In 2016, when spring precipitation was below average, kg CP • ha$^{-1}$ was similar between sites with prairie dogs and those without prairie dogs; however, with near-average spring precipitation in 2017, prairie dog colonies contained greater kg CP • ha$^{-1}$ than sites without prairie dogs. These findings have direct implications for livestock enterprises and livestock production and performance.

Our research has identified several topics concerning livestock and forage performance within areas occupied by prairie dogs that are in need of further investigation. We suggest further research is needed: 1) to more directly quantify the potential benefits of consuming digestible organic matter in the absence of standing dead material (as observed on prairie dog colonies). We recommend feeding trials or in-situ foraging studies that use fecal NIRS or similar methods to assess direct digestibility; 2) to directly assess the effect of prairie dogs on animal performance, specifically cattle weight gain in the presence and absence of prairie dogs at varying level of pasture occupancy, in a grassland-shrubland ecotone; and 3) to directly assess how prairie dog density and colony age may have contributed to the variable effects of prairie dogs on herbaceous biomass that we observed in this study. We suggest future research should quantify herbaceous biomass across a broad gradient of prairie dog densities over multiple years with variable precipitation.

Vegetation of low forage quality requires herbivores to spend additional time and effort foraging to increase net biomass intake to achieve desired nutrition concentrations (Fryxell, 1991). Plant nutrition and digestibility is negatively associated with maturation and biomass (Van Soest, 1994), and thus plants that experience repeated herbivory, as in the case of forage on prairie dog colonies, express decreased herbaceous biomass and increased forage quality, specifically for CP and digestibility measurements, because of their immature phenological growth stage. In these circumstances, large herbivores are faced with a trade-off to 1) maximize time spent searching a habitat patch for forage that is low in biomass but high in nutrition (necessitating increased foraging time to achieve base requirements of ruminant intake) or 2) conserve energy through decreased foraging behavior and maximize time by consuming readily available vegetation that is greater in biomass but lower in nutritional quality and digestibility (Charnov, 1976; Bergman et al., 2001).

Our results, coupled with foraging theory, begin to address the questions: 1) does the effect of prairie dog herbivory on forage quantity and quality create trade-offs between a limited quantity of a resource at a higher quality? And 2) can cattle mitigate this interspecific competition by strategic distributional decisions (Rosenzweig, 1995)? Trade-offs between forage quantity and quality are addressed by scientific studies in northwestern Mexico, which demonstrated both bison and cattle used black-tailed prairie dog colonies in disproportionate amounts when compared with their availability (Chipault and Detling, 2013; Sierra-Corona et al., 2015; but see Guenther and Detling, 2003). This preferential grazing on prairie dog colonies, coupled with our study results, suggests increased forage quality on prairie dog colonies might facilitate large ungulate distribution and foraging strategies and provide benefits to livestock in times of above-average spring precipitation. Conversely, prolonged periods of below-average precipitation can eliminate beneficial effects of prairie dog colonies by limiting instantaneous intake rate of forage and livestock may need to spend additional time foraging in areas without prairie dogs to compensate for biomass reduction (Vermeire et al., 2004; Augustine and Springer, 2013).

In the Northern Plains, rangeland-based livestock operations are heavily reliant on rainfall events and remain susceptible to year-to-year variability and long-term climatic changes (Derner et al., 2018). Thus, the mitigating effect of prairie dogs on forage quality and herbaceous biomass, which is closely related to spring precipitation, is also subject to uncertainty. Forecasted climate change models for this region project increased winter and spring precipitation, with rising temperatures that can lengthen growing seasons (Shafer et al., 2014). Drought forecasts predict an increase in the maximum precipitation received in a single day, while the annual longest consecutive dry-day period is expected to remain similar or even decrease over the next 30–70 yr; these predictions are notably unique compared with the rest of the United States (Derner et al., 2018). Increasing atmospheric $CO_2$ is also predicted to increase total forage production while negatively affecting digestibility of forage (Augustine et al., 2018). These trends could potentially lead to increased utilization of prairie dog colonies by livestock and native ungulates seeking improved forage quality.

