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Exploring the Efficacy of Prairie Dog Boundary Management and its Application Toward Density Control

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ABSTRACT

Despite providing numerous ecosystem services, black-tailed prairie dogs (*Cynomys ludovicianus*) can negatively impact livestock production, presenting a challenge for rangeland management. Lethal control along public-private boundaries is one approach to balance competing stakeholder desires. A novel approach to reduce but not eliminate prairie dogs on public land ("density control") was proposed to increase forage availability for livestock while maintaining other prairie dog-associated ecosystem services. Little research on this approach exists, but we posit that where boundary management leads to population reduction but not elimination (the case on many U.S. Forest Service National Grasslands), boundary management is one form of density control. We reviewed the literature on boundary management and density control, and then evaluated boundary management as one form of density control using a before-after control impact design in the Thunder Basin National Grassland of Wyoming. We found scant literature describing either management approach; resources reporting efficacy were typically management documents not found in traditional literature searches. Boundary management did not reduce adult prairie dog density relative to untreated areas ($\beta_{\text{treatment}} = 0.28$, 95% CI [−0.28, 0.85]), but pup numbers were lower following treatment ($\beta_{\text{treatment}} = -1.43$, 95% CI [−2.12, −0.79]). Bird communities and overall plant biomass were largely unaffected by treatment, although forb biomass was 5x higher on sites that experienced treatment. Forbs often increase within the months following prairie dog reductions; this paired with high numbers of prairie dogs on treated areas in the following spring indicate treatment was temporarily effective but that prairie dogs rapidly re-colonized. Studies of these management approaches are rare and difficult to access by managers, which is concerning because we found little support for positive impacts (i.e., increased forage) of density control at local scales. While it may be effective for small colonies, boundary management that results in partial lethal control (density control) may be economically and ecologically ineffective.

Introduction

Management of burrowing rodents is a challenge worldwide, and management of prairie dogs (*Cynomys* sp.) specifically is an ongoing challenge on North American rangelands (Miller et al. 2007). Prairie dogs influence soil aeration and water filtration through burrowing, create habitat for other burrow-dwelling species like burrowing owls (*Athene cunicularia*; Davidson et al., 2012; Augustine and Baker, 2013), and are an important prey species for several raptors and mesocarnivores including the endangered black-footed ferret (*Mustela nigripes*; Oldemeyer et al. 1993; Miller et al., 1994; Bodenchuk et al., 2013). Black-tailed prairie dogs (*C. ludovicianus*) live at high densities and actively clip vegetation to maintain visibility of predators (10 dogs/acre, Hoogland, 1995). Consequently, these animals create short-statured vegetation patches that provide habitat for species such as horned lark (*Eremophila alpestris*) and mountain plover (*Charadrius montanus*; The IUCN Red List of Threatened Species, 2022). Vegetation on colonies is also maintained in an early growth stage and has higher relative abundance of forbs, providing higher quality forage for native ungulates and livestock (Hoogland, 1995; Miller et al., 2007; Davidson et al., 2012; Connell et al., 2018).

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While prairie dogs contribute a multitude of ecosystem services, significant dietary overlap with cattle (*Bos taurus*) and potential for physical injury to cattle or horses and riders from burrows are perceived as major threats by livestock producers (Miller et al., 2007; Merriam, 1901). The latter is uncommon (Hoogland, 1995) and is a condition that bison coexisted with for millennia (Koford, 1958), although consequences can be dire when accidents do occur. In terms of dietary overlap, prairie dog colonies exhibit sparse vegetation and abundant bare ground, reducing forage availability and subsequently weight gains of cattle (Derner et al., 2006). Research indicates these effects are most problematic in dry years and in areas with large proportional cover of prairie dog colonies (Derner et al., 2006; Connell et al., 2019; Augustine and Derner, 2021). Further, during wet periods, forage biomass can be greater on-colonies (Connell et al., 2019), and cattle will preferentially graze these areas (Sierra-Corona et al., 2015; Augustine and Derner, 2021).

The dichotomy of prairie dogs providing valuable ecosystem services but potentially reducing forage quantity for cattle creates a persistent challenge for land managers. To address this challenge, numerous tools have been proposed to assist with prairie dog management across the Great Plains. In the late 19th and early to mid-20th centuries, lethal control of prairie dogs via fumigants, poison bait, and shooting was common across both public and private lands (Witmer and Fagerstone, 2003), with this activity subsidized and encouraged by the federal government (Miller et al., 1994). Ultimately, widespread lethal control led to the functional extinction of the black-footed ferret, a species that depends on prairie dogs as a food source (Miller et al., 1994). Given the current Endangered status of the black-footed ferret, nonlethal prairie dog control methods including visual obstruction barriers (Franklin and Garrett, 1989), deferred grazing (Cable and Timm, 1988), chemosterilants (Garrett and Franklin, 1983; Nash et al., 2007), and translocation (Guernsey et al., 2023) have become increasingly common. In recent decades, a non-native disease, sylvatic plague (*Yersinia pestis*), has complicated prairie dog management because it leads to high mortality in both ferrets and prairie dogs (Antolin et al. 2002). As such, activities aimed at reintroducing prairie dogs and promoting colony growth while preventing plague outbreaks are critical (Oldemeyer et al., 1993; Miller et al., 1994; Jachowski et al., 2011; Eads and Biggins, 2019).

On public lands managed to sustain multiple uses, the tools to accomplish both plague mitigation and population management are often used in tandem to achieve balance among livestock production and conservation objectives. On U.S. Forest Service National Grasslands, widespread lethal control is now rare and often constrained to conflict areas, such as boundaries between public and private lands. Boundary management, in which rodenticides are applied within some predefined buffer on the public side of public-private land boundaries (Griebel et al. 2008; USFS 2020), is commonly used to reduce conflict with grazing lessees and adjacent private landowners. These boundary management zones (BMZs) are intended to reduce the potential for prairie dog encroachment onto private lands, but efficacy of this technique is not well documented.

There is also evidence that reducing the spatial connectivity of prairie dog colonies could reduce the risks of both large epizootics and rapid colony growth (Barrile et al., 2023), but it is unclear how much current boundary management practices can change colony configuration. Partial lethal control has rarely been a management goal, but reducing populations to a target level without completely removing them (i.e. population density control) has recently gained traction as a way to retain some ecosystem services while mitigating negative impacts on livestock production (USFS 2020). However, the spatial scale at which 'partial lethal control' of a colony would occur or be most effective has not been clearly identified. Population density control is a relatively new frontier in prairie dog management and investigation into its efficacy is needed.

