

# Journal of Mammalogy

Volume 103 | Issue 5 | October 2022



**OXFORD**  
UNIVERSITY PRESS

Online ISSN: 1545-1542  
Print ISSN: 0022-2372  
[jmammal.oxfordjournals.org](http://jmammal.oxfordjournals.org)





## Boom and bust cycles of black-tailed prairie dog populations in the Thunder Basin grassland ecosystem

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Black-tailed prairie dogs (*Cynomys ludovicianus*) exhibit boom and bust cycles in landscapes where they are affected by outbreaks of plague caused by the introduced bacterium *Yersinia pestis*. We examined spatiotemporal dynamics of black-tailed prairie dog colonies in the Thunder Basin National Grassland, Wyoming over a period of 21 years. The colony complex experienced three plague epizootics during that time, and consequently three boom and bust cycles. The entire prairie dog colony complex collapsed over a 1-year period during the first and third epizootics, and over a 3-year period during the second epizootic. The boom and bust cycles were characterized by relatively rapid contractions in total area occupied by prairie dogs during a plague outbreak (e.g., >99% decline from 10,604 ha to 47 ha over 1 year [2017–2018]) followed by much slower recovery times (e.g., an increase from 410 ha to 10,604 ha over 11 years [2006–2017]). Prairie dogs occupied a total of 10,604 ha during at least one survey within the study period, but much of the area was not continuously occupied over time. We found that each of the three plague outbreaks occurred in years with highly connected prairie dog colonies and slightly above-average temperatures and summer precipitation, which were preceded by a dry year. Although plague outbreaks were associated with climatic conditions, we were unable to detect a role of climate in driving colony expansion. Our results illustrate the cyclic and extreme nature of fluctuations in black-tailed prairie dog colony size and distribution in a landscape where plague occurs and illuminate some of the drivers of these cycles. Further, our work shows how introduced diseases can dramatically influence populations of a keystone species, with important consequences for the broader ecological system.

Key words: boom and bust cycle, burrowing rodents, climate, introduced disease, keystone species, landscape connectivity, plague, population dynamics, prairie dogs, *Yersinia pestis*

Boom and bust population cycles are common in nature. The predator–prey population oscillation between the snowshoe hare (*Lepus americanus*) and the Canada lynx (*Lynx canadensis*) is a classic example, whereby the rise and fall of lynx populations follow that of the hare, their primary prey, over about a 10-year cycle (Bjørnstad and Grenfell 2001; Krebs et al. 2001). Increasingly, anthropogenic disturbances are disrupting wildlife population dynamics and creating boom and bust population cycles that are not reflective of historical patterns.

Such disturbances altering wildlife population dynamics include changing climate, ocean warming, parasite infestations, food limitations, pesticides, extreme weather, eutrophication, overharvesting, conversion or disruption of habitats, and disease outbreaks (Uthicke et al. 2009; Krkošek et al. 2013; Pitt et al. 2014; Ogden et al. 2019).

Introduced diseases—such as chytridiomycosis in amphibians and white-nose syndrome in bats—often cause high mortality in populations of naïve hosts that lack a shared

coevolutionary history (Cully et al. 1997; Pauli et al. 2006; Busch et al. 2011; Epstein et al. 2016; Langwig et al. 2016), and may broadly alter population dynamics over time and space (Daszak et al. 2000; Grenfell et al. 2001; Thompson et al. 2010; Krkošek et al. 2013; Eads and Biggins 2015). Sylvatic plague, caused by the bacterium *Yersinia pestis* introduced into the western United States from Asia ca. 1900, is an example of a highly virulent disease that causes catastrophic population collapses in prairie dogs (often <1% survival; Link 1955; Cully and Williams 2001; Augustine et al. 2008b; Salkeld et al. 2016). Large, stable prairie dog colony complexes were ubiquitous throughout central North America prior to European settlement (Knowles et al. 2002; Cully et al. 2010; Keuler et al. 2020). Today, plague epizootics, along with extensive historical eradication efforts (Redington et al. 1929; Knowles et al. 2002), have destabilized prairie dog populations and the productive and diverse ecosystems they create (Cully and Williams 2001; Cully et al. 2010; Eads and Biggins 2015; Keuler et al. 2020). Prairie dog colonies now exhibit “boom and bust” population cycles, expanding and contracting over time as a result of interactions among sylvatic plague, climate/weather variability, and grazing by large herbivores (Gage and Kosoy 2005; Snäll et al. 2008; Cully et al. 2010). The typical black-tailed prairie dog population cycle manifests over a 5- to 15-year time horizon and involves steady increases in colony size and abundance followed by plague-driven colony collapse, which nearly instantaneously resets the boom and bust cycle (Cully et al. 2006, 2010; Augustine et al. 2008b; Hartley et al. 2009; Johnson et al. 2011). Even when colonies recover, some do not reach their pre-plague spatial extent before another plague epizootic occurs (Seery and Matiatos 2000; Hartley et al. 2009, but see Augustine et al. 2008b). Plague can also remain in an enzootic phase between epizootics, causing persistent, low-level mortality within the affected colony complex (Biggins et al. 2010; Matchett et al. 2010; Liccioli et al. 2020).

Understanding boom and bust cycles of black-tailed prairie dogs is important for grassland conservation and management. Prairie dogs are keystone species in North America's grasslands, and associated species depend on stable colony complexes that were historically abundant across the central grasslands of North America prior to European settlement and the introduction of plague (Knowles et al. 2002; Kotliar et al. 2006; Augustine et al. 2008b; Davidson et al. 2012; Eads and Biggins 2015). Plague-driven crashes of prairie dog populations can result in consequent declines in species that associate with the grassland habitats they create, including burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*), and those dependent or are heavily reliant on prairie dogs as prey, including black-footed ferrets (*Mustela nigripes*) and ferruginous hawks (*Buteo regalis*; Seery and Matiatos 2000; Augustine et al. 2008a; Eads and Biggins 2015; Duchardt et al. 2019a). On the other hand, booming colonies often impact the management goals of livestock producers, due to competition that can occur between livestock and prairie dogs for available forage (Lee Lamb and Cline 2003; Derner et al. 2006; Delibes-Mateos et al. 2011; Augustine and Springer 2013), particularly

