LANDSCAPE EFFECTS ON DISEASE AND DEMOGRAPHY IN THE BLACK-TAILED PRAIRIE DOG, *CYNOMYS LUDOVICIANUS*

by

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B.S. University of Texas, Austin, 2001

A thesis submitted to the Faculty of the Graduate School of the University of Colorado in partial fulfillment of the requirement for the degree of

Master of Arts

Department of Ecology and Evolutionary Biology

2009

This thesis entitled:

Landscape effects on disease and demography in the

black-tailed prairie dog, *Cynomys ludovicianus*

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content and the form meet acceptable presentation standards of scholarly work in the

above mentioned discipline.

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Landscape effects on disease and demography in the black-tailed prairie dog,

Cynomys ludovicianus

Thesis directed by Associate Professor Sharon K. Collinge

Abstract

Landscape context can strongly influence wildlife disease incidence by precipitating shifts in host community structure and altering movement of hosts and vectors across the landscape. The black-tailed prairie dog (*Cynomys ludovicianus*) has undergone significant population declines due to sylvatic plague (*Yersinia pestis*), and understanding the combined effects of human-mediated landscape change on disease dynamics and host demography are crucial for the conservation of this species. In this thesis, I investigated putative correlates between landscape structure and plague occurrence at prairie dog colonies in Boulder County, Colorado during the 2005 plague epizootic. I used AICc to evaluate the relative support of logistic regression models of plague occurrence, and predicted that disease occurrence would be negatively associated with streams, urbanization, water bodies, roads, and isolation from other plague-positive colonies. The best supported models of plague occurrence in this study included negative effects of urbanization, streams, isolation from plague positive colonies and positive effects of prairie dog colony cover, colony area, and water bodies at the 250m scale. Urban colonies were afforded some protection against plague, highlighting the

importance of protecting urban colonies in Boulder County. In addition, I estimated prairie dog survival rates from 2003-2006 in Boulder County in order to investigate the short- and long-term effects of plague on prairie dog survivorship. Eight colonies infected with plague in 2005-06 suffered mortality rates exceeding 99%. Survival rates of prairie dogs in colonies founded since the 1994 plague epizootic were not significantly different from older colonies unaffected by plague in 1994, suggesting that demographic signals of plague events diminish over time. Finally, an investigation of prairie dog survivorship in relation to landscape and colony characteristics failed to uncover significant relationships between maximum survival estimates and measures of landscape composition, colony area, and prairie dog density, indicating that, in the absence of plague, landscape characteristics may be less important determinants of prairie dog survival than are patch-level characteristics. Taken together, these results underscore the ongoing threat plague presents to prairie dog populations in Boulder County, and suggest that the intervening landscape matrix plays a critical role in plague transmission by altering terrestrial animal movements.

Dedication

To my Pops, for sharing with me the rich tapestry of his life, and for teaching me the value of hard work, humor, and adventure.

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INTRODUCTION

Given the near domination of the agricultural lands and urban population centers that now characterizes the western United States, it is perhaps difficult to imagine the Great Plains grasslands as they once were. Early accounts given by the first European arrivals to the Great Plains reflect the historic extent and variety of native grassland ecosystems. When Francisco Vasquez de Coronado arrived in 1540 in search of the fabled Seven cities of Gold, he described the Great Plains in nautical terms, comparing the vast tracts of grasslands he was crossing to the rolling waves of an ocean, without landmarks or an end in sight (Savage and Page, 2006). Beginning in force with the Homestead Act of 1862 and stretching to present day, grassland habitats have been worked and altered, with native grasslands largely supplanted by agricultural crops and ranchlands (Samson, 2004). In recent decades, the "Wild West" has given way along the western margin of the Great Plains to what Riebsame and others describe as the "New West" (1997) with human populations rapidly expanding and rates of development in many areas far exceeding that of the national average (Hansen et al., 2002). This rapid transformation and degradation of the Great Plains, while serving an economic purpose and accommodating human population growth, has also had generally unfortunate and sometimes dire consequences for native wildlife.

The conservation status of the black-tailed prairie dog (*Cynomys ludovicianus*) exemplifies the negative consequences of habitat loss and degradation in grassland ecosystems. The black-tailed prairie dog is a diurnal colonial rodent whose historic range

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corresponds with the short and mixed grass prairies once common in North America. At the beginning of the 20th century, prairie dogs were reported to number a staggering five billion individuals (Merriam, 1902). Knowles and others have recently argued that early estimates of prairie dog abundance fell short of the true abundance and historic distribution of this species, suggesting that black-tailed prairie dogs covered 160 million hectares or more (Knowles et al., 2002). Today, prairie dog abundance has been reduced to less than 2% of what it once was (Miller, 1994) while the geographic extent of the species has been decreased to less than 1% of its historic range (Gober, 2000). In addition to habitat loss, these alarming population declines can be attributed to intentional poisoning and shooting as well as the introduction and establishment of sylvatic plague in the western US. Importantly, prairie dogs likely fill a vital role in grassland ecosystems as both a keystone species and ecosystem engineer (sensu Paine, 1969 and Jones, 1994), and as a result prairie dog population declines could have wide-spread effects on closely associated species.

Although studies have investigated both the deleterious effects of plague on prairie dogs (Cully and Williams, 2001) and the effects of landscape structure on prairie dog colonies (Johnson, 2004), few studies have yet to focus on the combined consequences of urbanization and disease on black-tailed prairie dogs (but see Collinge et al., 2005). For instance, while landscape characteristics associated with urbanization have been shown to reduce the risk of plague exposure in prairie dog colonies (Collinge, 2005), the exact nature of the relationship between prairie dog demographic rates, disease transmission, and urbanization are still poorly understood. In an effort to fill this knowledge gap, this thesis addresses landscape effects on demography and disease in

prairie dogs. In Chapter 1, I investigate the short- and long-term effects of plague on prairie dog survivorship using mark-recapture data collected in Boulder County, Colorado from 2003-2006. In this chapter, I also explore potential associations between prairie dog survival and landscape and colony characteristics. In Chapter 2, I investigate putative correlates of plague occurrence in black-tailed prairie dog colonies in Boulder County. Using a geographic information system and logistic regression models, I model plague occurrence as a function of landscape and colony characteristics.

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CHAPTER 1

LANDSCAPE AND COLONY FEATURES ASSOCIATED WITH
BLACK-TAILED PRAIRIE DOG SURVIVAL
IN BOULDER COUNTY, COLORADO

Abstract

Despite significant population declines due to habitat loss, deliberate poisoning and shooting, and sylvatic plague, the black-tailed prairie dog (*Cynomys ludovicianus*) continues to play an important functional role in the short and mixed grass prairies in which they live. In this study, prairie dog survival rates were estimated from 2003-2006 in Boulder County, Colorado in order to investigate the short- and long-term effects of plague on prairie dog survivorship, as well as to explore potential associations between landscape and colony characteristics and prairie dog demography. Eight colonies infected with plague during the course of this study suffered from mortality rates exceeding 99%, underscoring the considerable and ongoing threat plague presents to prairie dog populations. Survival rates of prairie dogs in colonies founded since the last large plague epizootic in 1994 were not significantly different from older colonies unaffected by plague in 1994, suggesting that demographic signals of plague events diminish over time. Finally, an exploratory investigation of prairie dog survivorship in relation to landscape and colony characteristics failed to uncover significant relationships between maximum survival estimates and measures of landscape composition, colony area, and prairie dog density. These results suggest that, in the absence of plague exposure, landscape composition and structure are perhaps less important determinants of prairie dog survival in Boulder County than are patch-level characteristics.

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) are the most widely distributed of the five recognized prairie dog species in N. America. Their historical range corresponds with the short and mixed grass prairies once common throughout the Great Plains. Prior to human interference, the geographic range of prairie dogs had remained relatively stable for over 400,000 years, according to the fossil record (Graham and Lundelius, 1994), and at the beginning of the 20th century, prairie dogs were reported to number a staggering five billion individuals (Merriam, 1902). Yet the historical abundance of this species stands in stark contrast to its current status. Today, prairie dog abundance has been reduced to less than 2% of what it once was (Miller, 1990, 1994) while the geographic extent of the species has been constricted to a mere 1% of its historic range (Gober, 2000). These precipitous population declines led the U.S Fish and Wildlife Service to designate black-tailed prairie dogs as "warranted but precluded" for listing as a threatened species in 2000 (Gober, 2000), though they have since been removed from consideration for listing (US Fish and Wildlife Service, 2004).

Despite their reduced numbers and dwindling habitat, black-tailed prairie dogs continue to play an important functional role in relict short and mixed grass prairies (Miller et al., 2000). Considered a keystone species (sensu Paine, 1969) and ecosystem engineer (sensu Jones et al.,1994), prairie dogs have a disproportionate effect on the structure and function of ecosystems relative to their abundance (Kotliar et. al., 1999, Miller et. al., 2000). Their burrowing activity increases plant productivity, soil porosity, and soil turnover, and creates shelter for small mammals (Whicker and Detling, 1993).

Many species are closely associated with prairie dog colonies, including the endangered black-footed ferret (*Mustela nigripes*), the tiger salamander (*Ambystoma tigrinum*), the burrowing owl (*Athene cunicularia*), and the swift fox (*Vulpes velox*) (Smith and Lonomolino, 2004). In addition, studies have demonstrated that black-tailed prairie dogs affect the diversity and abundance of a wide variety of species including small mammals (Smith & Lonomolino, 2004, Conlin, 2005), fleas (Brinkerhoff, et al., 2008), and birds (Agnew et al., 1986). Given their ecological importance, changes in prairie dog abundance and distribution could have widespread effects on associated species and possibly lead to further degradation and simplification of grassland ecosystems.

Prairie dog population declines are largely attributable to habitat loss, intentional eradication efforts, and disease (Miller et al.,1994, Biggins and Kosoy, 2001). Extensive habitat loss and degradation of the native grassland ecosystems of the Great Plains have significantly reduced suitable prairie dog habitat and decreased connectivity among colonies (Lomolino and Smith, 2003, Samson, 2004). Wide-spread poisoning and shooting by ranchers as well as a nationally sponsored eradication program have further depressed prairie dog numbers (Norris, 1987). Finally, sylvatic plague, caused by the bacterial pathogen *Yersinia pestis*, poses a serious ongoing threat to populations that encounter the bacterium. In colonies exposed to plague, mortality rates often exceed 99% (Biggins and Kosoy, 2001). Plague events thus typically lead to colony extirpations and an increase in isolation among the colonies that remain (Cully and Williams, 2001).

