








## ARTICLE

# Disease and weather induce rapid shifts in a rangeland ecosystem mediated by a keystone species (*Cynomys ludovicianus*)

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## Abstract

Habitat loss and changing climate have direct impacts on native species but can also interact with disease pathogens to influence wildlife communities. In the North American Great Plains, black-tailed prairie dogs (*Cynomys ludovicianus*) are a keystone species that create important grassland habitat for numerous species and serve as prey for predators, but lethal control driven by agricultural conflict has severely reduced their abundance. Novel disease dynamics caused by epizootic plague (*Yersinia pestis*) within prairie dog colonies have further reduced prairie dog abundances, in turn destabilizing associated wildlife communities. We capitalized on a natural experiment, collecting data on prairie dog distributions, vegetation structure, avian abundance, and mesocarnivore and ungulate occupancy before (2015–2017) and after (2018–2019) a plague event in northeastern Wyoming, USA. Plague decimated black-tailed prairie dog populations in what was then the largest extant colony complex, reducing colony cover in the focal area from more than 10,000 ha to less than 50 ha. We documented dramatic declines in mesocarnivore occupancy and raptor abundance post-plague, with probability of occupancy or abundance approaching zero in species that rely on prairie dogs for a high proportion of their diet (e.g., ferruginous hawk [*Buteo regalis*], American badger [*Taxidea taxus*], and swift fox [*Vulpes velox*]). Following the plague outbreak, abnormally high precipitation in 2018 hastened vegetation recovery from prairie dog disturbance on colonies in which constant herbivory had formerly maintained shortgrass structure necessary for certain colony-associates. As a result, we observed large shifts in avian communities on former prairie dog colonies, including near-disappearance of mountain plovers (*Charadrius montanus*) and increases in mid-grass associated songbirds (e.g., lark bunting [*Calamospiza melanocorys*]). Our research highlights how precipitation can interact with disease-induced loss of a keystone species to induce drastic and rapid shifts in wildlife communities. Although grassland taxa have co-evolved with high spatiotemporal variation, fragmentation of the remaining

North American rangelands paired with higher-than-historical variability in climate and disease dynamics are likely to destabilize these systems in the future.

#### KEYWORDS

disturbance, grassland birds, Great Plains, mesocarnivore, mountain plover, prairie dog, ungulate

## INTRODUCTION

Ecological theory was built on the concept of systems at equilibrium either under short or long timescales (Holling, 1973; Wilson & MacArthur, 1967). However, many ecological systems are better described under a nonequilibrium model (Briske et al., 2017; Rapacciuolo & Blois, 2019), especially those ecosystems that co-evolved with frequent disturbance. These systems are by nature more difficult to characterize and predict, but rapid change in the Anthropocene (e.g., climate change; Gaüzère et al., 2018; disease, Holdo et al., 2009) threatens to further destabilize all ecological systems, leading to novel outcomes. Destabilization could have dramatic, undesirable consequences for imperiled systems expected to simultaneously support human use and retain ecological function, such as rangelands.

Rangelands (typically grasslands, shrublands, or other aridlands) are poorly described by single-equilibrium models and are shaped by highly variable disturbance and climate regimes (Briske et al., 2017). Although rangelands have historically occupied nearly half of the planet's terrestrial surface, nearly all of these lands have been converted to some form of human use (Sterling & Ducharme, 2008). Within North America, 40% of the Great Plains have been converted to rowcrop agriculture (Augustine et al., 2019), and the pace of cropland conversion remains rapid (Gage et al., 2016; Wright & Wimberly, 2013). Most remaining grasslands and shrublands in North America are managed as dual-purpose rangelands, providing forage for livestock and habitat for wildlife.

Although research supports the compatibility of managing rangelands for both livestock and biodiversity conservation (Augustine & Derner, 2021; Fuhlendorf et al., 2012; Riginos et al., 2012), the balance is delicate, and made increasingly complex on rangelands occupied by burrowing rodents such as prairie dogs (*Cynomys* spp.). As with many burrowing mammals (Davidson et al., 2012), black-tailed prairie dogs (*Cynomys ludovicianus*; from this point forward “prairie dog”) play an integral role as keystone species within the North American Great Plains. Through herbivory, clipping, and

burrowing, prairie dogs generate habitat for associated wildlife species including burrowing owls (*Athene cunicularia*) that nest in prairie dog burrows and mountain plovers (*Charadrius montanus*) that select for the short, sparse vegetation they engineer (Duchardt et al., 2020). Prairie dogs also serve as a food source for predators, including raptors, foxes (*Vulpes* sp.), coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), and the endangered black-footed ferret (*Mustela nigripes*; Hoogland, 2013; Lomolino & Smith, 2004).

Despite their keystone role (Kotliar et al., 1999), prairie dogs are considered a nuisance or noxious species in some states in the USA because of their capacity to compete with livestock for forage, and they are lethally controlled throughout their range (Augustine & Derner, 2021; Derner et al., 2006; Miller et al., 2007; Wyoming Weed and Pest Council, 2019). Due to the combined effects of habitat loss and control efforts that began in the 19th century, prairie dogs currently occupy a small fraction of their historical range (Knowles et al., 2002; Luce, 2003). Additionally, prairie dogs have been decimated by epizootic outbreaks of sylvatic plague (*Yersinia pestis*). This nonnative pathogen was introduced to North America in the early 1900s and often resulted in >99% mortality in localized populations (Cully et al., 2006). Plague has been present throughout much of the prairie dog's range for the past one to three decades (Cully Jr. et al., 2010). The combined pressures of disease, habitat loss and control efforts that have severely reduced prairie dog populations have resulted in cascading declines in associated wildlife species (Ceballos et al., 2010; Davidson et al., 2012; Dobson & Lyles, 2000; Hoogland, 2013). Despite observed range-wide declines in associated species and detection of community shifts following long-term changes in prairie dog abundance (e.g., Ceballos et al., 2010), few studies have captured species-specific responses to plague events (e.g., Augustine et al., 2008; Seery & Matiatos, 2000), and assessments of community-level responses are even more rare. As such, the direct and indirect effects of plague events on associated vertebrate communities are still poorly understood (Eads & Biggins, 2015).

Drastic fluctuations in local prairie dog abundances across time due to plague (“boom-and-bust” cycles [Davidson et al., 2022]) are likely to impact wildlife

communities by reducing the availability of both prey and habitat. However, in considering the impacts of plague at the community level, it is important to recall that many rangeland wildlife species possess innate coping strategies for habitat variability. Periodic disturbance and unpredictable climate are the defining characteristics of rangelands (Samson & Knopf, 1994), and spatial and temporal variability has driven a suite of adaptations in species that inhabit these systems. For example, bison (*Bison bison*) and other ungulates track (Merkle et al., 2016), and sometimes engineer (Geremia et al., 2019) variable patterns of green-up following disturbance, and migrant songbirds can dramatically shift their breeding ranges in response to extreme precipitation years (e.g., Bateman et al., 2015). However, climate projections for the North American Great Plains consistently predict greater variation in precipitation with increased heavy precipitation events (Conant et al., 2018), which may present a novel degree of variability beyond those experienced historically. Although rangeland fauna co-evolved with, and may be better able to respond positively to variability, than wildlife in more stable or equilibrational ecosystems, the degree of variability predicted under climate change is unprecedented and may interact with other novel drivers such as disease (e.g., Biggins et al., 2021).

Compounding the challenges of climate change and novel disease interactions is a continued decrease in habitat availability. Variability in suitable habitat was historically buffered by broad-scale habitat availability, such that animals could alter their distribution to obtain needed resources in a given season. This is no longer the case as rangelands, and particularly grasslands, continue to be fragmented with less habitat remaining each year (Augustine et al., 2019). Quantifying the magnitude and speed at which species associated with prairie dogs respond to these novel drivers would enable the creation of models for holistic prairie dog management on the remaining grassland habitat, but this information has been previously unavailable.