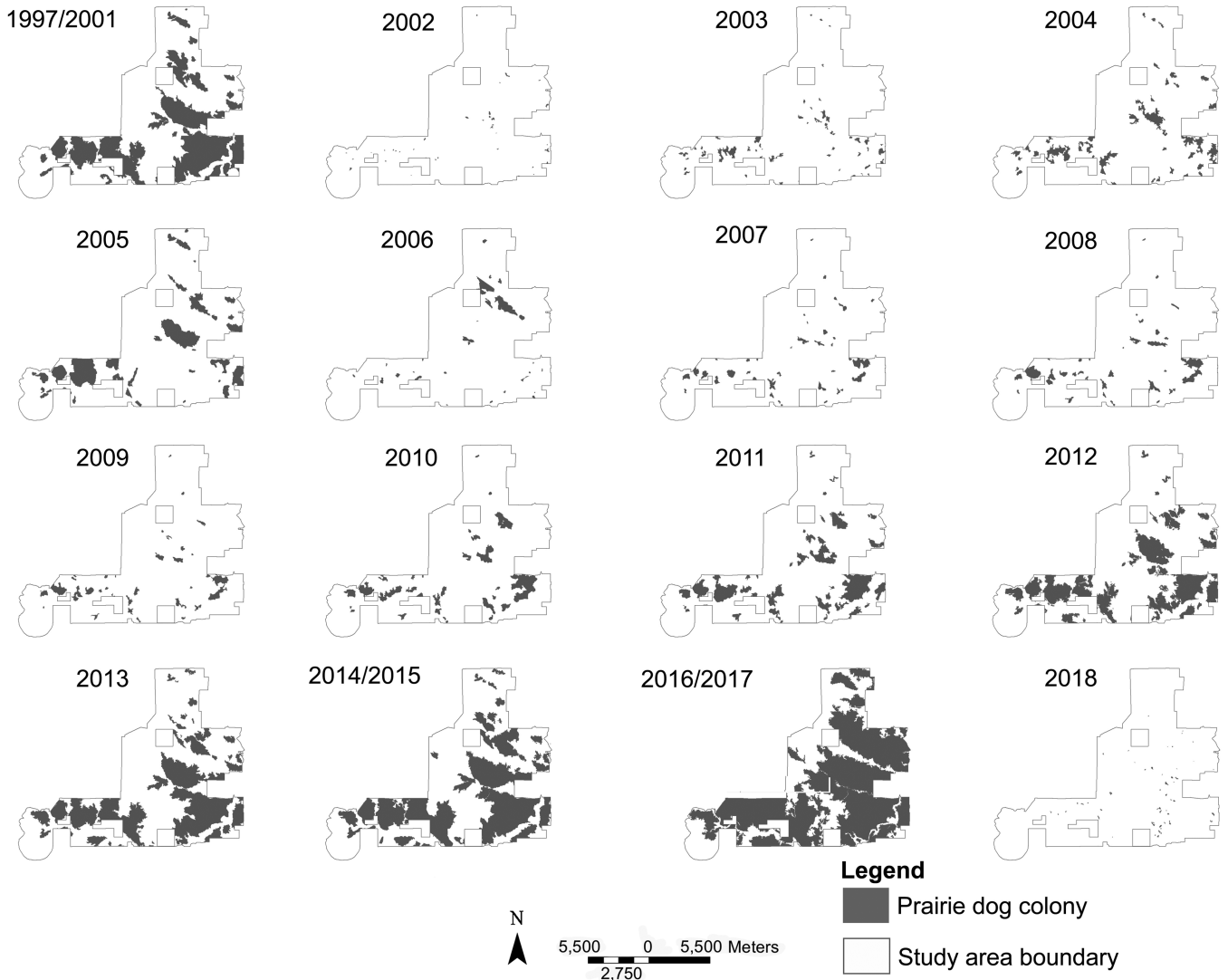
during dry years (Connell et al. 2019). Wildlife and land managers, livestock producers, and conservationists all have vested interests in finding ways to help stabilize prairie dog colonies to reduce system volatility for both wildlife communities and livestock production. Fundamental to this goal is understanding the magnitude, timing, spatial scale, and drivers of prairie dog colony boom and bust cycles over time.

Here, we report on the dynamics and drivers of these cycles over two decades and three plague epizootics in the Thunder Basin ecoregion, Wyoming, United States. We address the following questions: (1) What are the spatial dynamics, spatial attributes, timing, and magnitude of prairie dog colony expansions and contractions over time? and (ii) Are prairie dog colony expansions or contractions driven by seasonal and/or annual precipitation or climatic extremes?

## MATERIALS AND METHODS

**Study area.**—Our study encompassed a 17,142 ha portion of the Thunder Basin National Grassland (TBNG) in northeastern Wyoming, United States (43°26'–43°35'N; 104°56'–105°11'W; Fig. 1). Elevation is around 1,300 m, and the study area encompasses a biodiverse ecotone situated at the intersection of northern mixed-grass prairie, shortgrass prairie, and sagebrush steppe ecoregions. Vegetation includes a shrub layer dominated by *Artemisia tridentata* subsp. *wyomingensis*. Common graminoids include the C<sub>4</sub> (warm-season) perennial grass *Bouteloua gracilis*, the C<sub>3</sub> (cool-season) perennial graminoids *Carex filifolia*, *Hesperostipa comata*, and *Pascopyrum smithii*, and the annual grasses *Bromus tectorum*, and *Vulpia octoflora*. Common forbs include *Alyssum desertorum*, *Plantago patagonica*, *Lepidium densiflorum*, and *Sphaeralcea coccinea*. The cactus *Opuntia polyacantha* is also common (Porensky et al. 2018). The TBNG ecoregion has a semiarid climate; average annual precipitation ranges from 250 to 350 mm (long-term mean = 319 mm) and mean monthly temperature ranges from –5°C in December to 22°C in July (Porensky et al. 2018). The ecoregion is a multiuse sagebrush-grassland ecosystem managed for livestock production, energy development, conservation, and recreation, and includes a complex of intermingled federal, state, and private lands. Most of the public lands within the ecoregion are moderately grazed by livestock.

Various management efforts were implemented during the 21-year study period to control prairie dog colony expansion in some areas, increase prairie dog colonies in other areas, or to reduce the potential of plague outbreaks (Supplementary Data SD1). This included: (i) shooting by the public (2017) and rodenticide application (2010–2014) to control prairie dog colony expansion; (ii) mowing, prescribed fire, shooting closures (2009–2016), and translocations (2010 and 2011) to increase prairie dog colonies; and (iii) dusting with insecticide (2010–2015) to help reduce flea abundance and the transmission of plague. These efforts generally occurred across small portions of the overall colony complex. For example, the proportion of the prairie dog complex dusted for flea control within our study area ranged from 4% (53 ha) in 2010 and



**Fig. 1.**—Spatial dynamics of the colony complex across our study area on the Thunder Basin National Grassland, Wyoming from 1997 to 2018. Data originate from sources including: Jack Cully (Cully et al. 2010), United States Forest Service reports, and the Thunder Basin Grasslands Prairie Ecosystem Association.

38% (808 ha) in 2011 to 15% (979 ha) in 2014/2015 and 0.1% (10 ha) in 2016/2017 (Supplementary Data SD1). Prairie dog translocations occurred across 48 ha in 2010 and across 67 ha in 2011. Shooting closures were implemented across the study area in 2010, but when the colonies began to increase substantially in 2016, the entire area was opened to shooting by the public in early March 2017.

**Prairie dog colony mapping data.**—Perimeters of black-tailed prairie dog colonies in the study area were mapped in 1997 and in most years between 2001 and 2018. Biologists traveled around the boundaries of targeted colonies on foot and with all-terrain vehicles (ATVs) and used handheld global positioning system (GPS) devices to record the outermost perimeter of each mapped colony. In most years (see exceptions described below), colony boundaries were delineated based on: (i) the locations of burrow entrances that showed evidence of recent prairie dog presence (digging, soil disturbance, trails between active burrows, and/or presence of green or brown

fecal pellets near burrow entrances); and (ii) sharp transitions between prostrate or recently cropped vegetation and zones of taller vegetation that did not show signs of cropping by prairie dogs (Augustine et al. 2008b; Cully et al. 2010).

Over the study period, mapping was conducted by multiple agencies and organizations, including the United States Forest Service (USFS), United States Geological Survey (USGS), Thunder Basin Grasslands Prairie Ecosystem Association (TBGPEA), university partners, and private contractors. Methods varied over the study period, as follows. Mapping in 1997 and 2001 was conducted by the USFS. In 1997, colony boundaries were based on the location of outermost active burrows and other signs of recent prairie dog activity, as described above. In 2001, some colonies were beginning to show rapid contraction relative to their 1997 boundaries, and other colonies that were previously active appeared to have been entirely extirpated by a recent plague event. During the 2001 mapping effort, colonies where no surviving prairie dogs were found were



not mapped, but if survivors were seen, even on a small portion of the colony, the full previous extent of the colony where intact burrows could be found was mapped to represent the area recently affected by plague. We used these mapped boundaries as the best estimate of pre-epizootic occupied colony area. Ten colonies present in 1997 were not mapped in 2001 due to lack of detection of any live prairie dogs at the time of mapping. In addition, two large colonies mapped in both 1997 and 2001 had errors in the mapping of the eastern boundary during the 2001 survey. We therefore combined the 1997 and 2001 maps into a single layer that represented the outermost extent of the prairie dog colonies prior to the plague epizootic in 2001. We note that the colonies mapped in 1997, but not 2001, likely expanded from their 1997 extent prior to the plague event, but we had no means to estimate this expansion. Therefore, the combined 1997/2001 mapped colony footprint is likely a slight underestimate of the actual maximum colony extent prior to the 2001 plague epizootic.

Mapping from 2002 through 2004 was conducted as described by Cully et al. (2010) and was intended to be a full census of all active prairie dog colonies in the study area following the 2001 epizootic. Mapping during the next 11 years (2005–2015) was conducted by the USFS and typically occurred from June through November each year. By 2014, prairie dog colonies had expanded and changing priorities had reduced available resources to such an extent that only one full round of mapping was completed during 2014 and 2015.

