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Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality

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Abstract. Potential competition between native and domestic herbivores is a major consideration influencing the management and conservation of native herbivores in rangeland ecosystems. In grasslands of the North American Great Plains, black-tailed prairie dogs (*Cynomys ludovicianus*) are widely viewed as competitors with cattle but are also important for biodiversity conservation due to their role in creating habitat for other native species. We examined spatiotemporal variation in prairie dog effects on growing-season forage quality and quantity using measurements from three colony complexes in Colorado and South Dakota and from a previous study of a fourth complex in Montana. At two complexes experiencing below-average precipitation, forage availability both on and off colonies was so low (12–54 g/m^2) that daily forage intake rates of cattle were likely constrained by instantaneous intake rates and daily foraging time. Under these dry conditions, prairie dogs (1) substantially reduced forage availability, thus further limiting cattle daily intake rates, and (2) had either no or a small positive effect on forage digestibility. Under such conditions, prairie dogs are likely to compete with cattle in direct proportion to their abundance. For two complexes experiencing above-average precipitation, forage quantity on and off colonies (77–208 g/m^2) was sufficient for daily forage intake of cattle to be limited by digestion rather than instantaneous forage intake. At one complex where prairie dogs enhanced forage digestibility and [N] while having no effect on forage quantity, prairie dogs are predicted to facilitate cattle mass gains regardless of prairie dog abundance. At the second complex where prairie dogs enhanced digestibility and [N] but reduced forage quantity, effects on cattle can vary from competition to facilitation depending on prairie dog abundance. Our findings show that the high spatiotemporal variation in vegetation dynamics characteristic of semiarid grasslands is paralleled by variability in the magnitude of competition between native and domestic grazers. Competitive interactions evident during dry periods may be partially or wholly offset by facilitation during periods when forage digestibility is enhanced and forage quantity does not limit the daily intake rate of cattle.

Key words: black-tailed prairie dog; Cynomys ludovicianus; *digestibility; forage intake rate; grazing; nitrogen; northern mixed prairie; semiarid grassland; shortgrass steppe; spatiotemporal variation; western Great Plains, USA.*

Introduction

Grasslands worldwide are increasingly managed to provide multiple goods and services, including livestock production, carbon sequestration, clean water, and the conservation of native biota. Competition between native herbivores and livestock is often a major concern for land managers seeking to optimize livestock production while still conserving native species. The potential for competition between livestock and native herbivores has long been assessed on the basis of dietary overlap, and this continues to be a common approach in contemporary studies of competition (e.g., Beck and Peek 2005, Odadi et al. 2007, Vila et al. 2009, Wingard et al. 2011). However, factors other than dietary overlap, including shifts in forage quality and intake rate, and differences in herbivore body size and digestive strategy can determine the nature of interactions among coexisting herbivores (Hobbs et al. 1996*a*). Indeed, coexisting ungulate herbivores in some African rangelands are proposed to facilitate one another through effects on forage quality, despite substantial overlap in grass species consumed (Arsenault and Owen-Smith 2002). Furthermore, both facilitation and competition between two herbivore species can occur in different seasons (Odadi et al. 2011).

Despite the substantial economic and conservation implications of competition between native and domestic herbivores worldwide, only a handful of studies have experimentally evaluated effects of native mammalian herbivores on livestock performance. In North America, Hobbs et al. (1996*a*, *b*) documented a threshold winter density of elk (*Cervus elaphus*), above which cattle

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forage intake, mass gain, and date of calving were reduced. Derner et al. (2006) showed that black-tailed prairie dogs (*Cynomys ludovicianus*) have increasingly negative effects on cattle mass gains as they increase in abundance within a pasture. In Africa, Odadi et al. (2011) found that medium-sized native ungulates, primarily plains zebra (*Equus callabus*), suppress cattle mass gains in dry seasons, but facilitate mass gains to nearly the same degree in wet seasons. In each case, the magnitude of competition was substantially lower than predicted on the basis of diet overlap.

Such experiments demonstrate that competition occurs under conditions specific to the study, and that multiple interacting and often offsetting mechanisms can collectively determine the strength of competition between two herbivore species. Given the spatial and temporal variation inherent in semiarid ecosystems at multiple scales, it is important to ask not just whether competition occurs, but where, when, and to what extent. Here, we focus on competition for forage. We consider three types of trade-offs that can potentially reduce competition for forage between two herbivore species that overlap substantially in diet. First, one species may simultaneously reduce the quantity and enhance the quality of forage available to a second species. To the extent that reduced forage quantity does not substantially reduce forage intake rate, it may be offset by a larger increase in forage quality and net intake of digestible nutrients. Second, if the effects of one species are spatially discrete (e.g., colonial or central-place foragers), reductions in forage quantity within part of the landscape may be offset by shifts in a second species' ability to move between affected and non-affected patches. Third, where forage quantity is reduced, the second species may be able to offset reduced instantaneous intake rates (IIR) of dry matter with increased time spent foraging each day, thus preventing any reduction in daily intake rate (DIR) of dry matter. While this latter mechanism may affect wild herbivores by reducing time available for other activities (e.g., finding mates, avoiding predators), this is less of a concern for domestic livestock.

In the case of prairie dogs and cattle in the North American Great Plains, recognition of the keystone role of prairie dogs for other native fauna has been paralleled by concern about the economic impact of prairie dog conservation on livestock production. Many native plants and animals in the western Great Plains rely on resources or conditions provided by prairie dogs (e.g., Kotliar et al. 1999, Desmond et al. 2000, Kretzer and Cully 2001, Smith and Lomolino 2004, Augustine and Derner 2012). Past studies also show that (1) prairie dog diet overlaps substantially with cattle, and (2) prairie dogs significantly reduce standing herbaceous biomass (reviewed by Vermeire et al. 2004, Detling 2006). As a result, there is clear potential for prairie dogs to negatively affect livestock mass gains through reduced forage quantity.

Controversy surrounding prairie dog–cattle competition arises in part from processes that may or may not compensate for reduced forage quantity (Vermeire et al. 2004, Detling 2006, Miller et al. 2007). In a study of shortgrass pastures in Oklahoma, cattle mass gains were higher in pastures without vs. with prairie dogs, but replication was limited and statistical differences between the treatments were not detected (O'Meilia et al. 1982). Although prairie dogs reduced forage quantity, O'Meilia et al. (1982) hypothesized that this was offset by increased forage quality. More recently, Derner et al. (2006) showed that in northeastern Colorado, prairie dog presence reduced cattle mass gains, particularly where prairie dogs occupied >30% of the pasture. However, neither study assessed trade-offs between forage quality and quantity. Extrapolation of experiments beyond local site and weather conditions requires an understanding of how prairie dog effects on forage quantity and quality vary spatially and temporally across their broad geographic range.

Studies quantifying prairie dog effects on forage quality are also surprisingly sparse. Seminal research on black-tailed prairie dogs in grassland ecosystems (Polley and Detling 1988, Whicker and Detling 1988, Holland and Detling 1990, Detling 1998) was conducted primarily in national parks where competition with livestock was not of concern. They showed that prairie dogs substantially reduced the standing biomass and increased the protein content of plants growing on colonies, but did not assess effects on forage digestibility. More recently, Johnson-Nistler et al. (2004) measured forage quantity, protein content, and digestibility at a complex of prairie dog colonies in the north mixed prairie of Montana. Prairie dogs reduced standing herbage by 62% (from 32 g/m^2 off colonies to 12 g/m^2 on colonies), while increasing the weighted-average N content of herbage from 1.28% to 1.73% (36% relative increase) and the weighted-average in vitro dry matter digestibility to a lesser degree, from 32.3% to 36.2% (12% relative increase; not statistically significant). Whereas forage quantity and N content results were consistent with earlier work, the limited effect on forage digestibility calls into question how prairie dogs may influence the intake of digestible nutrients by large herbivores. Grass protein content is often not a limiting factor for cattle during the growing season (Karn 2000, Grings et al. 2004), whereas forage digestibility, which is linked to both plant protein and fiber content, can strongly influence ruminant mass gains.