In the Thunder Basin National Grassland of northeastern Wyoming, both boundary management and density control have been discussed as potential tools within a recent management plan amendment (USFS 2020). Boundary management is intended to reduce public-private conflict linked with encroachment while density control is intended to maximize multiple ecosystem services. Because of the novelty of density control as an objective, research on its direct and indirect effects is necessary prior to widespread application (USFS 2020). Boundary management can be interpreted as one form of density control because it reduces the density of prairie dogs at the colony scale, by removing prairie dogs in one portion of the colony. While this treatment often occurs at a colony edge to prevent expansion onto private land, in some cases encroachment has already occurred and as such, lethal control can sometimes be applied in a strip through the middle of a colony. As such, the direct and indirect effects of boundary management can be examined both for their own sake, and for consideration as one potential means of density control. We set out to examine the direct and indirect effects of boundary management in the Thunder Basin National Grassland and interpret these results as mimicking one potential form of density control. We identified the following three main objectives:

1) Review the literature on prairie dog boundary management and density control to assess existing research and efficacy of both management techniques;
2) Evaluate the effects of boundary management on adult and juvenile prairie dog abundance in treated areas, in subsequent years; and
3) Evaluate the secondary effects of boundary management on associated avian and plant communities.

We expected to find that boundary management was relatively understudied, and that it has a moderate ability to reduce prairie dog abundance. Due to its moderate efficacy, we expected boundary management as a proxy for density control to have low-to-moderate impacts on associated avian and plant communities.

Study Area

Our research was conducted on public lands within the USFS-Thunder Basin National Grassland in WY, USA, with a focus on the core area of prairie dog conservation and management (see Duchardt et al., 2023). Mean annual precipitation ranges from 25 to 35 cm, mainly falling as rain in spring and summer. Summer high temperatures average around 27°C but can exceed 37°C. The reference 'NOAA, 2018′ is cited in the text but is not listed in the references list. Please either delete the in-text citation or provide full reference details following journal style.

The Thunder Basin National Grassland is composed of grazed public lands managed by the USDA-Forest Service intermingled with private and state lands. The primary anthropogenic use of the region is cattle grazing, followed by oil and gas extraction and coal mining. In recent years the area has seen extreme fluctuations in prairie dog colony cover with the highest ever recorded at over 10,000 hectares in our focal area in 2017 to only 50 hectares in 2018 following an epizootic plague event (Davidson et al., 2022; Duchardt et al., 2023). Stakeholder concern about high colony cover in 2017 led to a Prairie Dog Management Plan Amendment by the Forest Service in 2020. This amendment targets 5859 hectares in the focal area and presents several tools both for conserving (e.g., using insecticides to reduce plague probability) and reducing prairie dogs (USFS 2020).

Methods

Objective 1. Literature review

We conducted a literature review to identify research and management plans that applied either boundary management or density control, with the goal of identifying best practices and efficacy of both management approaches. We defined a priori systematic search terms that combined some aspect of management with terms associated with black tailed prairie dogs: 1) Management ["boundary management" OR "population management" OR "density control" OR "selective control" OR "boundary control" OR "population control" OR "population reduction" OR "density reduction"] AND 2) prairie dog ["prairie dog" OR "Cynomys ludovicianus"]. We then determined relevance based on the publication title, excluding any literature that was clearly not focused on prairie dog management. We downloaded all hits that were deemed relevant to prairie dog management, including grey literature, and we searched the document for each of the above terms in quotations individually to determine context. We fully reviewed each relevant document and recorded if it either indirectly addressed one of the management approaches but did not implement it or if the document indeed implemented one of the approaches. For sources that did implement one of the approaches, we recorded whether they employed boundary management, density control, or both, and summarized the efficacy or outcomes of the approaches if possible. We initially performed our search using Scopus and Google Scholar, recording the number of hits on each platform. However, both search engines did a poor job of capturing agency reports based on personal knowledge; consequently, we also conducted a limited review (first 100 results) of these same search terms on the Google search engine.

Objectives 2 and 3. Direct and indirect effects of treatment

To monitor the effects of boundary management on the target species and associated taxa, we conducted surveys of prairie dogs, vegetation, and the avian community before and after application of boundary management in the Thunder Basin National Grassland. We used a subset of existing survey locations (Duchardt et al. 2019) to establish six study sites where we collected data from May through July from 2021 to 2023 (Fig. 1). A subset of additional data were was also collected in 2024, as explained below. Each site contained three plots approximately 4.05 ha in size, which were assigned to one of three treatment types: 1) prairie dog colonies that were not controlled at any time during the study (untreated colony), 2) colonies that experienced lethal control via rodenticide because they fell within the boundary management zone (BMZ; treated colony), and 3) locations without prairie dogs (unoccupied; Fig. 1). All plots were at least 250 m apart from one another within each site, but distance between the treated and untreated colony plots averaged 1.2 km (Fig. 1). We note that all six areas slated for control were associated with larger colonies on one or both sides of the BMZ (Fig. 1); colony sections within BMZ represented between 5% - 75% the total colony area for a given colony, though it is sometimes difficult in this landscape to differentiate individual colonies given high connectivity (see Davidson et al. 2022). We highlight that while plots were selected for this study, distribution of the BMZs was determined by federal managers and partners in this landscape. Where possible, we aligned study plots with existing long-term data collection locations that had been selected for on and off colony habitat in a stratified-random approach, while any newly established sampling sites were selected to maximize similarity of soils among plots within a site (Soil Survey Staff, 2020).

No survey locations had experienced lethal control using toxicants in the 10–15 years before the start of the study. Boundary control management was slated to take place during winter 2021–22, but occurred at only one of the six study sites during that winter. All BMZ plots were treated with rodenticide between October and January of 2022–2023 and in the same time period 2023 – 2024; black-tailed prairie dogs are active year-round, and poisoning is restricted to fall and winter to minimize potential take of nontarget species (USFS 2020). Rodenticide applications were coordinated by Wyoming Weed and Pest Department, and used zinc-phosphide-laced grain baits (2%) applied near burrows (see Witmer et al. 2023 for detailed application methodology). Prebaiting with nontoxic grain occurred at least 48 h before to increase bait uptake (Witmer and Fagerstone, 2003). Limited surveys by Forest Service staff indicated few or no prairie dogs in treated areas within the days following treatment, indicating high efficacy of treatment.

