

APPARENT SURVIVAL, DISPERSAL, AND ABUNDANCE OF BLACK-TAILED PRAIRIE
DOGS

by

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Abstract

Black-tailed prairie dogs (*Cynomys ludovicianus*) are a species of management and conservation concern. Prairie dogs have lost both habitat and occupied area due to plague, which is caused by the bacterium *Yersinia pestis*, pest control, and habitat conversion to agricultural land. Our goals were to estimate survival rates and dispersal rates, and to compare methods for estimating abundance of black-tailed prairie dogs for both management and conservation. We trapped black-tailed prairie dogs at four small National Parks from April 2009 through August 2011. Prairie dogs were trapped and marked for two trapping sessions per year in order to estimate seasonal rates of apparent survival. Apparent survival rates were estimated using the package RMark in R to construct models for program MARK. We found estimates to vary according to field site, sex, year, and season (summer or winter). Possible reasons for the differences in survivorship among sites could be presence of disease, quality of forage, predation, or frequency of dispersal. Visual counts were also conducted each trapping session beginning in April of 2010 to estimate abundance. Mark-recapture, mark-resight, and visual counts were compared to determine which method would be the most effective for estimating abundance of prairie dogs. We found mark-resight to produce the most precise estimates of abundance. While it costs more money to conduct a mark-resight estimate than visual counts because of repeated sessions, they produced significantly different results from one another 75% of the time, which was especially apparent on sites that had some form of visual barriers such as tall vegetation and uneven ground. However, if further information is needed in terms of sex ratios, age ratios, or the exact number of prairie dogs, then mark-recapture is the only method that can be used. Land managers need to address the level of accuracy needed, topography, and vegetation height before choosing which sampling method is best for the prairie dog towns in question. Finally, we looked at rates of intercolony and intracolony dispersal by placing 149 VHF collars and 6 GPS collars on prairie dogs at three colonies. Intracolony dispersal was also monitored through visual observation and trapping records over the three years of the study. We found 23 intracolony and eight intercolony dispersal events. Combined, these three studies offer insight not only into monitoring of prairie dog populations but also potential influence by plague both within and among colonies of prairie dogs.

Table of Contents

List of Figures	v
List of Tables	vii
Acknowledgements	viii
Preface.....	ix
Chapter 1 - Introduction.....	1
Literature Cited	4
Chapter 2 - Apparent annual survival of black-tailed prairie dogs at four small National Parks ...	6
Abstract.....	6
Introduction.....	6
Materials and Methods.....	8
Study Area	8
Study Species	8
Data Collection	9
Statistical Analysis.....	10
Model Selection	11
Results.....	12
Seasonal Survival Rate	12
Juvenile Winter Return Rate.....	13
Estimates of Apparent Annual Survival Rate	14
Encounter Rate.....	14
Weight.....	14
Discussion.....	15
Apparent Seasonal Survival	15
Juvenile Return Rates	16
Estimates of Annual Apparent Survival Rate	16
Comparisons to Previous Studies.....	17
Conclusions.....	18
Literature Cited	20

Chapter 3 - Comparison of methods for estimating abundance for prairie dogs	30
Abstract	30
Introduction.....	30
Methods	32
Study Site	32
Capture and Marking	32
Visual Counts.....	33
Abundance Estimates.....	34
Results.....	36
Comparison of Population Estimates.....	36
Discussion.....	37
Total work-hours.....	37
Prairie dog health and safety.....	38
Accuracy of estimates.....	38
Overall impressions	39
Use for other sites	40
Literature Cited	41
Chapter 4 - Intercolony and intracolony dispersal by black-tailed prairie dogs	47
Abstract.....	47
Introduction.....	47
Materials and Methods.....	49
Study area.....	49
Trapping	50
Radio telemetry	51
Observations	52
Results.....	52
Discussion.....	54
Literature Cited	59
Chapter 5 - Conclusions.....	69
Literature Cited	72

List of Figures

Figure 2.1. (A) Apparent seasonal survival rate (\pm SE) of male black-tailed prairie dogs. (B) Apparent seasonal survival rate (\pm SE) of female black-tailed prairie dogs. Bent’s Old Fort is the only site that showed significantly different rates between the seasons with higher rates during the winter than the summer ($\chi^2 = 10.3, P < .01$). Apparent survival rates are based on a 60-day time step. Summer (Su) represents the 2 time steps between the spring and summer trapping periods and the winter (Wi) represents the 4 time steps between the summer and spring trapping periods. 26

