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Research Article

Long-Term Effects of Black-Tailed Prairie Dogs on Livestock Grazing Distribution and Mass Gain

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ABSTRACT The conservation and management of black-tailed prairie dogs (*Cynomys ludovicianus*) have been contentious issues in grasslands of central North America for much of the past century, primarily because of the perception that they compete with livestock for forage. Studies quantifying the magnitude of competition between prairie dogs and cattle are difficult to conduct because of the large spatial and long temporal scales needed to quantify how competition varies in response to interannual variation in precipitation and prairie dog abundance. We examined variation in mass gains of yearling steers in shortgrass steppe of northeastern Colorado, USA, with and without prairie dogs from 2008–2019, a period that encompassed a full cycle in prairie dog abundance from a nadir following plague-induced population collapse, to peak abundance following population recovery, to plague-induced population lows again. Analyses of cattle grazing distribution with global positioning system (GPS)-collars revealed preferential grazing on colonies following a period of unusually high vegetation production, and preferential grazing off colonies following a period of rapid vegetation senescence, but these patterns were not clearly related to cattle mass gains. Across all 12 years of the study, average daily mass gain (ADG) during the growing season was 0.97 kg/steer/day in pastures where prairie dogs were controlled annually, and 0.95 kg/steer/day in pastures where they were not. Average daily mass gain was a quadradic function of precipitation and a linear function of prairie dog occupancy within a pasture, with a generalized linear mixed model predicting an 8.0% decrease in ADG as prairie dog occupancy increased from 0 to 60% of a pasture with average growing-season precipitation. We did not detect a significant interaction between precipitation and prairie dog occupancy, but one limitation of our study is that the only drought year (2012) occurred when prairie dogs occupied low percentages (10–25%) of the study pastures. Prairie dogs had a small but detectable negative effect on cattle mass gains during the growing season in shortgrass steppe. The magnitude of this effect can be used by managers in combination with market conditions and the spatial extent of prairie dog colonies to estimate economic effects of prairie dogs on livestock operations.

KEY WORDS Central Plains Experimental Range, *Cynomys ludovicianus*, competition, cattle production, rangeland management, shortgrass steppe.

Black-tailed prairie dogs (*Cynomys ludovicianus*, prairie dogs) are colonial, burrowing herbivores that historically were abundant and widely distributed across the western Great Plains in central North America (Hoogland 2006). Prairie dogs serve as both a keystone species and an ecological engineer in the western Great Plains because they create burrows and modify grassland structure in ways that create habitat for a diverse array of vertebrates including grassland birds, small mammals, reptiles, and arthropods (Desmond et al. 2000, Kretzer and Cully 2001, Dinsmore et al. 2005, Augustine and Baker 2013). Furthermore, prairie dogs serve as a prey base for many mesocarnivores including ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), prairie rattlesnakes (*Crotalus viridis*), American badgers (*Taxidea taxus*), and swift fox (*Vulpes velox*), and large complexes of prairie dog colonies are essential for the recovery of the endangered black-footed ferret (*Mustela nigripes*; Davidson et al. 2012, U.S. Fish and Wildlife Service 2013).

The conservation and management of prairie dogs have been contentious issues in the western Great Plains of North America for much of the past century, primarily because prairie dogs and cattle consume similar diets, and prairie dogs are perceived as reducing forage availability to a level that negatively affects livestock performance, or forces livestock managers to reduce their stocking rate (Vermeire et al. 2004, Detling 2006, Miller et al. 2007, Delibes-Mateos et al. 2011). As a result, 2 key questions for wildlife and rangeland managers in the western Great Plains are 1) to what extent does the suppression of prairie dog

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populations via rodenticides enhance livestock production and 2) how can prairie dog populations be managed spatially to maintain their ecological role while minimizing effects on livestock? Studies attempting to quantify the magnitude of competition between prairie dogs and cattle are difficult to conduct because of the large spatial and long temporal scales needed to quantify how competition varies in response to interannual variation in precipitation and prairie dog abundance (Detling 2006). Semi-arid rangelands of the western Great Plains are characterized by dramatic and unpredictable spatiotemporal variation in precipitation and forage production (Augustine 2010), and livestock producers often must adaptively reduce stocking rates or acquire new forage resources when drought occurs (Kachergis et al. 2014, Smart et al. 2021). Measurements of forage production and quality on versus off prairie dog colonies at multiple locations across the Great Plains suggest that prairie dogs can suppress, have no effect, and enhance livestock performance during dry, average, and wet years, respectively (Johnson-Nistler et al. 2004, Augustine and Springer 2013, Connell et al. 2019).

Prior to European settlement, black-tailed prairie dog colonies were relatively stable and spatially extensive within the western Great Plains (Knowles et al. 2002). The introduction of plague, caused by the bacterium *Yersinia pestis*, from Asia to California, USA, in 1908 enabled this disease to spread to black-tailed prairie dog populations in the Great Plains by the 1940s (Biggins and Eads 2019). Plague combined with extensive prairie dog population control efforts that began in the late 1800s (Knowles et al. 2002) led to range-wide declines in prairie dog populations. Even in areas where prairie dogs are not controlled with rodenticides, plague epizootics periodically cause a >95% decline in the size of individual colonies (Cully and Williams 2001, Stapp et al. 2004), or even entire colony complexes distributed across landscapes of >100,000 ha within a single year (Augustine et al. 2008, Cully et al. 2010). Epizootic outbreaks of plague typically occur at intervals of 5–15 years, with colonies expanding slowly back to pre-epizootic sizes in the intervening years (Augustine et al. 2008, Hartley et al. 2009, Cully et al. 2010). The exact timing and location of epizootics are unpredictable, and are influenced by complex interactions among precipitation, temperature, the bacterium, fleas that transmit it, prairie dog health, amplifying alternate hosts, and the movements of other mammals among colonies (Stapp et al. 2004, Salkeld et al. 2016, Eads and Biggins 2017). Given that these population fluctuations occur against a backdrop of interannual variation in weather and forage availability, quantifying the magnitude of competition between prairie dogs and livestock for forage presents a major challenge.