To test the effectiveness of boundary management in controlling prairie dogs, and as a proxy for density control, we employed a Before-after Control-impact (BACI) design on treated ($n = 6$) and untreated ($n = 6$) colonies before and after treatment. In each year of the study, we surveyed prairie dogs from a single point to a radius of 114 m (approximately 10-acre plot [4.08 ha]), using pinflags placed in each cardinal direction to assist in delineating North, East, South, and West quadrants for more accurate counts. One of our goals was to assess potential reproductive response to treatment; thus, surveys were conducted in mid to late May each year to coincide with pups emerging from burrows but before they grew to similar sizes as adults. We conducted surveys between 30 min after sunrise and 12:00 pm; although detection may vary across the day, Powell et al. (1994) found little temporal variation in counts after juvenile emergence. After a 15-minute acclimation period, we conducted two 10-minute surveys. During each 10-minute survey, we counted the number of adult prairie dogs, and the number of juvenile prairie dogs (pups) during multiple scans, taking the highest number observed per quadrant (Maximum Above Ground Count, MAGC). For each prairie dog age class, the maximum value from the two surveys was used in analysis. We did not apply time-based or distance-based adjustments to the counts to account for detection probability, because we were most interested in relative differences among treatments and across time, but acknowledge that some unexplained variation in counts may be due to unmodelled detectability. While MAGC methods are biased low compared to mark-recapture approaches, surveys at this spatial scale have shown a strong correlation between MAGCs and estimates based on mark-recapture (Severson and Plumb 1998; Facka et al. 2024); our main objective was to detect population changes and to pilot methods that could be easily implemented by Forest Service staff in the future and as such MAGCs were deemed appropriate.

We conducted point counts to assess avian responses to boundary management. Surveys were conducted on treated and untreated colony plots, as well as uncolonized plots ($n = 18$ plots each year), once each year from mid-May to mid-June 2021–2023 from sunrise to approximately 11 am (Duchardt et al. 2019). We conducted six-minute counts and included all birds seen or heard at the site within an unlimited radius, but did not include observations >200 m in our analysis. Surveys were not conducted on days with high wind or rain. Observers were trained by individuals with >7 years of bird sampling experience in this system. We recorded species, method of detection (aural/visual), and distance from the point using a laser rangefinder.

Following point count surveys, we used a Robel pole (Robel et al. 1970), with centimeter instead of decimeter increments, to collect visual obstruction data along a 30 m transect running north from the point count location. We collected these data in late May to align with breeding bird habitat structure. We took read-

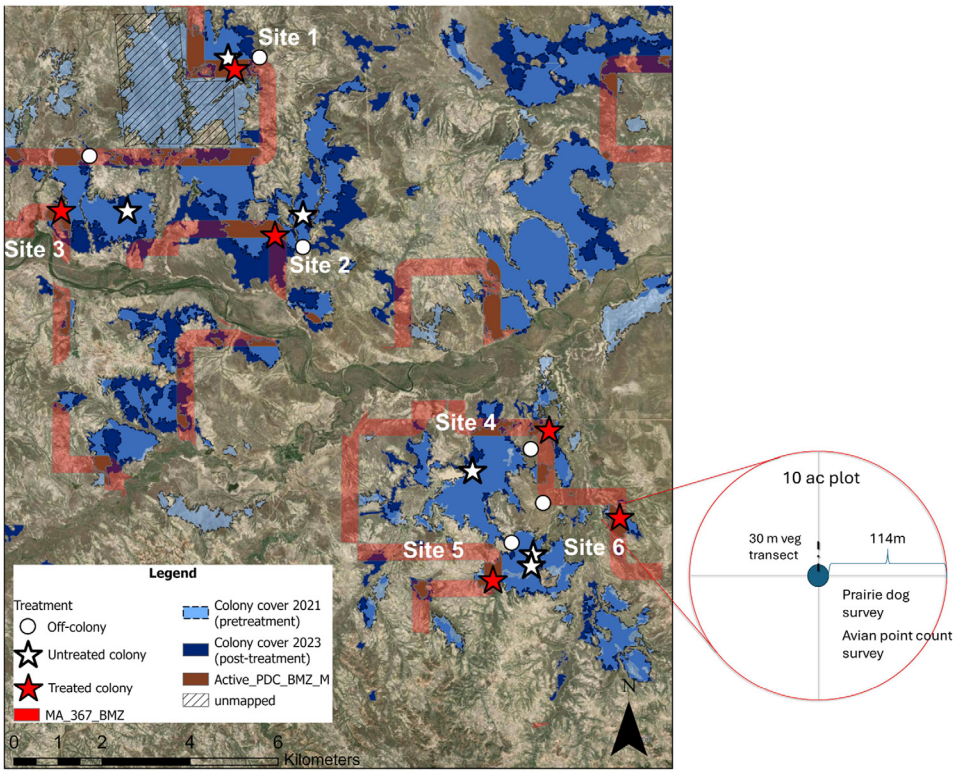

Figure 1. Study design for assessment of boundary control in Thunder Basin National Grassland, WY from 2021–2023. Inset depicts design of study plots. Polygons show pretreatment and post-treatment extent of prairie dog colonies. Hatched area indicates portion of private land without permission for prairie dog mapping in 2023.

ings from two directions (E and W) every 5 m for a total of 14 readings and averaged these readings for each plot ($n = 18$). Observers recorded the centimeter band at which tallest vegetation intersected the pole (maximum vegetation height) and the lowest band not completely obscured by vegetation (visual obstruction), along with obstructing plant species. We measured forage biomass in July using 0.5m^2 Daubenmire frames (Daubenmire, 1959) at two locations along the same 30 m transect in each plot ($n = 36$). On each transect, biomass was clipped 8 m E of the transect at 10 m and 20 m along the transect in the first year, and shifted 3 m forward in each year to avoid re-clipping. We separated clipped vegetation by functional group, dried samples for 48 h at 60°C, and weighed to generate estimates of dried biomass in g/m2. Functional groups included grasses, forbs, and several other categories not relevant to this analysis. For each transect and each year, we averaged the two measurements taken at each plot to generate plot-scale biomass estimates.

All data were collected 2021–2023. Additional prairie dog MAGCs were also conducted in the summer of 2024 to better assess long-term responses, but resources were not available to conduct additional surveys in that year. Therefore we analyze data from 2021–2023 but also report average MAGC for 2024.