Figure 2.2. Juvenile return rates between summer and spring trapping sessions. (A) Juvenile return rates (\pm SE) at all four National Parks between the summer of 2009 and the spring of 2010. (B) Juvenile return rates (\pm SE) at three National Parks between the summer of 2010 and the spring of 2011. Sample size (n) is included next to each point. 27

Figure 2.3. (A) Estimated apparent annual survival rate (\pm SE) of black-tailed prairie dogs from spring of 2009 to the spring of 2010. (B) Estimated apparent annual survival rate (\pm SE) of black-tailed prairie dogs from spring of 2010 to the spring of 2011. Standard error bars are included and survival rates are based on a 60-day time-step. 28

Figure 2.4. Comparison of the estimated apparent annual survival rates (\pm SE except for Hoogland and Facka) of black-tailed prairie dogs at four small national parks to published data of apparent annual survival rates from three other studies conducted by Hoogland (2005), Facka et al. (2010), and Biggins et al. (2010). Closed points represent males and open points represent females. Squares represent sites that potentially have plague and circles are sites without known plague in the area at the time of the study. 29

Figure 3.1. A comparison of estimated abundance (\pm SE) for black-tailed prairie dogs in 2010 (A) and 2011 (B) using four different methods: minimum number known alive (MNKA), visual counts with Severson and Plumb (2001) correction (VC), mark-recapture (MR), and mark-resight (MS) for each of the 4 ha study areas. 46

Figure 4.1. GPS collar locations for the five yearling male prairie dogs located at Scotts Bluff National Monument. Outer square of 8 small points represents a 4ha area with the 2.25ha trapping grid (100 points) inside. Collars b and e) were from 2010 and collars a, c and d) were from 2011. MCP (95%) estimates are shown as a polygon around the prairie dog

coterie. All points outside the edge of the polygon are considered exploratory movements.

..... 68

List of Tables

Table 2.1. Number of trapping days for all four field sites in the Midwest, spring 2009 - summer 2011.....	24
Table 2.2. Mark-recapture modeling using the robust design model to calculate apparent survival (ϕ), heterogeneity (π) encounter rates (p), and abundance (N) of black-tailed prairie dogs at four small national parks.....	25
Table 3.1. Mark-recapture modeling using the closed capture with full heterogeneity model to estimate abundance.	43
Table 3.2. Mark-resight modeling using the mark-resight model with logit-link to estimate abundance.	44
Table 3.3. Comparison between four methods: minimum known number alive (MNKA), visual counts (VC), mark-recapture (MR) and mark-resight (MS) to estimate abundance of black-tailed prairie dogs.....	45
Table 4.1. Number of collared prairie dogs at Fort Larned, Scotts Bluff, and Bent's Old Fort combined from 2009-2011 field seasons.	63
Table 4.2. Results of collars from all three years of the study. Study sites were all combined..	64
Table 4.3. Number of black-tailed prairie dogs at each field site for every year of the study that died before dispersal or went missing.....	65
Table 4.4. Percent of results of collars for each age and sex class for all sites and all years combined.....	66
Table 4.5. Intracolony dispersal of black-tailed prairie dogs at each site for each season. Winter is the time between July/August trapping and April/May trapping. Summer is the time between April/May trapping and July/August trapping. Percentage = seasonal percentage of total intracolony dispersed prairie dogs. One prairie dog season of dispersal could not be determined leaving the total percentage of dispersal less than 100%.....	67

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Preface

Each of the three main chapters is formatted for submission to different journals. The chapters on survival and dispersal are formatted for *Journal of Mammalogy*. The chapter on comparing methods for estimating abundance was formatted for the *American Midland Naturalist Journal*. Although I am the primary author, this thesis is written as publications from multiple authors.