As a result of these significant pressures, black-tailed prairie dogs occur in relatively small, spatially isolated colonies embedded within a heterogeneous matrix of human-dominated habitats and remnant grasslands (Miller et al., 2000, Cully and

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Williams, 2001, Johnson, 2004). The current spatial structure of prairie dog colonies coupled with observed patterns of local extinction and colonization events suggest that prairie dog populations may constitute metapopulations (Lomolino and Smith, 2001; Roach et al., 2001). Metapopulations are defined as groups of subpopulations that are each subject to independent population dynamics and local extinction events. Recolonization of unoccupied patches following these extinction events occurs via limited dispersal events from other subpopulations (Hanski and Gilpin, 1997). According to metapopulation theory, extinction rates are determined primarily by patch size (which limits local population size) and geographic isolation of patches (Bender and Fahrig, 2005). Yet, the landscape context within which these patches are embedded should clearly also be considered (Wiens, 1997), particularly in landscapes fragmented by human activities, where animal movement may be significantly impeded by an inhospitable intervening landscape matrix (Collinge, 2009).

Despite considerable uncertainty regarding the effect of urbanization on black-tailed prairie dogs, basic demographic characteristics have not been carefully explored within an urban setting. To address this gap in knowledge, I developed three model sets to investigate prairie dog survival in Boulder County, Colorado. This study draws from a large mark-recapture dataset collected from 2003-2006 in order to investigate the role of black-tailed prairie dogs in the epidemiology of plague. The objectives of this current study were three-fold. First, a plague epizootic that struck eight colonies during the course of this study provided an opportunity to calculate mortality rates in colonies exposed to plague. Due to the sporadic nature of plague epizootics and the time-intensive methods necessary to estimate survival, few studies have documented robust estimates of

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black-tailed prairie dog mortality rates in colonies affected by plague (Pauli, 2006). Second, I tested for demographic differences between prairie dog colonies that were and were not infected during the last large plague epizootic in 1994. I predicted that "new" colonies, established where colonies were decimated by the 1994 epizootic, would have higher survival rates due to increased resources and a release from population growth-inhibiting density effects. Finally, to investigate potential associations between survival and landscape and colony characteristics, I ran simple and multiple linear regression models. I predicted that both landscape and patch level characteristics would significantly affect prairie dog survivorship.

Methods

Study area

Boulder County is located in the geological zone known as the Colorado Piedmont, situated between the Great Plains and the Front Range of the Rocky Mountains. The Colorado Front Range has experienced rapid urban growth far surpassing that of the national average in recent decades (Hansen et al., 2002). Pressure exerted by increased human densities and development has driven land-use change in the region, resulting in a complex landscape mosaic of urbanization, irrigated and dryland farming, cattle ranching, and remnant short and mixed-grassed prairies. Land conversion has all but supplanted native grasslands in the area; most lowland tall grass prairie has been converted to irrigated hayfields, while upland mixed grasslands are used for cattle grazing (Bock and Bock, 1998). Although little native grassland remains in Boulder County, the County and City of Boulder have demonstrated a strong commitment to

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preserving the remaining undeveloped patches as public land. To date, the City of Boulder and Boulder County have jointly set aside over 16,187 ha of grassland properties that are protected from development. Approximately 4,093 ha of this greenbelt are permanently dedicated as Habitat Conservation Areas (HCA) for prairie dogs, although the total area presently inhabited by prairie dogs is less than half of this. Surprisingly, HCAs in Boulder County may represent as much as 70% of the total amount of dedicated prairie dog habitat set aside by state agencies in Colorado (City of Boulder Urban Management Plan, 2006).

Study Colonies

Twenty-four black-tailed prairie dog colonies inhabiting both short- and mixed-grass patches of public land within Boulder County were selected (Figure 1.1, Table 1.1). Prairie dog colonies varied in size, relative isolation, and landscape context. Colony area ranged from 5.13 to 222.95 ha in the year preceding the 2005 plague epizootic, with a mean of 53.23 ± 14.3 ha and a median of 18.69 ha. Short-grass sites are dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), pasture sagebrush (*Artemisia frigida*), and woolly plaintain (*Plantago patagonica*). Mixed-grass sites are dominated by blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), blazing star (*Liatris punctata*), prairie sage (*Artemesia ludoviciana*), and aster (*Aster falcatus*) (Bennett, 1997; Collinge, 2000). During a previous plague epizootic reported in 1994, nine of these colonies were confirmed plague positive and five confirmed plague negative (termed "historically plague positive and plague negative colonies" by Markeson, 2005). When another plague

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epizootic struck in 2005, nine colonies again contracted plague, including some but not all of those colonies affected in 1994. In both cases, plague drove drastic population declines in affected colonies. These epizootics have offered a relatively rare opportunity to survey prairie dog demography directly before, during, and after a plague epizootic.

Figure 1.1

Black-tailed Prairie Dog Colonies in Boulder County, CO
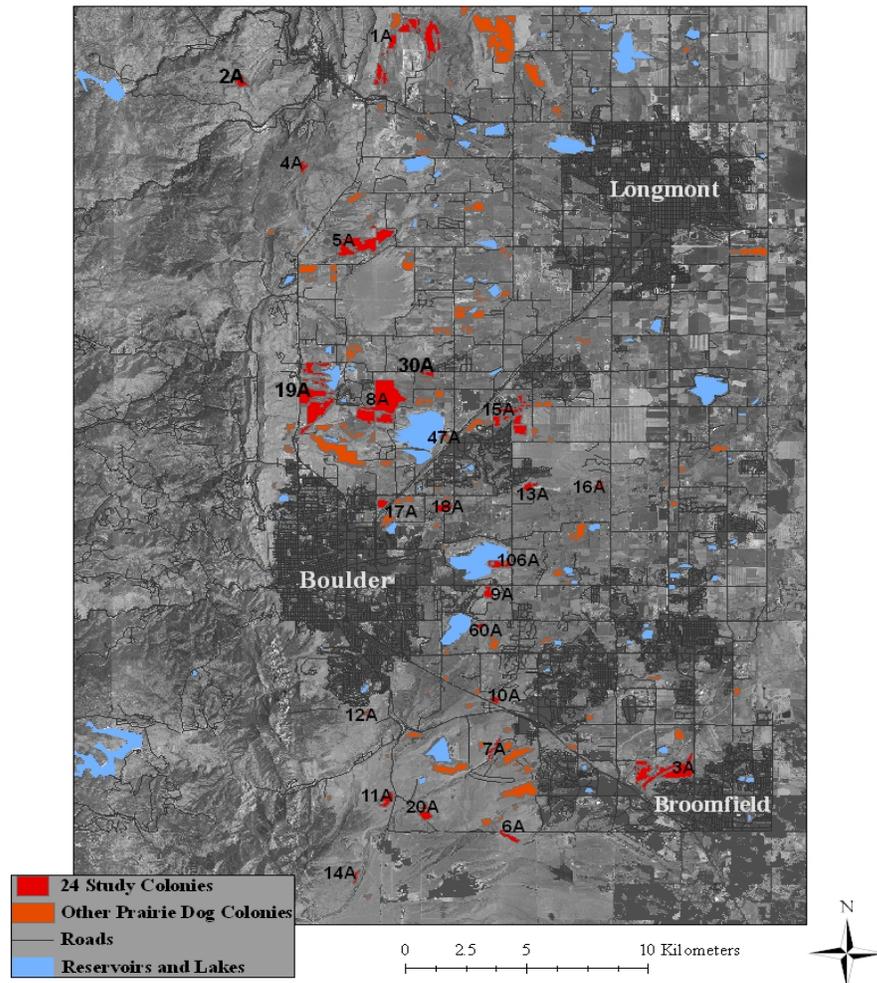
Prairie dog colonies in Boulder County. This map depicts 24 study colonies as they were in 2004, the year before the 2005 plague epizootic. Over the course of the study, eight of 24 colonies contracted plague and were effectively extirpated. In 2007, another colony died off.

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Table 1.1. Prairie dog study colonies, property names, and plague status.

Colony	Property Name	Plague
1A	Dowe Flats	2005+
2A	Hall Ranch West	Negative
3A	Rock Creek Farm	Negative
4A	Heil Ranch North	2005+
5A	Centennial	2005+
6A	Zaharias/Thomas	Negative
7A	Superior	Negative
8A	Axelson	2006+
9A	Aweida II	Negative
10A	Galluci	Negative
11A	Flatirons Vista	Negative
12A	Dover Blacker	2006+
13A	Kaufmann/Wood Brothers	Negative
14A	VanVleet/Jeffco	Negative
15A	Stepanek	Negative
16A	Culver	Negative
17A	Belgrove/McKenzie	2006+
18A	Andrus	Negative
19A	Beech	2006+
20A	Waneka/Kelsall	Negative
30A	Johnson/ Dawson	2006/07+
47A	South Dam Boulder Res	2007+
60A	Klein	Negative
106A	Ute Industrial Park	Negative

Prairie dog trapping and visual counts

Prairie dogs were captured from June-August in 2003-2006 using standard mark-recapture methods at 24 colonies in Boulder County. Colonies were sampled for 4 days using a grid of 49 Tomahawk live traps, with 25-meter spacing between individual traps. Traps were baited and locked open for a period of 3 days prior to trapping, and between trapping hours on trapping days. Animals were anesthetized before and during processing following the protocols approved by the University of Colorado's Institutional Animal Care and Use Committee and the Centers for Disease Control (Collinge et al., unpublished). Individuals were weighed, sexed, and measured for body and tail length. Newly captured animals were permanently marked using passive integrated transponder

(PIT) tags (Biomark Inc., Boise, Idaho). PIT tag numbers were recorded from recaptured animals. A small tissue sample was cut from the ear for genetic analyses, and approximately 0.5-0.7 ml of blood was extracted from the femoral vein for disease screening. Fleas were counted and collected, and prairie dogs were released at point of capture upon reviving from sedation.

Visual counts were performed at each study colony from June-August in 2003-2005 to estimate prairie dog density. Three 50 x 50m grids were established with at least 50% of the survey area lying within the prairie dog trapping grid. Field observers arrived at least 20 minutes in advance of beginning visual counts to allow prairie dogs to grow accustomed to human presence. For three consecutive days, observers counted prairie dogs within each of the three grids at 20 minute intervals. Counts were then summed across grids for each sampling interval. The maximum count per day was determined, and these values were averaged across the three days of sampling. Visual counts thus provide a relative index of prairie dog density rather than an absolute measure of density. Although recent advances in mark-resight techniques have improved on the estimation of prairie dog density (Magle, 2007) visual counts remains an effective and efficient field method for determining relative differences in density among colonies (Menkens et al., 1990; Johnson and Collinge, 2004).

Survival rate estimation

Mark-recapture data were analyzed using the robust design model in program MARK (White and Anderson, 1999, Kendall, 1999). The robust design model takes advantage of information commonly collected in multi-year mark recapture studies when each session is comprised of several consecutive or nearly consecutive sampling days, and the length of time between trapping sessions is longer than within sessions. The robust design method draws on two types of mark-recapture models, the Jolly-Seber (JS) method and the closed population models. The JS model is an open population model that includes additions to and removals from the population (by natality, immigration, emigration, and mortality) (Pollock et al, 1990). Survival rate estimators in this model are robust to heterogeneity in detection probability, and are used to determine survival estimates for the period of time between trapping sessions (Kendall, 1999). Closed-population models, on the other hand, assume closure over the length of the study period. Unlike the JS models, abundance estimators in the closed-population models are robust to heterogeneity in detection probability, and are used to estimate abundance. The robust design thus exploits information from both within and between trapping sessions to derive estimates of abundance, survival, and movement using maximum likelihood methods.