TBGPEA conducted mapping efforts in 2016 that initially focused on various research priority areas on both federal and nonfederal lands. In concert with private partners, wildlife consultants, and local agencies, TBGPEA began a second complete survey in 2016 that continued into 2017, when colonies began to show signs of contraction typically associated with a plague epizootic. To complete the full 2016/2017 survey in a manner that would quantify the maximum extent of colonies prior to the effects of plague (and in a manner equivalent to what was done in 2001), all colonies were mapped based on the distribution of outermost intact burrows, even if those burrows did not show signs of ongoing occupancy by prairie dogs. Mapping efforts occurred from mid-August through late October in 2016, and from mid-June through late October in 2017.

TBGPEA began coordinating mapping in conjunction with the USFS in 2018. Due to substantial contraction of all colonies within the study area by that time, mapping was conducted in two phases to ensure the entire study area was consistently searched for burrows showing signs of prairie dog activity. In the first phase, a grid of survey points spaced at 600-m intervals was placed across all areas that were occupied by prairie dogs or showed signs of intact burrows during the 2016/2017 survey period (Supplementary Data SD2). All grid points were visited from late April through mid-July 2018. At each point, observers watched and listened for prairie dogs for up to 5 min while scanning the immediately surrounding area in all directions with binoculars. In addition, an area approximately 50 m in radius around each survey point was searched on foot for any signs of activity, such as live prairie dogs, burrows with

active digging or fresh dung pellets, recent trails between burrows, or closely cropped vegetation. In the second phase, biologists returned to all points where any sign of prairie dog activity was recorded during Phase 1 and conducted more detailed mapping of active colony boundaries. During Phase 2 of mapping, each active burrow was marked with a pin flag, except for the few larger colonies where interior activity was confirmed. Observers then walked or drove an ATV around the outer perimeter of the flags with handheld GPS units to generate polygons of active colonies. This approach was used due to the extremely small average size of most active colonies that year and to ensure that all active burrows were included, to the extent possible. In 2018, active colonies were defined as those with five or more live prairie dogs seen or heard in that location on the day of mapping, or at least five active burrows (identified by signs such as presence of fresh scat, digging, or clipping of vegetation) located within 50 m of one another. Mapped burrow groups separated by >50 m were considered as separate colonies. For areas where fewer than five prairie dogs and/or active burrows were detected, a single GPS coordinate was recorded and this point did not contribute to total area of the complex for 2018.

*Climate data.*—Climate data for the study period were obtained from National Oceanic and Atmospheric Administration (NOAA) divisional time series data for Wyoming Climate Division 7: the Cheyenne Niobrara drainage (NOAA 2020). This division includes the entire study area and is centered around the junction of Weston, Campbell, Converse, and Niobrara counties. We extracted data on maximum temperature, precipitation totals, and modified Palmer Drought Severity Index (PDSI) for each month between 1 January 1996 and 30 September 2018. We calculated annual metrics by water year (1 October of the previous year to 30 September of the current year) to reflect the accumulated impacts of temperature and moisture on plant growth. Maximum temperature represented the average value of maximum temperature in the hottest month and precipitation represented the sum across the water year. We also calculated precipitation for spring (April–June) and summer (July–August), because seasonal precipitation can influence prairie dog offspring production and population expansion (Davidson et al. 2014; Grassel et al. 2016; Hayes et al. 2016; Stephens et al. 2018; Bruggeman and Licht 2020). Spring was defined as roughly the period between initial green-up and peak green-up using Moderate Resolution Imaging Spectroradiometer (MODIS) data (Didan 2015; DAAC 2018). Because of the potential for lag effects of weather on prairie dog dynamics (e.g., Bruggeman and Licht 2020), we also examined a 1-year lag effect of each of the variables previously described. For the combined years 2014/2015 and 2016/2017, we used the year prior to the combined period (i.e., 2013 and 2015, respectively) as the previous year. For combined years 1997 and 2001, we used 2000 as the previous year. Current year values for combined years represent the average values between the 2 years.

*Data preparation.*—We visually examined the spatial data for potential sources of error for each year of our study and



discussed potential anomalies with individuals involved in the mapping efforts. While most of the changes in colony area over time were determined to be consistent with normal distribution patterns due to plague, we also identified a few inconsistencies due to differing mapping goals and methods across the study years and addressed these issues, where possible. Our first step was to identify a spatial extent which minimized inconsistencies and data errors associated with mapping during the study's time frame. Our total study area was 17,142 ha and was located near the center of the TBNG. Next, because 10 colonies detected in 1997 were not mapped in 2001, we merged data from these 2 years under the assumption that all colonies that existed in 1997 persisted until 2001 (the colony extents were similar during these 2 years and there was no evidence of a plague event between the 1997 and 2001 mapping efforts). Similarly, we merged data for the years of 2014 and 2015, as well as 2016 and 2017, because mapping efforts took more than 1 year to complete during these boom cycle years. We also found that maps from 2002, 2003, and 2004 showed that four colonies mapped in both 2002 and 2004 were overlooked during the 2003 survey. To account for those missing data points, we used the expansion rates of 21 other colonies of comparable size (range 0.2–8.9 ha) to those missed in 2003 to calculate the estimated expansion rates of the four missing colonies.

**Data analysis.**—We evaluated the 21-year data set of mapped prairie dog colonies using a combination of qualitative assessment and quantitative modeling to: (i) uncover patterns in boom and bust cycles; and (ii) interpret those patterns in conjunction with measures of landscape connectivity and weather data. We mapped the spatiotemporal dynamics of the colony complex within our study site and qualitatively evaluated changes in total colony area, including the magnitude and distributions of those changes, across the boom and bust periods. We also evaluated metrics of landscape composition or configuration that can provide complementary information to understand landscape processes (Turner and Gardner 2015) and used univariate models and box plots to explore how weather might interact with colony area and connectivity to drive boom and bust cycles.

We generated landscape metrics for the 15 of the 16 survey periods and plotted them to evaluate quantitatively how these metrics varied from year to year. Although joined total colony areas from the years 1997/2001, 2014/2015, and 2016/2017 adequately represented the maximum acreage extents from those periods, the incomplete mapping coverage of certain regions in 2003 made metrics of landscape configuration inappropriate to calculate for that year, so we did not include colony data from 2003 in our landscape analysis. As a result, we evaluated 15 survey periods instead of 16. We first converted vector data to raster format (30 m  $\times$  30 m pixel size) and then used the landscapemetrics package (Hesselbarth et al. 2019) in program R (R Development Core Team 2020) to calculate four metrics of landscape configuration: mean nearest neighbor distance (MNND), clumpiness, contagion, and percent core area. MNND represents the average distance between one patch (i.e., colony) and the next nearest patch (McGarigal et al. 2012).

Clumpiness measures connectedness (like adjacencies) to other patches of the same type, while contagion evaluates the probability of adjacency to unlike cells (both fall within the family of aggregation metrics, but the former represents greater aggregation approaching one, while the latter represents greater aggregation approaching zero). These first three metrics can influence the ability of plague to spread among different colonies. Core area represents the percent of the landscape around active colonies that has the potential to influence habitat suitability for associated species (Duchardt et al. 2019b). We defined this core area as >90 m from a given colony's edge, based roughly on territory sizes for avian species known to respond to distance to colony edge (Duchardt et al. 2019b).

We chose to evaluate drivers of colony growth (boom) separately from drivers of plague events (bust), so we could better uncover the different mechanisms that likely drive the boom and bust periods. To determine if and how climate influences colony expansion, we evaluated univariate models incorporating the effects of temperature and precipitation on change in colony area from both the current and previous years, and only included years when a plague event was not documented (i.e., all years but 1997/2001, 2005, and 2016/2017,  $n = 12$ ). We examined 10 univariate models including spring and summer precipitation, annual precipitation, annual modified PDSI, and annual maximum temperature, as well as the 1-year lag of each variable, and compared these to a null model. We evaluated the histogram of the response variable as well as model residuals to select the appropriate data distributions. We log-transformed change in colony area because this variable was highly skewed, and then used a Gaussian distribution. We did not evaluate quadratic effects or multivariate models because of our limited sample size. We used generalized linear models in program R (R Development Core Team 2020) and used Akaike's information criterion adjusted for small sample size ( $AIC_c$ ) to compare models (Burnham and Anderson 2002).