Chapter 1 - Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) are an important species to study due to their status as both an ecological pest (Cully and Williams 2001; Hansen and Gold 1977; Hanson et al. 2007) and a keystone species (Kotliar et al. 2006). Black-tailed prairie dogs have lost approximately 97% of the total area they historically occupied (Endangered and Threatened Wildlife and Plants, 2009). The causes for this decline are from pest control, habitat conversion from grassland to cropland, and the introduction of the exotic disease, sylvatic plague, caused by the bacterium *Yersinia pestis* (Cully and Williams 2001; Miller and Cully 2001).

Black-tailed prairie dogs are a diurnal, colonial, ground-dwelling sciurid (Hoogland 1995; Manno et al. 2007). Within colonies, prairie dogs live in territorial family groups called coteries (Dobson et al. 1997; Hoogland 1995; King 1955). Black-tailed prairie dogs have the largest geographic distribution out of the five species of prairie dogs (Hoogland 1995). Although many studies have worked with black-tailed prairie dogs, few have looked at differences between colonies across a wide range of their occupied habitat.

Given their role as a keystone species of the prairie, there is a greater need to maintain disease free and stable populations of prairie dogs to support such species as endangered black-footed ferrets (*Mustela nigripes*), burrowing owls (*Athene cunicularia*), and tiger salamanders (*Ambystoma tigrinum*). Furthermore, they alter the plant community and ecosystem processes that affect a large range of species found within their habitat range (Kotliar 2000). As they are also considered a pest species, it is imperative to balance both the need for conservation and reduce the amount of conflict with private landowners. Conflicts arise because prairie dogs potentially compete with cattle for grass (Detling 2006; Miller et al. 2007).

In order to help resolve this conflict, we need to improve our understanding of the basic biology of prairie dogs and methods used to assess their population status. Furthermore, with the introduction of *Y. pestis* into the ecosystem, there is greater need to re-assess our current knowledge, taking into account the effects that plague can have on metapopulations of prairie dogs and thus the greater prairie ecosystem. This is evidenced by the fact that prairie dog colonies in known plague areas are smaller and more isolated than those without plague (Cully et

al. 2010). This change in colony composition then affects every other species that relies or interacts with prairie dog and their habitat.

The goal of our research was to study populations of black-tailed prairie dogs in both short and mixed grass prairie located on four small National Parks in Colorado, Nebraska, and Kansas. Specifically, we aimed to (1) estimate apparent survival rates at each field site and detect whether it changes seasonally, yearly, or is different among sites or between sexes. Results can be used to improve our management programs of black-tailed prairie dogs, (2) learn more about the rate of prairie dog dispersal, where they are most likely to disperse to off colony sites, and test whether dispersal is age or sex biased, and (3) assess the best methods to estimate total abundance within a colony, which can be used by the parks to manage their populations. Furthermore, our results will help us understand possible reasons for differences between colonies on a broad scale, and assess the possible impact of disease presence.

It is important to learn what the expected survival rates of prairie dogs are and compare our results to other studies conducted at different locations. Is survivorship similar or different, and why? We were interested in whether there were differences between the seasons of spring to summer (summer) and summer to spring (winter) as well as differences between yearly estimates both within and among field sites. We also wanted to know if survival rates differed between the sexes. With this knowledge, we hoped to develop a better understanding of the factors driving changes in survival such as prairie type, disease, or forage quality. We used the robust design model with full heterogeneity in Program MARK to analyze our data because of its ability to estimate survival for all time periods. Furthermore, the parameter estimates using the robust design model, are considered more precise due to its two-levels of sampling (Kendall 2010). The robust design uses a Cormack-Jolly-Seber model (open model) to estimate apparent survival and a closed capture model to estimate true encounter rate. With more knowledge of dispersal rates, we can also determine whether site-fidelity is biasing our results by falsely lowering the apparent survival rates.

To study dispersal, we attached radio-collars to prairie dogs over a three-year period during the spring and summer, which is when most dispersal is thought to occur (Garrett and Franklin 1988; Hoogland 1995; Knowles 1985). Knowledge of where, how often, and which age and sex classes disperse, we may be able to find ways to minimize the number of prairie dogs traveling onto private land and to understand the connectivity of prairie dog towns to one

another. The latter is potentially an important factor in plague dynamics. Little is known about how plague travels between prairie dog colonies and prairie dogs carrying plague-infected fleas are certainly a possibility. With increased knowledge of prairie dog dispersal, we may be able to minimize contact between infected and un-infected towns to protect them, while at the same time increase connectivity through the use of habitat manipulations such as burning or mowing, to promote reestablishment of prairie dogs after an epizootic (e.g. through source-sink dynamics).

