Interacting effects of disease and weather variability on rangeland biodiversity associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies

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Key words: disturbance, ecology, ecotone, mountain plover, grassland wildlife

Abstract
Rangeland ecosystems worldwide are experiencing novel pressures during the Anthropocene, including land conversion, disease dynamics, non-native species, and climate change. These issues can be compounded in rangelands occupied by burrowing rodents. Often considered keystone species important for maintaining rangeland biodiversity, these species often experience widespread control efforts because of their potential to reduce forage for livestock. We examined the effects of climatic variation and disease on bird communities associated with a North American burrowing rodent, the black-tailed prairie dog (*Cynomys ludovicianus*). Following an outbreak of sylvatic plague (*Yersinia pestis*) in the prairie dog population, we observed rapid shifts in taxa reliant on either prairie dog engineering or prairie dogs as a prey source. Responses in species sensitive to vegetation structure were amplified due to above average precipitation for 16 months following the plague event, leading to rapid accumulation of biomass. These results highlight not only the rapidity with which communities respond to the removal of prairie dogs, but also emphasize the tenuous status of these communities with increasing climatic variability and decreasing tolerance for prairie dogs on the predominantly agricultural lands within their range.

Introduction
Social, burrowing rodents play an important ecological role in rangelands around the globe (Davidson et al. 2012). Within the Great Plains of North America, herbivory, clipping, and burrowing by black-tailed prairie dogs (*Cynomys ludovicianus*; hereafter "prairie dog") generates habitat for many wildlife species of conservation concern, and the species serves also serves as a prey resource for predators including raptors and the endangered black-footed ferret (*Mustela nigripes*). These same behaviors lead to direct conflict with livestock (Miller et al. 2007), thus prairie dog populations are routinely controlled to mitigate their effects. Control efforts can have negative impacts on associated wildlife, especially those that depend on the species for habitat suitability or food. In addition to intentional control, prairie dogs can experience outbreaks of sylvatic plague (*Yersinia pestis*; hereafter, "plague"), a non-native disease that can result in >95% mortality (Cully et al. 2010). Control efforts and disease have reduced prairie dog populations range-wide warranting increased attention on how disease dynamics and climatic variation can influence the vegetation structure of rangelands and associated wildlife community dynamics. We evaluated prairie dog disturbance, vegetation structure, and avian community dynamics within the Thunder Basin National Grassland of Wyoming USA to evaluate how individual species and bird communities respond to the removal of prairie dogs via plague and concurrent interannual variation in climate.

Methods and Study Site
We performed our study within the U.S. Forest Service Thunder Basin National Grassland in northeastern Wyoming, USA (43.9482° N, 104.8620° W). This region is located on the ecotone between mixed-grass prairie and sagebrush steppe and is thus typified by patches of mid-stature grasslands and shrublands. Prairie dog colonies ranged between 10 and 4000 hectares in size and vegetation on colonies included short-statured graminoids generally no more than a few inches in height, and annual forbs. Total colony area increased from 2015–2017, but prairie dog numbers declined sharply following an outbreak of plague in the summer of 2017.

We worked with partners to map prairie dog colonies in the study area each year between 2015–2019 by delineating colony boundaries based on prairie dog burrows. We assessed avian responses to prairie dog disturbance by surveying established transects each year during the avian breeding season. Transects were located both on and off prairie dog colonies to capture variation in community structure with disturbance (see

Duchardt et al. 2018 for detailed methods). At each survey location, we also assessed visual obstruction using a Robel pole, because of known associations between visual obstruction and grassland bird habitat suitability (Robel 1970, Fisher and Davis 2010).

We used general linear models to test the interactive effects of prairie dog disturbance, plague, and precipitation on vegetation structure. We then quantified responses of individual bird species to fluctuations in prairie dog disturbance and precipitation and used non-metric multidimensional scaling (NMDS) to visualize how bird communities responded to these fluctuations. We performed ordinations only on the bird communities expected to respond directly to structural changes in vegetation due to the removal of prairie dogs (i.e., raptor species were not included in ordinations). All analyses were performed in base R or the VEGAN package (R Development Core Team 2020).