In this study, I developed three sets of robust design models to investigate separate but related questions pertaining to prairie dog survival. First, I created a candidate model set to confirm and quantify the detrimental effects of the 2005 epizootic on survival of prairie dogs. In this set of competing models, colonies were grouped according to whether or not they contracted plague and compared to a null model in

which plague status was not considered. Second, I created a set of candidate models to investigate potential demographic differences between colonies affected and not affected by plague during the 1994 plague epizootic. In order to separate the potentially confounding effects of the most recent plague epizootic, only those colonies that did not contract plague during the study period were used in this analysis (colonies 3, 6, 10, 11, 18, 19, 20, 30, 47, 60, 106). Mark-recapture data from colonies grouped in this way were compared to models in which all colonies were combined. Finally, to test putative associations between landscape and colony characteristics and survival estimates, I analyzed mark-recapture data from each of the 24 study colonies separately. For each of the three model sets described above, I developed a similar set of candidate models, including time-dependent and time-constant abundance, survival, encounter, and re-encounter probabilities.

Survival model selection

As a general modeling approach, I developed possible models for encounter (capture) and re-encounter (recapture) probabilities (p and c, respectively), and used the most parsimonious of these models to model survival, abundance, and movement probabilities (*S, N, γ′*, and *γ″,* respectively) (Burnham and Anderson, 2002). Once created, the support for each competing model was assessed using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham and Anderson, 2002) as provided by MARK. AICc is a function of the model fit (quantified as the negative log likelihood) that includes a penalization for increasing numbers of model parameters. The best supported model is the one with the lowest AICc value, and all competing models

are ranked relative to this one. Models within 2AICc units of the best supported model are considered to carry similar support (Lebreton et al., 1992). For data analyzed separately by colony, I used a model averaging procedure based on Akaike weights (Burnham and Anderson, 2002) available in MARK to calculate weighted estimates of survival and abundance per colony. These weighted estimates account for model selection uncertainty by including appropriately weighted predictions from all of the 'best' models (Lebreton et al., 1992), which in this case were those models with AICc scores within two units of the minimum observed score.

Landscape context and colony characteristics

I developed a raster-based geographical information system (GIS) to quantify landscape context at two spatial scales surrounding each colony (ArcInfo, ESRI, version 9.2). I created spatial buffers of 250m and 1km from the perimeter of each colony. Within each buffer, I used the 30m resolution 2001 National Land Cover Data (NLCD) to quantify urbanization. In the 2001 NLCD classification system, four land cover types are designated as development, including a category called "open space" which I excluded for the purposes of this study. I acquired vector-orientated files of prairie dog colonies and streams from the City and County of Boulder and converted these into raster files. Raster formatted files are essentially grids of a specified cell size where each cell takes on a value corresponding to the underlying land cover type. I reclassified each raster file such that the land cover type of interest was designated a value of 1 while everything else was specified as 0. I then used the Zonal Statistics tool to determine the percentage of

grid cells composed of each land cover type found within the two spatial buffers. Colony size was calculated using Xtools, a GIS extension application.

Statistical Analysis

Multiple linear regression was used to model the effect of landscape context and colony characteristics on individual colony survival estimates. In an effort to capture the spatial scale at which key demographic processes occur, this exploratory analysis included landscape metrics quantified at two spatial scales, 250m and 1km. Landscape context predictor variables included urbanization, stream, and prairie dog colony cover surrounding study colonies. Patch-level predictor variables of maximum survival included prairie dog density within the study colonies as well the area of the colony (in hectares). Statistical analyses were run in R (www.R-project.org). Models were evaluated using an AICc, as described above.

Results

Prairie dog trapping

A total of 1506 individuals were caught in 2786 captures at 24 colonies during summer trapping 2003-2006. Average within-session recapture rates were 0.48 ± 0.2 (mean ± 1SD) in 2003, 0.23 ± 0.09 in 2004, 0.26 ± 0.14 in 2005, and 0.33 ± 0.16 in 2006. I have excluded colonies decimated by plague from the calculation of yearly mean recapture rates. These colonies, although sampled, had no captures in 2006, and would thus skew the annual mean recapture rate. Inter-annual recapture, which refers to the recapture rate of animals caught in a previous year were as follows: 0.09 ± 0.08 in 2004, 0.21 ± 015 in 2005, and 0.25 ± 0.18 in 2006 (again excluding colonies with no captures

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in 2006). It is unclear why inter-annual recapture rates in 2004 were so low. Whether these low rates are a true reflection of relatively poor survivorship during the preceding year or whether it was a behavioral response on the part of individual prairie dogs was not formally tested within the framework of program MARK. Within this four year study period, there was no evidence of dispersal among colonies; no marked individual was recaptured away from its colony of first capture.

Mark-recapture analyses

As expected, survival estimates in colonies suspected or confirmed plague positive during the 2005 plague epizootic were much lower than in colonies that escaped exposure. Candidate models that treated the mark-recapture data as two separate groups (plague positive and plague negative) overall were far better supported based on AICc than models treating the data as one group. Indeed, there was a 695-unit difference between the AICc of the best supported model when the data were separated as compared to the best supported model when the data were aggregated. The best supported model garnered overwhelming relative support, with an Alaike weight of 0.98. The top model incorporated an effect of plague, and modeled survival, capture and abundance probabilities as fully time-dependent. Capture and recapture probabilities were set equal to one another, and the movement parameters γ' and γ'' were set to 0.

Survival estimates in plague positive colonies did not differ markedly from plague negative colonies in the two years prior to the plague outbreak, whereas survival rates declined dramatically in colonies that were plague-positive in 2005 (Figure 1.2). Annual survival estimates for colonies that were plague-negative in 2005 were 0.40 (SE = 0.09,

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95%CI = 0.22, 0.42) in 2003-2004, 0.26 (SE = 0.05, 95%CI = 0.17, 0.37) in 2004-2005, and 0.34 (SE = 0.06, 95%CI = 0.24, 0.46) in 2005-2006. Annual survival estimates for recent plague positive colonies were 0.26 (SE = 0.06, 95%CI = 0.16, 0.39) in 2003-2004, 0.31 (SE = 0.05, 95% = 0.22, 0.43) in 2004-2005, and 0.007 (SE = 0.006, 95%CI = 0.0009, 0.05) in 2005-2006. The 95% confidence intervals of plague positive and negative survival estimates overlap extensively in each time interval except for 2005-2006. During this time interval, colonies were exposed to plague and populations began to crash, suffering from mortality rates greater than 99% (survival estimates = 0.007, SE = 0.006, 95%CI = 0.0009, 0.05).

Figure 1.2

Annual Prairie Dog Survival Rates
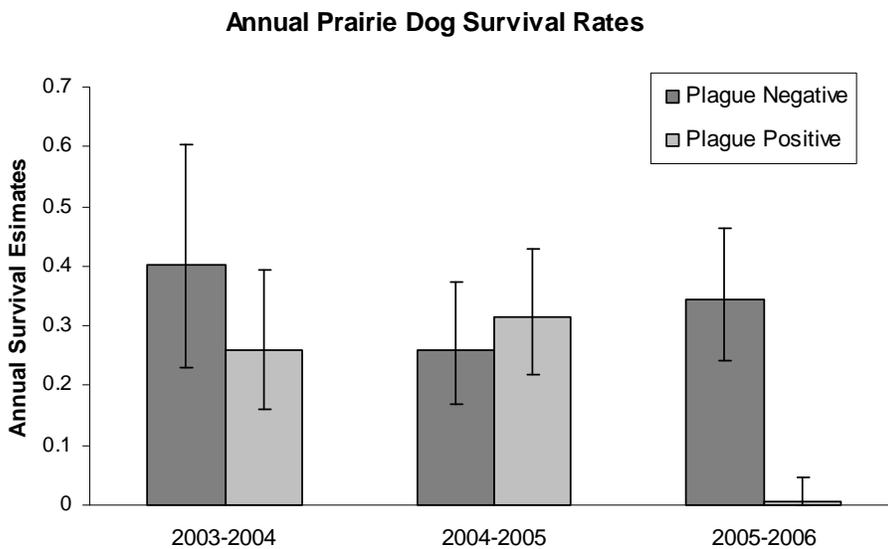
Annual survival estimates of plague positive and plague negative colonies. N plague negative in 2003-04 = 13, N plague positive in 2003-04 = 7; plague negative 04-05 = 16, plague positive = 8; plague negative 05-06 = 7, plague positive = 8. The 95% confidence intervals are shown.

When the mark-recapture data were analyzed according to plague history, there were no clear differences between prairie dog survival estimates at colonies that were affected by plague in 1994 compared with those that were not. Models that did not differentiate between plague positive and negative colonies were much better supported. The best supported model within this analysis modeled survival, capture, recapture, and abundance probabilities with full time dependence. All other models were untenable in comparison; the next closest one had a ΔAICc value of 21.2. The movement parameters γ' and γ'' in this model were set to 0, indicating that the null model (no movement) was best supported. In this analysis, annual survival estimates were 0.28 (SE = 0.05, 95%CI = 0.19, 0.38) in 2003-2004, 0.33 (SE =0.05, 95%CI = 0.23, 0.44) in 2004-2005, and 0.19 (SE = 0.02, 95%CI = 0.15, 0.25) in 2005-2006.

The mark-recapture data were also analyzed separately for each colony to determine annual colony survival estimates for use in further analysis (Figure 1.3). Estimates for individual colonies were calculated based on the most parsimonious group of models using a weighted model averaging function in MARK. From 2003-2006, the average annual survival rate across 24 study colonies was 0.36 ± 0.04 (mean ± standard error) and median survival rate was 0.34. Mean maximum survival rate was 0.26 ± 0.061 in colonies affected by plague in 2005-2006 and 0.48 ± 0.05 in colonies unaffected by plague during this time. Mean minimum survival was 0.09 ± 0.043 in these same plague-positive colonies and was 0.42 ± 0.04 in plague-negative colonies.