In order to assess the best methods to estimate colony abundance, we compared the following methods: (1) minimum known number alive (MKNA), (2) visual counts, (3) mark-capture, and (4) mark-resight. Our assessment considers both the monetary cost and the landscape characteristics of the colonies. It is important for managers of small parks to be able to estimate the abundance of prairie dogs to better manage for sustainable populations that do not spillover onto private land, and also to monitor the health and stability of the colony. Detection of a shrinking population may be an indication of the presence of plague or other epizootic diseases.

This thesis is organized into five chapters with the first being this Introduction. In Chapter 2, we look at the apparent survival rates of black-tailed prairie dogs at four small National Parks. In Chapter 3, we compare techniques for estimating abundance of prairie dogs at three small National Parks and provide evaluations of each method and when it may be the most effective choice for a manager to employ on a colony. In Chapter 4, we use radio-telemetry to track the rate of both long distance (intercolony) and short distance (intra-colony) dispersal by prairie dogs. The last chapter, Chapter 5, is a summary of the findings and conclusions from these three field studies.

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Chapter 2 - Apparent annual survival of black-tailed prairie dogs at four small National Parks

Abstract

Black-tailed prairie dogs (*Cynomys ludovicianus*) are a species of both management and conservation concern. The total area occupied by black-tailed prairie dog colonies has undergone severe declines due to plague, caused by the bacterium *Y. pestis*, pest control, urbanization, and habitat conversion to agricultural land. Because of their dual role as both a keystone species and a pest species, there is need to understand if populations are rising or falling and to understand the causes for these changes. Here we used the Robust Design model in the program RMark to estimate the apparent survival rates of black-tailed prairie dogs at four small National Parks. With this model, we were able to estimate apparent survival rates for each site during all three years of the study. We found estimates to vary according to field site, sex, year, and season (summer or winter). Possible ecological factors for the differences between sites could be disease, quality of forage, predation, or frequency of dispersal.

Introduction

The survival rate of a population is an important parameter to understand, especially for vertebrate species of management concern. Survival rates can be used determine whether a population is growing, stable, or declining. Mark-recapture analysis is a good way to estimate apparent survival rates, which can then be compared among sites to understand differences among populations. Apparent survival rates are different from true survival rates in that we cannot separate site-fidelity from true survival. The rates may vary as a result of emigration, survival, or a combination of the two. Mark-recapture methods allow calculation of age structure and to identify differences due to sex, location, or season (Boag and Murie 1981; Paradis et al. 1993; Sherman and Morton 1984).

Black-tailed prairie dogs (*Cynomys ludovicianus*) are diurnal, colonial, ground-dwelling sciurids that are a species of management concern (Hoogland 1995, 2006; Manno et al. 2007). Historically, prairie dogs were thought to have occupied over 31.85 million hectares of habitat, but today occur on approximately 0.97 million hectares (USFWS 2009), which is a loss of

approximately 97% of their historical range. The causes for this decline are from pest control, habitat conversion from grassland to cropland, and the introduction of the exotic disease, sylvatic plague, caused by *Yersinia pestis* (Antolin et al. 2002; Miller and Cully 2001). There is an urgent need to manage prairie dog populations for both conservation and control, as they are considered to be a keystone species (Kotliar et al. 2006) and an agricultural pest (Hansen and Gold 1977; Hanson et al. 2007).

To better manage prairie dog populations, we need to understand the variation in survival rates of populations across their habitat range. Most work with prairie dogs has been conducted in areas that contain multiple colonies on large landscapes such as National Parks, National Grasslands, or other public lands (Biggins et al. 2010; Cully et al. 2010; Hoogland 1995; Newby 2005). All of these previous studies were conducted on colonies that were less isolated with respect to other colonies than our study sites (see below), which may allow for more stability due to differences in source-sink dynamics, dispersal rates, or other factors. The most extensive examination of survival rates of black-tailed prairie dogs was from Hoogland's (1995) 17-year study at Wind Cave National Park, which used life-table analysis to estimate demographic rates.