Prior experimental tests of prairie dog effects on livestock mass gain suggested a small negative effect, varying from no effect to up to 15% reduction in livestock mass gain in certain locations and years, but sample sizes and statistical power were limited (O'Meilia et al. 1982, Derner et al. 2006). In addition, estimates of the magnitude of effect on livestock performance are also likely to be contingent on how stocking rates are managed over time (Vermeire et al. 2004). Recently, Brennan (2019) reported that, during a period of average to above-average precipitation, when stocking rates were reduced in direct proportion to the percent of a pasture occupied by prairie dogs, livestock mass gains on a per head basis were unaffected by prairie dog presence. Livestock production on a per unit area basis, however, declined in direct proportion to the magnitude of the reduction in actual stocking rate (Brennan 2019), which has substantial negative economic consequences for producers (Derner et al. 2006). Reducing the stocking rate in proportion to the area occupied by prairie dogs essentially assumes that any forage produced on colonies is unavailable to livestock. But researchers have reported that under some circumstances, cattle either do not avoid grazing on prairie dog colonies (Guenther and Detling 2003, Brennan 2019), or in some cases even preferentially graze on colonies relative to off-colony grassland (Sierra-Corona et al. 2015). A key unanswered question is whether sufficient on-colony forage could be used by cattle during the growing season such that livestock performance would be unaffected by prairie dogs if stocking rates were managed in accord with fluctuating weather conditions but without regard to prairie dog occupancy.

Our first research objective was to quantify the degree to which prairie dogs compete with cattle by measuring differences in cattle mass gain in pastures with and without prairie dogs in the shortgrass steppe of eastern Colorado, USA. Our second objective was to quantify the degree to which cattle forage on versus off prairie dog colonies under varying weather and forage growth conditions, and whether this could serve as an indicator of the degree to which prairie dogs negatively affect cattle mass gain. A third objective was to describe the temporal dynamics of prairie dog colonies over the course of an entire plague-induced population cycle. Our study design enabled us to assess the magnitude of decline in cattle mass gain if managers do not reduce their stocking rate in response to prairie dog presence. We hypothesized that under these conditions, prairie dogs would negatively affect cattle mass gains in years with below-average precipitation, and this effect would become more severe with increasing occupancy levels. We additionally hypothesized that the magnitude and direction of effects of prairie dogs on livestock mass gains would be reflected in the degree to which livestock preferentially grazed on versus off colonies in a given year.

STUDY AREA

We conducted this study at the United States Department of Agriculture (USDA)-Agricultural Research Service's (ARS) Central Plains Experimental Range (CPER), a Long-Term Agroecosystem Research (LTAR) network site that encompasses approximately 6,400 ha of shortgrass steppe in northeastern Colorado (40°50′N, 104°43′W). Mean annual precipitation is 340 mm and mean growing-season precipitation (Mar–Aug) is 258 mm. During 2008–2019, growing-season precipitation varied from 116 mm in 2012 to 361 mm in 2009. The CPER is subdivided into 65–390-ha pastures, which have been grazed by cattle since the station was established in 1939. Topography consists of gently undulating plains at a mean elevation of 1,640 m.

Soils consist of deep, well-drained, fine sandy loams to loamy sands on alluvial flats and upland plains. Parent materials of soils are primarily Holocene alluvial and eolian deposits derived from local sources (Kelly et al. 2008). Sandy soils are often associated with eolian deposits, whereas soils formed from mixed alluvium have greater clay and silt content (Kelly et al. 2008). Soils in study pastures located in the western and southern portion of CPER (Fig. 1) correlate to the Loamy Plains Ecological Site (USDA 2007*a*). Plant communities on Loamy Plains are dominated by C_4 perennial shortgrasses (blue grama [*Bouteloua gracilis*] and buffalograss [*B. dactyloides*]), which contribute >70% of forage production (Lauenroth and Burke 2008). Subdominant plants include C_3 perennial grasses (western wheatgrass [*Pascopyrum smithii*] and needleandthread [*Hesperostipa comata*]), the succulent plains pricklypear cactus (*Opuntia polyacantha*), and the perennial forb, scarlet globemallow (*Sphaeralcea coccinia*). Pastures located in the eastern and northern portion of CPER (Fig. 1) were dominated by soils that correlate to the Sandy Plains, Overflow, or Salt Flat ecological sites (USDA 2007*b*, *c*, *d*). All 3 of these ecological sites are similar in terms of total forage production, and are more productive than the Loamy Plains. The Sandy Plains and Overflow ecological sites are dominated by C_3 perennial grasses (western wheatgrass and needleandthread), with C_4 shortgrasses also present. The Salt Flat ecological site is co-dominated by western wheatgrass and C_4 saltgrasses (alkali sacaton [*Sporobolus airoides*] and inland saltgrass [*Distichlis spicata*]). For analyses, we grouped study pastures into 2 blocks, with one consisting of pastures dominated by the Loamy Plains ecological site, and the other consisting of pastures dominated by a combination of Sandy Plains, Overflow, and Salt Flat ecological sites. On all soil types, grazing by prairie dogs reduces the relative abundance of perennial grasses, reduces total vegetation cover, and increases the relative abundance of perennial and annual forbs and exposure of bare soil (Augustine et al. 2014). When colonies contract because of plague, cover of perennial C_3 midgrasses and C_4 shortgrasses recovers rapidly (Hartley et al. 2009, Augustine et al. 2014).

The range of the black-tailed prairie dog extends from southern Saskatchewan, Canada to northern Mexico. The CPER is located near the geographic center of this range. Most of CPER was homesteaded prior to 1930, and the lands were subsequently purchased by the United States