The geographic range of the black-tailed prairie dog in the western Great Plains encompasses substantial variation in plant communities, soils, and climatic conditions, all of which influence forage quantity and quality. Annual precipitation ranges longitudinally from 30 to 55 cm, mean annual temperature ranges latitudinally from <0° to >20°C, and plant production is directly related to precipitation, temperature, and grassland species composition (Lauenroth and Milchu-

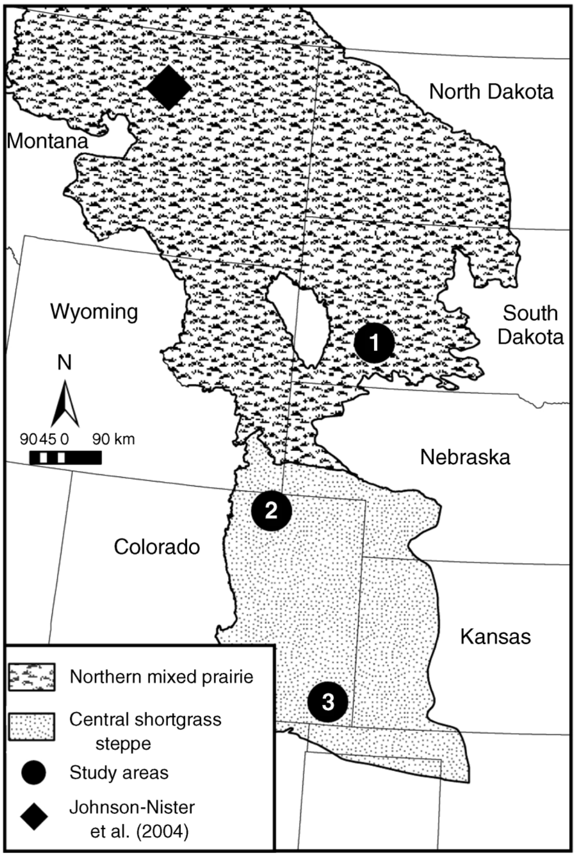

FIG. 1. Locations of study areas in the western Great Plains, USA, relative to the distribution of the northern mixed prairie and central shortgrass steppe as mapped by The Nature Conservancy (1999) and described by Lauenroth and Milchunas (1992) and Coupland (1992). The black diamond shows the area studied by Johnson-Nistler et al. (2004). Black circles show (1) the Buffalo Gap National Grassland, (2) the Pawnee National Grassland, and (3) the Comanche National Grassland.

nas 1992, Lauenroth et al. 1999, Detling 2006). We quantified spatiotemporal variation in forage quantity and quality at three prairie dog colony complexes in the western Great Plains (Fig. 1), and obtained additional data on forage quality and quantity from a fourth complex (Johnson-Nistler et al. 2004). Our objectives were to assess (1) spatial variation in the trade-offs between forage quantity and quality among prairie dog colony complexes located in the northern mixed prairie (dominated by a mixture of mid-height, C_3 and short, C_4 perennial grass species) vs. the shortgrass steppe (dominated by short, C_4 perennial grasses), (2) temporal variation in forage quality/quantity trade-offs among years, related to above- and below-average precipitation conditions, and (3) temporal variation in forage quality/quantity trade-offs over the growing season at each complex. We use our measurements of forage quantity in combination with previous experiments quantifying IIR of large ruminants (reviewed by Wilmshurst et al. 2000) to predict the relative decrease in IIR of cattle foraging on colonies compared to off-colony sites, and compare this with the relative increase in forage digestibility and [N]. We show how this balance, which provides a means of evaluating competition and/or facilitation between two herbivores, varies across locations and seasons in the Great Plains of North America.

MATERIALS AND METHODS

Study area

All sampling occurred on three national grasslands in the western Great Plains. The first site, Buffalo Gap National Grassland (BGNG), is in South Dakota (43°51′ N, 102°07′ W) in the northern mixed prairie ecoregion (Coupland 1992, Lauenroth et al. 1999). Our studies occurred in the portion of BGNG that surrounds Badlands National Park. Long-term mean annual precipitation (MAP) is 434 mm, and mean annual maximum and minimum temperatures (MAMMT) are 16.5° and 1.3°C, respectively. Vegetation is dominated by the C_3 perennial grass *Pascopyrum smithii*, and often includes the C_3 annual grass *Bromus tectorum* and C_4 perennial shortgrass *Bouteloua gracilis* along with a diversity of forbs. Precipitation received during our study period was above average, with 457 mm during July 2008–June 2009 and 469 mm during July 2009–June 2010. All study sites occurred on the Loamy 17–20 inch (43–51 cm) Precipitation Zone and the Dense Clay ecological sites (USDA 2011*a*, *b*) on flat or gently sloping terrain and were grazed by cattle at moderate stocking rates during May–October each year. Prairie dog density averages 29.6 prairie dogs/ha (Griebel 2011).

The second site was the Pawnee National Grassland (PNG) in northeastern Colorado (40°41′ N, 104°27′ W; MAP, 340 mm; MAMMT, 16.4° and 0.3°C), and the third was the Comanche National Grassland (CNG) in southeastern Colorado (37°09′ N, 102°51′ W; MAP, 412 mm; MAMMT, 19.7° and 2.0°C). Both are located in shortgrass steppe (Lauenroth and Milchunas 1992, Lauenroth et al. 1999) with vegetation dominated by the C_4 shortgrasses, *Bouteloua gracilis* and *Buchloe dactyloides*. Prickly pear cactus (*Opuntia polyacantha*) is codominant at PNG but rare at CNG. During our study period, precipitation at the PNG site was above average in the first year (July 2008–June 2009, 485 mm) and in the second year (July 2009–June 2010, 442 mm). Precipitation at the CNG site was below average in the first year (July 2008–June 2009, 318 mm) and near average in the second year (July 2009–June 2010, 427 mm). PNG study sites occurred on Loamy, Shaly, and Sandy Plains ecological sites; CNG study sites all occurred on the Loamy Plains ecological site (USDA 2007*a–c*). Study sites were on flat or gently sloping terrain and were grazed by cattle at moderate stocking rates during May–October (PNG) or May–November (CNG) each year. Magle et al. (2007) measured densities of 23.5–26.0 prairie dogs/ha on PNG. Estimates are not available for CNG, but annual monitoring by the national grasslands shows similar post-plague colony expansion rates in both shortgrass complexes.

Field sampling

We examined spatial variability in forage quantity and quality on vs. off colonies in 2009. At the northern mixed prairie complex (BGNG), we sampled 10 paired on–off colony sites. For each colony, we overlaid colony boundaries mapped in 2008 with a soils map, and identified a soil polygon that extended across the colony boundary by >100 m. We randomly selected 1 point on and 1 point off the colony within the soil polygon such that points were >50 m from the colony boundary and the soil polygon boundary. We randomly selected a direction for a 100-m transect radiating from each point, excluding directions that passed within 50 m of a colony or soil type boundary. Selected transects were overlaid on a digital elevation map and discarded and reselected if they differed in slope (by >3°) and/or aspect.

At the shortgrass steppe complexes (PNG and CNG), prairie dog colonies have expanded and contracted due to outbreaks of epizootic plague (Stapp et al. 2004, Augustine et al. 2008). For both of these complexes, we used records of colony boundaries mapped during 1999–2008 to identify all colonies where a single soil polygon overlapped (1) a portion of the colony that was actively occupied by prairie dogs in 2008, (2) a portion of the colony that had previously been occupied during 2005–2007 but where prairie dogs have been removed by plague, and (3) an area with no record of prairie dog occupancy during 1999–2008. We again only used sites with sufficient space for selection of transects located >50 m from edges of these categories. For each complex, we randomly selected five colonies to sample in 2009. We used the same procedure as at BGNG to randomly select the starting point and direction of a 100-m transect in each of the three categories, which we hereafter refer to as the active colony, plagued colony, and no prairie dog treatments. We did not sample the plagued colony treatment at BGNG because historically this area has been free of plague. However, we note that plague affected portions of BGNG for the first time beginning in 2008. The on-colony sites we sampled at BGNG were not affected by plague during 2008–2010. For each transect at each complex, we harvested aboveground plant biomass in July of 2009 in 10 100 × 20 cm plots placed at 10-m intervals along the transects. In each plot, biomass of each plant species was collected separately.

In 2010, we focused on temporal variability in forage quantity and quality by reducing our spatial replication to only three of the colony sites at each complex, but sampling these nine colony sites in late May, mid-July, and early September, with an approximate six-week interval between sampling at each site. For each round of sampling, we began at the southernmost site (CNG) and finished at the northernmost site (BGNG). For these nine colony sites, we sampled along the same transects as in 2009, but shifted the initial plot location by 2.5 m in a consistent direction, which ensured we did not sample previously clipped plots.

Plant samples were returned to the laboratory, oven-dried at 55°C, sorted to separate current-year's growth from standing dead biomass remaining from the previous year, and weighed. We examined the list of all plant species sampled during the study, and identified those species that are rarely grazed by cattle based on literature sources (Klipple and Costello 1960, Milchunas et al. 2008) and consultation with rangeland management specialists at each national grassland (Appendix A). We defined rarely grazed species as those species that experience <5% use in pastures stocked to attain 30–40% of total plant production (Klipple and Costello 1960) and/or species that have both a low preference rank (<1.0) and make up <1.5% of bites recorded in shortgrass pastures (Milchunas et al. 2008; Appendix A). We calculated forage quantity by summing biomass of those species in each plot that were not classified as rarely grazed species.