We worked at small colonies at four National Park Service Units for three years. Due to the short term nature of our study, we used the robust design model in program MARK to analyze our mark-recapture data. This model made it possible to obtain estimates of apparent survival for every year of the study. The ability to obtain precise estimates from a relatively short-term study is an advantage over a traditional Cormack-Jolly-Seber analysis, which may not provide estimates of apparent survival for all time periods if time-dependence is present in the parameters (Kendall 2010; White and Burnham 1999; White et al. 2001).

As populations of black-tailed prairie dogs decline, due to continuing habitat conversion or as they are affected by plague, they may become more isolated across their range. Understanding demographic rates such as survival, in small colonies will become ever more important. Our study sites were in four small National Parks located in Kansas, Colorado, and Nebraska. We compared apparent survival rates between age and sex classes among sites and tested whether covariates such as prairie type (short or mixed-grass) and year may account for differences in apparent survival. In addition, we compared the use of the Robust Design model in program MARK for our short-term study of three years to Hoogland's (1995) long-term study at Wind Cave National Park. We hypothesized that the parks will show differences in apparent

annual survival rates, which may be due to regional variation of habitat. We also hypothesized that prairie dogs would show seasonal variation in apparent survival rates, which may be due to differences in activity levels of prairie dogs and/or predator abundance during different times of the year.

Materials and Methods

Study Area

The study was conducted at four small National Park Service areas in the western Great Plains: (1) Fort Larned National Historic Site, KS; (2) Scotts Bluff National Monument, NE; (3) Bent's Old Fort, CO; and (4) Sand Creek Massacre National Historic Site, CO. There was no domestic livestock grazing, and shooting of any animal was prohibited, at all four National Park sites. All parks were surrounded by agricultural land. Both Colorado sites were in short-grass prairie while Scotts Bluff and Fort Larned were located in mixed-grass prairie. The Sand Creek prairie dog colony experienced a plague epizootic between 2009 and 2010, which precluded further analyses there. Bindweed (*Convolvulus arvensis*) was present at all four sites. Bindweed is also known to contain alkaloids which may have negative health effects on mammals that consume it (Schultheiss et al. 1995). Due to the toxicity of bindweed, it is not considered to be a preferred food source by prairie dogs. Bindweed was the dominant plant species at Bents Old Fort and was also abundant at Scotts Bluff. Scotts Bluff had the least amount of occupied habitat with a large part of the 4 ha plot covered by sweet clover (*Melilotus officinalis*) and summer cyprus (*Kochia scoparia*) which grew to be taller than three feet in some locations making it an undesirable location for prairie dogs which need low vegetation for viewing predators. Sand Creek had the most native vegetation, followed by Fort Larned.

Study Species

Black-tailed prairie dogs are small ground-dwelling sciurids. Adult prairie dogs live 2-8 years with females tending to live longer than males. Males weigh 5% - 15% more than females (Hoogland 1995). Black-tailed prairie dogs inhabit the largest area out of the five species of prairie dogs. The species is found as far south as Mexico and north into Canada. Black-tailed prairie dogs are the most social ground squirrel (Armitage 1981; Hoogland 1995) and live in colonies that consist of a number of family groups called coterie. Each coterie typically has one

to two adult males, multiple adult females and yearlings, and juveniles. Coterries have been found to contain 1 to 26 adults and yearlings at a given time (Hoogland 1995).