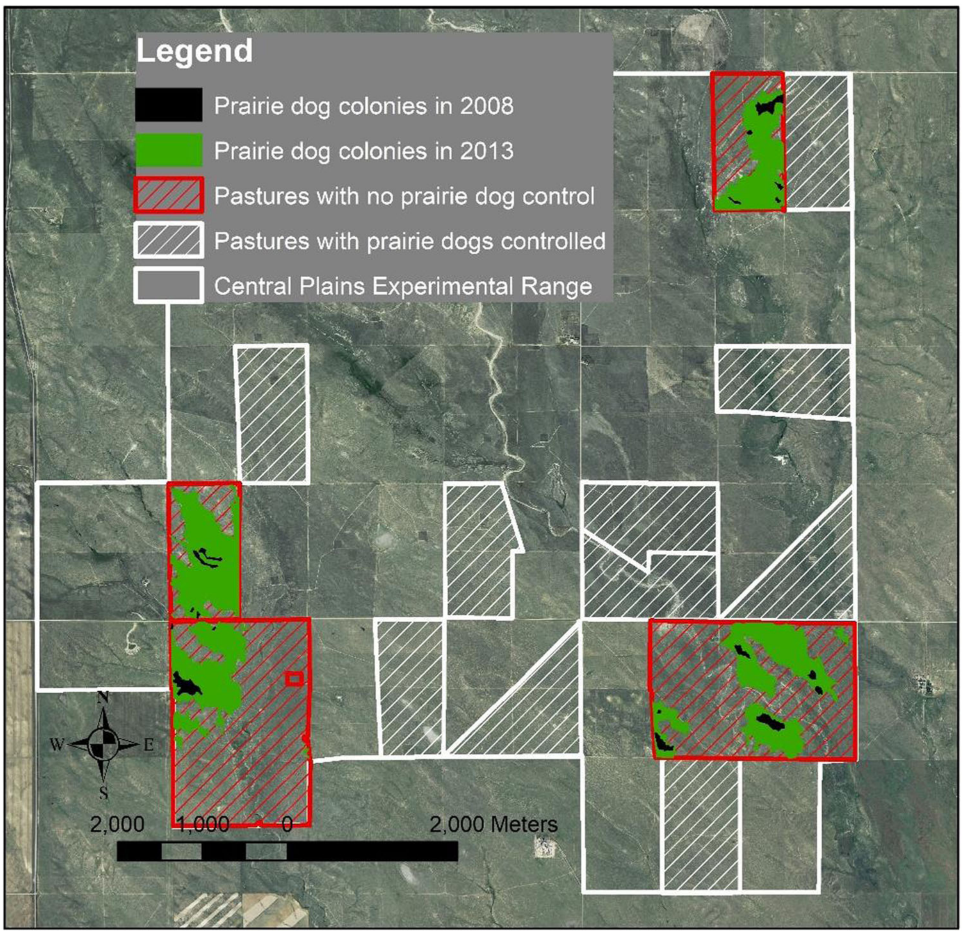

Figure 1. The Central Plains Experimental Range in northeastern Colorado, USA, with locations of pastures with and without prairie dog control via rodenticides in which we studied cattle mass gains in 2008–2019.

government in the 1930s as farms and ranches became unviable during the Dust Bowl years. Presumably, most prairie dogs were extirpated from CPER during the homesteading era. The CPER was created in 1937, and the first scientist to work there (D. F. Costello) wrote in his memoir (~1949; on file at CPER) "We have never made a complete list of the wildlife of the experimental range… The lone prairie dog in [pasture] 15-W eventually died of ennui, or a coyote got him." Prairie dogs remained extirpated from CPER from the 1940s through the 1980s, and then subsequently recolonized 4 locations on the property in the 1990s. Mapping of prairie dog colony boundaries began in 1997 using global positioning system (GPS) devices (Sidle et al. 2012) with 6 documented colonies in 5 different pastures totaling 22 ha. Subsequent annual mapping showed that colonies expanded continuously for the next 9 years (Derner et al. 2006), reaching a maximum of 961 ha in 2006. During 2006–2007, epizootic plague drastically reduced prairie dog abundance, to a low of 25 ha of active colony area mapped in 2008. Our study period began in 2008, and it encompassed a full cycle in prairie dog abundance from the nadir in 2008 following plague-induced population collapse, to peak abundance during 2013–2015 following population recovery, to plague-induced population lows again during 2014–2017. Other widespread native herbivores present at the study site include pronghorn (*Antilocapra americana*) and black-tailed jackrabbits (*Lepus californicus*).

METHODS

Beginning in 2008, we designated 4 pastures at CPER (2 130-ha and 2 390-ha pastures) containing active prairie dog colonies as areas where prairie dogs would be allowed to coexist with cattle. We mapped the boundaries of active black-tailed prairie dog colonies in these pastures during September or October each year during 2008–2019 following methods described by Sidle et al. (2012). On the remainder of CPER (~5,360 ha), prairie dogs have been controlled annually since 2008 with rodenticides (implemented by the USDA Animal and Plant Health Inspection Service-Wildlife Services; Fig. 1).

In 2008, 6 pastures where prairie dogs were controlled (i.e., controls) and the 4 pastures containing prairie dogs were stocked with yearling steers at a moderate rate during the grazing season (mid-May to Oct). In 2009, the number of moderately stocked control pastures was increased to 10. Of the 10 control pastures, 4 were 65 ha during 2008–2012, and then expanded to 130 ha during 2013–2019. The remaining 6 control pastures were 130 ha. Within any given year, stocking rates varied by ≤8% across study pastures. During 2008–2012, stocking rates for all study pastures were set at a constant annual moderate rate of approximately 18 animal unit days (AUD)/ha (Fig. 2). For the second half of the study, we varied stocking rates adaptively among years in response to weather and forage conditions. Following a drought in 2012, stocking rates were reduced by 30% below the 18 AUD/ha rate in 2013, and then returned to 18 AUD/ha rate in 2014. Following consecutive years of above-average forage production during 2014–2015, stocking rates were progressively increased during 2016–2018, reaching a peak at 24 AUD/ha in 2018, and then reduced to 20 AUD/ha in 2019 (Fig. 2). Although stocking rates varied from year to year during 2013–2019, stocking rates remained constant across all study pastures (both with and without prairie dogs) within each year. Two of the 4 prairie dog pastures and 5 of 10 control pastures were in the Loamy Plains block, and remaining pastures were in the second block.

Cattle Measurements

We determined average cattle mass gains (kg/animal/day) each year by weighing individual animals (yearling steers) at the beginning (mid-May) and end (early Oct) of each grazing season, and dividing by the number of grazing days. Protocols for handling, weighing, and collaring of

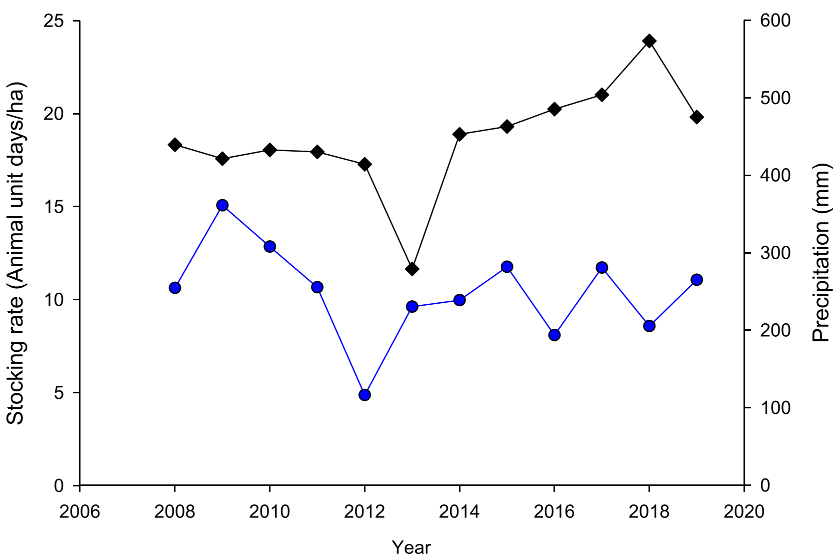

Figure 2. Mean annual growing-season precipitation (Mar–Aug; blue circles) and annual cattle stocking rates (black diamonds) used in this study at the Central Plains Experimental Range, northeastern Colorado, USA, 2008–2019.

the cattle were approved by the Institutional Animal Care and Use Committee of the USDA-Rangeland Resources and Systems Unit, Central Plains Experimental Range (protocol number CPER-3). On occasion, 1 steer within a herd exhibits substantially greater or lower growth rate than the remainder of the herd, likely because of health issues or genetic variation. We calculated mean steer mass gain for each pasture in each year, identified any individuals whose gain differed from the pasture mean by >2 standard deviations, and removed these outliers from the analysis. We then calculated mean daily mass gain for each pasture, and used pasture means in our statistical analyses.