Analytical methods

The Forest Service did not apply full lethal control due to ongoing litigation during the first winter of the study, resulting in only one of six treatment sites experiencing lethal control in 2021–2022. In the winter of 2022–2023, approximately 800 ha of BMZs were treated, including all six of our BMZ study plots. To address this and evaluate the direct effects of prairie dog control on prairie dogs and the indirect effects of prairie dog control on associated avian and plant species, we evaluated the difference in observed prairie dog abundance pre and post control treatment using only data from 2021 (before treatment) and 2023 (after treatment). In this way, our analytical approach to direct effects of BMZ treatment follows a BACI design ("before-after control-impact).

We used generalized linear models with a Poisson distribution to evaluate whether boundary management altered prairie dog maximum counts across our six study sites (Objective 2). We generated a global model that incorporated the change in prairie dog counts as a function of the interaction between time (before and after treatment) and treatment, with a random effect of site. We generated models for the response of pups, adults, and all prairie dogs, and interpreted a significant interaction with a more negative slope in the treatment category as an indication of treatment effects. We fit models using the *glmer* function in the lme4 package within program R (R Core Team 2023).

We also evaluated indirect effects of boundary management and prairie dogs on vegetation and the bird community following a similar BACI approach with generalized linear models in each year as described above (Objective 3). Because we were interested specifically in the interactive effect of treatment and year we did not explore a precipitation covariate (because this was perfectly correlated with year), but we address this caveat later in the text and present cumulative precipitation from January–June each year (NOAA 2023). We explored additive and interactive effects of treatment and year with the expectation that if treated plots led to increased forage we would observe a positive interaction between year and forage/vegetation metric relative to untreated areas, while a positive impact on birds would be observed relative to areas unoccupied with prairie dogs. We also modeled additive and interactive models with prairie dog presence, as well as year alone. We compared all five models with a null model using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002); we used a model comparison approach to indirect effects so that we could compare models both with and without treatment effects. We also included random effect of site

as described in prairie dog models above. All models were run using the *glmer* function in the lme4 package in program R (R Core Team 2023). Vegetation response variables included vegetation structure (height of tallest vegetation and visual obstruction) and vegetation biomass (forb, grass, and total biomass); in each year for each plot, we used the average value of each metric where multiple readings were collected at the plot scale as our response variable.

Avian community response variables included avian species richness and number of detections of horned larks (*Eremophila alpestris*) and western meadowlarks (*Sturnella neglecta*). We selected these two species because they had enough observations to facilitate modeling, and they are known to respond strongly to vegetation structure. Meadowlarks prefer mid-grass structure more commonly available off-colonies, and horned larks are short-structure obligates (Duchardt et al. 2019). We did not adjust for detectability because: 1) our dataset was small, and 2) we were more interested in relative differences among treatments than in avian abundance per se. We acknowledge potential biases in this approach, but highlight that observers had extensive experience in the system and that these species have high detectability within this system (as opposed to more cryptic species like mountain plovers) especially because observers often used vocalizations (calls or songs) for initial identification, which is less affected by light levels or vegetation obstruction. Avian response variables were modeled with a Poisson distribution while vegetation variables were modeled with a Gaussian distribution.

Results

Objective 1. Literature review

Our literature search yielded 315 hits in Scopus and 1,180 in Google Scholar. All records returned in Scopus were also found by Google Scholar (Table 1). We considered 18 of these hits to be relevant to boundary management or density control, with an additional ten resources identified in the Google search engine, and two resources found through snowball sampling (i.e., found in the literature cited of other resources).

The peer reviewed literature comprised 26% of relevant resources, with the rest composed of agency reports, conference proceedings, theses, and other grey literature (Table 1). Most resources that discussed boundary management employed or recommended lethal control via toxicants or fumigants, although some advised translocation, visual barriers (either constructed or vegetative), or deferred grazing to help deter re-colonization (Table 1). Similarly, most resources that discussed intentional reduction of prairie dog densities referred to toxicants as the most common tool (38%). Some literature on the efficacy of chemosterilants indicates these may be an effective means of reducing density (e.g., Yoder et al. 2017, Shiels et al. 2022), but our search did not reveal any resources that provided a comparison between fertility control and lethal control.

Empirical research regarding the efficacy of boundary management was lacking; we identified only three resources that reported efficacy results of boundary management. Griebel et al. (2008) explored the effectiveness of boundary management on colonies in the Conata Basin of South Dakota and observed that prairie dog counts were significantly lower, but not zero ($\bar{\mathbf{x}} = 0.4$ dogs $\pm$ SD 0.9) on fully poisoned colonies in 800 m (1/2 mile) BMZs. Colonies that were partially treated with zinc phosphide had higher counts ($\bar{\mathbf{x}} = 5.2$ dogs $\pm$ SD 4.6), but the scale of these counts was not reported, nor were densities prior to treatment. Researchers stated that encroachment of prairie dogs into the BMZ was limited both due to the size of the BMZ, as well as livestock grazing exclusion applied to increase vegetation height and deter prairie dog immigration. In western South Dakota, Terrall et al. (2005) evaluated the role of management buffer widths up to 100 m for what was essentially boundary management, although this term was not used. They found that while buffer size did not influence recolonization of the buffer or a target area beyond the buffer, livestock grazing exclusion from the treated areas facilitated vegetation growth to such an extent as to deter recolonization. Finally, Knowles (1986) evaluated population recovery following poisoning at different intensities in northeastern Montana. He found that colonies that received partial treatment at edges, cores, or 300 m bands through colonies reached pretreatment population levels within 1–2 years. Colonies that were heavily treated across their entire extent and had a 95% population reduction recovered to pretreatment levels within 3–5 years.

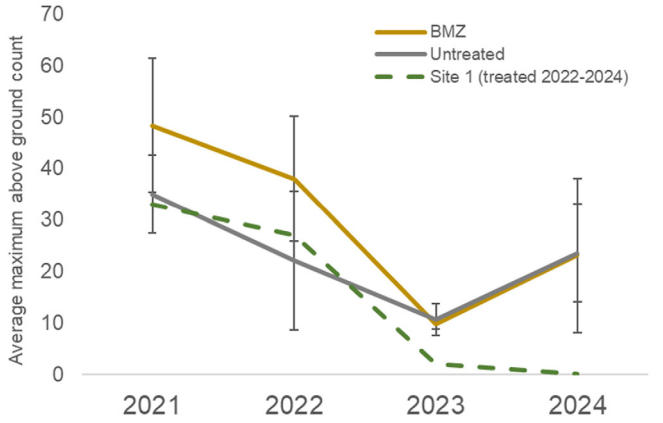

Figure 2. Mean detections of prairie dogs each year in Boundary management zones (gold) and untreated colony (grey) areas, with standard errors. Data from plot E30 is shown separately (green) due to this being the only plot treated twice during the study (winter 2021–2022 and 2022–2023).