Data Collection

The study was conducted from 2009 to 2011, with two trapping sessions conducted each year, one during the spring (April/May) and the other during the summer (July/August). Each trapping session involved 4 - 14 days (Table 2.1). Trapping sessions were shorter during the first year by an average of 6 days, but were extended during the following two years because longer sessions were needed to increase our sample size and increase the precision of our model parameter estimates. We tried to trap before the juveniles emerged in the spring and yearling males were expected to disperse (Garrett and Franklin 1988), but early timing was not always possible. Prairie dogs were live-trapped using single door collapsible Tomahawk live traps (either 16-in x 5-in x 5-in or 19-in x 6-in x 6-in Hazelhurst, WI) that were placed one trap per stake on a 2.25 hectare plot. The stakes formed a 10 by 10 grid, with 15 m between traps. At times, up to 40 additional traps were added during the 2010 and 2011 trapping season in areas with higher densities of prairie dogs. By adding extra traps, we hoped to eliminate the chance that some prairie dogs were being out-competed for a chance to enter traps by individuals who always entered traps first and often. Sweet feed, a common horse feed, was used as bait for all traps. Traps were baited and opened before sunrise in the morning and checked three to four hours afterwards. Traps were checked earlier on days when the temperature exceeded 90 degrees. In the spring, while days were cooler, we conducted a second trapping session following the first by rebaiting traps. In the summer, a second trapping session was conducted in the evenings. Traps were opened approximately four to five hours before sunset and checked two hours later in order to clear traps of prairie dogs before it was dark. Our trapping protocol was approved (Approval No. 2994) by the Institutional Animal Care and Use Committee at Kansas State University. We also followed the guidelines of the American Society of Mammalogists for the use of live mammals in research (Sikes et al. 2010).

Prairie dogs were permanently marked using 12.50mm X 2.07mm pit tags (Biomark Inc, Boise, ID) and dye-marked using blue-black Clairol hair dye. The hair dye only lasted for a single trapping occasion (about two weeks), while the pit tag was expected to last for the duration of the study. A study conducted by Schooley et al. (1993), found that the chance of

losing a pit tag for Townsend's ground squirrels was less than 5% during the first 10 days and had no losses up to two years later. We assumed that prairie dogs lost their pit tags at a comparable rate to ground squirrels. Each animal was identified to sex and aged as either an adult or a juvenile based on size. After an animal was pit-tagged and dye-marked with an individually unique number, it was released at the point of capture. The point of capture and the burrow that it ran to were also recorded in order to identify coterie boundaries. Each subsequent time a prairie dog was captured, the animal was immediately released and the point of capture and escape burrow location were recorded.

Statistical Analysis

We used the robust design model with full heterogeneity (Huggins 1989; Pollock 1982) which uses both open and closed models to estimate survival and population abundance (Kendall et al. 1995, 1997). A closed population means that the population did not change in size or composition during that period. Essentially, this means closure to losses, immigration or gains from local demography or movements during a trapping session. The open period is between trapping sessions when animals can disperse, immigrate, give birth, and die. During the closed periods, we were able to estimate encounter rates. Between closed periods, assuming there is no temporary emigration, the robust design model uses an open population model to obtain estimates of apparent survival (Kendall 2010). We used the package RMark (Laake and Rexstad 2009) within Program R ver. 2.14.0 (R Development Core Team 2010) to construct models for Program MARK (White and Burnham 1999). The model was designed with a time-step of 60 days. The logit link function was used to run all models.

We modeled apparent survival (ϕ), individual heterogeneity with two mixtures (π), encounter or initial capture (p), re-encounter or recapture (c), and population size (N) probabilities in program RMark (Kendall 2010; White et al. 2001). The closed capture part of the robust design analysis uses the capture-recapture information from the secondary occasion to improve the estimation of capture and recapture probabilities. It has shown that survival rates are more precise when estimated under this method than the traditional Cormack-Jolly-Seber method (Kendall et al. 1995; Pollock 1982). We analyzed sexes separately. We only analyzed survival rates in adults (prairie dogs ≥ 1 year) because juveniles were expected to have a different survival rate, and juveniles were only captured during the summer trapping season.

We were unable to look at annual survival of juveniles because they had already emerged and were exposed to predation for a couple of months prior to our trapping season which would have produced a biased estimate of apparent survival. Furthermore, due to a small sample size, we would have been unable to precisely estimate all the parameters needed for a Cormack-Jolly-Seber model. We were, however, able to calculate return rates for juveniles between the summer and spring (winter) trapping sessions. We ran models for each National Park separately.

Using the delta method (Powell 2007) we were able to calculate the variances for estimates of apparent annual survival rates of adult prairie dogs at each of the parks using our seasonal estimates. We modified the equation for annual apparent survival both to reflect the differences in length of each seasonal estimate where the summer to spring trapping period is approximately twice the length of time that the spring to summer trapping period is and because we used a 60 day time step within RMark. We used the following equation: $S_{ann} = (S_{sp-su})^2(S_{su-sp})^4$ where S_{sp-su} represents the estimated apparent seasonal survival rate from the spring to summer trapping period and S_{su-sp} represents the estimated apparent seasonal survival rate from the summer to spring trapping period. Apparent survival rates were compared between field sites, sexes, and seasons using Program Contrast (Hines and Sauer 1989). All other statistical analyses were conducted with Program R ver. 2.14.0 (R Development Core Team 2010).