To examine the degree to which cattle forage on prairie dog colonies, we studied cattle foraging distribution in 3 prairie dog pastures (2 were 130 ha and 1 was 390 ha) during 2013–2016. In 2013 and 2014, we measured cattle distribution using GPS-collars (Lotek 3300LR collars; Lotek Engineering, Newmarket, ON, Canada) placed on 3 or 4 steers per pasture for 2 time intervals (collar deployments) per year, the first beginning in mid-June and the second beginning in mid-August, that lasted for 27–29 days. In 2015 and 2016, we used the GPS-collars to measure cattle distribution during 4 consecutive 27–29-day intervals that began in early June and continued until the end of September. Collars weighed 1.2 kg, were set to record GPS positions at 5-minute intervals, and included a dual-axis activity sensor that recorded up-down (y-axis) and side-to-side (x-axis) movements and percentage of time the y-axis sensor was in the down position. We used a previously developed classification tree model based on the distance traveled in a 5-minute interval and activity sensor measurements to discriminate between GPS fixes associated with grazing versus fixes associated with non-grazing behavior (Augustine and Derner 2013). We analyzed cattle distribution based on those GPS coordinates recorded by the collars when the cattle were estimated to be grazing (i.e., grazing locations).

Vegetation Phenology

Because we hypothesized that the degree to which cattle grazed on prairie dog colonies would vary with the productivity of the vegetation, we quantified seasonal and annual variation in vegetation productivity using the normalized difference vegetation index (NDVI). We calculated NDVI from a fusion of measurements by the Terra and Aqua moderate resolution imaging spectroradiometer satellites, which generated a quasi 8-day time series at a 250×250-m pixel resolution for the years in which we conducted the cattle grazing distribution study (2013–2016). We used the Savitzky-Golay filter to smooth data and fill gaps following Gaffney et al. (2018), thereby generating a smoothed daily NDVI time series. We averaged the daily NDVI values across all pixels within the boundary of CPER to provide a study-site-scale index of vegetation phenology and overall productivity each year. The integrated area under the NDVI curve is positively related to net primary production at CPER (Gaffney et al. 2018).

Statistical Analyses

We first analyzed cattle mass gains using a generalized linear mixed model in which mass gain was the response variable, annual growing-season precipitation (Mar–Aug) and pasture occupancy by prairie dogs (as a categorical variable [controlled or not controlled]) were fixed effects, year within pasture was included as a random effect with first-order auto-regressive covariance structure to account for repeated measures over time, and block (differentiating pastures with loamy vs. sandy soils) was included as a random effect. We then considered 3 additional models. The first included main effects of annual precipitation and pasture occupancy by prairie dogs as a continuous variable (percent of the pasture occupied each year, which was 0% for controls and could potentially vary from 0–100% for non-controlled pastures). The second included the 2 main effects plus an interaction between precipitation and prairie dog occupancy, and the third included the 2 main effects and a quadratic effect of precipitation. We considered the latter because Derner and Hart (2007) reported average daily mass gain was a quadratic function of precipitation. Because the 2 smaller prairie dog pastures (each 130 ha, the same as control pastures) both reached higher levels of prairie dog occupancy than the 2 larger prairie dog pastures (each 390 ha), we also evaluated the same statistical models using only the 2 smaller prairie dog pasture replicates, to test whether the magnitude of effects would change notably. We performed all analyses using Proc GLIMMIX in SAS version 9.4 (SAS Institute, Cary, NC, USA).

For each collar deployment interval, we overlaid all of the grazing locations pooled across all collared steers onto a 25×25-m grid of pixels within each study pasture to obtain a count of grazing locations per pixel. We also used a digital elevation map to classify each pixel into 1 of 4 topographic position classes (flat plains, open slopes, lowlands, and uplands; Gersie et al. 2019), and we calculated the distance from the center of each pixel to the nearest fence and nearest drinking water location. Lowlands consist of incised stream channels, floodplains near channels, and shallow valleys; open slopes consist of flat plains tilted at >2% slope, and uplands consist of ridges, hilltops, and upper hillslopes (Gersie et al. 2019). For each year, we used the mapped boundaries of the prairie dog colonies to classify each pixel as occupied or unoccupied by prairie dogs. We then fit count-based regression models of grazing locations per pixel as a function of topographic position class, prairie dog occupancy, and distance to fence and water (Gersie et al. 2019). For each collar deployment and study pasture, we examined whether the model coefficient for prairie dog occupancy was positive or negative, and whether it was significantly different from zero ($P < 0.05$). We considered a statistically significant effect of prairie dogs on cattle grazing distribution to occur when coefficients from the 3 study pastures were all significantly positive or negative.

RESULTS

During 2008–2019, the area occupied by active prairie dog colonies in pastures where prairie dog populations were not controlled by rodenticide varied dramatically. Prairie dogs occupied 1–3% of study pastures in 2008, as a result of a spatially synchronized plague epizootic that affected all colonies during 2006–2007 (Augustine et al. 2014). During the current study, peak prairie dog occupancy occurred at 65% of the 130-ha replicate in block 1 in 2013, and at 68% of the 130-ha replicate in block 2 in 2014 (Fig. 3). The 2 larger replicates (390 ha each) only reached peak occupancy levels of 29% and 38% in blocks 1 and 2 respectively (Fig. 3). Prairie dog colonies contracted dramatically because of epizootic plague in all 4 pastures sometime during 2014–2017, but the exact year of contraction was not synchronous across the study site (Fig. 3).