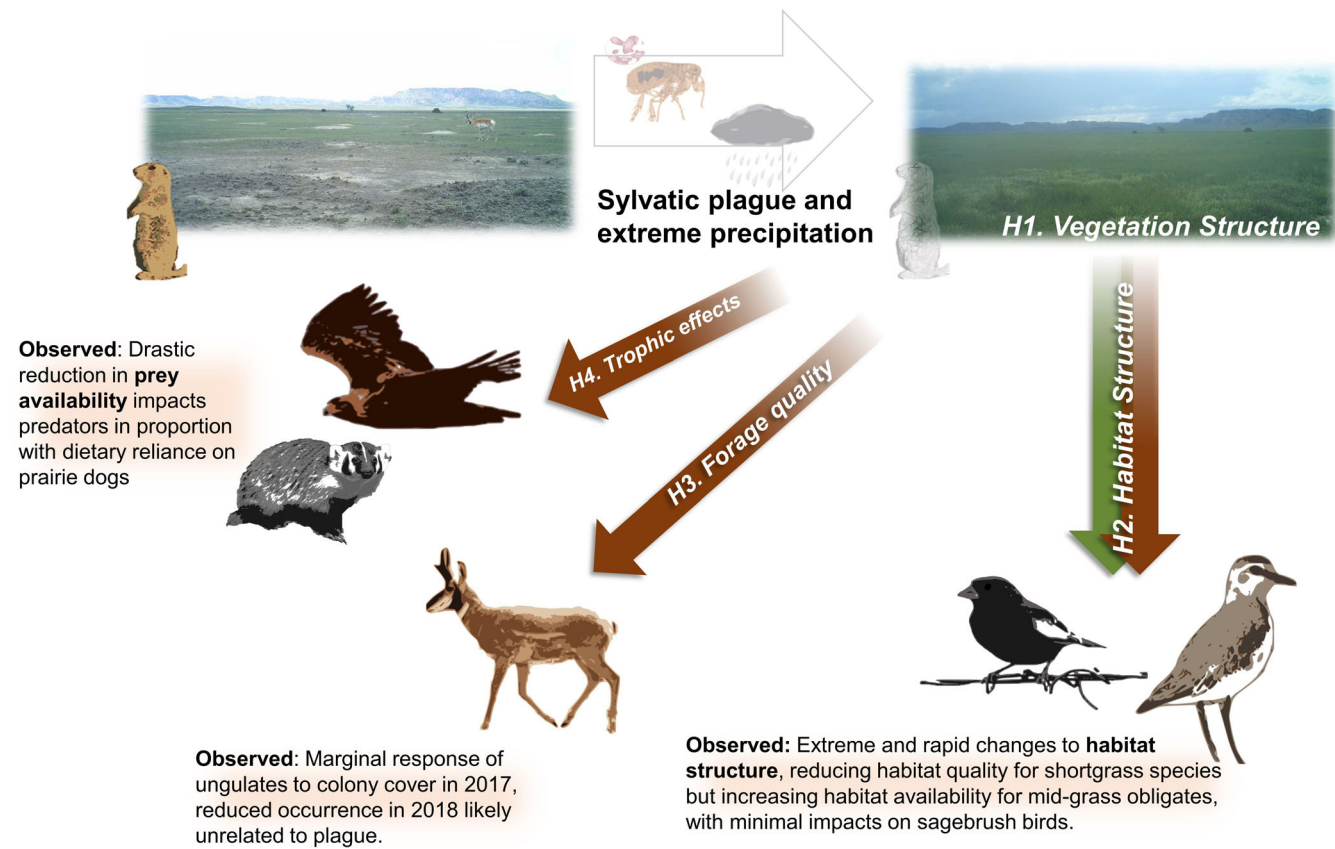
We capitalized on a natural experiment in which we tracked responses in vegetation, avian communities, and the occupancy of mesocarnivores and ungulates, before and after a plague event in a prairie dog colony complex at a grassland–shrubland ecotone. Following a severe plague outbreak combined with above-average precipitation years, we were able to examine the combined impacts introduced by disease, disturbance, and extremes in precipitation that have contributed to transforming vertebrate communities in the northern Great Plains. We hypothesized that widespread plague would yield taller and denser vegetation on colonies (H<sub>1</sub>. Vegetation structure; Figure 1), which would lead to decreased habitat suitability for shortgrass songbirds but increased suitability for mid-grass obligates (H<sub>2</sub>.

Habitat structure; Figure 1). Although taller and denser vegetation would yield greater forage availability, we hypothesized that decreased forage quality (due to the loss of herbivory and clipping by prairie dogs) would reduce the use by ungulates (H<sub>3</sub>. Forage quality; Figure 1). Prairie dogs maintain forage in an early phenological state (Connell et al., 2019; Whicker & Detling, 1988) and can trigger a shift from graminoids to forbs (Duchardt et al., 2021). Decline in the major prey resource (prairie dogs) was hypothesized to lead to declines in mesocarnivore occupancy and use in this landscape (H<sub>4</sub>. Trophic effects; Figure 1). We predicted that population responses would be most dramatic and swift for the carnivores in our study system that relied on prairie dogs for a large proportion of their diet (e.g., ferruginous hawks [*Buteo regalis*], American badger, and swift fox [*Vulpes velox*]; Kagel et al., 2020; Nicholson et al., 2006; Seery & Matiatos, 2000), with the magnitude of their declines increasing with their dietary reliance on prairie dogs. We anticipated bird communities, which respond more to vegetation structure, would differ most at 2 years post-plague. This is because in other systems in which plague has occurred, responses in vegetation structure and associated species have typically taken multiple years, probably due to the slow recovery of vegetation structure (Augustine et al., 2008, but please refer to Seery & Matiatos, 2000).

## METHODS

### Study area

We collected data between 2015–2019 in the Thunder Basin Ecoregion of northeastern Wyoming, USA (Appendix S1: Figure S1). Thunder Basin is located at the ecotone between the Great Plains and sagebrush (*Artemisia* spp.) steppe, with mean annual precipitation ranging between 25 and 35 cm, generally falling during spring and summer (Porensky et al., 2018). This rangeland system is a mosaic of vegetation communities including sagebrush, shortgrass prairie, mixed-grass prairie, ponderosa pine (*Pinus ponderosa*) woodlands and plains cottonwood-dominated (*Populus deltoides* ssp. *monilifera*) riparian areas. Our research focused on a mosaic of sagebrush–grasslands, grasslands, and prairie dog colonies. In sites without prairie dogs, shrub species included Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) and other sagebrush species, greasewood (*Sarcobatus vermiculatus*) and broom snakeweed (*Gutierrezia sarothrae*). Common graminoids included blue grama (*Bouteloua gracilis*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and threadleaf sedge (*Carex flifolia*). Prairie dog colonies were dominated by western wheatgrass, plains prickly



**FIGURE 1** Conceptual figure describing the impacts of disease and climate on vegetation structure and associated species within the Thunder Basin Ecoregion, Wyoming, USA. Top panels show the vegetation structure in late May 2017 (left; pre-plague) and in 2018 (right; post-plague). Hypotheses of interest are noted in white text, along with predicted positive or negative effects (green or brown, respectively). We also note observed trends and how these aligned with hypotheses. Original photographs for creation of graphics are from C. Duchardt, J. Hennig, or the public domain.

pear (*Opuntia polyacantha*), and short-lived forb species (e.g., woolly plantain [*Plantago patagonica*], desert madwort [*Alyssum desertorum*], common pepperweed [*Lepidium densiflorum*]). Typical of most extant prairie dog complexes, the Thunder Basin Ecoregion has experienced multiple cycles of colony growth followed by outbreaks of sylvatic plague (2000 and 2007; Cully Jr. et al., 2010), with the most extreme event in the last 20 years occurring at the end of the growing season in 2017 (Davidson et al., 2022).

## Study design

### Prairie dog colony mapping

Prairie dog colony mapping occurred within the study area annually between 2015 and 2019. Mapping was conducted by multiple stakeholders including the U.S. Forest Service and Thunder Basin Grassland Prairie Ecosystem Association (TBGPEA). Mapping was conducted either on foot or in an all-terrain vehicle

(ATV) using a global positioning systems (GPS) device to map outer boundaries of colonies, similar to Cully Jr. et al. (2010). Boundaries consisted of outer active burrows, with activity denoted by vegetation clipping, recent digging, or fresh scat. Following a plague event in the summer and fall 2017, mapping efforts were complicated by extreme contraction in active colonies. In response, we used a two-phase approach to mapping in 2018 (Davidson et al., 2022), with the first phase consisting of surveys conducted in April–July of point grids spaced at 600 m intervals to detect signs of prairie dog occupancy. In autumn, phase two consisted of revisiting areas with activity and mapping active burrows. Mapping in 2019 consisted of revisiting previously identified occupied areas and mapping in those areas. Please refer to Davidson et al. (2022) for additional methodological details. We did not directly quantify prairie dog density in the study area over time, but did observe burrow densities of 150/ha and confirmed active (via scat or active digging) burrow densities of 68/ha in 2017 (Duchardt et al., 2021).