## Implications

Black-tailed prairie dogs generally compete with livestock for graminoid forage, but in years of average or above-average rainfall prairie dog herbivory may not significantly reduce herbaceous biomass. Moreover, prairie dogs increased most forage quality metrics of nutrition, including digestibility, with many of these positive effects extending through the growing season. These findings suggest livestock can sometimes benefit from access to prairie dog colonies, similar to pre-European bison-prairie dog interactions, which may have conservation implications for the black-tailed prairie dog. The conservation of prairie dogs within their native grassland habitat is important for ensuring the continued provisioning increased groundwater recharge and benefits to soil (Martínez-Estévez et al., 2013), grassland biodiversity (see Augustine and Baker, 2013 for implications specific to our region of study), and other benefits provided via the ecosystem engineering activities of this unique burrowing mammal (Kotliar et al., 1999).

These benefits, coupled with comparable herbaceous biomass on prairie dog colonies in years with average or above-average spring precipitation, could serve to mitigate direct competition with livestock for forage and therefore alleviate forage-centric tensions surrounding the presence of prairie dogs on rangelands. In fact, given current climate projections for this region, the long-term maintenance of native rangelands that can provide high-quality nutrition for livestock may be facilitated by conservation of the black-tailed prairie dog. However, benefits are dependent on spring precipitation; in years of average spring precipitation, livestock may require periodic access to areas without prairie dogs to meet bulk intake requirements, and in years of below-average spring precipitation livestock may not be able to meet their bulk forage intake requirements solely on prairie dog colonies. In addition, when prairie dogs occupy the majority of a pasture during seasons of below-average precipitation, cattle weight gain can be negatively affected (Derner et al., 2006). Producers should be especially cognizant in years of below-average precipitation when prairie dog-induced reductions of herbaceous biomass become pronounced.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.10.004.

## Acknowledgments

## Appendix A

Livestock grazing utilization during the study period (2015–2017) in Thunder Basin National Grasslands, Wyoming. We collected data at sites with prairie dog colonies and from separate, spatially distinct areas without prairie dogs (≥ 280 m from colony edge). Livestock grazing information provided by the Thunder Basin Grazing Association.

| Site | Prairie dogs presence or absent | Pasture size (ha) | Date in | Date out | Livestock type | Animal unit months |
|---|---|---|---|---|---|---|
| 1 | Prairie dogs present | 874 | 7/16/2015 | 9/20/2015 | Cows/calves | 177 |
| | | | 8/1/2016 | 8/31/2016 | Cows/calves | 46 |
| | | | 9/1/2016 | 9/20/2016 | Ewes | 124 |
| | | | 9/28/2016 | 10/4/2016 | Cows | 30 |
| | | | 8/1/2016 | 9/20/2016 | Cows/calves | 132 |
| | | | 9/28/2016 | 10/4/2016 | Ewes | 44 |
| | | | 8/1/2017 | 9/20/2017 | Cows/calves | 131 |
| 1 | Prairie Dogs Absent | 660 | 5/8/2015 | 5/15/2015 | Cows | 32 |
| | | | 7/2/2015 | 8/3/2015 | Ewes/lambs | 52 |
| | | | 5/10/2016 | 5/30/2016 | Cows/calves | 14 |
| | | | 5/10/2016 | 5/30/2016 | Yearling steers | 31 |
| | | | 8/2/2016 | 9/4/2016 | Ewes/lambs | 68 |
| | | | 5/8/2017 | 5/11/2017 | Cows/calves | 16 |
| | | | 7/16/2017 | 8/26/2017 | Ewes/lambs | 70 |
| | | | 12/9/2017 | 2/15/2018 | Cows/calves | 82 |
| 2 | Prairie dogs present + absent | 12 655 | 1/1/2015 | 6/11/2015 | Cows/calves | 2 025 |
| | | | 12/20/2015 | 3/18/2016 | Cows/bulls | 1 631 |
| | | | 12/10/2016 | 3/3/2017 | Cows | 1 683 |
| | | | 11/18/2017 | 12/31/2017 | Cows | 911 |
| 3 | Prairie dogs present + absent | 2 809 | 1/1/2015 | 6/1/2015 | Bulls | 155 |
| | | | 9/1/2015 | 5/1/2016 | Bulls | 248 |
| | | | 9/1/2016 | 5/1/2017 | Bulls | 196 |
| | | | 9/1/2017 | 12/31/2017 | Bulls | 140 |
| 4 | Prairie dogs present + absent | 3 650 | 5/10/2015 | 7/4/2015 | Cows/calves | 877 |
| | | | 5/25/2016 | 8/2/2016 | Cows/calves | 864 |
| | | | 5/20/2017 | 7/13/2017 | Cows/calves | 904 |
| | | | 6/12/2017 | 7/13/2017 | Bulls | 32 |

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