We found no resources that evaluated the efficacy of density control to reduce prairie dogs to target densities nor the secondary effects on ecosystem services. However, Collins et al. (1984) evaluated forage benefits from prairie dog control in South Dakota and estimated that the costs of lethal control were generally not recouped in terms of forage benefits for several years, potentially decades. They calculated that 7.2 hectares of colony must be controlled to yield 1 additional animal unit month (AUM) of grazing, and that half of the colony required re-application of lethal control in the following year.

Objective 2. Prairie dog responses to boundary management

Boundary management reduced, but did not eliminate, prairie dog encroachment onto nonfederally-owned lands across our study area (Fig. 1). In some locations encroachment onto nonfederally managed lands was low (e.g., Site 1 and Site 3, Fig. 1) but in others, acreage in nontarget areas was higher after treatment (e.g., Site 2, Fig. 1). On both treated and untreated sites, we observed a 3–5 fold reduction in prairie dog counts between the first and third year of the study ($BMZ_{2021} = 45.8$ prairie dogs/4.04 ha plot [SD = 26.78], $BMZ_{2023} = 8.5$/plot [SD = 3.73]; $Untreated_{2021} = 35$/plot [SD = 18.61], $Untreated_{2023} = 10.67$/plot [SD = 7.53]. Additional MAGC conducted in summer of 2024 indicated increased prairie dog abundance at both treated and untreated sites but little difference between the two (Fig. 2). Site 1 (Fig. 1), which was the only site to receive three consecutive years of treatment, had the lowest counts in 2023 and no observed prairie dogs in 2024.

Model results indicated strong support for a decline in prairie dog counts between 2021 and 2023 irrespective of treatment ($\beta = -1.19$, 95% CI [−1.48, −0.91]). Results indicated that on aver-

Table 1
Results of literature search targeting effects of boundary management and density control on prairie dogs or associated ecosystem services, including the search engine used to identify the resource, and the type of resource.

Resource	Type	Search engine	Boundary Management		Density Control	
			Empirical	Other	Empirical	Other
Collins et al. 1984	Peer-reviewed	Google Scholar, Scopus				X^{p}
Yoder et al. 2017	Peer-reviewed	Google Scholar, Scopus				X^{c}
Shiels et al. 2022	Peer-reviewed	Google Scholar, Scopus				X^{c}
Nebraska National Forest 2006	Agency report	Google Scholar	X^{p}			
Knowles 1986	Peer-reviewed	Google Scholar		X^{p}		X^{p}
Nash et al. 2007	Peer-reviewed	Google Scholar				X^{c}
Cable and Timm 1988	Conference proceedings	Google Scholar				X^{d}
Bodenchuck et al. 2013	Conference proceedings	Google Scholar		X^{g}		
Eddy 2011	Thesis	Google Scholar		X^{b}		
Witmer et al. 2008	Peer-reviewed	Google Scholar		X^{b}		
Garrett and Franklin 1983	Peer-reviewed	Google Scholar				X^{c}
Hendrie 2004	Thesis	Google Scholar		X^{b}		
McColloch et al. 2005	Agency report	Google Scholar				X^{p}
Vosburg 1996	Thesis	Google Scholar				X^{s}
Defenders of Wildlife 2020	Other	Google Scholar		X^{g}		X^{g}
Pauli 2005	Thesis	Google Scholar				X^{s}
Witmer 2019	Conference proceedings	Google Scholar				X^{c}
Defenders of Wildlife 2007	Other	Google Scholar		X^{g}		
Griebel et al. 2008	Agency report	Google	X^{p}			
Wind Cave National Park 2006	Agency report	Google		X^{g}		
Stapleton Development Corporation 2000	Agency report	Google		X^{b}		
Parks Canada Agency 2021	Agency report	Google		X^{g}		
City of Lakewood, 2012	Agency report	Google		X^{g}		
Cooper and Gabriel 2005	Agency report	Google		X^{g}		
USFS [Buffalo Gap] 2005	Agency report	Google		X^{g}		
Ruckelhaus 2017	Agency report	Google		X^{g}		X^{g}
USFS [Thunder Basin] 2020	Agency report	Google		X^{g}		X^{g}
Texas Black-tailed Prairie Dog Working Group 2004	Agency report	Google				X^{pds}
Terrall et al. 2005	Conference proceedings	[snowball]	X^{pd}			
Witmer and Fagerstone 2003	Staff publication	[snowball]		X^{p}		

"Snowball sampling" represents sources that were not identified in our initial search but occurred in the literature cited of an identified source. Where either empirical research exists or resources at least discussed the management approach, we use superscripts to indicate which type of treatment was discussed (b = visual barriers, c = chemosterilant, d = deferred grazing, p = poison or fumigants, x = shooting). Where direct types of treatment were not discussed in detail, references have a "g" superscript, for "general."

age (including before and after treatment) sites in the BMZ had greater observed counts than untreated sites ($\beta = 0.27$ CI, 95% CI [0.09, 0.45]), and treatment effect (the interaction between treatment and time covariates, hereafter, treatment) was also significant ($\beta_{\text{treatment}} = -0.50$, 95% CI [−0.91, −0.089], Fig. 3A). After further examination into models evaluating treatment effects on both pups and adults, it appears this treatment effect was mainly driven by a decrease in pups following treatment ($\beta_{\text{treatment}} = -1.43$, 95% CI [−2.12, −0.79]; Fig. 3B), while adult numbers did not significantly change with treatment ($\beta_{\text{treatment}} = 0.28$, 95% CI [−0.28, 0.85], Fig. 3C).

Objective 3. Indirect effects of boundary management

We found no model support for effects of treatment or prairie dog presence on avian species richness or abundance of horned larks or western meadowlarks (Table 2). Effect of year alone was competitive (within 2 AIC_c) for richness and horned lark abundance but was still worse than the null model. The interaction between year and treatment best explained maximum vegetation height; parameter estimates for both treated ($\beta_{\text{treated}} = -3.01$, 95% CI [−5.73, −0.29]) and untreated ($\beta_{\text{untreated}} = -2.84$, 95% CI [−5.57, −0.12]) plots were negative relative to areas without prairie dogs, but did not significantly differ from one another in any year. Further, the interaction term between treatment and the final year (post treatment) overlapped zero ($\beta_{\text{treatment}} = 1.75$, 95% CI [−2.1, 5.6], Fig. 4). No other models were competitive (within 2 AIC_c of the top model). When examining models predicting visual obstruction, we did not find support for an effect of treatment over time. The best model included additive effect of treatment and time but the parameter estimated for treated areas overlapped zero (Table 2, Fig. 4).Visual obstruction was estimated to be highest across treatments in the final year of the study (β_{2023}=1.75, 95% CI [0.81, 2.70]).