## Avian and vegetation sampling

We conducted pre- and post-plague sampling at locations corresponding with avian point-count transects established in 2015 (Duchardt et al., 2019). One set of transects was randomly placed with the constraint that transects fell entirely within prairie dog colonies (“colony transects”), a second set was located randomly with the requirement that transects crossed the edge of a prairie dog colony with four points located outside the colony and one to four within the colony, depending on colony size (“edge transects”), and a third set was located nonrandomly in areas without prairie dogs and characterized by extensive sagebrush–grassland habitat (“sagebrush–grassland transects”). All transects contained between five and eight points spaced 250 m apart. Only a subset of these transects (five undisturbed sagebrush–grassland, eight colony, 23 edge; Appendix S1: Figure S1) were surveyed in all years between 2015 and 2019; subsequently, we only used these data for this analysis ( $N = 263$  point-count locations).

We conducted avian surveys between sunrise and 10:00 AM on days with low wind and no rain (Pavlacky et al., 2017) from mid-May to mid-June, 2015–2019. By traveling to many points via ATV we ensured more effective detection of mountain plovers, which display more cryptic behavior in response to observers on foot (Dinsmore et al., 2002). Between mid-June and late-July each year, we measured maximum vegetation height and visual obstruction (a metric incorporating both vegetation height and density) using a Robel pole (Robel et al., 1970). We collected these measurements every 5 m along 30-m transects originating at the point-count location and running perpendicular to the axis of the point-count transect.

## Mesocarnivore and ungulate sampling

We used previously established camera traps (please refer to Connell et al., 2018) and supplemented these with additional camera locations to begin characterizing the mammalian communities at these sites. We established 12 camera traps (Browning BTC-5HD, 20 s delay, two shot) in 2016 as part of a study to detect wildlife use of sites on historical fire scars, prairie dog colonies, and undisturbed areas (Connell et al., 2018). In 2017, we added 17 camera traps (Bushnell Trophy Camera 119636TCP) at a subset of the avian point-count locations described in section *Avian and vegetation sampling*. We selected locations for camera placement as follows: all point-count locations were characterized by duration of prairie dog occupancy (0–15 years), and we randomly selected point locations along a gradient of occupancy duration

(Appendix S1: Figure S1). These cameras were deployed from mid-May 2017 through April 2019. All cameras were placed ~1 m high with an unobstructed viewshed away from fences.

We reviewed all photographs to determine the presence of any animal species and recorded the number of each taxon present per photograph. We trained each individual involved in photo processing in species identification, and all data used in analyses were reviewed by individuals with >10 years field experience working with North American Great Plains and sagebrush wildlife (C. Duchardt and N. Dufek [please refer to “*Acknowledgments*”]). To align with the timing of breeding bird surveys and vegetation data, we extracted and analyzed camera trap data from mid-May to mid-August in 2017 and 2018 for analysis.

## Precipitation data

We obtained precipitation data for each year from the NOAA divisional time series data for Wyoming Climate Division 7, the Cheyenne Niobrara drainage (NOAA, 2022). This division includes the entire study area and was centered at the convergence of Weston, Converse, Campbell, and Niobrara counties. We extracted data on cumulative annual precipitation for each year between 2015 and 2019.

## Analytical framework

### Avian and vegetation responses

We summed detections of each bird species on and off active colonies annually, correcting for number of survey points per transect (i.e., divided by number of points). Some target species had few detections (e.g., burrowing owl); therefore, we did not adjust for detectability and instead used number of detections as a proxy for abundance (but please refer to Duchardt et al., 2018, 2020 for detectability-adjusted abundances prior to plague in this system). To help mitigate detectability issues, we used a post-hoc detection radius of 200 m for all songbirds and shorebirds; after this distance, we observed detectability dropping off markedly in other data collected in this system. Because most raptors were detected >200 m, we used an unlimited radius for raptor detections. The majority of passerine and shorebird detections were aural, while raptors were typically detected in flight; therefore, differences in vegetation structure were likely to have had little impact on detectability.

We used distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) using the “vegan” package in R (Oksanen et al., 2020) to examine avian community structure and change on and off prairie dog colonies following the plague outbreak. This technique employs RDA based on Bray–Curtis distance, providing a more rigorous test of covariate importance than other nonmetric approaches (e.g., NMDS; Kruskal, 1964) while still being robust to non-normal data (a common feature in data based on avian point counts). Prior to conducting the ordination, we applied a Wisconsin square-root transformation to relativize the data and reduce the influence of dominant species relative to less abundant species (van der Maarel, 1979). We summarized point data at the transect level for “colony” and “sagebrush” transects. We split edge transects each year into “inside” or “outside” colony points according to each year’s colony distribution. We tracked avian community change over time at both the transect level and in areas historically colonized versus uncolonized by prairie dogs. To assess the potential roles of plague and precipitation in the system, we included the environmental variables of annual precipitation and percent prairie dog colony cover within 200 m of the transect. We also included a categorical variable that represented sagebrush dominated versus other (colony and edge) because we assumed some variation in bird communities was driven by shrub cover. We then used a permutational ANOVA in *vegan* (`anova.cca, by=‘term’`) to test for the significance of each of these variables (Legendre & Legendre, 1998).

We averaged readings of visual obstruction and maximum vegetation height at the point level annually. We then used the *glm* function in the *stats* package in base R to model the responses of maximum vegetation height and visual obstruction at the point level to annual precipitation and percentage prairie dog colony cover within 30 m of the point (the length of our vegetation transect). We considered models that included each of these factors individually, as well as both the additive and interactive combination of the two factors. We used Akaike’s information criterion corrected for small samples ( $AIC_c$ ; Burnham & Anderson, 2002) to compare each set of models with a null model.

## Mesocarnivore and ungulate occupancy

We estimated single season occupancy of five mesocarnivores (swift fox, red fox [*V. vulpes*], coyote, American badger, bobcat [*Lynx rufus*]) and three ungulates (elk [*Cervus canadensis*], mule deer [*Odocoileus hemionus*], pronghorn [*Antilocapra americana*]) in the summers of 2017 and 2018. We present detections of cattle (*Bos taurus*) as a control

because, although cattle grazing behavior may be affected by prairie dog activity (e.g., Sierra-Corona et al., 2015), cattle movement among pastures was human driven and therefore not expected to be impacted by plague. We fitted single season occupancy models (MacKenzie et al., 2017) to weekly camera trap detections using the *unmarked* R package (Fiske & Chandler, 2011). To minimize temporal autocorrelation, we recorded presences per species at each camera trap station at 1-week intervals from mid-May through mid-August in 2017 and 2018 (similar to Davidson et al., 2018). Because the average distance between cameras was >2 km, we did not model spatial autocorrelation in detection probability. We predicted that the proportion of prairie dog colony cover would be a significant driver of site occupancy, so we calculated the proportion of a 2 km radius buffer around each camera trap that was occupied by prairie dogs. We used this buffer size as it approximates average home range sizes in swift fox (Kamler et al., 2003; Pechacek et al., 2000), and because a larger radius would lead to increased overlap among some cameras. We evaluated three models per species to assess whether the proportion of the surrounding area occupied by prairie dogs was an informative predictor of mesocarnivore and ungulate occupancy in 2017. These included an intercept-only model, a linear effect of proportion of colony on occupancy, and a quadratic effect of proportion of colony on occupancy. We included a quadratic effect because we had previously observed nonlinear responses of songbirds to aspects of colony cover in this system (Duchardt et al., 2019). We did not include any covariates in the detection portion of the model because we were mainly interested in how the presence of prairie dogs influenced occupancy. We only used the proportion of colony cover covariate in the 2017 models because prairie dogs were functionally absent in 2018 (Appendix S1: Figure S1). Consequently, we only ran an intercept-only model to estimate occupancy in 2018. We used  $AIC_c$  to rank models and report beta coefficients and standard errors of detection and occupancy from the top model. To understand the influence of plague on regional-scale occupancy rates of mesocarnivores and ungulates, we compared mean occupancy between 2017 (pre-plague) to 2018 (post-plague). We did this by predicting mean site occupancy from intercept-only models, and determining whether 95% confidence intervals overlapped between 2017 and 2018 estimates.

## RESULTS

Prairie dog colony cover in the core area increased from 2015 to 2017 (Table 1). Maximum colony coverage reached 10,391 ha on public lands in 2017. The entire complex, including colonies on private lands, exceeded 16,000 ha in 2017, but these areas were not surveyed in

**TABLE 1** Responses of prairie dog colony cover, vegetation structure, and multiple wildlife taxa to changing climate and disease dynamics from 2015 to 2019 in the Thunder Basin Ecoregion, Wyoming, USA. Mesocarnivore and ungulate data were collected from camera traps deployed 2017–2018.