Forage quality

In 2009, we measured forage quality on two types of samples. For one-half of the plots from each transect, we ground together the biomass (including standing dead biomass) of all forage species (i.e., excluding biomass of rarely grazed species). For the remaining five plots, we ground only the current-year growth of the dominant grass species (*Bouteloua gracilis* and *Buchloe dactyloides* for the shortgrass sites and *Pascopyrum smithii* for the northern mixed prairie site), excluding standing dead biomass. Oven-dried samples were ground to pass a 1-mm screen. Samples were analyzed for in vitro dry matter digestibility (IVDMD) following the method of Tilley and Terry (1963) as modified by White et al. (1981). The ruminal inoculum was obtained from four fistulated cross-bred steers that received a daily ration of free-choice grass hay (minimum crude protein, CP, 8%), 1.14 kg 38% cottonseed cube (CP, 40.5%), and 2–3 kg of alfalfa hay (minimum CP, 21%). Ruminal pH values ranged 6.7–7.2. Two blind duplicate samples of each ground sample were analyzed for IVDMD. Samples were analyzed for nitrogen concentration using a LECO CHN-2000 Series Elemental Analyzer (LECO, Saint Joseph, Michigan, USA). In 2010, we only analyzed IVDMD and N concentration on samples consisting of the combined current-season growth and residual standing dead biomass of forage species.

Data analyses

We used a mixed-model analysis of variance (ANOVA) to test for differences in plant biomass, in vitro digestibility, and nitrogen concentration between active prairie dog colony vs. paired non-colony sites (Proc Mixed, SAS version 9.2; SAS Institute, Cary, North Carolina, USA). For the 2009 measurements (no repeated measures over time), data were analyzed as a split-plot ANOVA with colony complex as the whole plot (completely randomized design) and allotment as the split plot (randomized complete block design). Tests for an interaction between prairie dog effects and interannual variation in weather were based on ANOVA for measurements at each complex in July 2009 and July 2010, using a repeated-measures design in addition to the split-plot design described previously. Tests for an interaction between prairie dog effects and seasonal variation were based on measurement in May, July, and September of 2010, using a repeated-measures design in addition to the split-plot design. We evaluated model residuals for normality, and applied logarithmic transformations to response variables as necessary to meet ANOVA assumptions.

For one of the response variables (see *Results*), measurements at one complex in May were substantially more variable than all other complexes and months, causing heteroscedasticity in the residuals that could not be removed by response variable transformation. We excluded that particular site and date combination from the ANOVA. Tests for interaction terms were an important part of our analysis, in particular testing whether (and how) the effect of prairie dogs varied among complexes, years, and over the growing season. Because tests for interaction terms have lower power than tests for main effects, we examined simple effects in any case where the test for an interaction term resulted in $P \leq 0.10$ (Meredith and Stehman 1991). In all cases, we report exact P values to allow readers to distinguish between significant effects ($P < 0.05$) and marginally significant effects that may still warrant attention ($0.05 < P < 0.1$).

We used results for forage biomass and digestibility from our three study areas plus data from Johnson-Nistler et al. (2004) to contrast predicted daily intake of digestible dry matter and daily foraging time for ruminants of varying body sizes (350–750 kg) grazing in an area lacking prairie dogs (off-colony conditions for 100% of daily forging time) vs. ruminants that spend 50% of daily foraging time on colony, and the remainder foraging off colony. These calculations depend upon constraints potentially imposed by (1) the instantaneous intake rate (grams per minute) that an ungulate can achieve on swards of varying biomass (i.e., the functional response; Wilmshurst et al. 2000), (2) the maximum amount of time that an ungulate can spend foraging within a 24-hour period, and (3) the maximum amount of forage that an ungulate can process in a 24-hour period based on digestive constraints. Functional response curves are necessary for scaling up measurements from minutes to days, and hence are central to many models of plant–herbivore interactions. However, their use requires careful consideration of the experimental conditions from which they are derived, as the three-dimensional configuration of vegetation (e.g., grass tillers vs. large forbs) and depletion during a foraging bout can influence scaling (Wallis de Vries et al. 1998). We used functional responses for large ruminants grazing experimentally constructed swards of grass tillers derived from a study of yearly bison (180 kg body mass; Bergman et al. 2000) and a study of four-year-old steers (750 kg body mass; Laca et al. 1994). Wallis de Vries et al. (1998) also noted the value of Laca et al.'s (1994) measurements for application to ruminants on grass swards. We follow Wilmshurst et al. (2000) in assuming a maximum of 13 h foraging time per day. Maximum daily forage intake is limited by the amount of indigestible material a ruminant can process. We calculated maximum daily intake rate (DIR) as constrained by digestive processes as a function of IVDMD and body size based on the relationships between voluntary intake and forage digestibility reported by Bergman et al. (2001; see regression equations in Figs. 1 and 2 therein). This relationship predicted a maximum daily intake of 2.6% of body mass for ungulates consuming forage with IVDMD of 60%. This is consistent with studies of cattle grazing native rangeland in the western Great Plains, which report daily intake values varying from 1.7% to 2.8% of body mass, (Cordova et al. 1978, McCollum and Galyean 1985, Fredrickson et al. 1993).

RESULTS

Variation among complexes

Forage quantity was measured in terms of commonly grazed species' biomass (CGSB) that grew during the current growing season and residual standing dead biomass (RSDB) that remained from the previous growing season. Prairie dog effects on CGSB varied among complexes (complex × prairie dog interaction, $F_{3,21.4} = 3.99$, $P = 0.021$; Fig. 2). For the northern mixed prairie complex, prairie dogs reduced CGSB by 63% on vs. off colonies in 2009 ($P < 0.001$; Fig. 2A). For the shortgrass complexes, prairie dogs had no effect on CGSB at PNG ($P = 0.84$; Fig. 2B). Prairie dogs reduced CGSB by 38% at CNG, which was a marginally significant reduction ($P = 0.096$; Fig. 2C). Biomass on plague-affected sites was intermediate between but did not differ significantly from active or off-colony sites ($P \geq 0.20$; Fig. 2B, C). Prairie dog effects on RSDB varied by complex (complex × prairie dog interaction, $F_{3,26.9} = 4.53$, $P = 0.011$). Prairie dogs reduced RSDB by 94% at the northern mixed prairie complex ($P < 0.001$; Fig. 2A), but did not significantly influence RSDB at either shortgrass complex ($P \geq 0.17$; Fig. 2B, C). We found no evidence that prairie dogs influenced biomass of rarely grazed species (consisting primarily of *Plantago patagonica* and *Opuntia polyacantha*) at any complex (complex × prairie dog interaction, $F_{3,22.2} = 0.91$, $P = 0.45$; prairie dog main effect, $P = 0.94$; Fig. 2).

The relative proportion of the forage biomass consisting of forbs varied in relation to prairie dog presence and complex location. Individual contrasts within each complex showed that at BGNG, forbs comprised substantially more of the forage biomass on colonies (31%) vs. off colonies (15%; $P = 0.0154$). At PNG, forbs comprised a marginally greater proportion of forage biomass on active colonies (30%) compared to both off-colony forage (11%; $P = 0.043$ for contrast with active colonies) and forage from plague-affected colonies (10%; $P = 0.041$ for contrast with active colonies). In contrast, at CNG, forbs comprised a relatively low and similar proportion of the forage on active colonies (4%), plague-affected colonies (6%), and off colonies (7%; $P \geq 0.79$ for all contrasts).

Forage quality was first examined in terms of IVDMD and N concentration for samples in which we combined the current-season's growth of commonly grazed species with residual standing dead from the previous growing season. Prairie dogs increased IVDMD on vs. off colonies at the northern mixed prairie complex (by 7.9% relative to off-colony forage; complex × prairie dog interaction, $F_{3,27.8} = 5.56$, $P = 0.004$; on vs. off colony contrast for BGNG, $P < 0.001$; Fig. 3A). In shortgrass steppe, we found marginal evidence that prairie dogs increased IVDMD at the PNG complex (by 3.1% relative to off-colony forage, $P = 0.057$), and no evidence of a prairie dog effect at the CNG complex ($P \geq 0.56$; Fig. 3A). Prairie dogs significantly increased forage [N] across all complexes from a mean of 1.08% off-colony to 1.41% on-colony (complex × prairie dog interaction, $F_{3,25} = 1.68$, $P = 0.20$; prairie dog main effect, $F_{2,25} = 10.71$, $P = 0.0004$; Fig. 3B).