Results

The prairie dog colony complex in Thunder Basin in 2017 represented the largest in the world. Visual obstruction on prairie dog colonies averaged 2.1 cm (SE 0.08), while undisturbed sites averaged approximately 3x that value (6.2 cm, SE 0.28). However, following the plague outbreak in late summer 2017, prairie dog numbers plummeted and occupied areas in 2018 were 0.5% of the maximum extent. The first year following plague coincided with the second greatest precipitation total of the past 100 years (53.8 cm). Removal of prairie dog disturbance combined with above average precipitation resulted in rapid accumulation of biomass on former prairie dog colonies in 2018–2019. Visual obstruction on former colonies tripled post-plague (6.2 cm, SE 0.24). Visual obstruction on undisturbed sites was also somewhat higher (8.2cm, SE 0.4; 1.4 times the average in 2015–2017). Model results indicated significant additive effects of both disturbance removal and precipitation on vegetation structure.

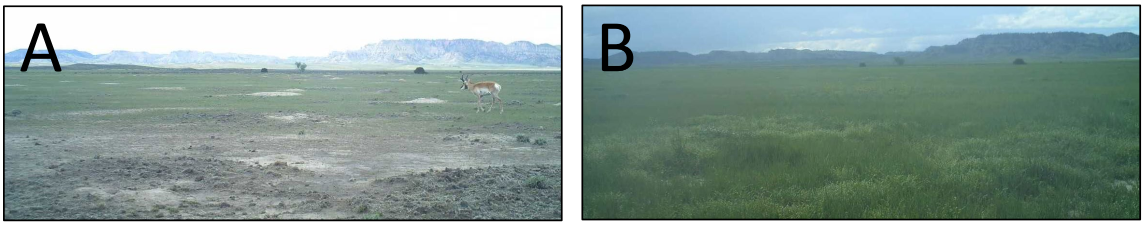

Figure 1. Vegetation on an active prairie dog colony in 2017 (A) compared to vegetation structure on the same colony location after plague (B)

We observed rapid changes in the bird community following the plague event of late summer 2017. We detected declines in golden eagles (*Aquila chrysaetos*) and ferruginous hawks (*Buteo regalis*), two raptor species that favour prairie dogs as prey. We also observed a steep decline in mountain plovers (*Charadrius montanus*), a species listed as Near Threatened on the IUCN Red List known to rely on vegetation structure of prairie dog colonies (Table 1). While abundances of many other species did not change, two nomadic mid-grass species, grasshopper sparrow (*Ammodramus savannarum*), and lark bunting (*Calamospiza melanocorys*) increased markedly in 2018–2019 (Table 1).

Table 1. Trends in precipitation, occupied prairie dog acres, and avifauna in the Thunder Basin National Grassland of Wyoming, USA in 2015-2019. Total precipitation is shown for the months most likely to affect vegetation structure during the breeding season. Species numbers represent raw counts at the same survey locations in each year.

Year	Mar.-Jul. precip (cm)	Prairie dog colony area (ha)	Species associated with prairie dogs: Burrowing owl	Ferruginous hawk	Golden eagle	Horned lark	Mountain plover	Species associated with midgrass structure: Grasshopper sparrow	Lark bunting	Western meadowlark	Species associated with shrubs: Brewer's sparrow	Sage thrasher
2015	14.06	5616	0	1	11	356	56	9	143	395	194	9
2016	7.81	6505	3	6	7	374	40	1	69	378	159	6
2017	8.92	10330	8	13	23	319	48	6	135	543	124	7
2018	15.69	47	6	0	6	338	3	62	858	467	86	1
2019	11.04	260	1	0	3	304	12	167	995	498	117	2

We conducted an NMDS ordination on bird communities located on and off prairie dog colonies. Our analysis yielded a two-dimensional solution with a stress of 0.11. Using the 'vegfit' function we overlaid the effect of disturbance and annual precipitation of bird communities. Although communities associated with prairie dogs and those associated with undisturbed habitat both changed substantially across the study period, changes in undisturbed sites were linked only to changes in precipitation, while shifts in bird communities on prairie dog colonies tracked along axes of disturbance and precipitation.