Wildlife and vegetation trends	2015 <sup>a</sup>	2016 <sup>a</sup>	2017 <sup>a</sup>	2018 <sup>a</sup>	2019 <sup>a</sup>	Conservation status
	Prairie dog core area (ha <sup>1</sup> ) <sup>a</sup>					
	5616	6505	10,391	47	265	
<b>Passerines and shorebirds<sup>b</sup></b>						
Mountain plover	0.18	0.11	0.16	0.01	0.04	IUCN-NT, FSS, SGCN
Lark bunting	0.49	0.26	0.50	3.11	3.57	
Grasshopper sparrow	0.03	0.00	0.02	0.22	0.61	FSS, SGCN
Brewer's sparrow	0.72	0.60	0.46	0.33	0.43	FSS, SGCN
Horned lark	1.24	1.31	1.11	1.17	1.12	
Killdeer	0.10	0.07	0.08	0.07	0.05	
Lark sparrow	0.17	0.13	0.08	0.11	0.14	
Loggerhead shrike	0.02	0.05	0.03	0.03	0.02	IUCN-NT, FSS
Sage thrasher	0.03	0.02	0.02	0.00	0.01	SGCN
Vesper sparrow	0.11	0.15	0.10	0.04	0.09	
Western meadowlark	1.40	1.33	1.72	1.56	1.72	
<b>Raptors and owls<sup>c</sup></b>						
Ferruginous hawk	0.00	0.02	0.05	0.00	0.00	FSS, SGCN
Golden eagle	0.04	0.03	0.09	0.02	0.01	SGCN
Red-tailed hawk	0.02	0.02	0.03	0.00	0.01	
Burrowing owl	0.00	0.01	0.03	0.02	0.00	FSS, SGCN
American kestrel	0.02	0.05	0.04	0.02	0.01	
Northern harrier	0.00	0.05	0.01	0.00	0.01	FSS
<b>Mammalian carnivores<sup>d</sup></b>						
Swift fox	...	...	0.25	0.07	...	FSS, SGCN
Badger	...	...	0.11	0.00	...	
Red fox	...	...	0.02	0.01	...	
Coyote	...	...	0.23	0.09	...	
Bobcat	...	...	0.03	0.00	...	
Raccoon	...	...	0.01	0.00	...	
Striped skunk	...	...	0.01	0.01	...	
<b>Ungulates<sup>d</sup></b>						
Pronghorn	...	...	0.69	0.36	...	
Mule deer	...	...	0.13	0.01	...	
Elk	...	...	0.11	0.03	...	
Cattle	...	...	0.12	0.15	...	
<b>Vegetation<sup>e</sup></b>						
Δ Visual obstruction inside/outside colony	4.70	3.61	3.63	2.59	1.45	
Δ Vegetation height inside/outside colony	17.91	10.90	9.56	5.70	3.19	

Abbreviations: FSS, Forest Service Sensitive Species (US Forest Service, 2018); IUCN-NT, International Union for the Conservation of Nature - Near-threatened (IUCN, 2021); SGCN, Wyoming Game and Fish Department - Species of Greatest Conservation Need (WGFD, 2010).

<sup>a</sup>Total hectares mapped in core area of study excluding private lands, as these were not mapped 2015–2016. Does not represent total prairie dog acres across the Thunder Basin study area.

<sup>b</sup>Number observed/number points surveyed. Detections were restricted to 200 m radius.

<sup>c</sup>Number observed/number points surveyed. Detections were unlimited radius.

<sup>d</sup>Number of site-weeks in which a species was detected in each year divided by the total number of unique site-weeks when cameras were active in that year (2017 = 363, 2018 = 265).

<sup>e</sup>Average reading (visual obstruction reading or maximum height) at sites occupied by prairie dogs subtracted from the average reading at unoccupied points in a given year. Because colonies expanded 2015–2017, but were functionally absent in 2018 and 2019, we used prairie dog occupancy status at the beginning of the study (2015) and tracked this across years.

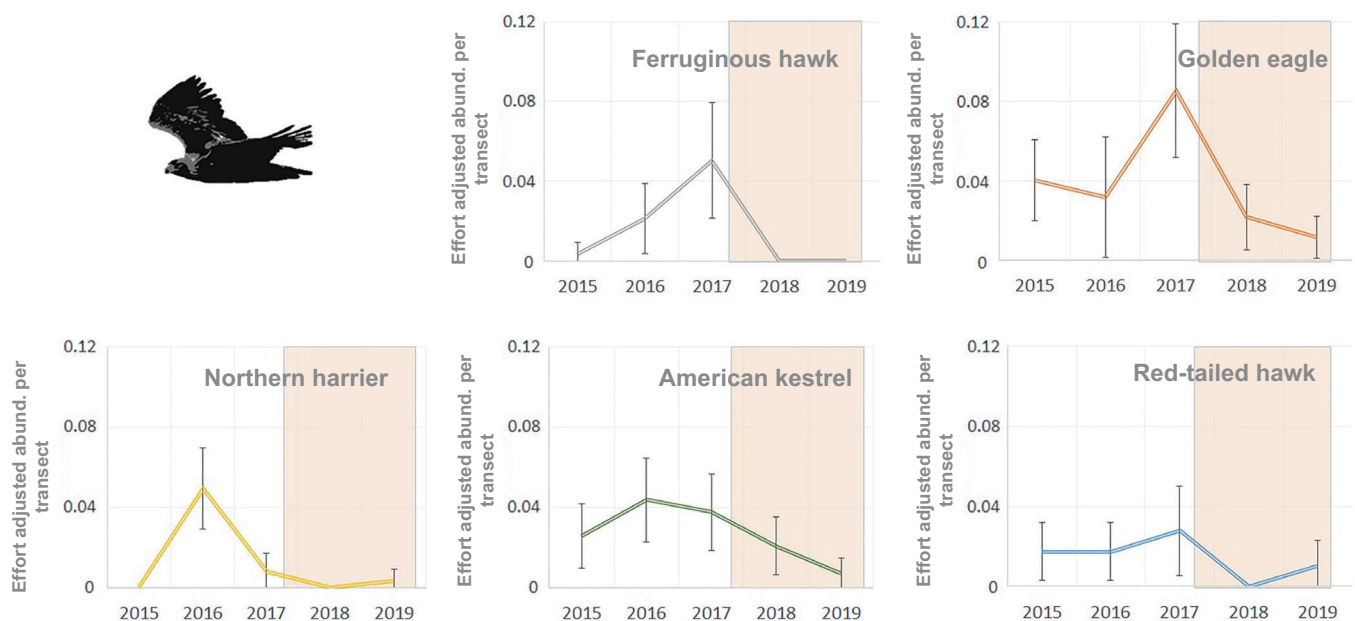
all years and are not discussed further. Plague was first detected in one localized area in mid-summer of 2017 (pers. observ. Dave Pellatz, Courtney Duchardt; Davidson et al., 2022); but by the following spring it had affected most of the region, leaving only 47 ha of colony in our focal study area in summer 2018. Prairie dogs occurred at low densities in areas where they persisted following the plague outbreak, typically in clusters of four or five individuals separated by >100 m. Consequently, prairie dog disturbance was functionally absent in 2018, except for one small complex (~400 ha) in the southeastern portion of the grassland, ~7 km from the nearest sampling location included in our focal study area. Concomitant with this reduction in prairie dog disturbance were climatic extremes observed in 2018 (Appendix S1: Figure S1). While 2017 was a relatively average year in terms of both moisture and temperature, 2018 represented the second wettest summer in these counties in half a century (NOAA, 2022); total precipitation from May through July was 13.7 cm in 2017 and 33.8 cm in 2018.

## Avian and vegetation responses

We observed 80 bird species during the 5-year period of study, including owls, passerines, raptors, shorebirds, and waterfowl. Across years and sites, the most common species observed were western meadowlark (*Sturnella neglecta*), horned lark (*Eremophila alpestris*) and lark bunting

(*Calamospiza melanocorys*; Table 1). Passerines associated with mid-grass structure, including western meadowlark, grasshopper sparrow (*Ammodramus savannarum*), and lark bunting, all reached their greatest abundances in the final 2 years of the study, following the plague event (Table 1). Conversely, mountain plover, which prefers early seral stage vegetation, declined to their lowest observed abundances in the year immediately following the plague event (effort-adjusted abundance was 16 times greater in 2017 vs. 2018; Table 1). Burrowing owls, which are dependent on burrow structures, were still observed in the first year following plague but their abundance decreased in 2019. Raptors that rely heavily on prairie dogs as prey also declined following plague (i.e., ferruginous hawk and golden eagle [*Aquila chrysaetos*]; Figure 2; Table 1) with no detections of ferruginous hawks after 2017. Red-tailed hawks (*B. jamaicensis*) showed modest but nonsignificant (based on 95% CIs) declines, whereas northern harrier (*Circus hudsonius*) and American kestrel (*Falco sparverius*) observations did not differ substantially in the latter part of the study period (Figure 2). Similarly, Brewer's sparrow (*Spizella breweri*) numbers were fairly constant across the study period, whereas the other sagebrush obligate passerine, sage thrasher (*Oreoscoptes montanus*), was relatively rare across all transects (Table 1).