We also examined IVDMD and N content for samples that only contained the current-season's growth of the dominant grass species (*Pascopyrum smithii* for BGNG and *Bouteloua gracilis* plus *Buchloe dactyloides* for CNG and PNG), in order to separate the effects of standing dead biomass from effects of fiber and protein content of current-season's growth. These samples represent forage quality that cattle could theoretically obtain if they foraged in a highly selective manner to avoid all standing dead biomass. However, in the field, standing dead and current-season's growth are typically finely intermixed within a grass tuft, preventing cattle from foraging this selectively. For the current-season's biomass, we found no difference for IVDMD on vs. off colonies (complex × prairie dog interaction, $F_{3,26.1} = 0.54$, $P = 0.657$; prairie dog effect, $F_{2,26.1} = 2.03$, $P = 0.15$; Fig. 3C) but significantly higher [N] on vs. off colonies (1.33% N on vs. 1.06% N off; complex × prairie dog interaction, $F_{3,25} = 1.52$, $P = 0.23$; prairie dog effect, $F_{2,25} = 12.57$, $P = 0.0002$; Fig. 3D).

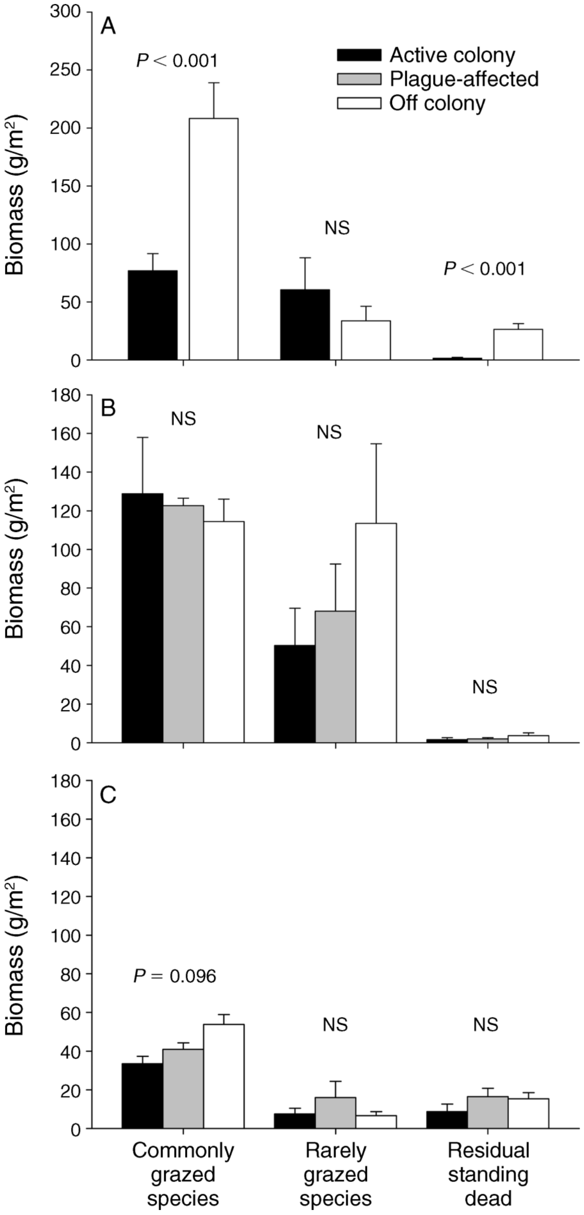

FIG. 2. Effects of black-tailed prairie dogs (*Cynomys ludovicianus*) on biomass of commonly grazed plant species, rarely grazed plant species, and residual standing stead at (A) the Buffalo Gap National Grassland (northern mixed prairie), (B) the Pawnee National Grassland (shortgrass steppe), and (C) the Comanche National Grassland (shortgrass steppe). The key indicates site status: active prairie dog colonies, former colonies where prairie dogs were removed by plague, and off-colony sites with no prairie dogs present in the past decade. Biomass was measured during mid-growing season in 2009. "NS" means not significant; error bars show +SE.

Interannual variation

We found no evidence that prairie dog effects on forage quantity varied in direction or magnitude among years (complex × prairie dog × year interaction, $P = 0.9105$; treatment × year interaction, $P = 0.92$; Fig. 2 vs. July values in Fig. 4). The interannual variation analysis indicated a negative effect of prairie dogs on residual standing dead biomass across years and complexes (all higher order interactions with prairie dog, $P > 0.22$; prairie dog main effect, $P = 0.0006$), which was inconsistent with the lack of effect detected at the shortgrass complexes based on the 2009 sampling. This was due to increased RSDB at the shortgrass complexes

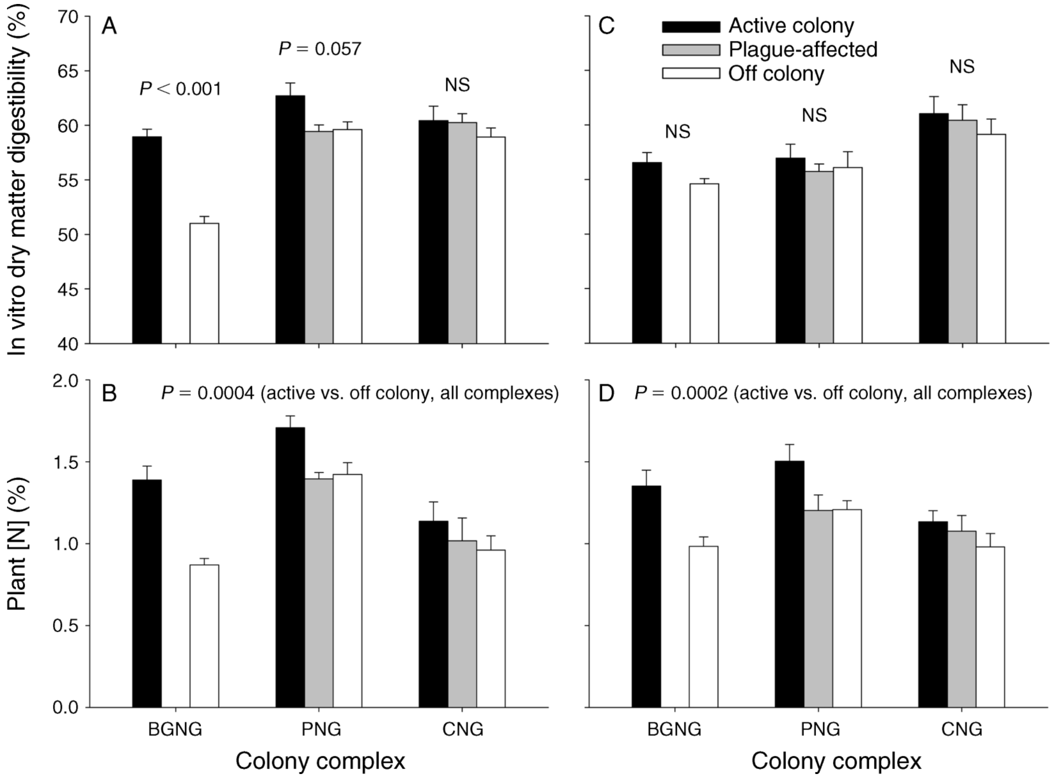

FIG. 3. In vitro dry matter digestibility and nitrogen concentration of forage collected on active prairie dog colonies, former colonies where prairie dogs were removed by plague, and off-colony sites with no prairie dogs present in the past decade. Sampling occurred during mid-growing season in 2009 at the Buffalo Gap National Grassland (BGNG, northern mixed prairie), Pawnee National Grassland (PNG, shortgrass steppe), and Comanche National Grassland (CNG, shortgrass steppe). Data are presented for (A, B) current-season's growth and residual standing dead combined and for (C, D) current-season's growth only. "NS" means not significant; error bars show +SE.

in 2010, particularly at PNG where above-average forage production occurred in 2009. As a result of this increase, there was greater potential for prairie dogs to influence RSDB in all three complexes in 2010.

For IVDMD, prairie dog effects varied among complexes (complex × prairie dog × year interaction, $P = 0.04$), so we examined interannual variation in IVDMD for each complex separately. At BGNG, prairie dogs consistently increased IVDMD in both years (8.0% increase in 2009, 5.1% increase in 2010; prairie dog × year interaction, $F_{1,7.55} = 2.13$, $P = 0.18$; prairie dog main effect, $F_{1,11.5}$, $P = 0.0002$). At CNG, we found no evidence that prairie dogs influenced IVDMD in either year (prairie dog × year, $F_{1,7.71} = 0.01$, $P = 0.92$; prairie dog main effect, $F_{1,3.07} = 0.38$, $P = 0.58$). At PNG, prairie dogs increased IVDMD in both years, but the magnitude of the effect was smaller than at BGNG (1.5% increase in 2009, 6.8% increase in 2010) and strength of evidence was weaker (prairie dog × year interaction, $F_{1,3.01} = 1.55$, $P = 0.302$; prairie dog main effect, $F_{1,1.96} = 10.98$, $P = 0.083$). For plant [N], prairie dog effects did not vary among complexes and years (complex × prairie dog × year interaction, $P = 0.32$, prairie dog × year, $P = 0.89$). Prairie dogs substantially increased plant [N] at all complexes and in both years ($P = 0.0003$), with plant N concentration of 1.33% ± 0.05% (mean ± SE) on colonies vs. 0.95% ± 0.06% off colonies at BGNG, 1.56% ± 0.13% on and 1.30% ± 0.12% off colonies at PNG, and 1.01% ± 0.06% on vs. 0.78% ± 0.04% off at CNG.