Seasonal survival rates for juvenile prairie dogs were calculated using return rates. We used return rates rather than a Cormack-Jolly-Seber model because we would have needed three trapping seasons to obtain estimates of p (Sandercock 2006). We were only able to trap juveniles once each year due to the constraints of our study plan. Hence, we chose to use return rates even though they may produce biased results because they were the only estimator available to us (Sandercock 2006).

Model Selection

Our goal was to identify patterns within the top models of the robust design between the four colonies. We chose the following seven models to best represent our estimate of apparent survival for our population in the study: difference in time (between seasons), differences between the sexes, the main effects (additive models) of time and sex, main effects and interaction of time and sex, seasonal variation (summer versus winter), main effects (additive models) of seasons, and main effects and interaction of seasons and sex.

The following five models were used in our analysis of the nuisance parameters of probability of capture and re-capture (superscript represents the primary periods while subscript represents the secondary periods): The probability of capture could be constant within the primary periods but different for each primary period M_0^t . The probability of capture could be different both within and between primary periods M_t^t . The probability of capture could be the same for each primary period but show a behavioral difference (trap-happy versus trap-shy) within the primary periods M_b^t . The probability of capture could be different for each primary period but some prairie dogs may show heterogeneity in their trap response within primary periods M_h^t . The probability of capture could be different for each primary period but some prairie dogs may show heterogeneity and behavioral differences in their trap response within primary periods M_{bh}^t (Kendall et al. 1995; Liu et al. 2009; Otis et al. 1978). Other models were not considered due to the large number of parameters that would have been estimated, which our sample size could not accommodate. In the case of models with heterogeneity, we used two mixtures and modeled a different estimate for π for each session (closed period). We modeled all gamma parameters set to zero.

No goodness-of-fit test was run as there is no test for the Robust Design model at this time (Liu et al. 2009). Support for each model was assessed using Akaike's Information Criterion which was corrected for small sample size (AIC_c). Models with a delta AIC_c of 2.0 or less were used for parameter estimation. If there was more than one top model, all those with at least 5% AIC_c weight were used in model averaging to calculate the parameter values. We assumed that the prairie dog population was closed within each primary period because each period was no longer than 14 days and we are not including any juveniles that may emerge from the burrows during the trapping period. Due to small sample sizes, we imposed some restraints on the estimations of initial capture (c) and recapture (p) probabilities.

Results

Seasonal Survival Rate

We estimated survival rates from 3,637 captures of 480 individuals (23 at Sand Creek, 105 at Scotts Bluff, 169 at Bent's Old Fort, and 183 at Fort Larned). There were no captures at Sand Creek after the 2009 season due to a plague epizootic. For this reason, Sand Creek will be treated separately in comparing the four sites. All of the sites other than Sand Creek had a best

fit model that included a difference in apparent survival between the sexes and seasons (Table 2.2).

All estimates of apparent seasonal survival rates are based and reported on a 60-day time-step. Bent's Old Fort and Fort Larned had the highest apparent seasonal survival rates. Scotts Bluff did not have any difference between years in its estimated seasonal survival. At Bent's Old Fort, males' apparent seasonal survival rates ranged from 58.2 to 63.9 during summer season and 85.8 to 86.8 through the winter season, whereas females' ranged from 55.6 to 65.5 and 89.4 to 90.4 respectively. At Fort Larned, males' apparent seasonal survival rates ranged from 85.2 to 92.2 in the summer and 77.0 to 82.0 through the winter, whereas females' ranged from 94.8 to 97.4 and 90.2 to 92.9 respectively. At Scotts Bluff, the male apparent seasonal survival rates were 73.3 in the summer and 80.3 through the winter, while female survival was 83.3 and 90.9 respectively. Sand Creek showed no differences between the sexes or seasons and had apparent seasonal survival rates of 41.8 for both seasons for its one year with a prairie dog population. Females showed higher seasonal apparent survival rates than males at all the sites except during the spring at Bents Old Fort and at Sand Creek all seasons. Female survival was only significantly higher than males at Fort Larned during the winter ($\chi^2_1 = 8.1, P < 0.01$), and at Scotts Bluff during the winter ($\chi^2_1 = 7.6, P < 0.01$). Seasonal apparent survival rates were higher in the winter than the spring at Scotts Bluff and Bent's Old Fort but winter rates were lower than spring at Fort Larned (Fig. 2.1). Only at Bent's Old Fort did apparent survival significantly differ between the two seasons ($\chi^2_1 = 34.9, P < 0.001$).