All three biomass models were best explained by the interactive model, but treatment effects varied. We observed the expected positive interaction between treatment and the final year of the study for total herbaceous plant biomass, though confidence intervals widely overlapped zero ($\beta_{\text{treatedx2023}} = 3.1$, 95% CI [−30.97, 37.12]; Table 2, Fig. 4). Herbaceous biomass in 2023 was also significantly higher than the previous two years ($\beta_{2023} = 51.74$, 95% [CI 27.67, 75.82]). The interactive treatment model also best explained grass biomass but interestingly, the interaction term between treatment and the final year was negative (Table 2, Fig. 4), indicating lower grass biomass on treated sites though again, confidence intervals overlapped zero ($\beta_{\text{treatedx2023}} = -16.82$, 95% CI [−27.59, 12.41]), and again, grass biomass was higher in 2023 (β_{2023}= 39.12, 95% CI [21.02, 57.23]). Forb biomass was the only response where we observed a significant positive treatment-time effect ($\beta_{\text{treatedx2023}} = 21.22$, 95% CI [3.78, 38.67]; Table 2), with 5x greater forb cover on treated plots in 2023 compared with 2022 (Fig. 4), while confidence intervals for all other parameters, including year, overlapped zero.

Discussion

We capitalized on a Forest Service initiative in Thunder Basin National Grassland to assess the efficacy of boundary management both as a standalone tool and as a proxy for density control. Our literature review revealed that both management methods are rel-

Table 2
Evaluating response of eight ecosystem metrics to treatment.

Metric	Model	K	AIC_c	ΔAICc	w_i	Prairie dog control prediction supported
Avian richness	Null	1	200	0	0.58	
	Year	3	201.3	1.4	0.3	
	Prairie dog + Year	4	203.8	3.8	0.09	
Western meadowlark	Null	1	221.5	0	0.84	
	Year	3	226	4.5	0.09	
	Treatment + Year	5	227.7	6.2	0.04	
Horned Lark	Null	1	158.5	0	0.53	
	Year	3	159.5	1	0.32	
	Prairie dog + Year	4	161.7	3.2	0.11	
Maximum Vegetation Height	Treatment * Year	9	266.4	0	0.65	
	Prairie dog * Year	6	269	2.6	0.18	
	Treatment + Year	5	269.9	3.5	0.11	
Visual Obstruction	Treatment + Year	4	215.8	0	0.46	
	Treatment * Year	9	218	2.2	0.15	
	Prairie dog+ Year	5	218.1	2.3	0.14	
Total Biomass	Treatment * Year	9	455.8	0	1	
	Prairie dog * Year	6	468.7	12.9	0	
	Treatment+ Year	5	474.9	19.1	0	
Grass Biomass	Treatment * Year	9	434.5	0	1	
	Prairie dog * Year	6	445.9	11.5	0	
	Treatment+ Year	5	454.8	20.3	0	
Forb Biomass	Treatment * Year	9	393.7	0	1	✔
	Prairie dog * Year	6	408.5	14.8	0	
	Treatment+ Year	5	412.4	18.8	0	

For each metric, we show the top three of six models ranked by AIC_c. Number of parameters (K), model weight (w_i) and ΔAIC_c are shown. Each model also includes a random effect of site. The final column indicates (with a checkmark) whether resulting model supported either a positive ecological (avian) outcome relative to areas without prairie dogs, or a positive forage/vegetation outcome relative to colonies where prairie dogs were not controlled.

atively poorly studied. In our study, prairie dog abundance across the grassland decreased over time, but shifts in abundance were only weakly related to boundary management treatments. Boundary management *per se* reduced, but did not eliminate, prairie dog encroachment onto nonfederally managed lands. Regarding boundary management as a proxy for density control, overall densities in the spring following treatment were only mildly impacted by control, and adult numbers were unaffected. Given the limited overall efficacy of the treatment, it was unsurprising that many ecosystem services (e.g., avian richness and abundance, vegetation height and biomass) did not significantly differ between treated areas and untreated areas.

Literature review

Our literature review was not designed to capture all research on lethal control of prairie dogs but was instead structured to focus on two management approaches: boundary management and density control. Accordingly, we likely missed papers with relevance to poisoning efficacy. However, our review mimicked those conducted during National Environmental Policy Act (NEPA) Environmental Assessments, or by managers wishing to apply one of these approaches. We found that little guidance exists for practitioners wishing to understand the direct or indirect effects of boundary or density control. Furthermore, most reporting on efficacy was found within management documents and other gray literature and therefore might not be recognized as "the best available science" by managers. This highlights the need for additional and accessible case studies for rangeland managers in the United States, and we anticipate these same challenges may occur with burrowing rodents worldwide.

Treatment efficacy

We highlight that "effectiveness" is a function of goals. In this study we wanted to examine boundary control *per se*, as well as boundary control as a proxy for as-yet untested density control. Boundary control *per se* was partially effective, in that it appeared to reduce encroachment onto non Forest-service lands, but did not eliminate it (Fig. 1). There is no required reporting on poisoning frequency or efficacy on private lands, but based on our knowledge of the system it appears that boundary control was more effective in areas where poisoning occurred not only in the BMZ, but also on the adjacent private land. Conversely, in areas where additional control on private land did not occur (e.g., Fig. 1 Site 2), poisoning within the BMZ appears to have had no retarding effect on colony growth.

As a form of density control, the goal of the treatment was to maintain ecosystem services generated by prairie dogs while increasing forage availability; the proposed mechanism for this was to reduce but not eliminate prairie dogs in target areas. This goal was largely not achieved in this study, though we highlight that here we tested only one form of density control ("strip" control), and studies of other methods such as controlling prairie dogs in patches throughout target area may be valuable. Relatively unchanged densities of adult prairie dogs in treated areas were unexpected because poisoning was done in a manner to maximize effectiveness (e.g., prebaiting; Witmer and Fagerstone 2003). By measuring prairie dog density ~6 months after treatment, our study was not well-suited to testing the immediate efficacy of poisoning; however, three lines of evidence indicate efficacy of the initial poisoning was high. First, Wyoming Weed and Pest staff that applied poison to different parts of the landscape across the winter did not observe evidence of ineffective treatment. Further, two game cameras managed as a part of a different project that were located within treated BMZ did not detect prairie dogs at those locations over the winter until February 2023. Third, the flush of forb growth in the BMZ indicates temporary reduction of prairie dogs (see discussion of this relationship below).