We conducted a distance-based redundancy analysis based on community data at the transect scale focusing on 20 species of shortgrass, mid-grass, and sagebrush



**FIGURE 2** Number of observations of five raptor species adjusted for number of points surveyed, with 95% confidence intervals, between 2015–2019 in Thunder Basin Ecoregion, Wyoming, USA. Orange polygons indicate the responses after the plague event in the summer of 2017.



passerines and shorebirds. We also included burrowing owls in this ordination because of their association with colony habitat but did not include raptors because the scale of their habitat use extended beyond individual transects. Distance-based redundancy analysis yielded an adjusted  $R^2$  of 0.20. Percentage prairie dog cover had the strongest relationship with bird community data ( $F_{1,291} = 31.8$ ,  $p < 0.001$ ), followed by annual precipitation ( $F_{1,291} = 16.5$ ,  $p < 0.001$ ) and whether transects were dominated by sagebrush ( $F_{1,291} = 5.2$ ,  $p < 0.001$ ) (Figure 3a). Shortgrass associates (mountain plover [MOPL], horned lark [HOLA], and to some extent burrowing owl [BUOW]) received low scores on both axes, and were associated with increasing prairie dog cover. Species either strongly or moderately associated with sagebrush (e.g., Brewer's sparrow [BRSP] and vesper sparrow [VESP]) were more abundant on sagebrush transects, whereas lark bunting (LARB) and grasshopper sparrows (GRSP) increased with increasing annual precipitation (Figure 3a).

Post-plague, centroids for avian communities in undisturbed sagebrush–grasslands (Figure 3a, green and yellow) that had previously few to no prairie dogs previously shifted mainly upon an axis of increased precipitation, while bird communities on colony core centroids (Figure 3a, red and purple) shifted along axes of both disturbance and precipitation. To better visualize site-level trajectories across the study period, we mapped vectors for both colony and sagebrush–grassland transects across the study period (Figure 3b). The magnitude of change on former colonies (measured as vector length in Figure 3b) was even more apparent at the site level, as distance in ordination space of bird communities on a given site before plague compared with afterwards was greater than distances between centroids measured at the treatment scale (Figure 3a), but the direction of change followed the same general trend as observed in centroids.

For vegetation structure, model comparison using  $AIC_c$  indicated strong support ( $\Delta AIC_c$  293.41 from the null) for an additive effect of precipitation ( $\beta_{\text{precip}} = 0.26$ ,  $SE = 0.05$ ) and colony cover ( $\beta_{\text{colony}} = -0.04$ ,  $SE = 0.003$ ) on visual obstruction, and an interactive ( $\Delta AIC_c$  859 from the null,  $\beta_{\text{int}} = -0.005$ ,  $SE = 0.002$ ) effect of precipitation ( $\beta_{\text{precip}} = 1.39$ ,  $SE = 0.11$ ) and colony cover ( $\beta_{\text{colony}} = -0.06$ ,  $SE = 0.03$ ) on maximum vegetation height (Appendix S1: Tables S2 and S3).

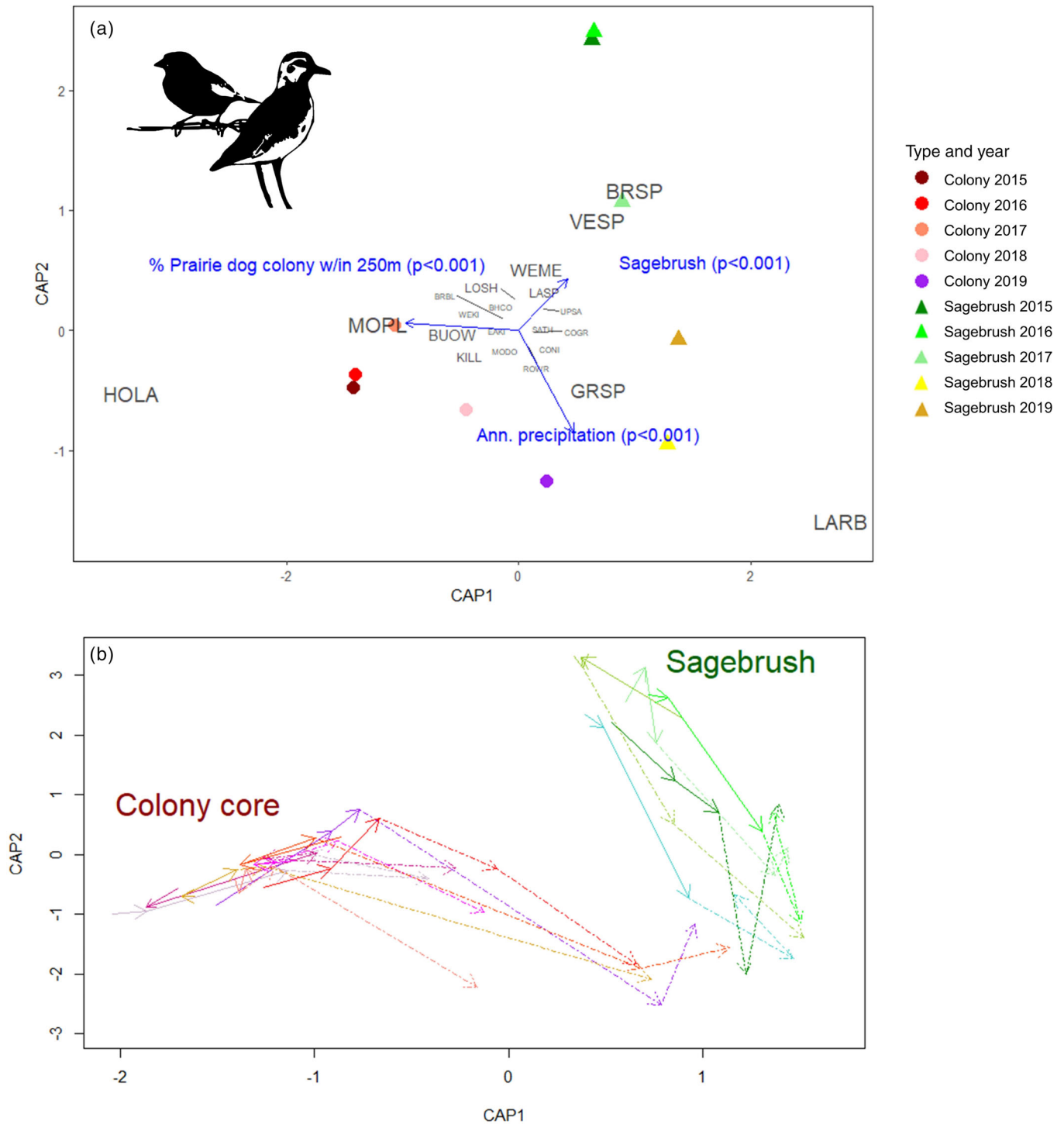
Visual obstruction on colonies during 2015–2017 ( $2.49 \text{ cm} \pm 95\% \text{ CI } 0.25$ ) was significantly lower than readings off-colonies ( $6.42 \text{ cm} \pm 0.61$ ). Visual obstruction on colonies occupied by prairie dogs 2015–2017 increased post-plague to  $5.88 \text{ cm} (\pm 0.6)$  and  $6.49 (\pm 0.73)$  in 2018 and 2019, respectively. Increases in visual obstruction on areas occupied inconsistently (either unoccupied for the entire study or having prairie dogs 1–2 years) were less

extreme ( $2018 = 8.47 \pm 1.05 \text{ cm}$ ,  $2019 = 8.06 \pm 1.15 \text{ cm}$ ), and were not different from formerly colonized areas in 2019. We also observed similar trends in changes of maximum vegetation height over time (Table 1).

## Mesocarnivore and ungulate occupancy

We examined more than 216,335 camera trap photographs between 2017 and 2018 (Figure 4). Pronghorn were the most frequently detected native mammal at the weekly scale and were observed on all sites. Estimated detection probability for ungulates varied widely, from 0.71 for pronghorn in 2017 to 0.12 for mule deer in 2018. Detection probabilities for mesocarnivores were lower than for ungulates, with an average of 0.22 and a maximum of 0.38 (coyote in 2017). Five species (American badger, swift fox, coyote, elk, and cattle) were observed on at least half of the sites in one or both years. Striped skunk (*Mephitis mephitis*) was the least widespread species and was observed at only three sites, with only six observations total. Because skunk observations were low, we did not include them in our occupancy models.