Collectively, these analyses show that with the exception of RSDB, the direction and magnitude of prairie dog effects on mid-growing-season forage quantity was consistent across the three complexes and two years.

Seasonal variation

Prairie dog effects on CGSB varied seasonally (prairie dog × month interaction, $P = 0.099$), but the seasonal pattern of this effect did not vary across complexes (complex × prairie dog × month interaction, $P = 0.1834$). In particular, we found an increasingly negative effect of prairie dogs on CGSB over the course of the growing season, with an average reduction across all complexes of 32% in May ($P = 0.057$), 42% in July ($P = 0.009$), and 54% in September ($P = 0.001$; Fig. 4A–C). Most plant growth occurred in the first half of the growing season at BGNG and PNG, whereas most

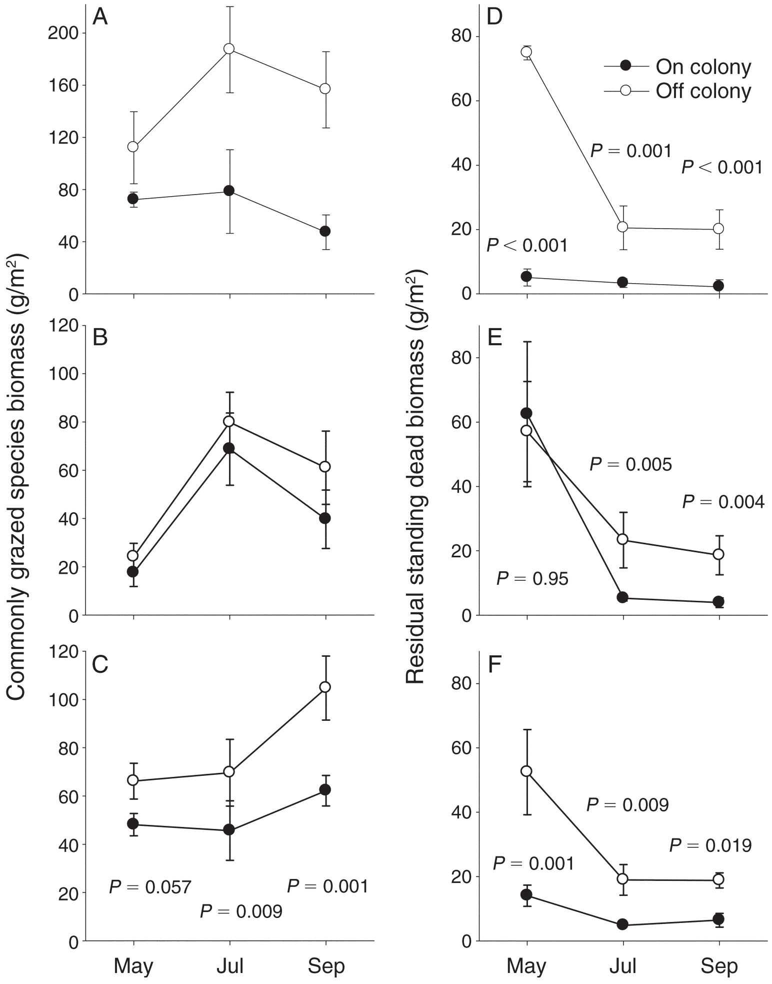

FIG. 4. Seasonal variation in (A–C) current-season's biomass of commonly grazed species and (D–F) residual standing dead biomass retained from the previous growing season on active prairie dog colonies and off-colony sites with no prairie dogs present in the past decade. Measurements are from (A, D) the Buffalo Gap National Grassland (northern mixed prairie), (B, E) the Pawnee National Grassland (shortgrass steppe), and (C, F) the Comanche National Grassland (shortgrass steppe). Error bars show ±SE.

growth occurred in the second half of the growing season at CNG (Fig. 4A–C). Off-colony vegetation at BGNG and PNG was primarily vegetative in the first sampling period, but had progressed to reproductive phases by mid- and late summer. At CNG, plants were primarily in vegetative growth phase in all samplings, associated with early-summer water limitation. Seasonal effects of prairie dogs on RSDB varied by complex (complex × prairie dog × month interaction, $F_{4,23.1} = 3.05$, $P = 0.037$), and within each month, prairie dog effects varied by complex (all three prairie dog × complex interaction slices by month; $P < 0.001$). In May, RSDB was dramatically lower on vs. off colonies at BGNG and CNG, but not PNG (Fig. 4D–F). In July and September, RSDB was substantially lower on colonies at all complexes (Fig. 4D–F).

The ANOVA for forage IVDMD suggested that prairie dog effects varied among complexes and months, but residuals exhibited high heteroscedasticity even after logarithmic transformation, due to greater among-site variability at PNG in May compared to all other complexes and months (Fig. 5). To meet ANOVA assumptions, we excluded the May measurements at PNG. The resulting ANOVA indicated that prairie dog effects on IVDMD varied over the growing season (treatment × month, $F_{2,19.9} = 11.10$, $P = 0.0006$), but the seasonal pattern of effects did not vary among complexes ($P = 0.31$; note the exception of a lack of any evidence for an effect at PNG in May). At BGNG and CNG, prairie dogs increased IVDMD more in May than in July and September. A consistent pattern of increased IVDMD on prairie dog colonies was observed across all complexes in July and September, with larger effects at BGNG and PNG compared to CNG. The high among-colony variance at PNG in May 2010 (Fig. 5B) was associated with large amounts of residual standing dead biomass that accumulated during the productive 2009 growing season (Fig. 4E). This was consistent with

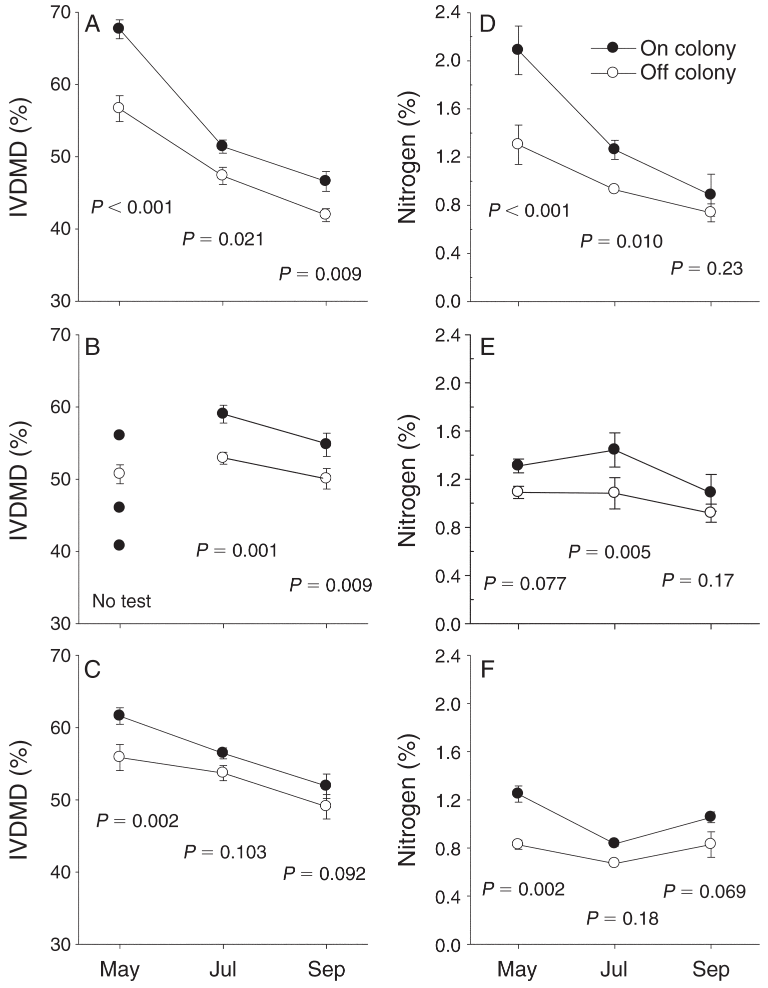

FIG. 5. Seasonal variation in the in vitro dry matter digestibility (IVDMD) and nitrogen concentration of forage (current-season's growth plus residual standing dead) on active prairie dog colonies and off-colony sites with no prairie dogs present in the past decade. Measurements are from (A, D) the Buffalo Gap National Grassland (northern mixed prairie), (B, E) the Pawnee National Grassland (shortgrass steppe), and (C, F) the Comanche National Grassland (shortgrass steppe). Error bars show ±SE.

the unusual finding that forage IVDMD and N content were lower in May than in July at PNG (Fig. 5B, E). By July, most residual biomass had been removed from the on-colony sites at PNG, leading to differences between on- and off-colony sites that were similar to patterns at the other complexes.