Figure 1.3

Maximum Prairie Dog Survival Rates 2003-2006
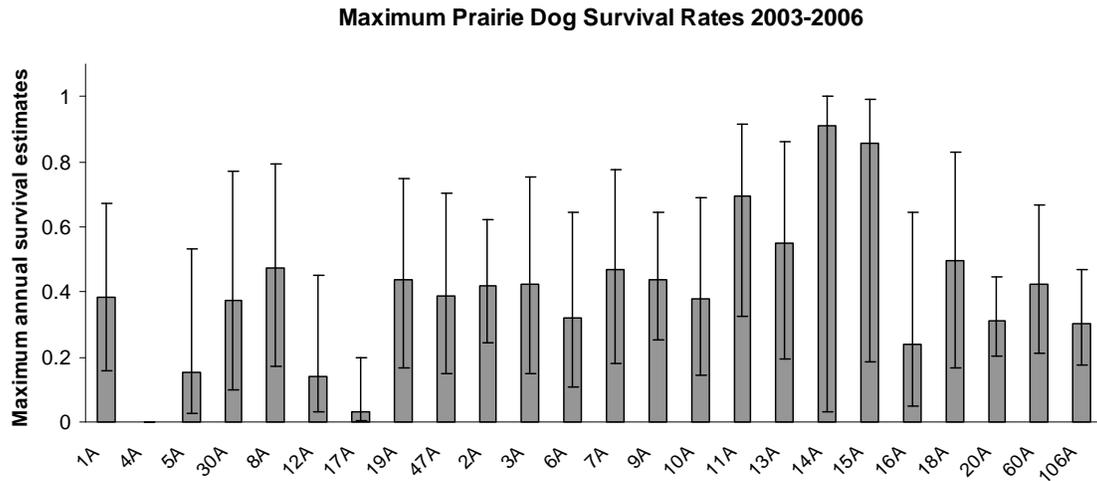
Maximum annual prairie dog survival estimates at 24 study colonies. Estimates were based on different survival intervals depending on the colony. The three survival intervals were 2003-04, 2004-05, and 2005-06. In 2005 and 2006, plague was confirmed present within the first 8 colonies (on the left). There were no inter-annual recaptures at colony 4A, resulting in survival estimates near 0. 47A was confirmed plague positive following this study period. 95% confidence intervals are shown.

Multiple linear regression analyses

I ran multiple linear regressions to model maximum colony survival as a function of colony characteristics and landscape context. Survival estimates for colony 4A (Heil Ranch) were not included in this analysis because the inter-annual recapture rate throughout the study period was 0, and as a result, survival estimates were unreliable. In this case, the null model had the lowest AICc value of all the models, indicating that the independent variables stream cover, urbanization, colony area, prairie dog density and

colony density were poor predictors of prairie dog maximum survival. No other models were within 2 AICc units of the null model, although the simple linear regression model including stream cover at 250m was close, with a ΔAICc value of 2.01. The next three best supported models were also simple linear regression models: urban land cover at 250m, area of colony, and prairie dog colony cover at 1km.

Discussion

Prairie dogs in Boulder County suffered clear demographic declines when exposed to and infected by plague during the epizootic of 2005. From 2003-2006, eight of 24 study colonies contracted plague and underwent severe population crashes that resulted in survival rates of less than 1%. These extremely high mortality rates are similar to those observed in other studies, and underscore the considerable threats posed by this disease to black-tailed prairie dogs. Results from a separate analysis indicated no significant differences in prairie dog survival rates of individuals in historically plague positive colonies compared to historically plague negative colonies. These results suggest that 10 years is likely sufficient time for the demographic differences expected in newly established colonies compared to older colonies to subside. Finally, this study failed to uncover associations between colony survival rates and several landscape- and patch-level variables, which may be indicative of the uncertainties in survival estimation, or a failure to determine the spatial scale at which ecological processes essential to prairie dog survival operate. Additionally, in the absence of plague exposure, other patch-level characteristics besides colony area and prairie dog density might influence survival more strongly in Boulder County.

Plague and prairie dog survivorship

As expected, prairie dog survival was negatively affected during the 2005 epizootic in Boulder County. In 2005-2006, when the epizootic was first reported, individuals in plague positive colonies experienced a 99% mortality rate. These results formally confirm largely anecdotal evidence that shows that black-tailed prairie dogs are highly susceptible to the bacterial agent of plague, *Y. pestis*, and suffer high rates of mortality as a result of infection (Barnes, 1982; Cully and Williams, 2001; Biggins and Kosoy, 2001; Antolin et al, 2006; Collinge et al, 2005). In the Gunnison's prairie dog (*Cynomys gunnisoni*), plague events have been more closely studied and are thus better documented, and declines generally reach levels > 97% (Lechleitner et al., 1968; Cully and Williams, 2001). Despite the relative paucity of data, patterns of decline in the black-tailed prairie dog seem to be quite similar. Cully and Williams (2001) reported, for example, that plague outbreaks generally cause a reduction of black-tailed prairie dog colony populations to less than 1% of pre-plague levels, and they described the complete collapse of colonies in the Rocky Mountain Arsenal National Wildlife Refuge and areas of the Comanche National Grasslands during the plague epizootic beginning in 1994. The only published demographic account of an intensively-studied black-tailed prairie dog colony undergoing a plague event reported reductions in juvenile and adult abundance by 95-96% (Pauli, 2006). Other studies that did not directly calculate survivorship but rather measured decreases in colony area suggest similarly drastic reductions in colony area during plague outbreaks (Stapp et al., 2004, Augustine et al., 2007).

In the comparative analysis of newly-established and older colonies, I hypothesized that newer colonies would experience higher growth and reproductive rates as a result of a decrease in density dependent effects and an increase in resource availability following a plague event. Contrary to my prediction, however, individuals in historically plague negative colonies exhibited no clear demographic differences when compared to historically plague-positive colonies, and models that treated the data as one group were better supported relative to models that treated the data as two groups. Demographic differences in new and old black-tailed prairie dog colonies have been documented in at least one other study, with new colonies showing significantly greater survival and recruitment rates (Garrett et al., 1982). A study following the growth and life-history changes of Gunnison's prairie dogs immediately following a plague epizootic suggests that the higher population growth rates seen in new colonies were due to higher juvenile growth and survival rates (Cully, 1997). Although this body of research suggests that newly founded prairie dog colonies may often be characterized by higher fecundity and survivorship following plague events, these studies generally looked at colonies immediately after recolonization, and it is unclear how long these demographic differences might persist. In this current study, nearly 10 years had passed since plague decimated these historically plague-positive colonies.

At least two factors might help to explain the diminishing demographic effect of recolonization. First, black-tailed prairie dogs reproduce annually, and while only 35% of female yearlings copulate, older females generally give birth to approximately four pups per year, for up to 6 years (Hoogland, 1995). With such high reproductive rates, it is perhaps not surprising that there is little support for a demographic signal in colonies that

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were previously extirpated by plague in 1994. Second, historically plague-negative colonies may not have reached critical thresholds in density or resource availability at which survivorship would be expected to decrease. In this study, resource availability was not assessed, and prairie dog densities were not compared between historically plague positive and plague negative colonies.

Prairie dog survivorship in a relatively urbanized area

Annual prairie dog survival rates in Boulder County varied considerably among colonies, but were on average lower than survival rates reported elsewhere. Survivorship in black-tailed prairie dogs follows a peaked curve for both sexes (Hoogland, 1995). Juveniles generally have the lowest rates of survival, while yearlings have the highest, and survival rates slowly decline in subsequent years (Hoogland, 1995). In one well-studied colony in Wind Cave National Park, South Dakota, survivorship was approximately 50% for juveniles, and peaked at 69% for 2-year-old females. In this study, cumulative cohort-specific life history tables were created based on detailed demographic data collected over 14 years. (Hoogland, 1995). At two other colonies located in this region, survivorship of prairie dogs during a two-year study ranged from 67%-97% for adults and 49% to 90% for juveniles (Garrett, 1982). In Boulder County, annual prairie dog survivorship in the 24 study colonies was 0.36% ± 0.04 (Mean ± SE) and a median survival rate of 34%. Clearly, high rates of mortality associated with plague explain to some degree the lower survival rates. However, this reasoning alone may be insufficient, since the average maximum (i.e. pre-plague) survival rate (40% ± 0.05) was also lower than the survival rates reported by Hoogland and Garrett.

Although substantial variation in estimates and differences in methodology clearly preclude direct comparison, lower observed survival rates of prairie dogs in Boulder compared to those reported in other studies is highly suggestive. These slightly lower survival rates may reflect differences in habitat quality and landscape context that might lead to decreased survivorship. Many of the black-tailed prairie dog studies in which survival rates have been directly documented have taken place in grasslands in national parks and national grassland systems that are, relatively speaking, more undisturbed than Boulder (e.g. Wind Cave National Park, Hoogland, 1995; Thunder Basin National Grasslands, Pauli, 2006). In contrast, colonies in Boulder are relatively small and embedded in an urbanized landscape matrix (Johnson and Collinge, 2004). Prairie dog densities in Boulder have been shown to increase in response to habitat loss and sharp urban-colony boundaries, and densities in more urban sites are substantially higher than those reported from more remote sites (Johnson and Collinge, 2004). Another study reported that individuals in an urban colony had a significantly lower average body mass compared to individuals inhabiting a rural one, suggesting differences in habitat quality (Dawson, 1991). Although it seems logical that individuals in urban colonies might experience lower survival as a result of crowding effects or decreased habitat quality, much work remains in order to understand the relationship between urbanization and demographic rates in prairie dogs. Moreover, to fully investigate differences among prairie dog survival rates in urbanized vs. relatively natural landscapes, sampling in these different landscape types would need to occur simultaneously and employ similar sampling methods.

Linear Regression Models

Results from the linear regression models indicate no significant linear relationships between maximum survival estimates and landscape and colony characteristics. There are several potential reasons why these explanatory variables proved to be poor predictors of survival. First, in terms of landscape context, prairie dog survival may be more dependent on unmeasured patch level characteristics than on the surrounding landscape. In fragmented systems, connectivity among habitat patches is thought to be a key determinant in species persistence (Soule, 1988). One way in which survival might be higher in more connected colonies, for example, is via an influx of healthy immigrating individuals with higher individual survival rates. However, animals that are large-bodied and exhibit an intermediate amount of movement across the landscape are expected to be more heavily influenced by landscape composition than small-bodied animals that move less frequently (Crooks, 2002). Dispersal events may indeed be essential to the persistence of prairie dog metapopulations, either by rescuing declining populations or recolonizing empty patches. However, it is unclear how frequently prairie dogs disperse, and dispersal attempts may be rare in urban landscapes (Magle, 2007). This may explain why the potentially positive impacts of connectivity (and the negative ones due to urbanization) were not predictive of survival in this study. Moreover, the best supported model of prairie dog density in Johnson's study included a squared term for road density (Johnson and Collinge, 2005) suggesting that landscape effects on survival may be non-linear and thus not captured in simple and multiple linear regression models.

It is perhaps more surprising that there was no observed linear relationship between survival rates and prairie dog density within colonies. Density-dependent factors regulate populations by increasing mortality or decreasing natality as population density increases. High population densities can lead to shortages in food resources, increased predation, and a greater intensity of intraspecific social interactions (Pulliam, 1994). While prairie dog survival might be expected to decrease with increasing density, the lack of a clear relationship does not preclude density dependence, since reproductive rates rather than survival rates may decrease in response to external stressors, as suggested by Lack (1954).

One of the many complicating factors in this simple analysis is that study colonies are of different ages as a result of plague outbreaks. In newly established colonies, densities, adult survival, and reproductive rates have been observed to be relatively high even when overall abundance is low (Garrett et al., 1982), presumably due to differences in resources. Although newer and older prairie dog colonies did not exhibit clear demographic differences in this study, differences in colony age, resource availability, and predation pressures could obscure relationships between survival and density.