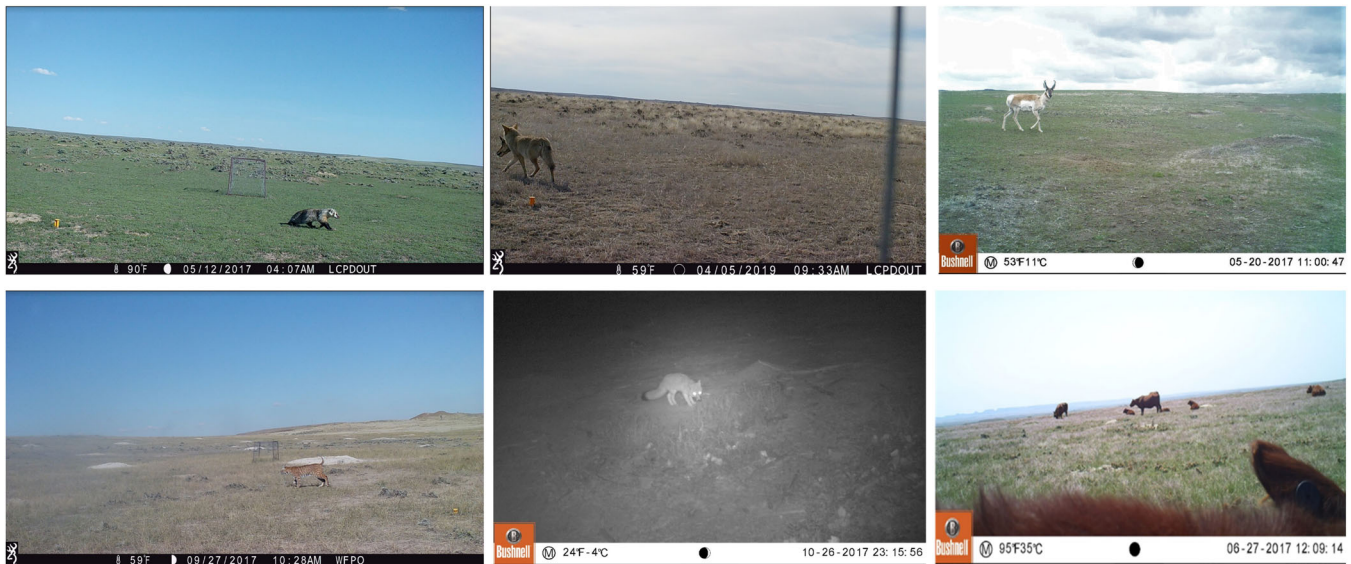
Prairie dog observations declined rapidly in July and August 2017 (pers. observ., Dave Pellatz, Courtney Duchardt; Figure 5), with lagged declines in badgers and swift fox by January 2018 (Figure 5). In contrast, we found no clear patterns of decline for ungulate species following plague-induced collapse of prairie dogs (Appendix S1: Figure S2). We found that the proportion of prairie dog colony cover within a 2-km radius of camera traps ( $p_{\text{col}}$ ) was included in the top-ranked occupancy models for four mesocarnivores in 2017 (Table 2; Appendix S1: Figure S3). Colony cover had the greatest influence on badger occupancy ( $\beta = 11.9$ ,  $SE = 4.9$ ,  $p = 0.01$ ), followed by swift fox ( $\beta = 6.8$ ,  $SE = 3.0$ ,  $p = 0.03$ ) and bobcat ( $\beta = 4.1$ ,  $SE = 2.1$ ,  $p = 0.05$ ). Colony cover was not included in the top-ranked model for red fox occupancy (Table 2). For both badgers and swift fox, probability of occupancy reached 0.75 at 25% colony cover, with predicted occupancy at 1.00 when 75% of the area within 2 km was occupied by prairie dog colonies (Appendix S1: Figure S3). Coyote occupancy also tended to increase with percentage colony cover, but this was not significant at the  $\alpha = 0.05$  level ( $\beta = 21.2$ ,  $SE = 15.9$ ,  $p = 0.18$ ). Red fox occupancy was unaffected by percentage colony cover. Percentage colony cover was included in the top-ranked model of pronghorn occupancy, but this effect was not significant ( $\beta = 96.7$ ,  $SE = 133.9$ ,  $p = 0.47$ ) and pronghorn occupancy was predicted to be 100% even at low (~15%) colony cover. We observed no effect of percentage colony cover on



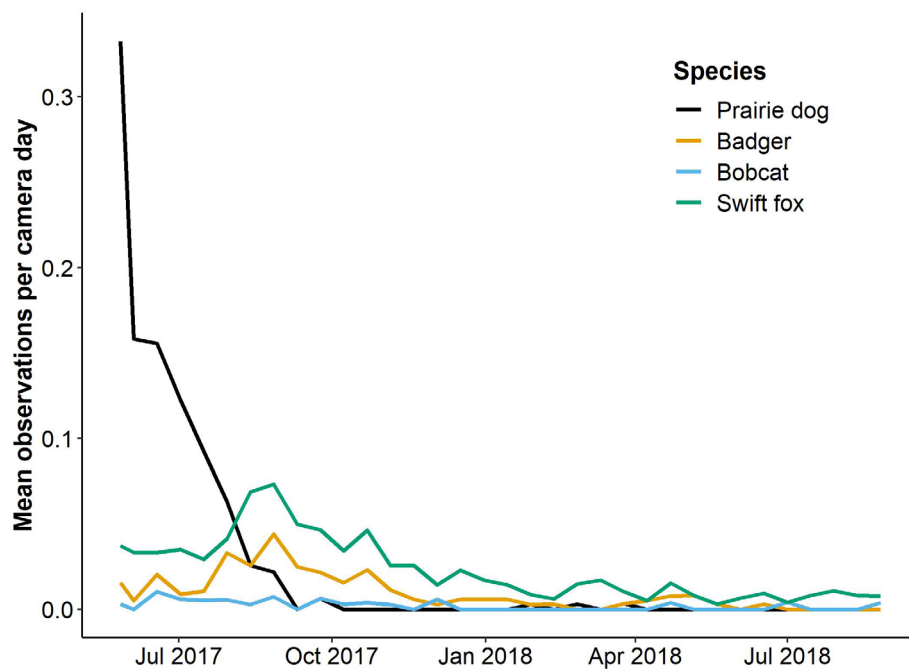
**FIGURE 3** Results of distance-based redundancy analysis in the Thunder Basin Ecoregion, Wyoming, USA generated from all transects in 2015–2019. Points in panel (a) represent centroids for colony core and sagebrush transects in all years, whereas species acronyms represent density centers for each species. Vectors in panel (a) (blue) represent environmental covariates. Vectors in panel (b) indicate direction and degree of community change in individual colony core (red/purple) and sagebrush (blue/green) transects over time, with the origin of vectors in 2015 and the endpoint in 2019. BHCO, Brown-headed cowbird; BRBL, Brewer’s blackbird; BRSP, Brewer’s sparrow; BUOW, burrowing owl; COGR, common grackle; CONI, Common nighthawk; GRSP, grasshopper sparrows; HOLA, horned lark; LARB, lark bunting; LASP, lark sparrow; LOSH, loggerhead shrike; MODO, mourning dove; MOPL, mountain plover; ROWR, rock wren; SATH, sage thrasher; UPSA, upland sandpiper; VESP, vesper sparrow; WEME, western meadowlark.

cattle or elk occupancy, whereas a quadratic effect was included in the best model for mule deer, indicating a peak in occupancy at 20% colony cover and declining at

higher coverage (but note that both terms in the model were nonsignificant (colony,  $p = 0.16$ ; colony<sup>2</sup>,  $p = 0.12$ ); Table 2).



**FIGURE 4** Example of camera trap images captured in the Thunder Basin Ecoregion, Wyoming, USA, between 2017 and 2018. Images, from left to right on the top row: American badger, coyote carrying pronghorn head, pronghorn. Bottom row: bobcat, swift fox, and cattle and prairie dogs.



**FIGURE 5** Mean daily observations of prairie dogs and associated mesocarnivores averaged over 2 week intervals, May 2017 through August 2018, Thunder Basin Ecoregion, Wyoming, USA.