Finally, prairie dog effects on forage N content showed potential variation among seasons and complexes (complex × treatment × month interaction, $F_{4,21} = 2.19$, $P = 0.10$). In May, prairie dogs substantially increased forage N concentration at BGNG and CNG, but only marginally at PNG (Fig. 5D–F). This pattern was parallel to findings for IVDMD (Fig. 5A–C) and the amount of residual standing retained from the previous growing season (Fig. 4D–F). Variation among sites in May at PNG was not as extreme for forage N as for IVDMD. Prairie dogs enhanced forage N content at BGNG and PNG in July (but not in September) and at CNG in September (but not in July; Fig. 5D–F).

Comparison of scenarios for cattle feeding on grassland lacking prairie dogs vs. cattle feeding 50% on and 50% off of prairie dog colonies showed that prairie dogs can both positively and negatively influence daily digestible dry matter intake and net daily energy gain of cattle. Our analyses predict predominantly negative prairie dog effects (competition) under below-average precipitation in both shortgrass and mixedgrass, and positive effects (facilitation) under above-average precipitation in both shortgrass and mixedgrass (Table 1; Appendices B and C). These predictions depend upon the specific functional response used, ruminant body size, and the proportion of daily time that cattle spend grazing on a prairie dog colony. Facilitation was more likely for smaller sized ruminants that can achieve IIRs measured by Bergman et al. (2000) as compared to larger animals with lower IIR as measured by Laca et al. (1994; Appendices B and C).

TABLE 1. Summary of the relative difference in forage biomass, predicted large ungulate instantaneous intake rate (IIR), in vitro dry matter digestibility (IVDMD), and nitrogen concentration in forage on vs. off black-tailed prairie dog (*Cynomys ludovicianus*) colonies sampled at four different colony complexes in the western Great Plains, USA.

Complex	Growing-season conditions†	Relative prairie dog effect (% of off colony)				Predicted effect
		Biomass	IIR	IVDMD	[N]	
Northern mixed prairie						
Phillips County BLM‡	dry	−61.8	−57.6	+12.1	+35.2	facilitation and competition
Buffalo Gap National Grassland	wet	−63.1	−46.1	+15.7	+59.8	facilitation
Shortgrass steppe						
Comanche National Grassland	dry	−32.1	−22.2	NS	+21.4	competition
Pawnee National Grassland	wet	NS	NS	+5.2	+18.7	facilitation

Notes: Relative change in IIR is the mean of the predicted change based on functional responses of Laca et al. (1994) and Bergman et al. (2000). For each variable, the relative difference is calculated as 100 multiplied by the difference between the on- vs. off-colony value divided by the off-colony value. NS indicates no significant difference on vs. off colonies. The predicted net effect of prairie dogs is based on a comparison of cattle feeding 100% of their time off colony vs. cattle feeding 50% of their time on and 50% of their time off colony. See Appendices B and C for details on calculations of prairie dog effects on daily cattle energy gain.

† Based on Palmer drought index for the two months preceding sampling, which provides an index of moisture availability relative to long-term mean conditions for the site.

‡ Data are from Johnson-Nistler et al. (2004). BLM stands for Bureau of Land Management.

DISCUSSION

Assessing the potential for competition between herbivores requires consideration of spatiotemporal shifts in forage quantity and quality, herbivore behavioral responses, and potential community and ecosystem-level feedback effects of the herbivores on plants. We assessed both spatial and temporal variability in prairie dog effects on forage resources. One important finding is that although prairie dogs substantially reduced the biomass of plant species that are commonly grazed by cattle, we did not find a compensatory increase in on-colony biomass of rarely grazed species such as cactus (*Opuntia polyacantha*) or wooly plantain (*Plantago patagonica*) at any complex. Thus, prairie dog effects on cattle mass gains are likely to operate primarily through their direct effects on the quantity and quality of forage, rather than shifts in abundance of unpalatable plant species. Prairie dogs did increase the relative abundance of forbs vs. graminoids within the available forage on compared to off colonies, with implications for forage quality.

A second key finding is that prairie dogs are predicted to both facilitate and compete with cattle depending on local weather conditions and dominant grass species (Table 1). For the two shortgrass steppe complexes, which have similar forage species composition, our results predict opposite outcomes for cattle. At the Comanche complex, which received below-average precipitation, we found (1) a substantial reduction in forage quantity on colonies, (2) no increase in forage digestibility, and (3) a small increase in forage [N]. Under the low-biomass conditions (34–54 g/m^2 available forage), IIR is predicted to be so low that it forces cattle to maximize daily foraging time and thereby constrains daily dry matter intake (Appendices B and C). With no compensating increase in forage digestibility, net daily digestible dry matter intake is also predicted to decline, thereby reducing livestock mass gains. Furthermore, as forage quantity declines in late summer/early fall with no corresponding increase in forage quality on colonies (Figs. 4 and 5), negative impacts on livestock performance are likely to increase. In contrast, under conditions of above-average precipitation at the Pawnee complex, we found (1) no reduction in forage quantity on colonies, and (2) increased forage digestibility and [N] on colonies. Here, DIR of cattle can remain unchanged or even increase due to reduced intake of indigestible material. In either case, net daily intake of digestible nutrients is predicted to increase, resulting in improved livestock performance. These opposite predictions for shortgrass steppe under dry vs. wet conditions parallel the recent findings by Odadi et al. (2011) of wildlife–cattle facilitation in wet seasons and competition in dry seasons in an African savanna. In both cases, the underlying mechanism is a wildlife-induced increase in forage quality under wet conditions and reduction in forage quantity under dry conditions.

For complexes in northern mixed prairie, our results and those of Johnson-Nistler et al. (2004) show a large reduction in available forage on colonies paralleled by smaller but significant increases in forage digestibility and/or [N], under both below-average and above-average precipitation (Table 1). These findings are consistent with Baker et al.'s (2012) report of a similar reduction in vegetation volume on vs. off prairie dog colonies across seven different complexes in the northern mixed prairie. Reduced forage quantity under both dry and wet conditions in this ecoregion may be related to the limited grazing tolerance of the dominant perennial grass species, *Pascopyrum smithii*, which responds to prairie dog grazing with reduced above- and below-ground productivity (Detling and Painter 1983, Polley and Detling 1988, Milchunas et al. 2008).

To extrapolate from forage measurements to livestock performance in northern mixed prairie requires knowledge of whether forage availability limits IIR to the point where increased foraging time cannot compensate for decreased IIR, and DIR declines. This is likely to occur where (1) forage quantity off colonies is so low that intake is limited more by IIR than digestion, and/or (2) the proportion of the pasture occupied by prairie dogs is large, again causing intake to be limited more by IIR and the inability of cattle to sufficiently increase daily foraging time to maintain DIR. In the northern mixed prairie, forage production is typically greater and individual plants taller compared to shortgrass steppe, such that off-colony intake is not constrained by IIR under moderate stocking rates and average or above-average precipitation, and cattle can achieve maximum daily intake rates in far less than 13 hours per day. However, in the more arid (western) portion of the region under below-average precipitation, available forage averaged only 32 g/m^2 off colonies and declined to 12 g/m^2 on colonies (Johnson-Nistler et al. 2004). For grasslands this short and sparse, IIR is predicted to constrain DIR, particularly for ruminants larger than 550 kg (Appendices B and C). For example, IIR declines by 54.8% (from 13.5 to 6.1 g/min) off vs. on colonies based on the functional response of Bergman et al. (2000) and by 60.5% (from 5.8 to 2.3 g/min) based on the functional response of Laca et al. (1994). Even given the large differences between the two functional response curves, both predict that IIR constrains DIR for a 750-kg cow (i.e., even when foraging 13 hours per day, they do not attain the maximum potential DIR determined by digestive constraints), such that DIR declines in direct proportion to time spent foraging on colonies. These predictions are consistent with Hobbs et al. (1996*a*), who found that cattle grazing pastures with <45 g/m^2 experienced significant reduction in DIR compared to cattle grazing pastures >45 g/m^2. If cattle forage on colonies in proportion to their abundance (Guenther and Detling 2003), reduced DIR could only be offset by the 12% increase in digestibility for smaller cattle (e.g., 350–550 kg) that are able to attain IIR as high as that reported by Bergman et al. (2000). In most cases, the net effect of prairie dogs is reduced daily nutrient intake and reduced cattle mass gain, the magnitude of which will increase with increased prairie dog abundance (Table 1).