Understanding the mechanisms that affect vital rates is fundamental to the study of population biology. The aggregate of individual mortality and reproductive rates dictate population growth rate, which is a parameter of fundamental interest for those charged with the difficult task for managing threatened or declining species (Sibley and Hone, 2003). Population growth rates can vary greatly from one generation to the next when unpredictable extrinsic factors such as plague events sporadically take place. Such

variation in time and space can have profound effects of population dynamics, and thus may be important components of conservation management plans (Rhodes and Odum, 1996). Studies of the natural history of black-tailed prairie dogs have greatly increased our understanding of prairie dog ecology in natural systems. However, with few but notable exceptions (Johnson and Collinge, 2005; Magle 2007, 2009; Brinkerhoff, 2008), prairie dogs inhabiting urban areas have been largely overlooked as research subjects. Given the continued risk to prairie dogs posed by plague, further investigation of the disease ecology of prairie dogs in urban settings may be of critical importance for the conservation of this species.

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CHAPTER 2

LANDSCAPE EFFECTS ON PLAGUE OCCURRENCE IN

BOULDER COUNTY, COLORADO

Abstract

Landscape context can strongly influence disease incidence by causing shifts in host community structure and impeding or facilitating movement of hosts and vectors across the landscape. In this study, I investigated associations between landscape structure and plague occurrence at black-tailed prairie dog colonies in Boulder County, Colorado during the 2005 plague epizootic. Drawing on previous research done in this system, I predicted that plague occurrence in Boulder County would be negatively associated with streams, urbanization, water bodies, roads, and isolation from other colonies exposed to plague. I used AICc to evaluate the relative support of logistic regression models of plague occurrence. The best supported models of plague occurrence included negative effects of urbanization, streams, isolation from plague- positive colonies and positive effects of prairie dog colony cover, colony area, and water bodies at the 250m scale. In direct contrast to previous work in this system, water bodies in this analysis exhibited a positive relationship with plague occurrence, indicating that increased urbanization may shift the balance with regard to the relative effects of landscape characteristics on plague risk. Taken together, these results suggest that the composition of the intervening landscape matrix in Boulder County, Colorado, plays a critical role in plague transmission.

Introduction

Habitat loss and fragmentation are widely acknowledged as the largest threats to biodiversity (Wilcox and Murphey, 1985; Harrison and Bruna, 1999). Human-mediated landscape change is the main driver of this ubiquitous phenomenon, and in many areas of North America, pressure exerted on natural systems due to urbanization accounts for observed reductions in the abundance, diversity, and distribution of species (Czech et al., 2000). Coincident with this wide-spread human-induced landscape change, outbreaks of wildlife disease as well as the emergence of zoonotic infectious diseases are also on the rise (Daszak et al., 2000; Dobson and Fouopoulos, 2001). Such diseases in turn pose further threats to wildlife species and endanger human health (Patz et al., 2004). A growing body of evidence suggests that these processes are, in many cases, closely linked (Patz et al., 2004), and attests to the growing importance of understanding the effects of landscape structure on disease dynamics (Wilson et al., 1994; Collinge et al., 2005).

Landscape epidemiology is a discipline that focuses on disease patterns across the landscape, and as such offers an approach that is particularly well suited for uncovering relationships between landscape structure and disease dynamics. Coined in the 1930s by the Russian parasitologist, Pablovsky, landscape epidemiology centers on spatial variation in infection risk and disease incidence (Pablovsky, 1966; Hess, 2002; Ostfeld et al., 2005). Renewed interest in the field reflects a growing appreciation for the inherently spatial process of disease spread. Many disease-causing pathogens are dependent upon contact with susceptible hosts for disease transmission and persistence. As a result, spatial variation in the abiotic and biotic conditions that govern host abundance, survival, and movement are critical components of disease dynamics (Hess, 2002). Moreover,

vector-borne diseases, including malaria, dengue, and yellow fever are transmitted by arthropod vectors that are highly sensitive to environmental conditions and are thus closely linked to spatial variation across habitats (Gubler, 2001). Importantly, these relationships are often not only influenced by conditions occurring at a highly localized scale, but also at a landscape scale (Ostfeld et al., 2005). Clearly, a complete understanding of disease incidence and risk in some disease systems requires a detailed knowledge about the effect of landscape context on the hosts, pathogens, and vectors involved.

One of the best-studied examples of the effect of landscape composition on the prevalence of wildlife disease is Lyme disease. Lyme disease is a multi-host tick-borne zoonosis caused by the spirochete *Borrelia burgdorferi*. It is the most common vector-born disease in the US, and its rapid emergence has been linked to land-use patterns such as the development of wooded areas and farmland reforestation (Gubler, 2001). Changes in the size and landscape context of forest fragments in the Northeast have precipitated shifts in host abundance and species composition, with important implications for disease incidence (LoGiudice, 2003, Collinge, 2009). Smaller forest fragments support high densities of the most competent reservoir host species, the white-footed mouse (*Peromyscus leucopus),* leading to a higher proportion of infected ticks (Allan et al., 2003).

Another zoonotic disease strongly influenced by landscape composition is plague. Plague is a vector-borne disease that is transmitted within and among mammalian species via the bite of an infected flea. Caused by the bacterium *Yersinia pestis*, this virulent disease can infect most mammalian species and is carried by over 80 different flea species (Eisen and Gage, 2008). The distribution of plague is world-wide, having greatly expanded since the 1880's (Gage and Kosoy, 2005). It is now endemic in many previously unaffected areas including portions of South America, South Africa, and the western United States (Dennis, 1998). Prior to the development of antibiotics, three massive pandemics scoured Europe and Asia, the largest of which killed an estimated 75 million people (Benedictow, 2004). Public fear surrounding the disease is still acute in areas where antibacterial medications are scarce, as evidenced during the mass hysteria following an outbreak of pneumonic plague in India in 1994 (Gage and Kosoy, 2005).

Introduced to North America in the early 1900's through the ports of San Francisco, plague is thought to have established in commensal rodents in the city before expanding eastward to around the 100th meridian (Cully and Williams, 2001, Adjemian et al., 2007). By the time plague had advanced across the Rocky Mountains and into the grasslands of Colorado in the 1940s, a surveillance program had been put in place to investigate potential reservoir wildlife hosts (Adjemian et al., 2007). Yet, over 60 years later, and in spite of important advances in plague research (Gage and Kosoy, 2005), basic questions about the dynamics of this disease still remain. For example, aspects of the transmission cycle in natural systems are still poorly understood. Plague has for some time been thought to persist in an enzootic state between outbreaks, potentially residing in host species that exhibit moderate to high resistance to the disease. Occasionally,

plague will move from these maintenance hosts into susceptible species, sparking an epizootic (Barnes, 1982). However, no reservoir species have been identified, and there is no convincing evidence that there are separate enzootic and epizootic plague transmission cycles (Gage and Kosoy, 2005; Cully et al., 2000).

Although many questions remain about the epidemiology of plague, recent work has advanced understanding regarding the landscape ecology of the disease. In research investigating associations between landscape structure and plague occurrence at black-tailed prairie dog colonies in Philips County, Montana, and Boulder County, Colorado, Collinge et al. (2005) uncovered similar landscape correlates of disease occurrence in both systems, despite marked differences in the landscape characteristics of each study area. In both study systems, plague occurrence was negatively associated with streams, water bodies, roads, and isolation from other colonies infected with plague (Collinge et al., 2005). In both cases, the largest of the spatial scales investigated (3km) emerged as the most predictive of plague occurrence. Over 20 years of plague occurrence data were compiled using confirmed and suspected cases of colony die-offs obtained from the Centers for Disease Control (CDC) and local management records (Collinge, 2005). This study provided a strong indication that landscape context influences plague occurrence.

In the present study I re-visit the question of landscape correlates of plague occurrence while departing in two important ways from previous work. First, in this current study, I employed a novel approach (but see Stapp et al., 2004 and Augustine et al., 2008) to determine plague events in prairie dog colonies from 2005-2006 in Boulder County using GIS shape files initially created for prairie dog management purposes. Using this technique I was able to account for every colony infected with plague during

the study period, and was not limited by the sometimes incomplete plague records kept by city and county officials. Second, I investigated associations between landscape structure and plague occurrence at a different spatial scale than in Collinge et al. (2005) In this study, I developed logistic regression models at three spatial scales: 250m, 500m, and 1km, whereas in Collinge et al. (2005) the scales used were 1km, 2km, and 3km. Based on this previous work, I predicted that plague occurrence during the 2005 epizootic in Boulder County would be negatively associated with streams, urbanization, water bodies, roads, and isolation from other colonies exposed to plague.

Methods

Study area

Boulder County is located on the Colorado Piedmont, between the Great Plains and the Front Range of the Rocky Mountains. In this region, remnant patches of short and mixed-grass prairie habitat are embedded in a heterogeneous landscape matrix of urban development, agricultural lands, and residential neighborhoods. The City and County of Boulder, recognizing the importance of the remaining grasslands for biodiversity, recreation, and traditional land use, jointly have set aside over 16,187 ha of protected grassland and mountain properties. Approximately 4,093 ha of this greenbelt are permanently dedicated as Habitat Conservation Areas (HCA) for prairie dogs. Outbreaks of plague are episodic in Boulder, and have occurred approximately every seven to ten years. The most recent epizootic struck in 2005, with new suspected cases reported as recently as summer 2008.

Plague Occurrence Data

I created a geographic information system to determine plague events at prairie dog colonies in Boulder County, Colorado. The City of Boulder and Boulder County conduct annual surveys of prairie dog colonies on their land by mapping currently active burrows along the perimeter of colonies. This method of annual, on-the-ground colony mapping provides documentation of the spatial dynamics of prairie dog colonies in Boulder County. Prairie dog colonies naturally contract or expand to some extent from year to year. However, because sylvatic plague is the only known natural cause of rapid colony die-offs (Hoogland, 1995, Cully and Williams, 2001), when colonies on managed lands rapidly decline or disappear from one year to the next it is likely due to colony exposure to the bacteria. Prairie dog maps from 2004-2007 were obtained from the city of Boulder and Boulder County and were analyzed to determine the fate of each colony during plague epizootic that began in 2005. All spatial analyses were conducted using ArcInfo (ESRI, 9.2).

Some data manipulation was necessary in order to follow individual colonies through time. In this work, I chose the individual colony rather than a complex of colonies as the unit of study (Snall, 2008). This choice was made in part because patterns of fragmentation in the relatively urbanized area of this study area tend to preclude the existence of the larger complexes typically observed in relatively undisturbed grasslands. Colonies that were composed of separate but closely-spaced fragments located within 50m of one another were considered as single colonies. Areas of activity separated by more than 50m were defined as separate colonies. A step-wise series of clips were performed to determine percent reduction of colonies from 2004-2007. A colony was

assumed to have contracted plague if the active colony area decreased by more than 70% from one year to the next. Prairie dog colonies exhibit spatial clustering (Collinge, 2005) and as a result may possess some degree of spatial autocorrelation. To correct for this and to insure independence among colony data points, I randomly chose a sub-sample of the prairie dog colonies for further analysis. I used a randomized iterative process to remove colonies from the analysis that were within 200 meters from one another.