When we examined regional-scale occupancy models of mammals pre- versus post-plague (i.e., 2017 vs. 2018), we found that low numbers of observations in 2018 led to some issues in prediction for mesocarnivore species. Bobcats were uncommon throughout the study area (12 detected in 2017, probability of occupancy 0.15, SE = 0.07), and none were detected in 2018, leading to model nonconvergence in that year. Badgers were

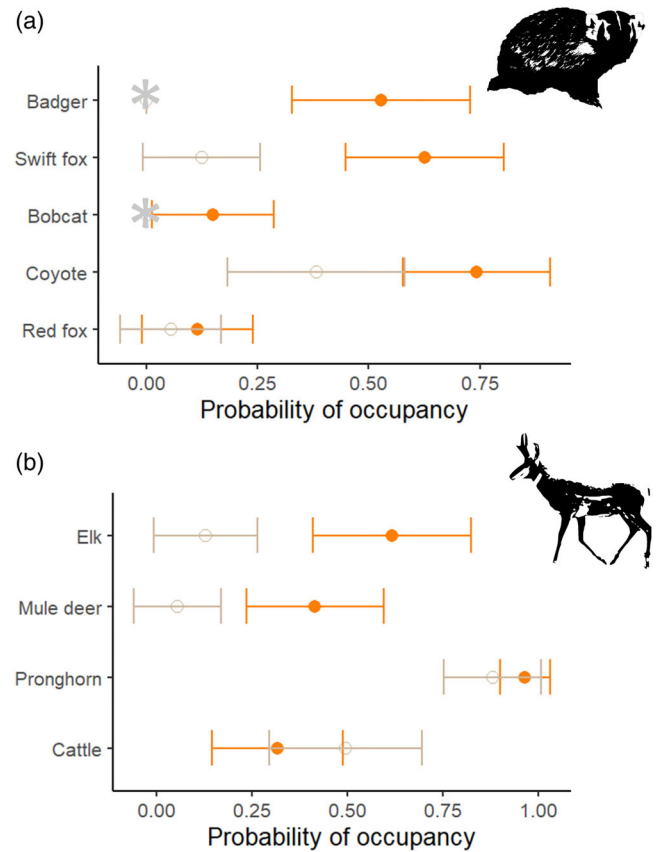
detected relatively frequently pre-plague (40 in 2017, probability of occupancy 0.5, SE = 0.1), but declined to only a single detection in 2018; this model converged, but generated estimates with confidence intervals overlapping both zero and one. For these two species, we only reported estimates generated from 2017 data (Figure 6a), but note that occupancy in 2018 was essentially zero. For species that we could model occupancy in

**TABLE 2** Akaike's information criterion corrected for small sample size ( $AIC_c$ ) rankings per species for modelling occupancy as a function the proportion of prairie dog colony within 2 km of a camera, Thunder Basin Ecoregion, Wyoming, USA, 2017–2018.

Model	$AIC_c$	$\Delta AIC_c$
<b>Mesocarnivores</b>		
American badger		
Colony	217.5	0.0
Null	235.4	17.9
Colony <sup>2</sup>	... <sup>a</sup>	... <sup>a</sup>
Bobcat		
Colony	82.5	0.0
Null	84.9	2.4
Colony <sup>2</sup>	...	...
Coyote		
Colony	360.2	0.0
Colony <sup>2</sup>	363.0	2.8
Null	370.1	9.9
Red fox		
Null	63.6	0.0
Colony	65.2	1.6
Colony <sup>2</sup>	66.8	3.2
Swift fox		
Colony	342.2	0.0
Null	350.6	8.4
Colony <sup>2</sup>	... <sup>a</sup>	... <sup>a</sup>
<b>Ungulates</b>		
Cattle		
Null	198.8	0.0
Colony	201.3	2.5
Colony <sup>2</sup>	203.5	4.7
Elk		
Null	243.8	0.0
Colony	246.3	2.5
Colony <sup>2</sup>	248.7	4.9
Mule deer		
Colony <sup>2</sup>	208.9	0.0
Colony	211.1	2.2
Null	212.7	3.8
Pronghorn		
Colony	439.2	0.0
Null	440.8	1.6
Colony <sup>2</sup>	441.8	2.6

Note: Quadratic model of colony cover is shown as "Colony<sup>2</sup>".

<sup>a</sup>Model did not converge.



**FIGURE 6** Mean probability of occupancy for five mesocarnivores (a) and four ungulates (b) before and after a sylvatic plague outbreak, mid-May to mid-August in 2017 (orange, filled) and 2018 (tan, unfilled), Thunder Basin Ecoregion, Wyoming, USA. Asterisks indicate model nonconvergence because of low badger ( $n = 1$ ) and bobcat ( $n = 0$ ) detections.

both years, swift foxes declined substantially after plague ( $Occu_{2017} = 0.63$ ,  $SE = 0.09$ ,  $Occu_{2018} = 0.01$ ,  $SE = 0.007$ ) and coyote numbers were marginally lower after plague ( $Occu_{2017} = 0.74$ ,  $SE = 0.08$ ,  $Occu_{2018} = 0.38$ ,  $SE = 0.1$ ). Occupancy rates of cattle and pronghorn did not change significantly among years, whereas occupancy rates of elk ( $Occu_{2017} = 0.62$ ,  $SE = 0.11$ ,  $Occu_{2018} = 0.13$ ,  $SE = 0.07$ ) and mule deer ( $Occu_{2017} = 0.41$ ,  $SE = 0.91$ ,  $Occu_{2018} = 0.055$ ,  $SE = 0.058$ ) declined following the plague event (Figure 6b).

## DISCUSSION

Following the outbreak of sylvatic plague in late 2017, we observed rapid changes in the Thunder Basin Ecoregion that supported three hypotheses of our system-level conceptual model (Figure 1). Due to the concomitant loss



of prairie dogs and extremely high precipitation, mean height and total biomass of herbaceous vegetation was greater during the final 2 years of our study ( $H_1$ ). We observed changes in passerine and shorebird community structure ( $H_2$ ) and decreased occupancy in multiple predator species, with the magnitude of change linked to species-specific degree of dietary reliance on prairie dogs as a food resource ( $H_4$ ). We found minimal support for  $H_3$ , which posited that ungulates would respond negatively to plague because vegetation was no longer maintained at an earlier phenological stage providing higher forage quality (please refer to Connell et al., 2019).

Incorporating prairie dog disturbance and precipitation into ordinations of rangeland bird communities helped to disentangle the effects of these two drivers on bird community structure (Figure 3a). The loss of prairie dogs mainly affected shortgrass obligates, with marked declines of mountain plovers (16-fold reduction), horned larks, and burrowing owls. Breeding mountain plovers and horned larks are reliant on disturbed habitat with high levels of bare soil exposure, features in this landscape that are found almost exclusively on prairie dog colonies (Duchardt et al., 2018, 2020). Burrowing owl density was relatively low throughout the study area, but our data indicate that this species declined 2 years after the plague event, likely because of lagged burrow collapses, which occur 1–2 years after prairie dog removal (please refer to Alverson & Dinsmore, 2014 for more on burrowing owls and plague). In addition, increased precipitation led to a community shift toward greater numbers of lark buntings and grasshopper sparrows in 2018 and 2019. Interestingly, these wet years in the northern Great Plains corresponded with drought in the southern Great Plains, where these species also breed. This probably compounded the importance of our study area for ground-nesting birds associated with mid-height grasses, as our study area may have provided habitat for individuals unable to breed in the more southerly part of their range. Bolstering this hypothesis, we recorded the first occurrence of Cassin's sparrows (*Peucaea cassinii*) in Weston County, Wyoming in 2018, a species generally restricted to the southern Great Plains but known to be somewhat nomadic in habitat use.

Passerines and shorebirds responded to changes in habitat structure influenced by plague and precipitation, but predators were more directly influenced by loss of prairie dogs as a prey resource. The two raptor species most reliant on prairie dogs as a food resource, ferruginous hawk and golden eagle (Katzner et al., 2020; Ng et al., 2020), increased during the prairie dog “boom” but declined rapidly once this resource was removed. Although it can sometimes be difficult to disentangle landscape-level responses from regional ones, neither breeding bird survey

data at the scale of Wyoming between 2015 and 2019 (Pardieck et al., 2020) or visual assessment of eBird data (eBird, 2021; eBird.org) indicated higher than average abundances of either of these species at the regional scale in 2017 or a population decline in 2018, supporting the role of prairie dogs in the response we observed. Similarly, the lack of “boom-and-bust” response in raptors that rely less on prairie dogs (e.g., red-tailed hawk, a generalist predator) or do not use prairie dogs as a food resource (e.g., American kestrel, which consumes mainly invertebrates as well as reptiles, birds, and small mammals, and northern harrier, which relies on mammals or birds generally smaller than prairie dogs) indicates that the years following plague were not marked by the reduction of other prey resources.