Under wet conditions, as we measured at the Buffalo Gap study site, forage both on and off colonies was substantially greater than at the Phillips County site (Table 1) even though prairie dogs reduced forage availability by $>60\%$ at both sites. Under these conditions, digestion rate rather than IIR is likely to constrain DIR for cattle. IIR is predicted to decline by 35.5% (from 37.1 to 23.9 g/min) by Bergman et al. (2000) or by 56.7% (from 30.1 to 13.0 g/min) by Laca et al. (1994) as forage availability declines from 208 to 77 g/m^2. Here, cattle can increase daily foraging time and hence intake of more digestible on-colony forage, thereby increasing their net daily energy gain (Appendix C). Consistent with the findings of Hobbs et al. (1996*a*), forage availability both on and off colonies was also well above the 45 g/m^2 threshold at which DIR declines. Precise predictions require consideration of interactions among daily foraging time, how IIR varies as a function of pasture characteristics, animal body size, and forage growth vs. depletion rates, but vary from facilitation at low prairie dog abundance to competition with complete prairie dog occupancy of a pasture. Although extrapolations for the northern mixed prairie are more complex than the shortgrass sites, our measurements predict that competition is likely with below-average precipitation at drier sites, while facilitation predominates with above-average precipitation and at more mesic sites.

Another important factor influencing competition between herbivores is seasonal variation in forage quantity and quality. The previous discussion focuses on mid-growing-season measurements of forage, but conditions can vary substantially over weeks and months in semiarid grasslands. We found that in general, prairie dog effects on availability of current-season's forage growth was minimal in early summer and increased with the progression of the growing season. In contrast, prairie dogs enhanced forage digestibility most in early summer, with smaller but still significant effects later in the growing season. Enhancement of forage digestibility early in the growing season likely resulted from a combination of two mechanisms. First, prairie dogs typically removed most standing dead biomass during the dormant season (Fig. 4D, F). While small herbivores may be expected to forage selectively and avoid low-quality forage, prairie dogs are colonial, central-place forgers that are often forced to utilize standing dead forage when supply is limited. Furthermore, black-tailed prairie dogs often clip but do not consume standing dead or unpalatable plant species in order to improve visibility on their colonies (Hoogland 1995). In one case where standing dead biomass was unusually abundant and prairie dogs had not yet removed it by the start of the growing season (Fig. 4E), forage digestibility also did not increase (Fig. 5B). A second factor that likely influenced digestibility was the increased relative abundance of forbs vs. graminoids in on-colony forage at the Buffalo Gap and Pawnee study sites, where we documented significant increases in digestibility. Conversely, we found no increase in forbs on colonies at the Comanche site, and an associated lack of effect on forage digestibility. We also found that prairie dogs did not significantly affect the digestibility of current-year's growth of the dominant grass species at any of the study sites. Collectively, these findings indicate that increased relative abundance of forbs and removal of standing dead biomass both are likely explanations for increased forage digestibility on colonies. In addition, late in the growing season, standing dead biomass was low both on and off colonies.

Increased forage quality on colonies at this time is likely related to declining quality due to plant maturation off colonies compared to more prostrate, regrowing plants on colonies. These patterns indicate that competition between prairie dogs and cattle will be absent or minimal early in the growing season, and increase in severity over the course of the growing season. Where managers can shift livestock distribution seasonally, grazing should be targeted in areas with concentrations of native herbivores early in the growing season and during periods of rapid plant growth in order to minimize competition.

In many grassland ecosystems, the regrowth of previously grazed grasses contains elevated [N] relative to ungrazed grasses (McNaughton 1984, Knapp et al. 1999); this has clearly been shown for plants grazed by prairie dogs (Polley and Detling 1988, Whicker and Detling 1988). Underlying mechanisms include an increase in soil N availability, and the maintenance of vegetation in vegetative growth stages that have higher protein levels (Polley and Detling 1988, Holland and Detling 1990). However, the relative effect of prairie dogs on both forage [N] and digestibility needs to be assessed to evaluate competition with livestock. We found that prairie dogs enhanced forage digestibility to a lesser degree than [N] in both shortgrass steppe and northern mixed prairie (Table 1). The relative effect on IVDMD is likely to be the more important consideration for livestock performance during the growing season, but forage [N] can also affect rumen microbial function. Rumen microbial populations require 6–7% crude protein or ~1% [N], which is generally accepted as a maintenance level for ruminants (Van Soest 1982). Forage [N] declined at Pawnee and Buffalo Gap over the growing season, reaching critically low concentrations by September. At Comanche, forage [N] was below 1% throughout the growing season, potentially related to the dry conditions. The ability of cattle to acquire forage with enhanced [N] from prairie dog colonies late in the growing season, and thereby enhance digestion of off-colony forage, could potentially reduce competition at this time, again depending on the proportion of the pasture occupied by prairie dogs. For managers concerned with livestock mass gains, native herbivore effects on forage IVDMD will be most important to consider during periods of plant growth, while effects on forage [N] will be more important during periods of plant senescence and in more productive rangelands where rapid accumulation of grass stem biomass and older leaves reduces [N] below 1%.

Our findings show that whether native and domestic herbivores compete in rangeland ecosystems depends on multiple interacting factors. To the extent that domestic herbivores are more strongly limited by forage digestion rates than by short-term forage consumption (i.e., cropping and chewing) rates during some seasons or under certain rainfall patterns, there exists an opportunity for coexisting herbivores to enhance the digestibility and [N] of available forage, and thereby enhance livestock performance. Competitive interactions should not be assessed on the basis of diet overlap and the effects of native herbivores on forage quantity alone, but rather on the basis of trade-offs between forage quantity and digestibility. In the case of prairie dogs, which are central-place foragers with effects that are concentrated in discrete colonies, cattle can move between on-colony and off-colony sites. Prairie dog effects can be evaluated by considering daily intake of digestible nutrients of cattle foraging both on and off colonies (e.g., Appendix C). Key factors in any site-specific evaluation include the proportion of a pasture occupied by prairie dogs, site productivity and growth form of dominant grasses, current-season growing conditions, and season of cattle grazing. In particular, our findings indicate that above-average growing season precipitation promotes facilitation, while competition is more likely with below-average precipitation. With the grazing-tolerant grasses found in the shortgrass steppe, above-average precipitation promoted a pulse of rapid plant growth and regrowth on colonies, resulting in similar quantities of available forage on and off colonies. With taller and less grazing-tolerant plants in the mixed grass prairie, above-average precipitation produced high forage biomass (with low quality) off colonies. Under these conditions, daily cattle intake rate is not limited by IIR and cattle could utilize forage on colonies to enhance digestibility and [N] of their overall diet. Thus, the high degree of spatiotemporal variation in vegetation dynamics characteristic of semiarid grasslands (Ellis et al. 1993, Knapp and Smith 2001) is also paralleled by variability in the magnitude of competition between native and domestic grazers.

A diversity of burrowing, mammalian herbivores are native to semiarid rangelands worldwide. These herbivores are frequently viewed as pests due to perceived competition with domestic herbivores (Delibes-Mateos et al. 2011). However, they also have been shown to create belowground refugia, alter vegetation structure, and thereby generate unique habitats for associated flora and fauna in rangelands of Asia (Smith and Foggin 1999), Australia (Noble et al. 2007), Europe (Galvez-Bravo et al. 2011), North America (Kotliar et al. 1999), and South America (Villarreal et al. 2008). Managers weighing trade-offs between livestock production and the conservation of such ecosystem engineers should recognize that both competition and facilitation can occur in a given year or location. Competitive interactions that may be visibly evident during dry or dormant seasons can be partially or wholly offset by facilitation during periods when forage quantity does not limit the daily intake rate of cattle and forage digestibility is enhanced. The relative importance of these two processes will depend on both the ecological conditions determining which predominates, and the economic conditions influencing whether losses to competition are financially equivalent to gains due to facilitation. Management options for controlling populations of native herbivores are often costly, and may only be economically feasible with government subsidies (Miller et al. 2007, Delibes-Mateos et al. 2011) or where local eradication is achieved. Where managers seek to balance livestock production and biodiversity conservation, the costs of controlling native herbivores should be weighed not only against their competitive effects during periods of low forage availability, but also in relation to the facilitative effects of native herbivores on forage quality and the value of the habitats that native herbivores create for other associated species.

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Literature Cited

Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313–318.

Augustine, D. J., and J. D. Derner. 2012. Disturbance regimes and mountain plover habitat in shortgrass steppe: large herbivore grazing does not substitute for prairie dog grazing or fire. Journal of Wildlife Management 76:721–728.

Augustine, D. J., M. R. Matchett, T. P. Toombs, J. F. Cully Jr., T. L. Johnson, and J. G. Sidle. 2008. Spatiotemporal dynamics of black-tailed prairie dog colonies affected by plague. Landscape Ecology 23:255–267.