Cattle Mass Gains

The ADG of cattle in pastures where prairie dogs were controlled varied among years, from a low of 0.73 kg/steer/day during the drought of 2012 to a maximum of 1.13 kg/steer/day in 2017 (Table 1; Fig. 3). Across all 12 years of the study, ADG averaged 0.97 kg/steer/day in pastures where prairie dogs were controlled, and ADG averaged 2.1% less (0.95 kg/steer/day) where they were not (Table 1). A generalized linear mixed model (GLMM) of ADG as a function of growing-season precipitation and presence or absence of prairie dog control (treatment) showed no treatment × precipitation interaction ($F_{1,145} = 0.01$, $P = 0.96$). When we refit the

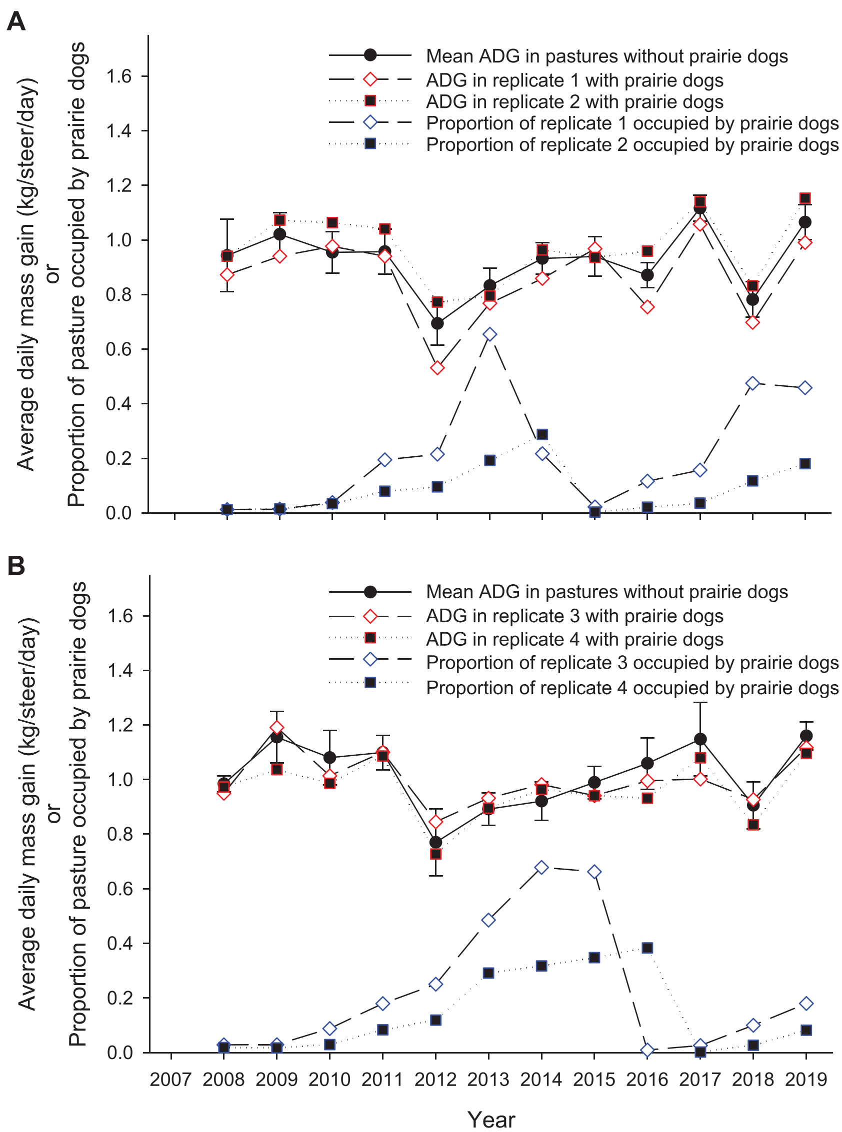

Figure 3. Average daily mass gain of steers (ADG; kg/steer/day) in A) pastures dominated by Loamy Plains ecological site (low productivity block; $n = 5$ pastures without prairie dogs and 2 pastures with prairie dogs), and B) in pastures dominated by Sandy Plains, Overflow, or Salt Flat ecological sites (high productivity block; $n = 5$ pastures without prairie dogs and 2 pastures with prairie dogs) at the Central Plains Experimental Range in northeastern Colorado, USA, 2008–2019. Error bars show 95% confidence intervals for the pastures without prairie dogs in each block. For the pastures with prairie dogs, blue symbols show the proportion occupied by prairie dogs each year for the replicate with the same symbol shape. At the start of this study in 2008, prairie dogs were rare in all 4 pastures because of an outbreak of epizootic plague during 2006–2007. Colonies in all 4 pastures expanded during 2009–2013, and then contracted because of plague in 2014 and 2015 in pasture 1, in 2016 in pastures 2 and 3, and in 2017 in pasture 4.

Table 1. Average daily mass gains (kg/steer/day) of yearling steers in pastures with and without control of prairie dogs via rodenticide during 2008–2019 at the Central Plains Experimental Range in northeastern Colorado, USA. Annual stocking rates were the same in both sets of pastures each year but varied annually. Values in parentheses are 1 standard error around the mean based on spatial variation among replicates within each year, and for the overall mean are based on temporal variation among the 12 years.

	Prairie dogs controlled		Prairie dogs uncontrolled	
Year	$\bar{x}$	**SE**	$\bar{x}$	**SE**
2008	0.97	0.02	0.93	0.02
2009	1.09	0.03	1.06	0.05
2010	1.02	0.03	1.01	0.02
2011	1.03	0.03	1.04	0.04
2012	0.73	0.03	0.72	0.07
2013	0.86	0.02	0.85	0.04
2014	0.93	0.02	0.94	0.03
2015	0.96	0.02	0.95	0.01
2016	0.97	0.04	0.91	0.05
2017	1.13	0.02	1.07	0.03
2018	0.84	0.03	0.82	0.05
2019	1.11	0.02	1.09	0.03
All	0.97	0.03	0.95	0.03

model without the interaction term, where ADG was a function of treatment and a quadratic function of growing-season precipitation, there was a highly significant influence of precipitation, but no significant effect of treatment (Table 2, model 1).

Prairie dogs were relatively rare in some years, and reached peak abundance in different pastures in different years (Fig. 3). When we evaluated a generalized linear mixed model of ADG as a function of growing-season precipitation and percent of pasture occupied by prairie dogs, we found no significant interaction between the effects of prairie dogs and precipitation ($F_{1,157.1} = 0.13$, $P = 0.72$). When we evaluated models that only included the main effects of colony occupancy and precipitation, both with and without a quadratic term for precipitation, we found the quadratic term for precipitation was a highly significant predictor of ADG, as were the main effects of precipitation and prairie dog occupancy (Table 2, model 2). The final model predicted a rapid rate of increase in ADG as growing-season precipitation increased from approximately 110 mm to 275 mm, followed by less rapid increases in ADG above 275 mm precipitation (Fig. 4). The effect of prairie dogs was statistically significant but small over the entire range of precipitation levels, with the GLMM predicting an 8.0% decrease in ADG as prairie dog occupancy increased from 0 to 60% of a pasture at average growing-season precipitation (Fig. 4). For comparison, our results predict a 24% decrease in ADG as growing-season precipitation declines from 240 mm (near-average) to 120 mm (drought; Fig. 4).