Because only three plague events occurred during the study period, we were unable to assess potential drivers of plague via logistic models. However, we wanted to evaluate if plague was potentially a function of both weather and landscape connectivity, as both variables have been found to play a role in plague epizootics in other regions (Stapp et al. 2004; Collinge et al. 2005b; Snäll et al. 2008; Savage et al. 2011; Eads and Biggins 2017). We hypothesized that years where landscape connectivity among colonies was high, but plague did not occur, might have different weather patterns from high connectivity years where plague did occur. We used MNND and plague occurrence to categorize our data into three groups for qualitative comparison. The first group included the years of each plague event (1997/2001, 2005, 2016/2017). The second group included all years when plague did not occur but MNND was equal to (i.e., within  $\sim 10$  m) or smaller than the highest value among plague years. The final group comprised years when MNND was substantially greater than in plague years. We then generated box plots for each of the groups with spring and summer precipitation, total annual precipitation, and annual maximum temperature, as well as the 1-year lag of each variable, to identify potential trends.



## RESULTS

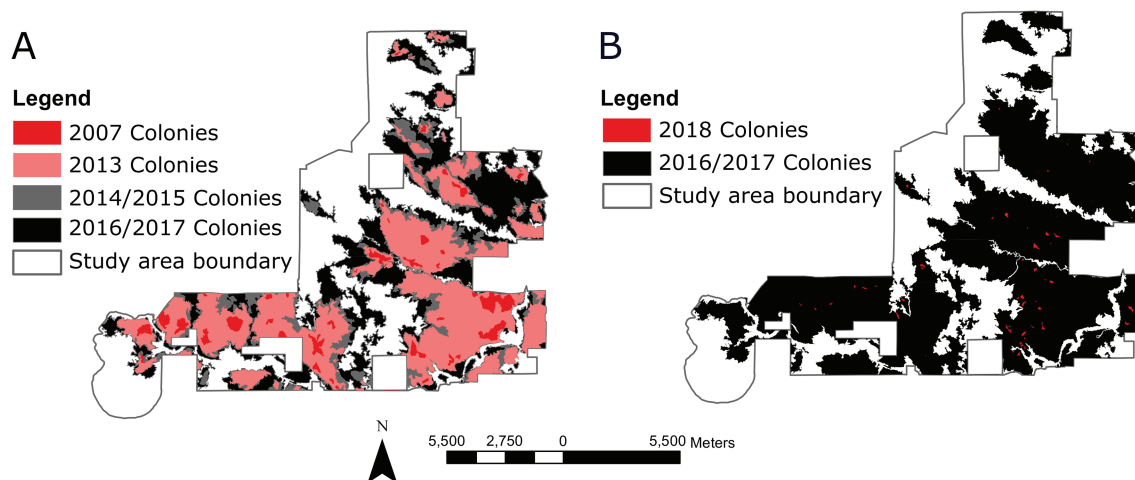
**Spatial scale of plague epizootics.**—Prairie dog colonies on the TBNG exhibited large fluctuations in total occupied area associated with three distinct plague epizootics during the 21-year study period (Fig. 1; Supplementary Data SD1). The presence of plague during these three cycles was only confirmed, as far as we know, during the third cycle in 2017 by laboratory analysis of a prairie dog carcass at the University of Wyoming Veterinary Lab (press release from Wyoming Department of Health, 7 July 2017). We are confident that plague was the cause of the previous two cycles because plague is the only pathogen known to cause such rapid, large-scale die-offs in prairie dogs (Barnes 1993; Cherry et al. 2019), and no large-scale poisoning or shooting efforts occurred during those time periods.

The first and third plague cycles were characterized by rapid colony contraction across the entire study area within a single mapping year (between 1997/2001 and 2002, and between 2016/2017 and 2018, respectively). In contrast, the second epizootic did not affect the entire colony complex synchronously within 1 year. Between 2004 and 2005, seven colonies in the southeastern portion of the study area contracted in size or were extirpated, but remaining colonies in the majority of the study area expanded, such that total complex area increased from 1,090 ha to 2,300 ha. Most of the colonies contracted dramatically between 2005 and 2006, such that total complex area declined from 2,300 ha to 410 ha. However, several colonies in the north-central portion of the study area still expanded between 2005 and 2006. These latter colonies collapsed between 2006 and 2007 in a manner consistent with plague, while the remainder of the complex started to expand between 2006 and 2007. Although the entire complex reached a minimum area in 2006, these results indicate that plague spread less rapidly across the complex over a period of approximately 3 years, in contrast to the larger-scale and synchronous contractions of all colonies during the 2002 and 2018 bust periods.

At the start of the 2005–2007 epizootic period, both total colony complex area and connectivity were notably lower than

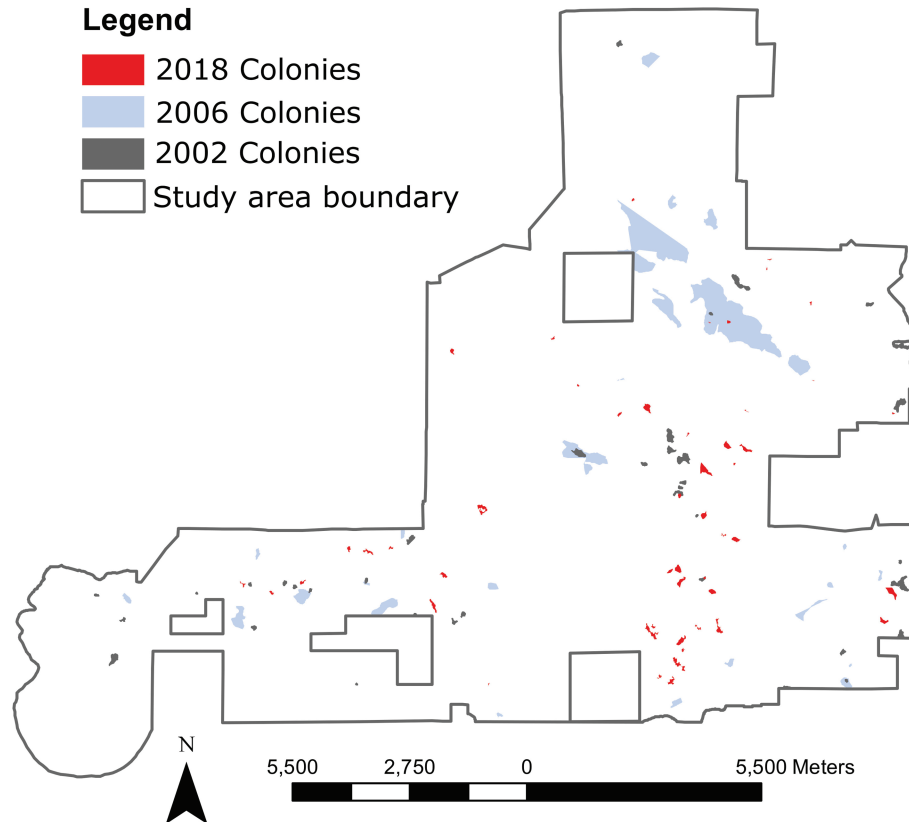
during the two temporally synchronous epizootics. Total complex area increased modestly from 2007 to 2010, after which it began to increase more rapidly each year, surpassing 2001 pre-plague size by 2013. The complex boomed to a maximum of 10,604 ha during the 2016/2017 survey, which was 21 times larger than the 499 ha documented in 2007, and nearly double the 2001 level (Fig. 2A). A third plague epizootic began in 2017 and continued into 2018, when the colony complex collapsed to only 47 ha, a >99% decrease in area occupied by prairie dogs (Fig. 2B). Interestingly, the size of the complex after the two synchronous epizootic outbreaks was similar, at 45 ha in 2002 and 47 ha in 2018.