While it is rare that a single poisoning treatment is 100% effective (Witmer and Fagerstone 2003), all evidence indicates densities immediately after treatment were substantially reduced. We hypothesize that unchanged adult densities in the summer following treatment were not due to ineffective poisoning, but instead to re-colonization of the BMZ from nearby coteries that were not treated. Because lethal control occurred in fall and winter, the entire system is grazed by livestock, and mean annual precipitation in our study area was much lower than in prior studies (e.g.,

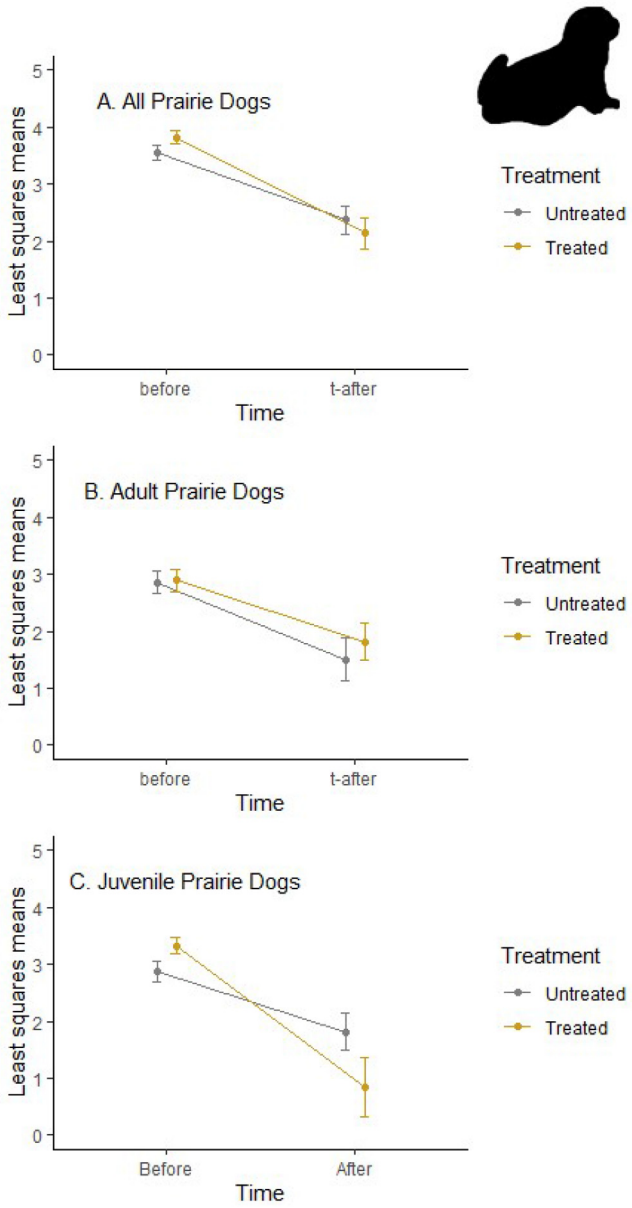

Figure 3. A) Least squares means of all prairie dogs **A**, adult prairie dogs **B**, and pups **C**, between 2021 and 2023 on treated (gold) and untreated (grey) colonies.

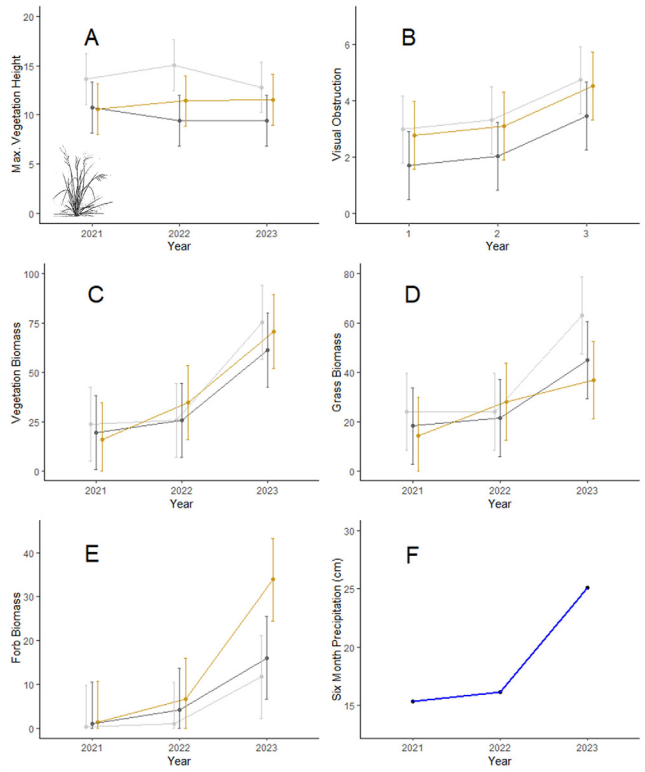

Figure 4. Least squares means for maximum vegetation height **A**, visual obstruction **B**, vegetation biomass **C**, grass biomass **D**, and forb biomass **E**, with 95% confidence intervals. Treated colonies are shown in gold, with untreated colonies in dark grey, and uncolonized locations in light grey. Panel **F**, shows January – June cumulative precipitation in each year.

Griebel et al. 2008), vegetation structure on these treated patches remained low and was likely ideal for prairie dog colonization (Knowles, 1986; Miller et al., 2007). Although prairie dogs typically disperse in the summer, they can also disperse year-round, especially following local changes in habitat structure or conspecific density (Hoogland, 1995). Reduced densities in treated areas may increase perceived habitat suitability in neighboring colonies, facilitating "diffusion" into these areas. Despite this hypothesis making a great deal of sense in light of prairie dog biology, few resources document it (e.g., Knowles 1986), and to our knowledge this information does not appear in management guidance. We are unable to confidently identify a direct mechanism driving reduced pup numbers post treatment, but diffusion into treated areas during winter or early spring may have precluded breeding, or have been biased towards dispersing males. Additional prairie dog aboveground counts conducted in 2024 supported this general trend of lower pup numbers, with a 30% reduction in pups on BMZs vs. untreated areas, but again total prairie dog numbers between treated and untreated sites were similar. We continued to observe large variation among treated sites; no prairie dog pups were observed in three of six treated plots, including Site 1, which was treated three years in a row and also had no adult prairie dogs. However, the treated plot at Site 6 had the highest number of pups of any site, treated or untreated (~5 pups per acre; Fig. 1). This highlights the unpredictable efficacy of this approach; it is likely that re-colonization is a function of aspects of site suitability including soil type and grazing management, but how these site-specific traits interact with management are not well understood.