When we fit the same set of GLMMs to the data using only the 2 prairie dog pasture replicates that were 130 ha each, results were nearly identical to the results with all 4 replicates. We again found no significant interaction between prairie dog occupancy and precipitation ($F_{1,131} = 1.02$, $P = 0.31$), and the linear and quadratic term for precipitation were highly significant ($F_{1,121.8} = 25.65$, $P < 0.001$, and $F_{1,119.9} = 8.85$, $P = 0.004$ respectively). The effect of prairie dog occupancy was also significant ($F_{1,79.42} = 5.83$, $P = 0.018$), with a coefficient of −0.00299 (1 SE = 0.00124). This coefficient predicted a decline in ADG by 8.4% as prairie dog occupancy increased from 0 to 60% of a pasture at average growing-season precipitation.

Cattle Grazing Distribution

When we analyzed models of the distribution of grazing steers in terms of number of grazing fixes per 25 × 25-m (625 m^2) pixel, across all 3 study pastures in 2013, cattle preferentially grazed in lowland topographic positions relative to flat plains, and avoided uplands and open slopes relative to flat plains, but did not exhibit any consistent pattern of preferential grazing either on or off prairie dog colonies. The growing season of 2013 followed a severe drought in 2012, so there was minimal standing dead vegetation in 2013, but greenup at the start of the growing season was rapid (approximately following the long-term mean), and was followed by a second mid-summer pulse of grass growth at the beginning of the second GPS-collar deployment period (Fig. 5). In 2014, overall greenness and forage production was substantially above average. Under these conditions, yearling steers again did not show any consistent preferential use of either prairie dog colonies or topographic patterns across the 3 study pastures.

Table 2. Results of 2 generalized linear mixed models for average daily mass gain of yearling steers at the Central Plains Experimental Range in northeastern Colorado, USA, 2008–2019. Model 1 included a binary categorical predictor for presence or absence of prairie dog control via rodenticides. Model 2 included a continuous, numerical predictor consisting of the percent of each prairie dog pasture occupied by prairie dogs each year.

		Type III tests of fixed effects					
Model	**Effect**	**Numerator DF**	**Denominator DF**	***F***	***P***	**Parameter estimate**	**SE**
Model 1	Intercept					0.803	0.192
	Precipitation (mm)	1	149.1	27.97	<0.001	0.007478	0.001414
	Precipitation $(mm)^2$	1	147.7	9.17	0.003	−0.00000882	0.0000029
	Pasture treatment (presence or absence of prairie dog control)	1	81.8	2.15	0.147	0.0458	0.0312
Model 2	Intercept					0.824	0.1890
	Precipitation (mm)	1	147.0	31.03	<0.001	0.007814	0.001403
	Precipitation $(mm)^2$	1	145.4	11.25	0.001	−0.00000971	0.0000029
	Prairie dog occupancy (% of pasture)	1	93.7	6.41	0.013	−0.00288	0.00114

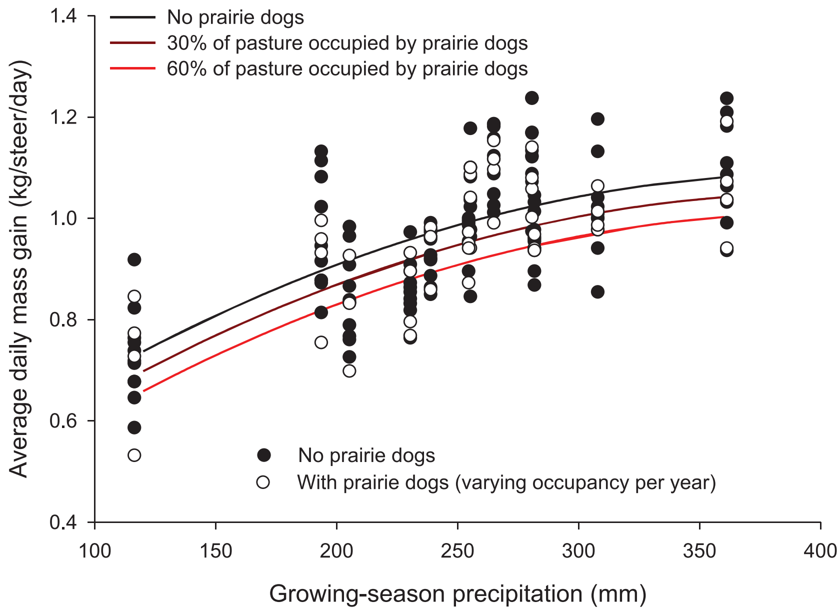

Figure 4. Average daily mass gain of steers (kg/steer/day) in relation to growing-season precipitation and degree of pasture occupancy by prairie dogs at the Central Plains Experimental Range in northeastern Colorado, USA, 2008–2019. Points show measured mass gains in pastures with ($n = 4$) and without prairie dogs ($n = 10$). Curves show mass gains predicted by a generalized linear model fit to the data. The red curve shows predicted mass gains for a pasture in which 60% of the area is occupied by prairie dogs. Actual occupancy of prairie dogs in pastures where they were not controlled varied from 0–65% over time depending on location and timing of plague outbreaks, with an overall average annual occupancy of 17% during the 12-year study.

In 2015, greenness and forage growth were substantially above-average for the second year in a row, such that off-colony portions of the pastures had residual standing dead grass carried over from the previous wet year and new growth during the first two-thirds of the growing season. Under these conditions, cattle preferentially grazed on colonies (and reduced grazing time off-colony) in all 3 study pastures during 12 June–5 August, which corresponded to the period of peak greenness (Fig. 5). For the remainder of August and through September, when vegetation was senescing, cattle did not graze preferentially on or off colonies in a consistent manner (Fig. 5).

In 2016, plant growth in early summer was near average throughout the growing season, and then senesced relatively rapidly in August and September compared to the previous 3 years. During the first 2 collar deployments in midsummer (10 Jun–6 Aug), cattle grazed preferentially off-colony in 1 study pasture ($\beta \leq -2.06$; $P < 0.04$). In the other 2 study pastures, the coefficient for colony selection was negative ($\beta < -0.07$), but these coefficients were not significantly different from zero ($P > 0.05$). During the third and fourth collar deployments (7 Aug–1 Oct), cattle grazed preferentially off colonies in all 3 pastures ($\beta \leq -1.97$, $P < 0.05$ in all 6 models; Fig. 5).