The spatial distribution of the prairie dog colonies across the complex varied substantially over time (Figs. 1 and 3; Supplementary Data SD3). Over the course of the 15 mapping periods, prairie dogs occupied a total cumulative footprint of 10,712 ha within the 17,142 ha study area, but much of that footprint was not continuously occupied by prairie dogs. We estimated that 17% of the total study area was occupied for only 1 of the 15 surveys, and only 2.7 ha (0.02%) were continuously occupied across all 15 surveys (Supplementary Data SD3). Areas occupied for 8 or more of the 15 surveys comprised a total of 8% of the study area. Although the initial location of colonies during the bust cycle years exhibited little overlap, particularly during the first year or two following a plague event (Fig. 3), prairie dogs persisted in or recolonized many of the same general areas following both the first and second epizootics during our study period (our study period ended in 2018, so we do not report here on recolonization patterns for after the third epizootic). That tendency was more evident by the third-year post-plague, when overlap between active colony locations pre- and post-plague increased to 29%. Additionally, as prairie dogs reached peak abundance in each of the expansion phases (i.e., in 1997/2001, 2005, and 2016/2017; Fig. 1), they consistently occupied the same areas. Specifically, 99.9% of the area occupied during 1997/2001, as well as 99.9% of the area occupied in 2005, was recolonized during 2016/2017 (Fig. 1). Conversely,



**Fig. 2.**—Examples of boom and bust cycles on the Thunder Basin National Grassland, Wyoming. Panel A shows expansion following the 2006 population crash, with expansion occurring in all directions, from 499 ha in 2007 to 10,604 ha in 2016/2017. Panel B shows colony collapse from 2016/2017 (10,604 ha) to 2018 (47 ha), showing reduction is occurring in all directions across the study area and a decline of over 99%.





**Fig. 3.**—Spatial distributions of colonies during “bust” years (2002, 2006, 2018) in our study area on the Thunder Basin National Grassland, Wyoming, illustrating that there was little overlap in the location of collapsed colonies during these years.

6,471 ha of the study area were never colonized during any of the post-plague recovery phases (Fig. 1).

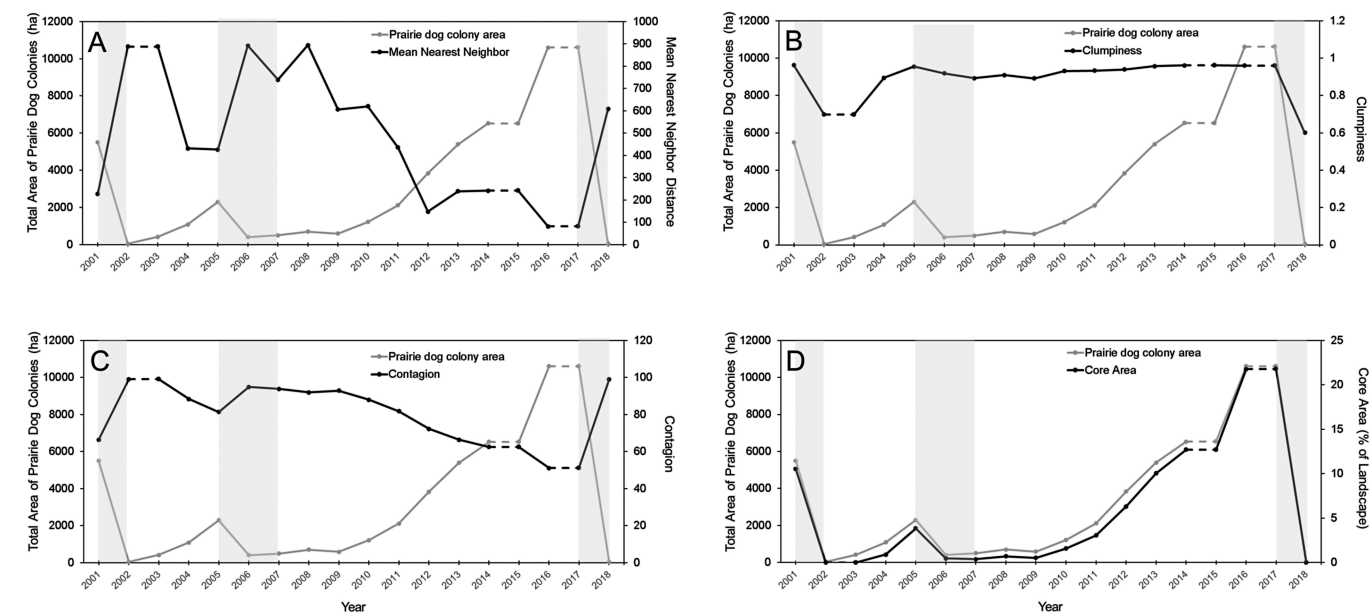
We did not observe a consistent relationship between the metrics of landscape aggregation and plague epizootics (Fig. 4). Because configuration and composition are closely tied, landscape metrics of spatial aggregation were, by nature, somewhat correlated with total colony size, which was higher prior to plague events. Contagion ( $r = -0.977$ ) and core area ( $r = 0.997$ ) were highly correlated with total colony area, and thus provided little additional information for interpreting these cycles. Notably, however, colony core area was particularly high in 2016/2017 (highest among all sample years), just before the 2017/2018 plague outbreak occurred (Fig. 4). Our two other metrics of spatial aggregation, MNND ( $r = -0.834$ ) and clumpiness ( $r = 0.517$ ), provided some additional insight. MNND was low preceding the first and third epizootic (228 m in 2001 and 82 m in 2017) but was substantially greater preceding the second (426 m in 2005). Colonies were similarly or more connected during the nonplague years of 2004 and from 2011 through 2015 (MNND ranged from 148 to 435 m) than they were during the plague event of 2005 (MNND was 426 m). The other 8 years (without plague) had MNND values  $>600$  m. Clumpiness, a measure of connectedness, was relatively consistent over time except following the first and third epizootics, when it declined by 27% and 37%, respectively. Among all four metrics, we observed no consistent threshold values beyond which epizootics occurred.

*Association with weather patterns.*—We found only weak support for any relationship between weather variables and colony growth (Table 1; Fig. 5). The model including maximum annual temperature indicated a marginally positive association with growth in colony size ( $\beta_{\text{maxtemp}} = 0.103$ ,  $SE = 0.052$ ). No other model was better than the null model. Our analysis of weather conditions in years when plague outbreaks occurred showed higher annual maximum temperature and summer precipitation compared to years with high colony connectivity but no plague, years with low connectivity and no plague, and the means for those weather parameters across the study period (Fig. 6). Additionally, precipitation was notably lower the year prior to a plague outbreak than in the first year of an outbreak. In years preceding a plague epizootic, the region received an average of 7.5 cm less of total annual precipitation compared to nonepizootic years with similar connectivity. Spring and summer precipitation levels in years preceding an epizootic were also well below the mean for the study period. However, total annual precipitation during the first year of plague events was similar and close to the mean, compared to years when no plague outbreak occurred.

## DISCUSSION

We found that boom and bust cycles characterized the colony dynamics of black-tailed prairie dogs in the Thunder Basin ecoregion of northeastern Wyoming. The area occupied by





**Fig. 4.**—Trends in four metrics of landscape configuration on prairie dog colonies in the study area on the Thunder Basin National Grassland, Wyoming between 1997 and 2018. Mean nearest neighbor (A) represents the average distance to the next nearest prairie dog colony. Clumpiness (B) measures connectedness (adjacencies) to other patches of the same type, while contagion (C) evaluates the probability of adjacency to unlike cells (both are aggregation metrics, but the former represents greater aggregation approaching 100, while the latter represents greater aggregation approaching zero). Core area (D) represents the percent of the landscape defined as “colony core,” here, as >90 m from an interior colony edge. Plague epizootic events are represented by the vertical light gray bars.

**Table 1.**—Results for univariate models predicting drivers of log-transformed prairie dog colony growth on the Thunder Basin National Grassland, Wyoming from 1997 to 2018. Table presents number of parameters ( $K$ ),  $AIC_c$  values,  $\Delta AIC_c$ , model weights ( $w_i$ ), log likelihoods of all models, and estimated  $\beta$  coefficients. No  $\beta$  coefficients were significant at an alpha of 0.05. PDSI, Palmer Drought Severity Index.