Landscape composition and colony characteristics

A raster-based GIS was created to analyze the landscape context surrounding each colony using ArcInfo (ESRI, version 9.2). Spatial buffers of 250m, 500m, and 1km were delineated around the perimeter of each study colony. Within these three spatial buffers I quantified percent land cover of urbanization, lakes and reservoirs, streams, roads and prairie dog colonies. The National Land Cover Database (2001), a raster database of 30m resolution, was used to estimate the amount of urbanization within the study area. Developed land in this database is divided into four categories: open space, low-intensity development, medium-intensity development, and high-intensity development. "Open space" is defined as developed areas in which impervious cover accounts for less than 20% of the land cover, and includes parks, reserves, golf courses, and other recreational areas. Since prairie dog colonies occupy a significant portion of the "open space" land cover, this developed land cover type was excluded from the analysis. Urbanization was thus categorized as low- to high- intensity developed land. I obtained reservoir, stream, and prairie dog colony data files from the city and county, and converted these into a raster file format. I also acquired data files of major and minor roads from the Colorado

Department of Transportation and converted these into a raster file. These files were re-classified into a binary raster format such that each grid cell containing a given land cover type was designated 1 while all others were designated 0. I then used the zonal statistics tool in ArcInfo to calculate the mean number of grid cells (percent cover) of each land cover type surrounding each study colony.

I quantified colony characteristics using ArcInfo and a GIS extension application named X tools. Colony area was calculated in hectares. In addition, I determined the distance from each study colony to the nearest plague positive colony. Referred to as the "effective epizootic isolation", by Collinge et al. (2005), this distance measures how close study colonies were in relation to plague positive colonies the year before the outbreak of plague. For example, the distance from a plague positive study colony to the nearest plague positive colony in 2005 is measured as the distance between these colonies in 2004. For more information on this isolation metric, refer to Collinge et al. (2005).

Statistical Analyses and Model Selection

Logistic regression was used to model plague occurrence in Boulder County as a function of colony characteristics and landscape composition at three spatial scales. Predictor variables were chosen based in large part on previous plague occurrence work carried out in this system (Collinge et al., 2005). Candidate models included at least one of the following predictor variables: colony area, distance to nearest plague positive colony, percent cover of lakes, streams, roads, prairie dog colony, and urbanization. No more than four independent variables were included in any candidate model to reduce over-fitting. Due to high spatial autocorrelation across scales, each spatial scale (250m,

500m, and 1km) was analyzed separately. I used Pearson's Correlation coefficients to test for collinearity between predictor variables within each scale and between scale-independent predictor variables. Percent urbanization and road cover were highly correlated and as a result were not included together in any models. Since the maximum likelihood fit to the logistic regression model is extremely sensitive to outliers (Pregibon, 1981), and can lead to non-informative yet significant results, I examined the data for such influential points. Overly-skewed data was log transformed. All non-spatial statistical analyses were performed in R (www.R-project.org.).

I used a model selection approach to evaluate the relative support of each candidate model given the data. Candidate models were ranked and weighted using an Aikaike's information criterion adjusted for small sample size (AICc, Burnham and Anderson, 2002). AICc provides a measure of model quality that takes into account parsimony and goodness of fit. The model with the minimum AICc value is selected as the best supported model given the data. Models within 2 AICc units of the best supported model are considered to be similar in their ability to describe the data (Lebreton et al., 1992). I calculated Akaike weights of the independent variable and the three spatial scales following Anderson (2000). Although an AIC value is provided automatically in R, I calculated it separately as recommended by Stafford and Strickland (2003).

Results

Colonies affected by plague

In 2005, a plague epizootic in Boulder County originated from or entered into the north-central part of the County, in the foothills near Lyons, Colorado. From 2005-2007, plague progressed generally from northwest to southeast across the county, with suspected cases reported as recently as summer 2008 (Whitney Johnson, personal communication). Using prairie dog colony maps made in 2004, 175 individual prairie dog colonies were identified in Boulder County (Figure 2.1). Of these, 138 active colonies were randomly selected and tracked from 2004-2007. A total of 59 colonies (42.7%) were extirpated by plague over the study period. In 2005, 18.1% (25/138) of colonies were struck, in 2006 another 18.1% (25/138) struck, and in 2007, 6% (9/138) were struck. Colonies identified in this study and affected early in the outbreak were located just east of the Foothills. As the epizootic progressed, colonies further east and south of the original cases were extirpated, creating a distinct spatial pattern of plague movement from west to east.

Figure 2.1

Plague Occurrence at Prairie Dog Colonies, 2005-07
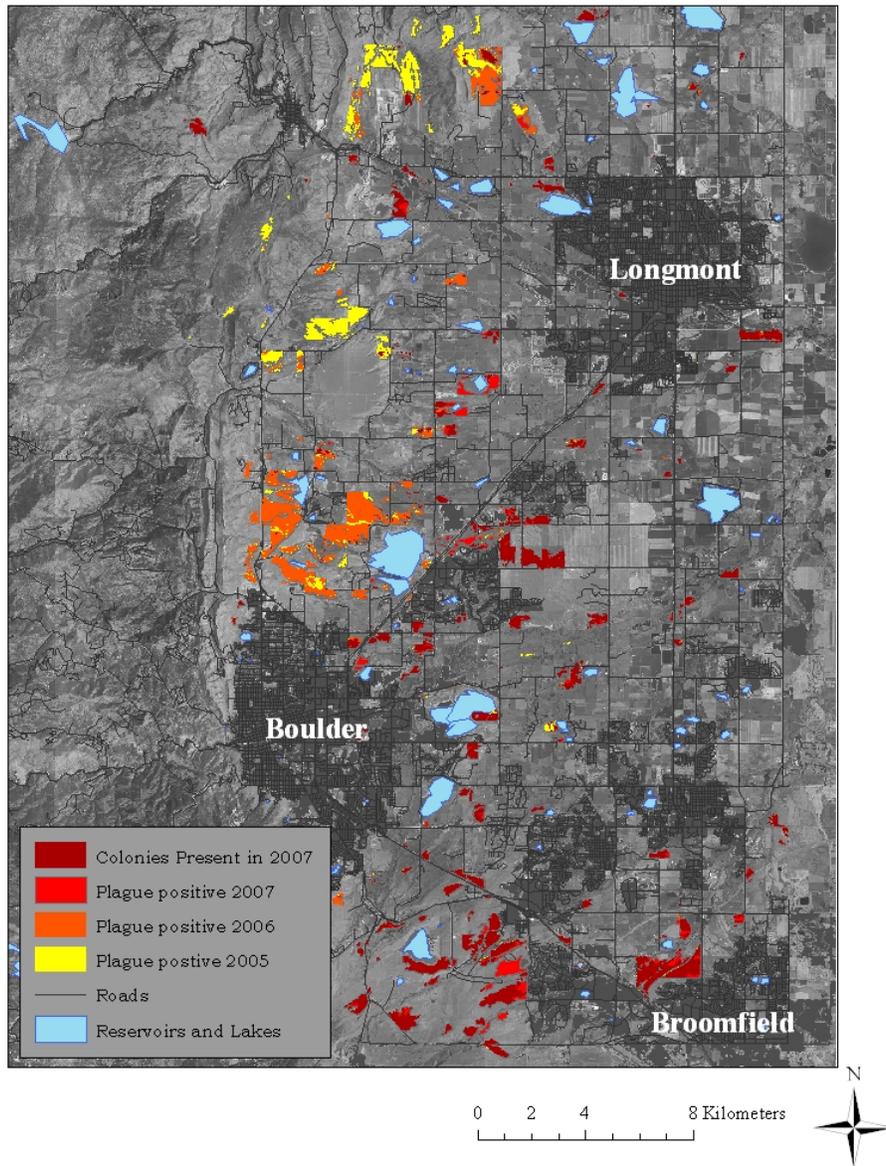
Plague occurrence in Black-tailed Prairie Dog colonies from 2005-2007 in Boulder County, Colorado. Plague positive colonies are shown in different colors as indicated on the legend. The plague epizootic began in 2005 and proceeded to cross the county in an eastern-southeasterly direction. Major roads and areas of urbanization are also shown.

Univariate analysis

Colony characteristics differed between prairie dog colonies that did and did not contract plague over the course of this study (Figure 2.2). Plague-positive colonies were on average larger than plague-negative colonies (p= 0.04, t statistic=1.76, d.f.=136). The mean colony area for plague positive colonies was 25.83ha ± 6.82 (mean ± SE) while for plague-negative colonies it was 14.22ha ± 2.6. As expected, distance to the nearest plague positive colony was also significantly correlated with plague occurrence. Plague positive colonies were on average significantly closer to other plague positive colonies than were plague negative colonies (mean distance plague positive= 2.65km ± 0.39, mean distance plague negative= 4.54 ± 0.27, p<0.001, t statistic= -4.12).

The landscape context of plague-positive and -negative colonies also differed in this univariate analysis (Table 2.1). The most pronounced difference in landscape context of plague-positive and plague-negative colonies was in percent cover urbanization. Plague-negative colonies were, on average, surrounded by more than twice the amount of urbanization than were plague-positive colonies. These differences in means were significant at each spatial scale tested (at 250 m scale, p=0.007, t statistic= -2.47; at 500m scale, p= 0.003, t statistic= -2.77; at 1km scale, p= 0.002, t statistic -2.91, d.f. for all scales= 136, see table 2.1 for means). Similar trends emerged for percent road cover surrounding plague-positive and –negative colonies. Although the differences were less striking in this case, plague-negative colonies were surrounded by more road cover at each of the spatial scales than plague-positive colonies (at 250 m scale, p=0.36, t statistic= -0.35; at 500m scale, p= 0.005, t statistic= -2.56; at 1km scale, p= 0.005, t statistic -2.62, d.f. for all scales= 136). However, despite small differences between

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plague-negative and positive colonies in the mean percent cover of prairie dog colonies, lakes, and streams, these differences were not significant, with the exception of stream cover at the 250m scale. In this case, plague-negative colonies were surrounded by more stream cover on average than plague positive colonies (p= 0.005, t statistic= -2.6, d.f.= 136).