We note that had we not included untreated plots, and only assessed BMZs pre and post treatment, we would have inferred a major effect of lethal control on prairie dog abundance. However, comparison of treated and untreated colonies revealed that prairie dog abundances decreased in 2023 across both treatment types. It is possible that these declines are a landscape-scale result of density control, but we think this to be less likely than other explanations. First, we note that sylvatic plague was detected in the system in 2023 (Tim Byers USFS, personal communication) and, while we did not observe large-scale die-off, this may have locally reduced densities in some parts of the grasslands.

Second, we have reason to believe that lower densities in 2023 may be related to colony expansion rather than density control. Although plot-scale observed densities declined across the study period, colony cover in the study area increased by almost 50% from 7800 acres in 2021 to 11600 acres in 2023 (unpublished data, Great Plains Consulting). Indeed, we noticed prairie dog colony expansion into two of our study plots that were originally chosen as "unoccupied" in 2021 (Fig 1. Site 2, Site 3). Colony expansion typically occurs when densities are high, with lower densities following ex-

pansion (Cincotta et al. 1988). If density control in a given area was effective, we would expect lowered densities along with a constant or reduced amount of colony cover in the landscape, but this is not what we observed.

Secondary effects

Since there was no significant effect of the boundary management treatment on adult prairie dogs, it is not surprising that there was also no evidence for effects on avian communities and only limited evidence for effects on vegetation. Duchardt et al. (2019) found that prairie dog presence or absence was not enough to explain variation in detection of sympatric bird species. We used two common species in our avian detection models, but species with greater degrees of association with prairie dog colonies (e.g., mountain plover) breed at such low densities in this landscape that this study was unlikely to capture variation in those species. A positive interaction of treatment by time was not found for most vegetation metrics and most importantly, did not significantly increase overall forage availability. Instead, we posit that higher production and vegetation structure in 2023 across all study plots was largely driven by increased precipitation, which was unsurprising in this herbaceous-dominated system.

We found support for a treatment by time interaction for four of five vegetation metrics but in most cases, this was not a result of increased forage or vegetation height on treated areas relative to untreated areas. Instead, it appears that the treatment year largely compounded by increased precipitation in the following spring and summer (Fig. 4F) leading to higher overall vegetation structure and biomass in all treatments. Again, had we not compared treated areas to untreated and uncolonized plots, we may have missed this fact. Vegetation height, structure, and biomass were intermediate in treated areas but confidence intervals were widely overlapping, indicating far more variation among sites within the treated areas. Perhaps more interesting, grass biomass was actually slightly lower in the treated areas compared to untreated sites and those without prairie dogs; grass forage is the main target among most ranchers and as such, this further indicates this approach, and this form of density control, does not generate increased target forage availability, at least in the short term.

However, we did observe a large increase of forb biomass on treated sites. The significant increase in forb biomass after prairie dog removal has also been documented in shortgrass steppe when prairie dogs were removed by an outbreak of epizootic plague (Augustine et al. 2014). Many forbs in this system are annuals, and these can quickly re-colonize bare areas after removal of prairie dogs. The increase in forb biomass on treated sites supports the hypothesis that after treatment, these areas experienced several months without large populations of prairie dogs, during which time forbs were able to germinate and grow before prairie dogs recolonized the sites. Increased forb abundance can provide important resources for pollinators (Hardwicke 2006) and are also important for native ungulates like pronghorn (*Antilocapra americana*; Sexson et al. 1981, Bleke et al. 2023) and can be a useful forage resource for livestock.

Management implications

We did not set out to assess the economic efficacy of these approaches, but given the inherent financial limitations to public land management, we believe some discussion of tradeoffs is warranted. Multiple resources we reviewed highlighted that lethal control is not economically feasible, especially when returns on forage is the major goal (Collins et al. 1984, Witmer and Fagerstone 2003). We posit that when reduction, not elimination, of prairie dogs is the goal, economic efficiency will be lower because it ensures that there will always be nearby source populations to recolonize the target area. Indeed, in the limited empirical evidence found in the literature, managers reported that boundary management targeting only portions of colonies had very low effectiveness (USDA Forest Service 2006), and was especially ineffective when not paired with at least temporary cessation of livestock grazing. Although we know of no studies exploring these sorts of treatments in other rangeland systems worldwide, we posit that similar trends may be observed with colonial burrowing animals elsewhere, and underscore the need for further research on this topic.

We also acknowledge that while MAGCs of prairie dogs are useful in detecting relative differences they do not incorporate prairie dog detectability (e.g., Facka et al. 2024); more rigorous methods like mark-recapture will be useful in future studies to further explore treatment efficacy but may be cost-prohibitive for federal agencies. Based on our admittedly limited data, we think that partial lethal control (either through density control or BMZs) has the potential to destabilize colony dynamics. Densities in the target area may be temporarily reduced but rebound quickly, while diffusion to the treated area may lead to lower densities somewhere else within the colony or colony complex. Moreover, these challenges do not consider the direct negative impacts that poisoning may have on nontarget wildlife (e.g., Vyas et al. 2013). In summary, the drawbacks to density control may outweigh the potential benefits.

In locations where eradication or prevention of future colonization is the goal, research indicates that visual barriers, especially natural barriers, may be effective (Franklin and Garrett, 1989; Terrall et al., 2005), although efficacy may be decreased if predominant species are naturally short in structure (e.g., blue grama; *Bouteloua gracilis*). Consequently, boundary management may be more effective if multiple years of control are paired with grazing exclusion to facilitate biomass accumulation. Temporary grazing exclosures can be cost-prohibitive but the emerging technology of virtual fencing (e.g., Campbell et al. 2019) might provide the means to facilitate cost-effective and lasting boundary management zones.

Declaration of Competing Interest

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

CRediT authorship contribution statement

Lindsey M. Buehler: Writing – original draft, Investigation, Formal analysis, Data curation. **David J. Augustine:** Writing – review & editing, Conceptualization. **Lauren M. Porensky:** Writing – review & editing, Conceptualization. **Courtney J. Duchardt:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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