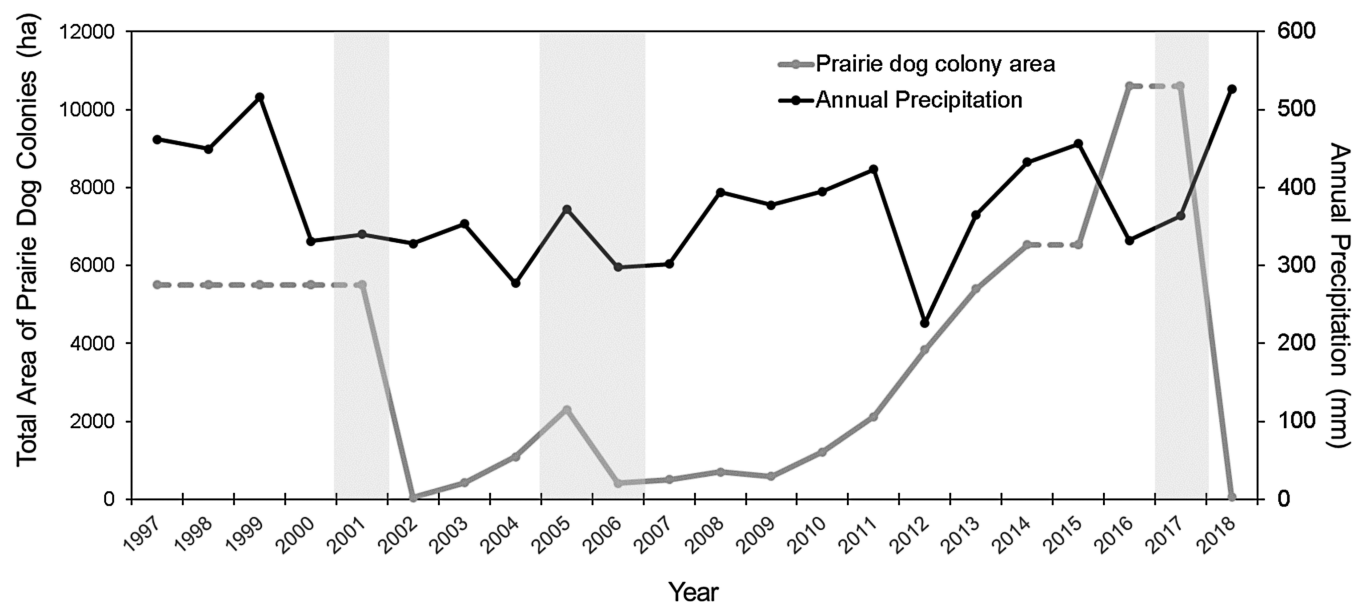
Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$	Log likelihood	$\beta$ estimate ( $SE$ )
Max temp	3	25.62	0	0.30	−8.31	0.103 (0.052)
Null	2	25.91	0.29	0.26	−10.29	—
Lag1.Spring precip	3	28.64	3.02	0.07	−9.82	−0.029 (0.033)
Lag1.Max temp	3	28.97	3.34	0.06	−9.98	0.04 (0.053)
Summer precip	3	29.11	3.49	0.05	−10.05	−0.038 (0.06)
Annual precip	3	29.21	3.59	0.05	−10.11	−0.017 (0.030)
Lag1.Summer precip	3	29.40	3.77	0.05	−10.20	0.038 (0.07)
Lag1.Annual precip	3	29.43	3.81	0.04	−10.22	−0.01 (0.03)
Spring precip	3	29.44	3.82	0.04	−10.22	−0.012 (0.034)
Lag1.PDSI	3	29.58	3.95	0.04	−10.29	−0.005 (0.088)
Annual PDSI	3	29.58	3.96	0.04	−10.29	−0.002 (0.082)

black-tailed prairie dog colonies fluctuated dramatically over the two decades of our study, driven largely by collapses induced by epizootic plague occurring over approximately 1- to 3-year time periods, followed by 4- to 11-year periods of steady colony expansion. The cycles observed on the TBNG behaved similarly to those documented in other portions of black-tailed prairie dog range where plague occurs (Cully and Williams 2001; Augustine et al. 2008b; Hartley et al. 2009; Johnson et al. 2011; Savage et al. 2011). However, unlike many colonies followed over time in these landscapes (Cully et al. 2010; Keuler et al. 2020), the TBNG prairie dog complex showed no precipitous, long-term decline or increase in fragmentation, at least over the 21-year period of our study. While the complex rebounded to less than half of its pre-plague (2000) size before the second plague outbreak occurred, similar to patterns documented for other colony complexes (Seery and Matiatos 2000;

Hartley et al. 2009), it recovered well beyond that size before the epizootic of 2017/2018. Notably, the TBNG colony complex mapped during 2016–2017 was the largest documented in North America at the time.

Prior to the introduction of plague, prairie dog colonies throughout their range were typically large, stable features on the landscape; the boom and bust cycles present today do not reflect natural, historical population dynamics of prairie dogs (Knowles et al. 2002; Augustine et al. 2008b; Cully et al. 2010; Keuler et al. 2020; Biggins et al. 2021a). Plague—a non-native disease to which prairie dogs have no natural, co-evolved immunity—consequently destabilizes the prairie dog ecosystem, with cascading impacts on associated species (Augustine et al. 2008a, 2008b; Eads and Biggins 2015; Keuler et al. 2020). For example, Duchardt et al. (2019a) documented rapid declines in mountain plovers, golden eagles (*Aquila chrysaetos*), and





**Fig. 5.**—Total area of prairie dog colonies in the study area on the Thunder Basin National Grassland, Wyoming (1997–2018) compared to total annual precipitation. Plague epizootic events are represented by the vertical light gray bars. Dotted lines indicate years where surveys did not occur (1998–2000) or partial surveys were averaged (2014–2015 and 2016–2017).

ferruginous hawks on the TBNG concomitant with the plague-induced population collapse of prairie dogs from 2017 to 2018. Such losses in prairie dogs are especially detrimental to those species that depend on large colonies to support their populations (e.g., 130–320 ha; Augustine et al. 2008a; Parker et al. 2019; Duchardt et al. 2020, 2021).