Figure 2.2
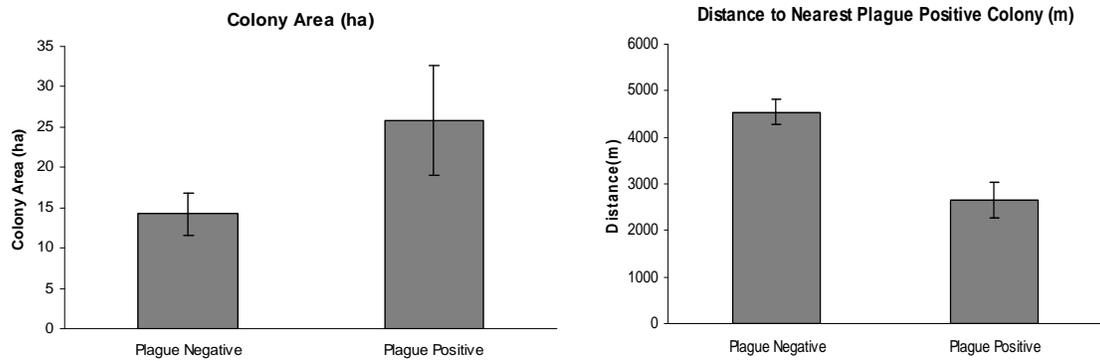
Mean landscape and colony characteristics for plague positive and negative colonies. Shown here is the mean colony area in hectares and distance to nearest plague positive colony in meters. Standard error bars shown.

Table 2.1 Landscape characteristics of plague positive and negative colonies. Mean percent cover is indicated ± SE

Landscape Cover and Scale	Plague Negative	Plague Positive
Prairie dog colony at 250m	0.026 ± 0.0080	0.021 ± 0.0048
Prairie dog colony at 500m	0.034 ± 0.0078	0.036 ± 0.0079
Prairie dog colony at 1km	0.049 ± 0.0105	0.057 ± 0.0149
Lakes at 250m	0.012 ± 0.0054	0.018 ± 0.0066
Lakes at 500m	0.017 ± 0.0063	0.025 ± 0.0084
Lakes at 1km	0.021 ±0.0057	0.021 ± 0.0070
Urbanization at 250m	0.086 ±0.015	0.038 ± 0.012
Urbanization at 500m	0.100 ±0.016	0.041 ± 0.011
Urbanization at 1km	0.124 ± 0.018	0.053 ± 0.014
Streams at 250m	0.002 ± 0.0002	0.001 ± 0.0002
Streams at 500m	0.002 ± 0.0002	0.001 ± 0.0002
Streams at 1km	0.002 ± 0.0001	0.001 ± 0.0002
Roads at 250m	0.002 ± 0.0002	0.002 ± 0.0003
Roads at 500m	0.003 ± 0.0003	0.002 ± 0.0002
Roads at 1km	0.003 ± 0.0003	0.002 ± 0.0002

Multiple Logistic Regression Analysis

Multiple logistic regression was used to model plague occurrence in Boulder County as a function of colony characteristics and landscape variables at three spatial scales. The best supported candidate model, using AIC for model selection, included a negative effect of distance to nearest plague-positive colony, a negative effect of percent cover of streams, a negative effect of percent cover of urbanization, and a positive effect of percent cover of prairie dog colonies within a 250m buffer surrounding sample

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colonies. Candidate models within ΔAICc of 2 are considered to have similar support and were considered indistinguishable from one another. In this analysis, all such candidate models shared similar predictor variables with identical effect signs. Each included a positive effect of percent cover of prairie dog colonies, and a negative effect of percent cover of urbanization, and each was at the 250m scale. In contrast to the best supported model, however, other similarly supported models included a positive effect of colony area and percent cover lakes on plague occurrence.

In addition to ranking the candidate models based on the relative support of each model given the data, Akaike weights were calculated for each independent variable as well as each spatial scale tested (Table 2.2). Percent cover of urbanization and prairie dog colonies within 250m of study colonies were the two best predictors of plague occurrence (w_{avg} = 0.027 and 0.026 per model, respectively). Stream cover ranked third among the most predictive independent variables with a weighted Aikaike weight of 0.011 per model. When separated by spatial scale rather than individual variable, models including variables measured within 250m of study colonies were by far the most predictive of plague occurrence, garnering close to 99% of the support in comparison to the 500m and 1km scales.

Table 2.2 Best supported logistic regression models of plague occurrence in prairie dog colonies using AICc criterion.

Model	Scale	AICc	dAICc	Aikaike Model Weight
Distance(-), Streams (-), Urbanization (-), Colony (+)	250 m	83.08	0.00	0.19
Distance(-), Area (+), Urbanization (-), Colony (+)	250 m	83.09	0.45	0.15
Distance(-), Lake (+), Urbanization (-), Colony (+)	250 m	83.93	0.84	0.12
Distance (-), Urbanization (-), Colony (+)	250 m	84.24	1.14	0.11
Area (+) Streams (-), Urbanization (-), Colony (+)	250 m	84.46	1.36	0.09
Streams (-), Lake (+), Urbanization (-), Colony (+)	250 m	85.04	1.95	0.07

Discussion

Plague occurrence in black-tailed prairie dog colonies was significantly associated with landscape metrics and colony characteristics in this study. As predicted, plague-positive colonies were larger in size (colony area covered) and were located closer to other plague-positive colonies than plague-negative colonies. Across all models and spatial scales, there was a well-supported and uniformly negative effect of urbanization and stream cover on plague occurrence. The percent land cover of prairie dog colonies was also highly predictive of plague occurrence. Although there are other plausible hypotheses, the most likely explanation for these results is that the composition of the intervening landscape matrix facilitates or impedes movement of hosts and vectors. All models with similar support relative to the best supported candidate model (within 2 ΔAIC units) were at the 250m spatial scale, indicating that critical aspects of local plague

dynamics may take place at a relatively fine scale. This study generally reaffirms associations observed in previous work in this study system with one significant and unexpected departure. Previous work showed a negative association of lakes on plague occurrence, whereas this study demonstrated a positive effect of lakes on plague risk in prairie dog colonies.

Colony characteristics and plague occurrence

Plague-positive colonies were larger in area than plague-negative colonies, and colony area was included in three of the six top models that received similar support using AICc. This result was expected, as several other studies also found positive relationships between colony area and disease risk (Cully and Williams, 2001; Smith and Lomolino, 2001; Stapp et al., 2004, Collinge et al., 2005). It has been suggested that larger colonies may sustain a higher abundance of putative reservoir species for plague, such as deer mice (*Peromyscus maniculatus*), and their associated flea species (Collinge et al., 2005). In this scenario, more host individuals might lead to an increase in contact rates between prairie dogs and infected small mammals or fleas. Deer mice have garnered much interest as a reservoir species for plague because they exhibit variable resistance to infection and are both abundant and ubiquitous (Gage and Kosoy, 2005). Yet, although deer mice were relatively more abundant at prairie dog colony sites than in paired off-colony sites prior to the 2005 epizootic, there is still a lack of compelling evidence implicating deer mice in plague epizootic transmission (Gage and Kosoy, 2005). Another explanation that might explain this pattern is that larger area colonies may attract more infected prairie dog dispersers or predators, potentially because of higher quality habitat

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or higher colony densities (Collinge et al., 2005). Whatever the mechanism, the fact that larger colonies are more likely to contract plague presents challenges to the conservation recovery efforts of closely associated species, including the endangered black-footed ferret, which requires a minimum of approximately 50 ha of black-tailed prairie dog habitat to survive (Miller et al., 1994).

In this study, as in previous work in this system, plague events were spatially clustered across the landscape. Colonies located in closer proximity to exposed colonies were more likely to contract plague when compared to more isolated colonies. Modeling efforts of plague incidence in humans and prairie dogs indicate that climatic variables including temperature and precipitation influence plague outbreaks in many parts of the western U.S.(Enscore et al., 2002; Collinge et al. 2005*b,* Snall, 2008). Increased small mammal abundance following an increase in plant productivity may provide the biotic link between rainfall and transmission if higher small mammal abundance increases transmission (Collinge et al., 2005*b*). In Boulder, however, the influence of precipitation on plague occurrence is less clear, potentially because landscape structure is more influential than weather. Incomplete transmission among closely situated groups of colonies may indicate that epizootics are not wholly driven by intra-specific transmission among prairie dogs (Cully and Williams, 2001). Moreover, during outbreaks, plague travels exceptionally quickly through colonies, and can reportedly cover long distances (Girard et al., 2004). Whether an amplifying small mammal host or flea species common to prairie dogs passes plague from colony to colony in a step-wise fashion or predators simultaneously spark local transmission events in clusters of colonies, the spatial pattern is clear. Plague spread is non-random at the landscape level, and exhibits a strong spatial

clustering pattern that suggests epizootics are driven in part by terrestrial animal movement.

Urban land cover and plague transmission

Urbanization, as measured by the amount of urban land cover surrounding colonies, was negatively associated with plague occurrence in Boulder County during the 2005 plague epizootic. This observed pattern was particularly striking in that colonies that did not contract plague over the course of this study were surrounded by, on average, twice the amount of urbanization as colonies that did contract the disease. Several mechanisms may explain this pattern. First, urbanization may impede movement of the hosts and associated flea vectors that carry plague (Collinge et al., 2005, Cully and Williams, 2001). More heavily urbanized areas may create physical barriers that decrease movement of infected prairie dogs or other closely associated infective rodent species. An inhospitable intervening landscape matrix might also induce behavioral responses in animals that could lead to decreased movement in urbanized areas. Recent mechanistic studies show that urbanization modifies the behavior in songbirds (Slabbekoorn, 2003), but few other studies to date have reported on the behavioral changes of animals in response to urbanization *per se*. In Boulder, the effects of urbanization on wildlife species are highly species specific (Johnson, 2004). Regardless, there is a clear consensus among landscape ecologists that the composition of the intervening matrix plays an important role in inter-patch movement by individuals (Fahrig and Merriam, 1994). If infected prairie dogs, other rodent species, or the mammals that prey on these species are reluctant

to cross urban areas, transmission of plague to colonies embedded in an urban matrix might be reduced as a result of urbanization.

Different microclimatic conditions in relatively urbanized colonies might also serve to decrease plague transmission. Recent contributions in the field of urban ecology have revealed important effects of urban heat islands on plants and animals (Schochat, 2006). Artificial structures such as rooftops and paving materials that characterize urban areas act as heat sinks because they reflect less sunlight and trap more heat at night (Schochat, 2006). One study that examined urban-rural temperature gradients, for example, noted a 1-4°C difference between urban areas and the surrounding countryside (Arnfield, 2003). Dampened seasonality associated with urban heat islands can have multiple, and sometimes opposite, effects on pathogens, vectors, and hosts (Bradley and Altizer, 2006). Regarding plague, warmer temperatures can decrease the efficiency of pathogen transmission in fleas as well as reduce their population growth (Gage and Kosoy, 2005; Snall, 2008). If urbanized colonies are sufficiently warm to reduce flea populations or decrease plague transmission, then variation in mircroclimate among colonies could explain these results. Micro-climatic data were collected in 2004 in select colonies in Boulder County that did and did not contract plague during the last large plague epizootic of 1994 (Markeson, 2005) Although there were no significant differences in maximum daily temperature among these colonies, sampling took place well in advance of the 2005 outbreak and might not reflect environmental conditions directly before or during the outbreak.