We also documented substantial declines in occupancy rates of mammalian predators after the plague epizootic, and species were affected in direct proportion to their dietary reliance on prairie dogs. In addition to the black-footed ferret, American badgers have the greatest dietary reliance on prairie dogs (e.g., Kagel et al., 2020) and habitat specialization often manifests where the two species overlap (Grassel & Rachlow, 2018). On a landscape scale, badger occupancy in Thunder Basin was most strongly affected by proximity to prairie dog colonies prior to plague and declined to a near-zero level after plague. Across their range, swift fox reliance on prairie dog colonies for prey or denning habitat appears to vary considerably (e.g., Kintigh & Andersen, 2005; Nicholson et al., 2006; Shaughnessy & Cifelli, 2004), but we found that swift fox occurrence was both positively associated with proximity to colonies pre-plague and declined substantially following the plague epizootic. These results highlight the importance of prairie dogs for supporting the swift fox population in this landscape. Interestingly, we observed frequent diurnal behavior in both predator species, similar to Kagel et al. (2020), which highlights that studies using nocturnally-biased survey techniques may miss the importance of prairie dog resources, especially for swift foxes because this species is often surveyed using spotlighting. We found that coyote occurrence was influenced by prairie dog abundance, but to a lesser degree than badgers and swift fox, showing that both increased occurrence with increasing proximity to prairie dog colonies pre-plague, and a modest decline following the plague epizootic. Finally, bobcats used prairie dog colonies within this grassland at low rates when prairie dogs were abundant, and then occurrence rate declined to zero following the plague epizootic, adding to our knowledge of the relationship between these two species that has rarely been described in the literature (e.g., Licht, 2010). We hypothesize that these declines were due, at least in part, to emigration from the study

area due to decreased food availability, but we were not able to directly assess mortality or decreased fecundity related to these changes in food availability.

Mule deer and elk displayed landscape-scale declines following plague, consistent with findings in South Dakota (Whicker & Detling, 1988). These species may use prairie dog colonies because of maintenance of forage in a nutritious, early phenological state (Connell et al., 2019) and the relatively high abundance of forbs on prairie dog sites (Duchardt et al., 2021). However, modeling of responses of ungulates to colony cover in 2017 did not clearly support this hypothesis, as elk showed no response to colony cover and mule deer only had a high probability of occupancy of areas with up to 30% colony cover, after which probability of occupancy declined (Table 2; Appendix S1: Figure S3). Furthermore, detection probabilities of mule deer in this study were fairly low. Mule deer declines in 2018 may have instead been driven by macro-scale factors affecting the population of this migratory species, and we note that the estimated mule deer population throughout northeastern Wyoming was reported to be well above the 5-year average in 2017 and declined by ~12% in 2018 (WGFD, 2017; WGFD, 2018; reported for the Cheyenne River herd). We observed no landscape-scale difference in pronghorn occupancy between years, and only a weak positive relationship between colony cover at the 2-km scale and probability of pronghorn occupancy in 2017. Although other researchers have indicated that ungulate species utilize prairie dog colonies for grazing (e.g., Krueger, 1986; Whicker & Detling, 1988), it is still unclear the degree to which ungulates may utilize prairie dog colonies across their range, and how spatiotemporal dynamics of prairie dog disturbance may influence ungulate populations.

Our conceptual model focused on disease as a driver of wildlife community structure independent of climate, but climatic variability can also influence the probability of plague epizootics (Eads & Biggins, 2017). There have been three major plague outbreaks in Thunder Basin in the past 20 years, with each occurring in a relatively average precipitation year following a dry one (Davidson et al., 2022). While this pattern does not hold true in every landscape (Savage et al., 2011; Stapp et al., 2004), other studies have also linked plague epizootics with transitions from dry to wet years (Eads & Biggins, 2017). The hypothesis explaining this mechanism is that dry conditions may suppress fleas, the main pathogen host, and *Y. pestis* (Eads & Biggins, 2017), but wet years can lead to both increases in prairie dog abundance and concurrent increases in flea-loads and aboveground activity. We also note that while we did not directly measure prairie dog abundance/density in this study, concurrent work in this system reported many areas of very high prairie dog burrow density in 2017

(Duchardt et al., 2021). Future efforts in this system include increased focus on prairie dog density as a driver of community response and we encourage other researchers and managers to also incorporate this metric into their work, in addition to monitoring colony size.

## Conservation implications

As with other burrowing rodents in rangeland ecosystems worldwide (Davidson et al., 2012), we found that prairie dogs play a critical role in structuring associated vegetation and wildlife communities in this system. Our research highlights drastic and rapid community shifts following the functional loss of prairie dogs in the landscape due to an epizootic outbreak of sylvatic plague. Boom-and-bust disease cycles such as the one we describe in our study are a major conservation challenge. Direct threats from disease and unreliable food resources make these systems untenable for black-footed ferret reintroductions (Matchett et al., 2010). Furthermore, unreliable prey resources destabilize predator communities (MacArthur, 1955; Petchey, 2000), and the lack of consistent habitat availability may negatively impact avian species with high site fidelity, such as mountain plovers and burrowing owls (Crowley et al., 2019; Graul, 1973; Klute et al., 2003; Pierce et al., 2017; Skrade & Dinsmore, 2010). This may lead to increased time spent moving through the landscape or prospecting (Ponchon et al., 2013) and delayed breeding, or to the selection of suboptimal habitat and reduced reproductive output (Battin, 2004), all of which could be compounded with the fact that much of the remaining landscape is highly fragmented by agriculture, energy extraction, and other human land uses.

Given the strained relationship between agricultural production and burrowing rodent conservation objectives (e.g., Miller et al., 2007), it may be surprising that these cyclical die-offs are also challenging from a livestock management perspective. Uncertainty is directly at odds with agricultural production and huge efforts have been made to improve our ability to predict rangeland productivity to allow stocking rate adjustments in a timely fashion (e.g., Hartman et al., 2020; Raynor et al., 2020). Although reduced prairie dog numbers yield increased vegetation biomass, the unpredictability of these cycles make capitalizing on additional forage difficult for agricultural producers. Essentially, the undesirability and unpredictability of these cycles is potentially the one thing that most, if not all, stakeholders can agree on. Future work could simultaneously focus on predicting these cycles and identifying the management tools to mitigate them. Insecticides to control fleas (Eads et al., 2021; Eads & Biggins, 2019) have generally been successful in stabilizing

and maintaining colonies, but less consideration has been given to strategic spatial application of these tools to maximize long-term effectiveness, or how the influence of colony configuration on epizootic plague spread could inform active management of colony complex configuration (Collinge et al., 2005; Cully Jr. et al., 2010; Johnson et al., 2011).

Although extreme precipitation following the plague outbreak could be viewed as “noise” interfering with the interpretation of prairie dog effects in this landscape, these extremes are likely to increase in the future and continue to interact with prairie dog colony dynamics (Reeves et al., 2020), making them a necessary consideration in understanding these ecological processes. We acknowledge that our study was only able to measure responses to the interaction of plague and high precipitation; we are extremely curious about how responses may have differed had 2018 been a dry year, and we see this as an avenue for future research. Future work could also focus on incorporating these drivers into a multi-equilibrium model (also known as “ball-in-cup” or “basin of attraction” model; Briske et al., 2017) to help managers to better understand the levels of variability that are likely to push communities past thresholds into alternative stable states and focus management on avoidance of undesirable thresholds.

These climatic extremes also highlight the importance of this landscape for nomadic, mid-grass bird species, especially in years when drought affects other parts of their range. This gives rise to another challenge: how should managers address the trade-offs in rangeland management for nomadic versus philopatric breeders? Some grasslands may only provide habitat for certain species in 1 of 10 years (e.g., Green et al., 2019), yet that 1 year is exactly when the peripheral habitat is most essential. The answer is not straightforward, but we believe it is one that should be tackled not by individual rangeland managers but instead via collaborative adaptive management at a regional scale, with emphasis on the creation of a consistent, real-time communication network among spatially disparate managers, stakeholders, and researchers working in rangeland ecosystems.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Duchardt, 2022) are available on Dryad at <https://doi.org/10.5061/dryad.pzgmsbcpx>. These include all field-collected data except prairie dog colony locations and boundaries, as these data are curated by the United States Forest Service and Thunder Basin Grasslands Prairie Ecosystem Association. Data available on Dryad also do not include associated spatial data because these pertain to species of conservation concern. Full data (including spatial location) are available to qualified researchers from the Department of Natural Resource Ecology and Management at Oklahoma State University.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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