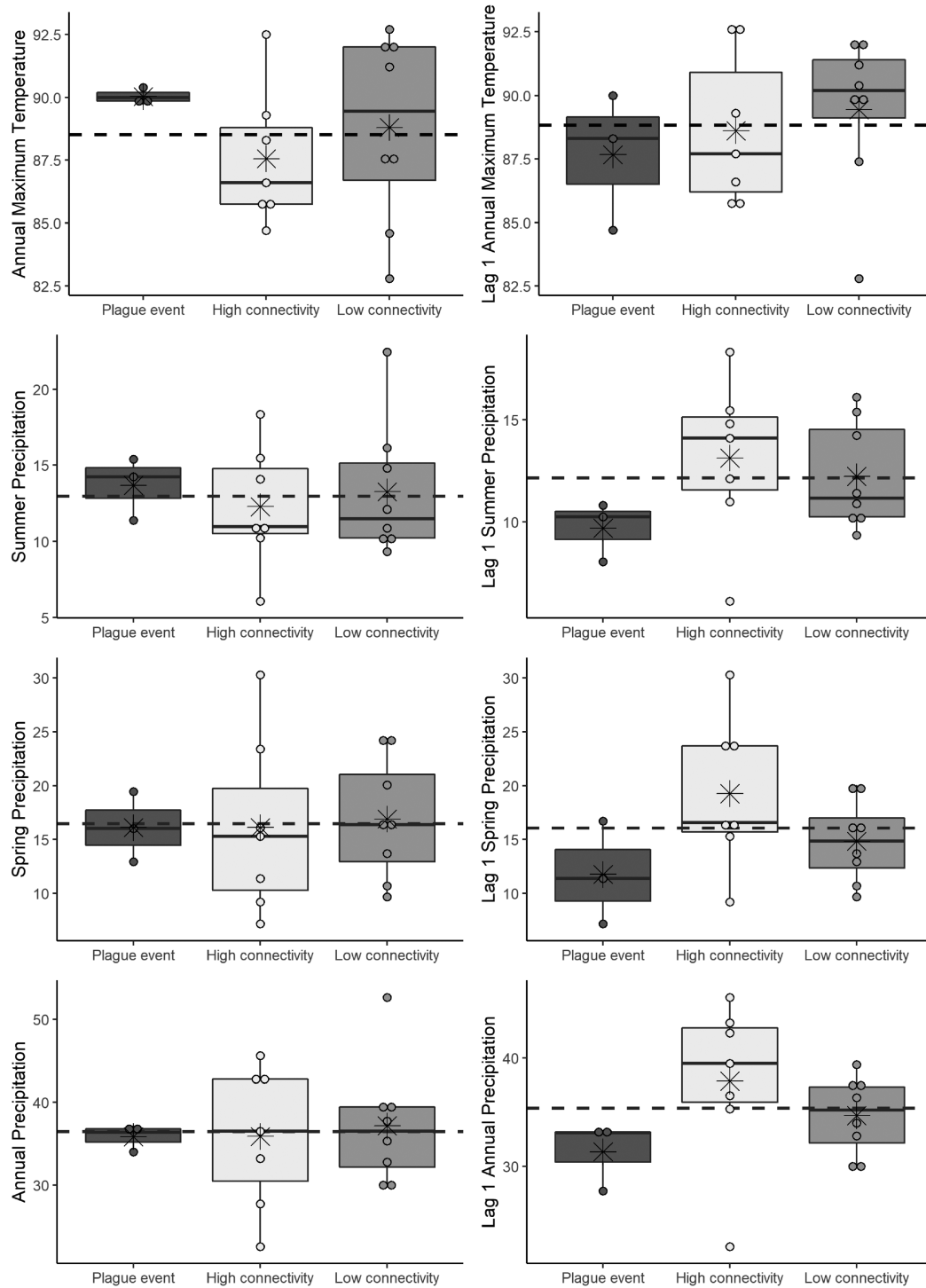
Colony collapses due to plague occurred across the entire prairie dog complex over a 1-year period during the first and third epizootics on the TBNG, and over a 3-year period during the second epizootic. Rapid declines in total complex area (e.g., >99% decrease between 2017 and 2018) and the comparatively slow population recovery times are similar to a plague cycle documented previously on the Comanche National Grassland in southeastern Colorado (Augustine et al. 2008b). In contrast, the patterns observed in the second epizootic, when colonies were less interconnected and contractions shifted in location over a series of years, are more similar to the scale and temporal patterns of epizootics documented in northeastern Colorado (Savage et al. 2011), western Kansas and Oklahoma (Johnson et al. 2011), and northern Montana (Augustine et al. 2008b). Because plague transmission often occurs over a period of months to more than a year before an observable die-off is detected, the epizootics on the TBNG could have begun even before population collapses were first reported (St. Romain et al. 2013).

Consistent with our findings for the TBNG, Johnson et al. (2011) found that epizootics spread more rapidly over a larger area in complexes with smaller intercolony distances. However, our finding that a rapid, synchronous epizootic occurred when the complex reached 10,604 ha (or 62% of the study area) and a slower-spreading, more patchy epizootic occurred when the complex reached 2,300 ha (or 13% of the study area) highlights the challenge in predicting when and where plague epizootics will occur. Although plague epizootics typically occur

when colonies become large and are in close proximity to each other to facilitate transmission (Collinge et al. 2005a; Snäll et al. 2008; Cully et al. 2010; Johnson et al. 2011; Savage et al. 2011), our findings illustrate how widely these factors can vary while still enabling the spread of plague. The lack of any colony contraction from 2013 to 2016, when the extent and connectivity of colonies were greater compared to some years when prior epizootics occurred, further illustrates the challenge in predicting epizootics. Additionally, colony distribution and connectivity are not always essential elements of an epizootic because plague is maintained in the environment in an enzootic phase, which allows outbreaks to erupt even among isolated colonies when conditions are right (Stapp et al. 2004; Biggins et al. 2010; Matchett et al. 2010; Lowell et al. 2015; Liccioli et al. 2020). Indeed, plague epizootics occur in response to complex interactions among climate, landscape connectivity, colony sizes, and metapopulation dynamics, as well as host and vector population densities, all of which remain poorly understood (Collinge et al. 2005a; Snäll et al. 2008; George et al. 2013; Eads et al. 2016b; Eads and Biggins 2017; Biggins and Eads 2019; Biggins et al. 2021a).

Analyses that consider the interaction of spatial features of prairie dog colony complexes with weather conditions that favor flea abundance and pathogen transmission have provided some insight to prediction of plague epizootics (Stapp et al. 2004; Snäll et al. 2008; Savage et al. 2011; Eads and Biggins 2017). One emerging hypothesis is that transitions from dry to wet years increase the probability of an epizootic (Eads and Biggins 2017). Such transitions may be important because dry conditions increase stress on prairie dogs, reducing body condition and creating the potential for future increases in flea loads (Eads et al. 2016b; Eads and Biggins 2017). The dry conditions can also suppress both fleas and *Y. pestis* (Eads and Biggins 2017). Yet when dry conditions are followed by wet weather





**Fig. 6.**—Box plots representing the range of climatic variables in three different colony connectivity categories between 2000 and 2018 in the study area on the Thunder Basin National Grassland, Wyoming. “Plague events” (dark gray) represent the conditions in each of the 3 years that plague occurred, while landscape connectivity was high (mean nearest neighbor (MNN) < 435 m). “High connectivity” (light gray) boxes represent conditions in years where colonies had similarly high connectivity, but plague did not occur. “Low connectivity” (medium gray) represents conditions when colonies had relatively low spatial connectivity (MNN > 600 m). Figures on the left represent conditions in a given year, while figures on the right represent the 1-year lagged conditions. Temperature is measured in °F, and precipitation is measured in cm. Dotted lines represent averages among all years of the study. Stars represent the mean.

with mild temperatures, the consequent increases in prairie dog densities, flea loads, and aboveground activity can coincide with conditions favoring fleas and plague transmission (Eads

and Biggins 2017). Although our sample size for plague events was small, we found that for those years in which colony connectivity was high, plague events corresponded with higher



temperatures and slightly above-average summer precipitation, and, most notably, when the prior year received substantially below-average summer precipitation. Similarly, Eads and Hoogland (2016) found that dry conditions increased both flea loads on prairie dogs and the likelihood of plague occurring when moisture returns and temperatures are mild. Our findings provide clear support for the idea that “paltry past precipitation predisposes prairie dogs to plague” (Eads and Biggins 2017), while also suggesting that the precipitation pattern may be more influential than temperature.

We did not find colony growth to be clearly correlated with climate. The model with maximum temperature was better than the null, but only by a small margin (i.e., within 2 AIC<sub>c</sub> of null model). Climate differs greatly across the geographic range of black-tailed prairie dogs and has varying effects on prairie dog populations in the different grassland systems where they occur. In the Northern Plains, black-tailed prairie dog reproduction has been shown to be positively correlated with previous summer–fall precipitation and negatively affected by severe winters (Grassel et al. 2016; Stephens et al. 2018). Colonies in the Northern Plains also have been documented to expand during dry periods, facilitated by reduced vegetation height and cover (Bruggeman and Licht 2020). Under drought stress, prairie dogs presumably require larger home ranges to obtain sufficient food resources, so prairie dog densities can decline even as the spatial extent of colonies expands (Bruggeman and Licht 2020). In the southern and far northern portions of their range, drought can suppress reproduction and population growth rates, causing colony contractions and local extinctions (Hoogland 1995; Facka et al. 2010; Hale et al. 2013; Davidson et al. 2014; Hayes et al. 2016; Stephens et al. 2018). Weather may have played a role in driving the boom periods of prairie dog colonies on the TBNG, but we were not able to detect it. This could be in part because the size of an area occupied by prairie dogs is not a direct measure of their population density, so only evaluating colony area may obscure the relationships between climate and prairie dog population dynamics. Future work should consider changes in both colony acreage and population density to better understand how climate influences boom periods. This is a complex ecological system and uncovering the drivers of the boom and bust cycles will probably require monitoring a suite of ecological variables and their interactions over long periods of time.