Urbanization might also reduce plague transmission by altering species composition and abundance within relatively urbanized colonies. Urbanization and other human-mediated landscape changes result in habitat loss, fragmentation, and increased edge effects (Collinge, 2009). These factors can in turn induce shifts in community structure and decreases in biodiversity, along with increased abundance of urban-tolerant species in urban areas (Bradley and Altizer, 2006). Recent studies investigating relationships between host community composition and disease dynamics (Ostfeld and Shmidt, 2001) provide an intriguing potential link between land use change and disease incidence. Research in this area has focused on the dilution effect, whereby incompetent hosts in species-rich communities dampen the transmission and prevalence of multi-host diseases. The dilution effect hinges upon there being differences in disease competence among the host community as well as a generalist vector species, and is intricately linked to the composition of species present in the communities of interest. A contrasting situation might also take place where simplified, species-poor communities lack the most competent species by chance alone. Communities in urbanized colonies might also have differences in the relative abundance of the species influential in plague outbreaks, leading to a decrease in disease transmission. In Boulder County, however, this is not likely the case. Research in this system has demonstrated no significant differences in the relative abundance of flea or rodent species between plague negative and plague positive colonies immediately prior to the 2005 epizootic (Brinkerhoff, *in press*), although species composition was not directly addressed.

Connectivity and plague spread

As predicted, the amount of prairie dog colony cover surrounding colonies was highly predictive of plague risk in this study. Specifically, colonies surrounded by a greater proportion of other prairie dog colonies were more likely to contract plague than those that were more isolated. The amount of prairie dog colonies found within a spatial buffer is in fact a measure of connectivity, and its inverse is isolation. Connectivity is inextricably linked to the movement of the species that live there (Collinge, 2009; Tischendorf and Fahrig, 2000). Particularly when habitat is discontinuous, the degree to which a species can move across a landscape has important consequences for species composition, abundance, and persistence (Hanski, 1998; Crooks et al., 2004). At least two non-mutually exclusive hypotheses may explain the positive correlation between colony cover and plague occurrence. Both are based on the premise that the movement of hosts, either infected with plague or infested with infective fleas, is facilitated by prairie dog colony habitat.

One explanation for the positive association between plague and connectivity is that dispersing prairie dogs infected with plague are spreading the disease to neighboring colonies. Intra- and inter- colony dispersal is common among yearling males (Hoogland, 1995). Females also disperse (Garrett and Franklin, 1988), though they generally exhibit fidelity to their natal coteries (Hoogland, 1995). Due to the high susceptibility of prairie dogs to plague and the relatively rapid mortality that occurs when individuals are infected, it is unlikely that infected individuals could survive long distance dispersal attempts. Moreover, successful dispersal may be relatively rare in an urbanized, fragmented landscape (Johnson, 2004; Magle, 2007). However, plague challenges of

prairie dogs in the lab have shown that the incubation time for infection by *Y. pestis* is 8-10 days (Cully and Williams, 2001), leaving open the possibility that infected dispersing prairie dogs might increase inter-colony plague transmission, particularly in colonies in close proximity to one another. Such intra-specific transmission would only provide a partial explanation for plague occurrence, because the spatial pattern of outbreaks is somewhat spotty and colonies are sometimes "skipped" (Cully and Williams, 2001).

The second hypothesis to explain this positive association pertains to predator species. Carnivores have varying responses to isolation and patch area, and species that exhibit moderate movement between patches are thought to be most sensitive to differences in connectivity (Harrison, 1991). In Boulder County, a greater amount of prairie colony cover may facilitate movement of mammalian host species that prey on prairie dogs, such as coyotes (*Canis latrans*), stripped skunks (*Mephitis mephitis*), and red foxes (*Vulpes vulpes*), potentially increasing plague transmission in the process. Several characteristics of carnivores make them likely candidates for moving plague between colonies. They have large home ranges, acquire species-specific fleas from their prey, and can be infected with plague by ingesting sick animals (Barnes, 1982; Brinkerhoff, unpublished data; Salkeld and Stapp, 2006). In part because they can become infected or acquire infected fleas by a number of different avenues, their role during and between epizootics is of particular interest (Brinkerhoff, 2008). However, intensive sampling of carnivores before and during the 2005 epizootic failed to uncover high rates of plague exposure or infection (Brinkerhoff, 2008), suggesting that carnivores might not encounter sick animals as frequently as suspected. It's also important to note

that the spatial scale at which colony cover was most predicative was 250m, and it is unclear how larger-ranging mammals perceive or respond to such a relatively fine scale.

Interestingly, stream cover was once again negatively associated with plague. Like the negative effects of roads and urbanization, this landscape variable may also impede or block movement of infected hosts or vectors. Collinge et al. (2005) also suggested that the streams, lakes, and roads in the vicinity of colonies may vary in microclimate or habitat in such a way as decrease transmission. In my study, the opposing effects of lakes and streams suggest that a unique riparian community likely does not explain these differences. This work underscores the point that the degree to which landscape structure affects disease spread, if at all, is closely linked to host, vector and pathogen characteristics. For example, a stochastic spatial model of rabies spread in Connecticut indicated that rivers acted as a significant geographical barrier to raccoon dispersal, slowing the rate of the spread of rabies by a factor of 7 (Smith et al., 2002). In contrast, the initial spread of myxomatosis among rabbits in Australia in 1950-51 was apparently facilitated rather than impeded by rivers, likely as a result of increased mosquito densities associated with water bodies (Ratcliffe et al., 1952).

Similarities and differences to previous work

This study confirms many of the associations observed in previous work in Colorado and Montana, with some notable differences. In that study, the most predictive models of plague occurrence in Boulder County were landscape context variables measured at the 3km spatial scale, and included negative effects of lakes, reservoirs, streams, roads, and epizootic isolation (Collinge et al., 2005). In my analysis, the best

supported models also included negative effects of streams, roads, urbanization, and road cover. In contrast to the previous study however, results of my analysis indicate a positive association of water bodies and plague occurrence rather than a negative one. In addition, colony area emerged as highly predictive of plague occurrence in my analysis, whereas in the Colorado analysis of the previous study, this variable was not included in the best supported models.

In regard to colony area, my analysis greatly benefited from the prairie dog management practices of the City and County of Boulder. Prairie dog colonies have been surveyed uninterrupted on an annual basis since 1996 (Collinge, 2005). GIS colony shapefiles from 2004-2007 allowed me to determine with relative precision the area of every plague positive colony in the year directly preceding colony extirpation. In the previous study, which investigated plague occurrence in Boulder County from 1981-2003, data pertaining to colony area in the year prior to plague outbreak was not in all cases available. Prairie dog colonies have been shown to rapidly expand under natural conditions as a function of adjacent available habitat, colony density, and area (Hoogland, 1995; Reading et al., 1993). Such variability in colony area might obscure the relationship between colony area and plague occurrence when data from the year before an outbreak is not available.

Surprisingly, the results of this analysis suggest a positive correlation of plague occurrence with lakes and reservoirs rather than a negative one, as was observed in the previous study. This unanticipated shift in effect might be explained in the following way. An increase in the amount of urbanization in proximity to prairie dog colonies since the last study may have precipitated changes in the landscape context of prairie dog

colonies. In this hypothesis, water bodies may still exert a negative effect on plague occurrence when compared to more open, unobstructed routes. In comparison to more heavily urbanized areas, however, water bodies (and the land surrounding it) may offer a more suitable route for hosts and vectors carrying plague, and may explain the positive effect of water bodies on plague occurrence observed in this study. In the previous study, urbanization was quantified using 1994 Colorado GAP data; I used the NLCD database of 2001 in my analysis. While urbanization likely increased from 1994-2001, human-mediated landscape change in Boulder County was not directly assessed in this study.

Conclusion

This study has shown links between landscape context and disease occurrence in Boulder, Colorado. Multi-host vector-borne diseases such as plague exist within a complex ecological fabric that can be both the cause and consequence of community structure, host behavior, vector abundance, and host contact rates. Results of this study suggest that the spatial context of disease dynamics is likely a highly influential aspect of disease occurrence, transmission, and persistence. In the plague system in particular, landscape characteristics such as streams, urbanization, and isolation likely serve as significant deterrents to plague spread.

Zoonotic diseases are currently emerging at an unprecedented rate, with an estimated 75% of these new diseases originating in wildlife (Daszak, 2002). In order to protect human health and conserve species highly susceptible to emergent diseases, it will become increasingly necessary in future years to understand the often complex ecological relationships that govern disease emergence and persistence in natural systems.

Moreover, as evidence continues to build that habitat loss, fragmentation, and

degradation often play a critical role in disease emergence and persistence (Patz et al.,

2004), a mechanistic understanding of the relationships between landscape structure and

occurrence may be of vital importance.

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CONCLUSION

In Chapter 1, I investigated black-tailed prairie dog survival in Boulder County, Colorado, with an original interest in determining whether urbanization had significant effects on survival. The plague epizootic in 2005 combined with a rich mark-recapture data set provided me the opportunity to determine robust estimates for mortality of prairie dogs using program MARK. The eight colonies that contracted plague over the course of the study suffered dramatic declines of over 99%. Two other analyses undertaken resulted in insignificant results. Specifically, historically plague negative and plague positive colonies exhibited no significant demographic differences, indicating that demographic signals of plague are likely not long lived in this species. These results also suggest that there may be no demographic differences in colonies that do and do not get plague, and that transmission of plague is likely independent of any colony effects. Finally, the results of the linear regression models of survival yielded insignificant results. Although there are other plausible explanations for why landscape characteristics and colony characteristics were not predictive of survival, including but not limited to highly uncertain survival estimates, I believe that, in the absence of plague exposure, patch-level characteristics are more important determinants to prairie dog survival than are landscape-level characteristics such as urbanization and colony cover.

In Chapter 2, I explored relationships between plague occurrence in Boulder County and landscape and colony characteristics using a model selection approach. Although my research approach was identical in most ways to work done by Collinge et al. (2005), there were two important differences. First, I used GIS shape files obtained from the City and County of Boulder to create a GIS. This allowed me to follow each

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colony present in 2004 through either 2007 or the year of that colony's extirpation. Second, I used smaller scales than did Collinge et al. (2005): 250m, 500m, and 1km. I found significant relationships between plague occurrence and landscape and colony characteristics. Specifically, the best supported models of plague occurrence included a negative effect of urbanization, roads, streams, colony isolation, and positive effects of colony area, and water bodies. Taking together, these results suggest that landscape composition impedes or facilitates movement across the landscape in ways that are as of yet speculative.

To some, the black-tailed prairie dog is an iconic symbol of relict grassland systems, to others, it is a pest. Yet, the black-tailed prairie dog has a rich evolutionary history in the short and mixed grasslands where it occurs (Graham and Lundelius, 1994). It is precisely as a direct effect of this long history that so many species associate so closely with prairie dogs, depending on colonies for shelter and prey (Miller, 1994). In part due to their fascinating colonial nature, prairie dogs are extremely susceptible to sylvatic plague, and this disease arguably poses the most significant risk to prairie dog populations today. Particularly in relatively urbanized landscapes like Boulder County, the largely human-mediated landscapes likely influence disease occurrence in prairie dog colonies. Management efforts to preserve the black-tailed prairie dog should thus consider landscape effects on prairie dogs.

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