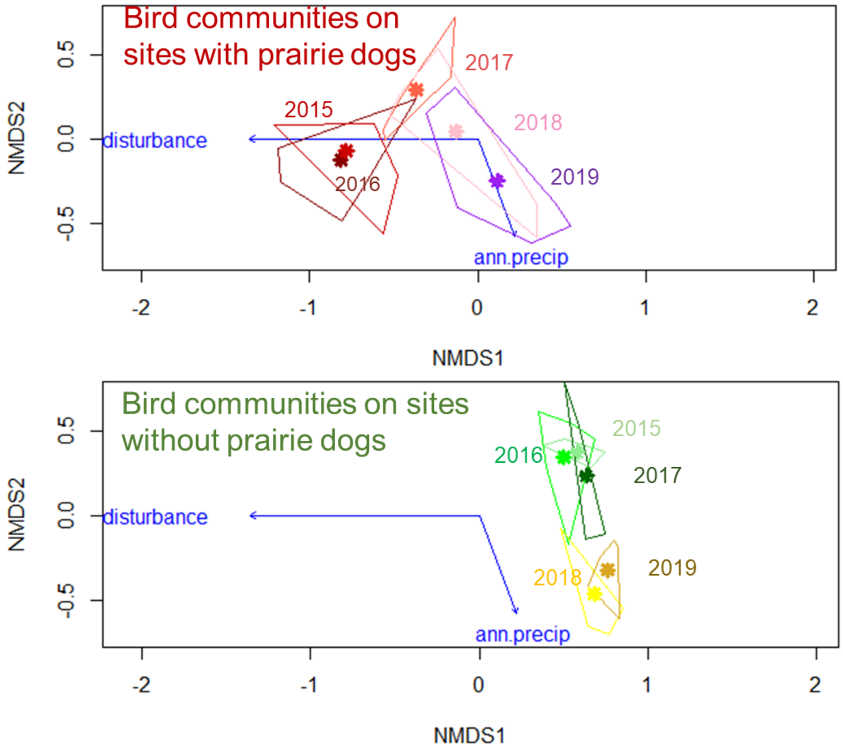

Figure 1. NMDS ordinations of avian communities from 2015–2019 in the Thunder Basin National Grassland in Wyoming, USA. Top panel shows shifting bird communities on prairie dog colonies (and the same areas following plague in 2018 and 2019) as a function of both disturbance and annual precipitation. The bottom panel depicts shifting communities on undisturbed sites in the same years, mainly linked with high precipitation in 2018.

Discussion

We observed rapid changes in both vegetation and bird community structure in the years following a plague outbreak in prairie dogs. Although few studies have tracked community responses to plague outbreaks in prairie dogs, previous studies have generally observed this process occurring more slowly. For example, in shortgrass prairie, researchers did not observe steep declines in mountain plover abundance until the second year following a plague event (Augustine et al. 2008). It is likely that in mixed-grass prairie these responses may be quicker; however, this was compounded by an abnormally wet year in this system.

Despite wetter years improving forage availability for livestock, producers are unlikely to be able to take full advantage of this availability if climatic shifts are rapid and unpredictable. Similarly, large "boom-and-bust" cycles of prairie dogs have negative impacts on both producers and wildlife. Grassland birds co-evolved with fluctuating disturbance and climatic variation, which explains the relatively high degree of nomadism in many of these species. However, some species, like mountain plover, exhibit moderate site fidelity and even nomadic species are limited by the ever-shrinking availability of grassland habitat in North America. Conflict between livestock and prairie dogs is likely to continue, and increasing variability predicted under climate models is likely to exacerbate these conflicts. Identifying the drivers of these boom-and-bust cycles and working with producers and stakeholders to identify workable solutions on multi-use rangelands will be necessary to maintain biodiversity in this system.

Acknowledgements

We would like to thank the USDA-Agricultural Research Service, University of Wyoming, The U.S. Forest Service, the Thunder Basin Grassland Prairie Ecosystem Association, and Great Plains consulting for assistance in project planning and data collection.

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