Application of deltamethrin dust to control for fleas that carry plague occurred in limited and localized pockets of TBNG colonies between 2010 and 2015, aligning with a major period of colony growth. However, we do not know if dusting interacted with climatic variables and colony connectivity to influence prairie dog colony expansion in the area; we suspect that it did not have a substantial impact given the small proportion of the complex dusted (Supplementary Data SD1). Additionally, plague was suspected based on apparent die-off in one location in early June of 2017 and confirmed by laboratory analysis of a collected prairie dog carcass several months after the study area was opened to recreational shooting (March 2017), following a 7-year ban. Recreational shooting

could potentially increase flea: host ratios that act as a trigger for epizootic plague (Biggins and Eads 2019). Because large and highly interconnected colony complexes like that observed on the TBNG in 2016/2017 are susceptible to plague epizootics when environmental conditions become suitable, we suspect the complex would have experienced an epizootic regardless of the recreational shooting policy. However, we do not know if shooting may have interacted with other environmental conditions to help trigger the 2017/2018 plague epizootic. We note these observations to encourage good record keeping of management approaches taken and future research to evaluate the potentially interactive effects of management approaches (e.g., dusting, recreational shooting) and weather patterns on prairie dog colony dynamics and plague outbreaks.

Prairie dog conservation on the TBNG is controversial due to the substantially mixed surface ownership and because large prairie dog colonies have the capacity to create operational and financial risk for livestock producers by reducing forage availability (Vermeire et al. 2004; Detling 2006), particularly during dry years when operations are already under stress (Connell et al. 2019). A key factor influencing the degree to which prairie dogs suppress perennial grasses and shift vegetation toward subshrubs and annual forbs unpalatable to livestock is the length of prairie dog occupancy on a given site (Coppock et al. 1983; Augustine et al. 2014). Historically, in a pre-plague landscape, colonies persisted for long periods of time during which prairie dogs substantially altered vegetation, creating heterogeneous landscapes with varying degrees of disturbance that supported many wildlife species (Coppock et al. 1983; Whicker and Detling 1988).

Our data indicated that, by blinking in and out over time and space due to plague, prairie dogs had limited long-term (i.e., 7 or more years) occupancy in any one area. Only limited portions of the study area were continuously occupied by prairie dogs for extended periods of time because of plague, even though there was spatial consistency in the areas that prairie dog colonized as they recovered from each of the three plague epizootics. These findings are similar to those by Augustine et al. (2008b) and are significant because available research suggests that 7 or more years of continuous occupancy are necessary for prairie dogs to have substantial long-term impacts on grassland vegetation in the western Great Plains (Coppock et al. 1983; Archer et al. 1987; Whicker and Detling 1988; Hartley et al. 2009; Augustine et al. 2014). Colonies on the TBNG did consistently occupy approximately 30% of our study area from 2013 through 2017, and short-term effects of prairie dogs on forage biomass and vegetation composition were likely to have been substantial (Augustine and Springer 2013) during this period of colony stability and expansion. Indeed, vegetation changes characterized by increased cover of annual forbs and bare soil and reduced perennial grass cover occurred on colonies in TBNG during this time, and were associated with increased use by mountain plovers, a species known to strongly associate with prairie dog colony habitat (Duchardt et al. 2020). However, because only 8% of the study area was continuously occupied by prairie dogs for 8 or more out of the



15 survey years, lasting impacts on vegetation composition and productivity were likely limited in extent (Hartley et al. 2009; Augustine et al. 2014).

In addition to areas of relatively consistent overlap in active colony locations pre- and post-plague, we also documented sizeable regions of the study area where prairie dogs have consistently been absent over time, even in years with extraordinary occupancy (e.g., 2016/2017) (Fig. 1). These regions are typically comprised of topographic (e.g., elevation, slope, aspect) or other features (e.g., soil texture, shrub presence) that reduce the probability of colonization by prairie dogs (Reading and Matchett 1997; Augustine et al. 2012). Understanding the presence, location, and factors that result in such natural exclusion zones is critical to prairie dog management efforts. Where managers are wanting to promote, translocate, or restore prairie dog colonies, efforts should be targeted in areas with the greatest potential for success.

Prairie dog “booms” on the TBNG are not necessarily population increases above long-term historical levels. For historical context, Redington et al. (1929) notes that a single prairie dog town extended 100 miles (160 km) long in the Thunder Basin ecoregion, and that between the years of 1923 to 1929, 445,073 ha of prairie dogs were poisoned in this complex located 40 miles (65 km) east of the study area. For perspective, the TBNG colony complex within our study area was 10,604 ha and about 20 km long at its peak in 2017, with the largest colony being about 8 km long. These numbers are an underestimate of true coverage in the Thunder Basin ecoregion beyond our study area, as many other colonies in other locations of the TBNG were observed but not mapped during the 2016/2017 survey. The prairie dog booms we have observed on the TBNG during our study period have been population recoveries following repeated collapses from a non-native disease, and appear to be below historical population and colony sizes (Redington et al. 1929; Knowles et al. 2002). Inevitably following the booms are plague-driven busts (Cully et al. 2010).

Research is needed to find viable options for managing these boom and bust cycles in a way that supports grassland biodiversity, rangeland health, livestock production, and rural communities, including within the context of climate change. In areas critical for associated species to thrive, such as the endangered black-footed ferret, population recoveries of prairie dogs and maintenance of their colonies can be facilitated through plague mitigation, helping to stabilize large colonies (Rocke et al. 2017; Biggins et al. 2021b). However, large colonies can conflict with livestock production goals, especially during dry periods (Augustine and Derner 2021), and this can negatively impact the willingness of livestock operations to coexist with prairie dogs. Lethal measures to control prairie dogs during boom periods can also be extremely costly (Collins et al. 1984). Economic analyses are needed to better understand the costs of controlling prairie dog populations relative to improvements in livestock production. The costs of control may not be offset by economic gains in livestock production, particularly if control efforts must be employed repeatedly and/or at large scales over time (Collins et al. 1984; Roemer and Forrest 1996, but see also

Crow 2020). Additional research is also needed to examine the efficacy of alternative approaches, such as grass banks, to mitigate the impact of expanding colonies on livestock production to help promote coexistence (Roemer and Forrest 1996; Pauli and Buskirk 2007).

Our study summarizes the spatiotemporal dynamics of black-tailed prairie dog boom and bust cycles in the Thunder Basin ecoregion from 1997 through 2018, helping to inform management and conservation decisions regarding the characteristics of these cycles within this landscape. Given the keystone role that prairie dogs play, the boom and bust cycles exhibited in our study undoubtedly influence populations of associated wildlife species (Augustine et al. 2008a; Davidson et al. 2012; Eads and Biggins 2015; Eads et al. 2016a; Duchardt et al. 2019a, 2021; Parker et al. 2019; Keuler et al. 2020). Thus, the results of our study have management implications for many species. Better understanding of the drivers, dynamics, and impacts of these cycles is needed to optimize the coexistence of livestock production, other land uses, and the conservation of black-tailed prairie dogs and associated species.

## ACKNOWLEDGMENTS

We thank the USFS, Great Plains Wildlife Consulting, Inc., Jack Cully, Tammi Johnson, Tim Byer, Christi Painter, Rachel Keller, Jennifer Ottinger, Bill Vetter, and numerous other biologists and field technicians for their data collection of prairie dog colony acreages and other associated data across the TBNG over the years. We also thank two reviewers for comments that helped to greatly improve the manuscript. This work is part of the Thunder Basin Research Initiative. Funding was provided by the National Institute of Food and Agriculture (award number: 2018-68008-28090). We thank TBGPEA, the Thunder Basin Grazing Association, Converse County Conservation District, and the United States Department of Agriculture–Agricultural Research Services for supporting and providing additional funding for this research.

## SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Detailed information on prairie dog mapping efforts and the colony complex over time within the study area, including plague patterns and management.

**Supplementary Data SD2.**—Example of the 2018 Phase 1 mapping effort in the Thunder Basin National Grassland, Wyoming.

**Supplementary Data SD3.**—Percent of total study area occupied by black-tailed prairie dogs in 1 or more years of the study period (1997–2018).

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*Submitted 10 April 2021. Accepted 30 March 2022.*

*Associate Editor was Timothy Smyser.*