DISCUSSION

How, when, and where to manage black-tailed prairie dog populations to conserve this keystone species while minimizing potential effects on livestock production continues to be a source of substantial controversy and contention in the western Great Plains (Miller et al. 2007, USDA Forest Service 2020). In shortgrass rangeland of Colorado, as prairie dog colony occupancy increases from 0 to 60% of a pasture, average daily mass gains of yearling steers during the growing season decline on average by 8%. The magnitude of this effect is smaller than that reported by Derner et al. (2006), who estimated that gains declined by 15% at 60% occupancy. Our results are based on a larger set of pastures and years, and likely provide an estimate of prairie dog effect on growing-season cattle mass gains that is more robust across varying pasture conditions and precipitation levels. For steers grazing for 140 days during the growing season, as in our study, our estimate of 8% weight gain loss amounts to individual steers ending the grazing season 10.8 kg lighter with 60% prairie dog occupancy compared to no prairie dogs. Over the course of our 12-year study, prairie dogs rarely occupied pastures at such a high level because of recurrent epizootic outbreaks of plague. Averaged over the entire 12 years, we did not detect a statistically significant increase in steer mass gains associated with prairie dog population control. Furthermore, we documented substantially greater effects of inter-annual variation in growing-season rainfall on mass gains, with the shape and magnitude of this effect being very similar to previous work in different pastures at our study site in a prior decade (Derner and Hart 2007). Overall, these results suggest that over an entire plague-induced cycle of prairie dog abundance, effects on livestock production during the growing season can be minimal. Significant reductions in mass gain can occur where and when prairie dogs are locally abundant.

One important consequence of plague-induced cycles in prairie dog abundance is that prairie dogs do not continuously occupy large areas over a sequence of several years. As a result, they do not induce long-term changes in plant community composition over large areas of the landscape (Hartley et al. 2009). In areas occupied by prairie dogs for a

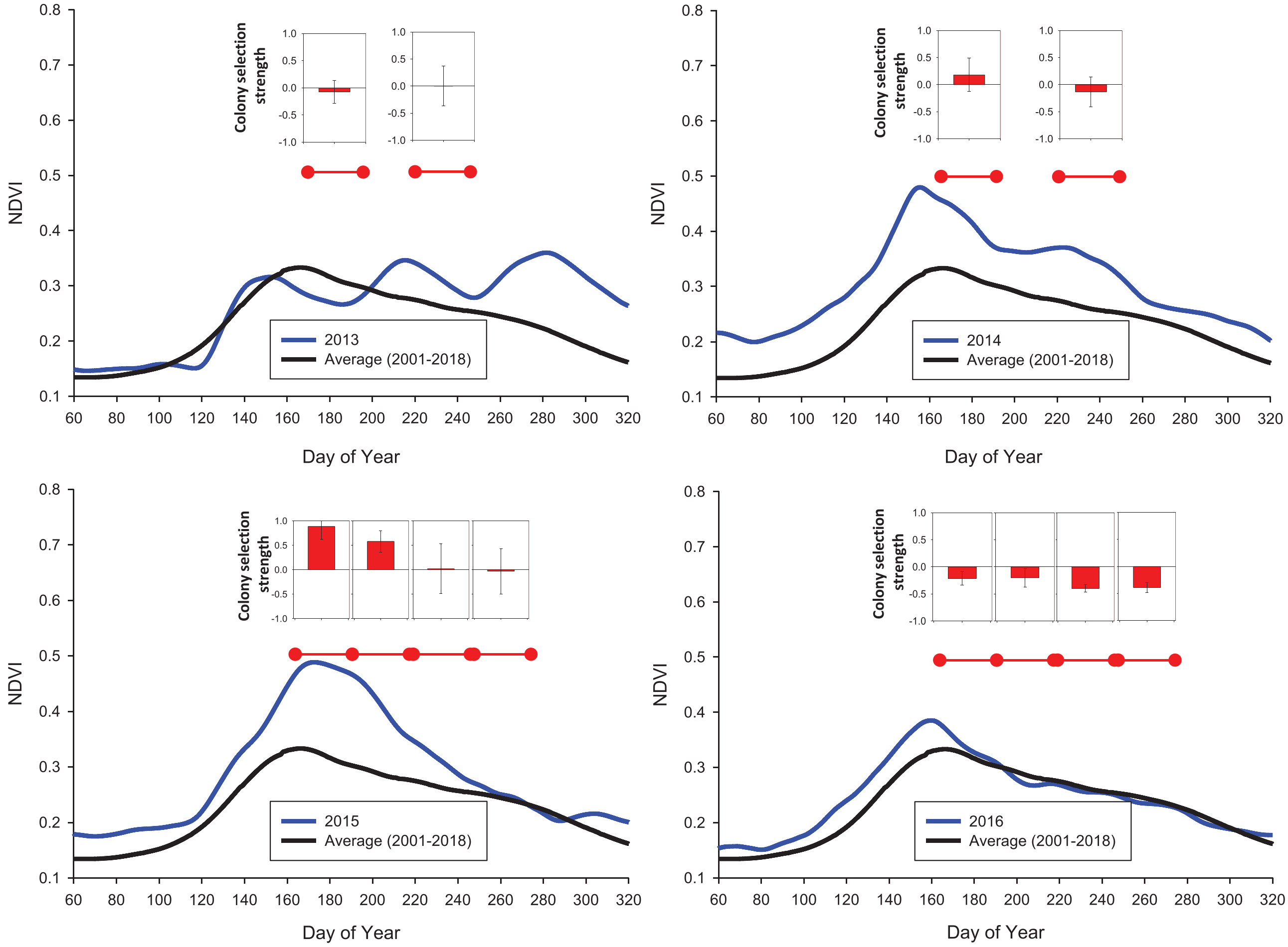

Figure 5. Variation in vegetation greenness (normalized difference vegetation index [NDVI]) in relation to the timing of measurements of cattle selection for or against prairie dog colonies while grazing shortgrass steppe at the Central Plains Experimental Range in north-eastern Colorado, USA, during each of 4 years (2013–2016). Red horizontal lines show the time periods within each year when we deployed global positioning system collars on cattle to measure grazing distribution, and inset graphs with red bars show the average magnitude of the prairie dog colony selection coefficient (positive values = preferential grazing on prairie dog colonies; negative values = avoidance of colonies). Error bars in the inset graphs show 1 standard error for the selection coefficient.

sequence of ≤6 years, plague-induced removal of the prairie dogs resulted in rapid recovery of perennial grass cover in the first post-plague growing season (Augustine et al. 2014). In contrast, areas occupied continuously for 7–10 years exhibited significant reductions in perennial grass cover and increased bare soil exposure for multiple years after plague-induced prairie dog removal (Augustine et al. 2014). Similarly, in northern mixed prairie, core areas of colonies that are occupied continuously for decades show increased bare soil exposure, increased dominance by unpalatable subshrubs and forbs, and loss of perennial grass cover, whereas the more recently colonized edges often have significant cover of closely cropped grasses (Coppock et al. 1983, Brennan et al. 2020). These colony edges can provide valuable foraging areas for livestock during the growing season (Brennan 2019), and in some cases, even during dormant season grazing (Sierra-Corona et al. 2015). Our finding that cattle mass gains were suppressed to a limited degree and only when colonies were extensive (e.g., by 4–8% when colonies occupied 30–60% of pastures) is consistent with the idea that negative effects of prairie dogs may primarily arise from the loss of perennial grasses on core colony areas that are occupied continuously in between plague epizootics. Because of recurrent plague epizootics on time scales of roughly 5–15 years across the western Great Plains, these core areas typically comprise a small portion of the landscape, even when colonies occupy a majority of a given pasture (Augustine et al. 2008, Hartley et al. 2009, Brennan et al. 2020). In our study, we did not map spatial variation in vegetation communities or cover within the colonies. Recent advances in remote sensing are enabling more accurate mapping of areas within colonies with elevated bare soil exposure and cover of unpalatable forbs (Brennan et al. 2020). Knowledge of the location and extent of such areas could potentially provide an improved estimate of the effect of prairie dogs on livestock performance, and perhaps assist with more targeted adaptive management approaches to minimize the effects.