Baker, B., D. Augustine, J. Sedgwick, and B. Lubow. 2012. Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs. Ecography. http://dx.doi.org/10.1111/j.1600-0587.2012.07614.x

Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen–sagebrush summer range. Rangeland Ecology and Management 58:135–147.

Bergman, C., J. Fryxell, and C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of wood bison. Functional Ecology 14:61–69.

Bergman, C., J. Fryxell, C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology 70:289–300.

Cordova, F. J., J. D. Wallace, and R. D. Pieper. 1978. Forage intake by grazing livestock: a review. Journal of Range Management 31:430–438.

Coupland, R. 1992. Mixed prairie. Pages 151–182 *in* R. Coupland, editor. Ecosystems of the world 8A: natural grasslands. Elsevier, New York, New York, USA.

Delibes-Mateos, M., A. T. Smith, C. N. Slobodchikoff, and J. E. Swenson. 2011. The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. Biological Conservation 144:1335–1346.

Derner, J., J. Detling, and M. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? Frontiers in Ecology and the Environment 4:459–464.

Desmond, M. J., J. A. Savidge, and K. M. Eskridge. 2000. Correlations between burrowing owl and black-tailed prairie dog declines: a 7-year analysis. Journal of Wildlife Management 64:1067–1075.

Detling, J. K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin 26:438–448.

Detling, J. K. 2006. Do prairie dogs compete with livestock? Pages 65–88 *in* J. L. Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C., USA.

Detling, J. K., and E. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57:65–71.

Ellis, J. E., M. B. Coughenour, and D. M. Swift. 1993. Climate variability, ecosystem stability, and the implications for range and livestock development. Pages 31–41 *in* R. Behnke, I. Scoones, and C. Kerven, editors. Range ecology at disequilibrium. Overseas Development Institute, London, UK.

Fredrickson, E. L., M. L. Galyean, M. E. Branine, B. Sowell, and J. D. Wallace. 1993. Influence of ruminally dispensed monensin and forage maturity on intake and digestion. Journal of Range Management 46:214–220.

Galvez-Bravo, L., A. Lapez-Pintor, S. Rebollo, and A. Gamez-Sal. 2011. European rabbit (*Oryctolagus cuniculus*) engineering effects promote plant heterogeneity in Mediterranean dehesa pastures. Journal of Arid Environments 75:779–786.

Griebel, R.L. 2011. Wall ranger district 2010 boundary and interior management zone report. U.S. Department of Agriculture, Forest Service, Buffalo Gap National Grassland, Wall, South Dakota, USA.

Grings, E., R. Short, M. Haferkamp, and R. Heitschmidt. 2004. Late summer protein supplementation for yearling cattle. Journal of Range Management 57:358–364.

Guenther, D. A., and J. K. Detling. 2003. Observations of cattle use of prairie dog towns. Journal of Range Management 56:410–417.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*a*. Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. Ecological Applications 6:218–227.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*b*. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecological Applications 6:200–217.

Holland, E., and J. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois, USA.

Johnson-Nistler, C. M., B. F. Sowell, H. W. Sherwood, and C. L. Wambolt. 2004. Black-tailed prairie dog effects on Montana's mixed-grass prairie. Journal of Range Management 57:641–648.

Karn, J. F. 2000. Supplementation of yearling steers grazing northern Great Plains rangelands. Journal of Range Management 53:170–175.

Klipple, G. E., and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the central Great Plains. U.S. Government Printing Office, Washington, D.C., USA.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39–50.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. E. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177–192.

Kretzer, J. E., and Cully, J. F., Jr. 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. Southwestern Naturalist 46:171–177.

Laca, E. A., E. D. Ungar, and M. W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. Applied Animal Behavior Science 39:3–19.

Lauenroth, W. K., I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystem in the central North American grassland region. Great Plains Research 9:223–259.

Lauenroth, W. K., and D. G. Milchunas. 1992. Short-grass steppe. Pages 183–226 *in* R. Coupland, editor. Ecosystems of the world 8A: natural grasslands. Elsevier, New York, New York, USA.

Magle, S., B. McClintock, D. Tripp, G. White, M. Antolin, and K. Crooks. 2007. Mark-resight methodology for estimating population densities for prairie dogs. Journal of Wildlife Management 71:2067–2073.

McCollum, F. T., and M. L. Galyean. 1985. Cattle grazing blue grama rangeland. II. Seasonal forage intake and digesta kinetics. Journal of Range Management 38:543–546.

McNaughton, S. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

Meredith, M., and S. Stehman. 1991. Repeated measures experiments in forestry: focus on analysis of response curves. Canadian Journal of Forest Research 21:957–965.

Milchunas, D., W. Lauenroth, I. Burke, and J. K. Detling. 2008. Effects of grazing on vegetation. Pages 389–446 *in* W. Lauenroth and I. C. Burke, editors. Ecology of the shortgrass steppe: a long-term perspective. Oxford University Press, New York, New York, USA.

Miller, B., et al. 2007. Prairie dogs: an ecological review and current biopolitics. Journal of Wildlife Management 71:2801–2810.

Nature Conservancy (TNC). 1999. TNC ecoregions and divisions of the lower 48 United States. Map. http://gis.tnc.org/data/MapbookWebsite/map_page.php?map_id=9

Noble, J., W. Muller, J. Detline, and H. Pfitzner. 2007. Landscape ecology of the burrowing bettong: warren distribution and patch dynamics in semiarid eastern Australia. Austral Ecology 32:326–337.

Odadi, W., M. Karachi, S. Abdulrazak, and T. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. Science 333:1753–1755.

Odadi, W., T. Young, and J. Okeyo-Owuor. 2007. Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. Rangeland Ecology and Management 60:179–185.

O'Meilia, M. E., F. L. Knoph, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 5:580–585.

Polley, H., and J. Detling. 1988. Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. Oecologia 77:261–267.

Smith, A., and J. Foggin. 1999. The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan Plateau. Animal Conservation 2:235–240.

Smith, G., and M. Lomolino. 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia 138:592–602.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Nino events. Frontiers in Ecology and the Environment 2:235–240.

Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for the *in vitro* digestion of forage crops. Journal of the British Grassland Society 18:104–111.

USDA. 2007*a*. Ecological site description for Loamy Plains (R067BY002CO). http://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY002CO

USDA. 2007*b*. Ecological site description for Shaly Plains (R067BY045CO). http://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY045CO

USDA. 2007*c*. Ecological site description for Sandy Plains (R067BY024CO). http://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY024CO

USDA. 2011*a*. Ecological site description for Loamy 17–20″ precipitation zone. (R064XY036NE). http://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R064XY036NE

USDA. 2011*b*. Ecological site description for Dense Clay. http://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R064XY045NE

van Soest, P. 1982. Nutritional ecology of the ruminant. Cornell University Press, Ithaca, New York, USA.

Vermeire, L. T., R. K. Heitschmidt, P. S. Johnson, and B. F. Sowell. 2004. The prairie dog story: Do we have it right? BioScience 54:689–695.

Vila, A., L. Borrelli, and L. Martinez. 2009. Dietary overlap between huemul and livestock in Los Alerces National Park, Argentina. Journal of Wildife Management 73:368–373.

Villarreal, D., K. Clark, L. Branch, J. Hierro, and M. Machicote. 2008. Alteration of ecosystem structure by a burrowing herbivore, the plains vizcacha (*Lagostomus maximus*). Journal of Mammalogy 89:700–711.

Wallis de Vries, M. F., E. A. Laca, and M. W. Demment. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. Applied Animal Behavior Science 60:301–315.

Whicker, A., and J. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778–785.

White, L. M., G. P. Hartman, and B. W. Bergman. 1981. *In vitro* digestibility, crude protein, and phosphorus content of straw of winter wheat, spring wheat, barley, and oat cultivars in eastern Montana. Agronomy Journal 73:117–121.

Wilmshurst, J. F., J. M. Fryxell, and C. M. Bergman. 2000. The allometry of patch selection in ruminants. Proceedings of the Royal Society B 267:345–349.

Wingard, G., R. Harris, D. Pletscher, D. Bedunah, B. Mandakh, and S. Amgalandaatar. 2011. Argali food habits and dietary overlap with domestic livestock in Ikh Nart Nature Reserve, Mongolia. Journal of Arid Environments 75:138–145.

Supplemental Material

Appendix A

List of species classified as "rarely grazed species," and hence not included in estimates of forage biomass (*Ecological Archives* A023-043-A1).

Appendix B

Parameters used to calculate the effect of black-tailed prairie dogs on daily cattle energy gain (*Ecological Archives* A023-043-A2).

Appendix C

Comparison of the daily energy balance of cattle foraging in the absence of black-tailed prairie dogs vs. cattle foraging 50% of their time on prairie dog colonies and 50% of their time off prairie dog colonies (*Ecological Archives* A023-043-A3).