Several important caveats pertain to these results. First, and perhaps most important, peak abundance of prairie dogs during our 12-year study period did not coincide with the severe drought in 2012. We did not detect a significant interaction between the effect of growing-season precipitation and the effect of prairie dog occupancy level, suggesting that each have separate and independent effects across the range of combinations tested. Prairie dog occupancy varied from 10% to 25% of treatment pastures during the 2012 drought; hence, we have not tested whether an interaction may occur when precipitation is low and prairie dogs occupy >25% of a pasture. The substantial direct effects of drought on cattle mass gains that we observed likely operates in part through forage limitation during the second half of the growing season. Given that previous analyses of prairie dog effects on forage quality and quantity in shortgrass steppe showed much larger effects on quantity than quality in drought (Augustine and Springer 2013), we hypothesize that competition between cattle and prairie dogs could still be exacerbated in dry periods where prairie dogs occupy >25% of a pasture.

Our results combined with those of Olson et al. (2016) and Brennan (2019) also shed light on adjustments to stocking rates in response to prairie dog abundance. In the Brennan (2019) experiment, stocking rates were reduced in direct proportion to prairie dog colony extent in study pastures, which prevented cattle from experiencing reduced mass gain during the growing season when coexisting with prairie dogs. In contrast, within each year we maintained the same stocking rates in pastures both with and without prairie dogs, while also flexibly changing stocking rates in both treatments across years in response to weather and forage conditions. For example, the experiment-wide stocking rate was reduced by 30% in 2013 following the 2012 drought, and increased by 30% over a 4-year period in response to exceptional forage production during 2014 and 2015. Given our finding that cattle only experienced minor mass loss as the area occupied by prairie dogs increased, stocking rates may not need to be reduced as drastically in response to prairie dog occupation of pastures as implemented in the Brennan (2019) study. At the same time, some lesser reduction in stocking rate may be warranted if the goal is to prevent a decline in individual cattle performance. Estimates of the extent of core colony areas with elevated bare soil exposure and unpalatable forb dominance (Brennan et al. 2020) could potentially provide a more appropriate estimate of the necessary magnitude of reduction in stocking rate. Economic analyses are also needed to compare strategies of reducing stocking rate versus maintaining stocking rate with reduced animal gains, and to compare both to the costs of controlling prairie dogs.

Our analyses of cattle grazing distribution responses to prairie dog colonies during 2013–2016 yielded 2 key insights. First, our findings during 2013 and 2014 were consistent with Guenther and Detling (2003), who reported cattle in shortgrass rangeland grazed prairie dog colonies in proportion to their availability. We were surprised that cattle did not graze preferentially off colonies in 2013, when the rangeland was still recovering from the 2012 drought. One potential explanation is that the 30% reduction in stocking rates in 2013 alleviated the need for cattle to increase grazing time off colonies. Second, results from 2015 and 2016 were consistent with the competition and facilitation hypothesis (Augustine and Springer 2013), in that cattle grazed preferentially on colonies during the period of greatest forage availability during our study and off colonies during an extended period of plant senescence in 2016 (Fig. 4). This did not translate, however, into a detectable interaction between effects of precipitation and prairie dogs on cattle mass gain. Our grazing distribution models did account for the influence of topography and our data indicated increased grazing intensity on lowlands and flat plains compared to open slopes and uplands, consistent with work by Gersie et al. (2019). Perhaps the influence of factors such as spatial variability in topography and soils, combined with temporal variability in growing-season precipitation, so strongly affect mass gains that effects of prairie dogs on grazing distribution do not translate clearly into effects on mass gains in this ecosystem. Additionally, we did not map spatial variation in plant communities within colonies, which could perhaps improve predictions of grazing distribution (Sierra-Corona et al. 2015).

Our findings illustrate temporal variation in prairie dog colony size over the 12-year study period with initial low abundance following the 2006–2007 plague event, followed by colony growth until 2015 (reaching a maximum of 65–68% pasture occupancy 1 to 2 years after the 2012 drought), followed by another plague-induced decline in prairie dog colony area to <2.2 ha per occupied pasture during 2015–2017, and then colony recovery and expansion in 2018 and 2019. Expansions in colony size occurred even though prairie dogs in the surrounding landscape were being controlled annually with rodenticides. This control strategy likely suppressed the potential for prairie dog dispersal among the spatially separate pastures where they were not controlled. Two of the study pastures were adjacent and could have more readily exchanged dispersing prairie dog individuals, but the other 2 pastures were >4 km from adjacent uncontrolled sites. Both declined to <1 ha of active colony area in 2016–2017, and then recovered to 8.2–18.0 ha in 2019, suggesting significant resilience of spatially discrete populations to plague. Although the genetic consequences of plague-induced bottlenecks are not known, persistence of localized and isolated populations through plague epizootics is consistent with researchers reporting that prairie dog populations in Colorado may be developing increased resistance to plague, as compared to more eastern populations in South Dakota, USA, that have not coexisted with plague for the past 70 years (Rocke et al. 2012, Russell et al. 2019).

MANAGEMENT IMPLICATIONS

Cattle mass gain during the growing season declined linearly by 8% as prairie dog occupancy of shortgrass pastures increased from 0 to 60%. In the absence of population control via rodenticide, prairie dog populations fluctuate dramatically in response to periodic, disease-induced population fluctuations. As a result, negative effects on livestock mass gains do not occur every year, and could be negligible over the course of a decade if years of peak prairie dog abundance do not coincide with drought. We suggest that decisions on the need to manage prairie dog populations could be based on the magnitude of the effect documented in our study, market values of cattle, and the costs of prairie dog control, but managers should also consider uncertainty in the potential for drought to coincide with peak prairie dog abundance (and associated lack of quantification of the consequence for livestock managers), the frequency and timing of plague, and costs of alternative forage sources during drought. If prairie dogs become increasingly resilient to plague in the future, it will become even more important to plan management strategies temporally and spatially to mitigate effects on livestock production under conditions expected in most years, as quantified here, and to understand the consequences of high prairie dogs occupancy rates during dormant seasons and droughts.

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