Juvenile Winter Return Rate

With the exception of Scotts Bluff males and females in 2009, juvenile prairie dogs, at all three field sites, had return rates over 50% (Fig. 2.2). Bent's Old Fort females in 2010 had the highest with 100% ($n = 6$) of the juveniles re-captured during the spring trapping session. Overall, Bent's Old Fort had the highest average return rate for both sexes combined of 67.17% ($n = 63$), followed by Fort Larned (63.65%, $n = 45$), and Scotts Bluff (49.26%, $n = 37$). A paired sample t-test showed no significant differences between the sexes when field sites were combined ($t_2 = 1.01, P = 0.42$).

Estimates of Apparent Annual Survival Rate

Estimates of apparent annual survival rates show similar trends to seasonal rates with apparent differences both between sexes and sites (Fig. 2.3). All sites were significantly different from one another ($P < 0.05$) except Fort Larned and Scotts Bluff. Bent's Old Fort was significantly lower than Fort Larned ($\chi^2_1 = 14.4, P < 0.001$), Scotts Bluff ($\chi^2_1 = 4.7, P < 0.05$) and Sand Creek ($\chi^2_1 = 21.7, P < 0.001$). Fort Larned was significantly higher than Sand Creek ($\chi^2_1 = 77.2, P < 0.001$). Scotts Bluff was significantly higher than Sand Creek ($\chi^2_1 = 64.1, P < 0.001$). Annual survival differed significantly among the sexes at Fort Larned ($\chi^2_1 = 10.3, P < 0.01$) and Scotts Bluff ($\chi^2_1 = 4.3, P < 0.05$).

Survival at Sand Creek was zero due to the epizootic of plague and will not be considered further. Fort Larned had the highest apparent annual survival rates (\pm SE) of the three study sites at .328 (± 0.05) for males and .669 (± 0.08) for females. Scotts bluff had apparent annual survival rates of .223 (± 0.07) for males and .473 (± 0.09) for females. Finally, Bent's Old Fort had the lowest annual survival rate at .192 (± 0.05) for males and .205 (± 0.05) for females.

Encounter Rate

The top models for Fort Larned and Scotts Bluff showed a difference in behavior with heterogeneity within each primary session (Table 2.2). Bent's Old Fort top models also showed a difference in behavior with heterogeneity within each primary session and across all the primary sessions. Sand Creek top models showed a difference in time within the primary sessions but they were equal across the primary sessions. All but Sand Creek had re-encounter rates (c) higher than the initial encounter rates (p) for each primary session.

Weight

Prairie dogs were each weighed the first time they were trapped each trapping session. Using 2010 and 2011 data, Bent's Old Fort had the highest average adult female summer weight (mean \pm SD) of (821.9g \pm 110.8, $n = 46$), followed by Scotts Bluff (812.8g \pm 82.7, $n = 28$) and then Fort Larned (767.6g \pm 105.3, $n = 79$). Scotts Bluff had the highest average adult male summer weight of (957.3g \pm 112.6, $n = 25$), followed by Bent's Old Fort (952.8g \pm 94.9, $n = 35$) and then Fort Larned (847.8g \pm 116.6, $n = 89$).

Discussion

Populations of black-tailed prairie dogs at four small National Parks showed that apparent survival varied seasonally within a colony and annually among colonies. These differences may be a result of exposure to disease, variability in rates of dispersal, differences in predation pressure, access to mates, or quality of forage. With the use of the Robust Design Model, we were able to identify these differences in a short term study with higher precision than we would be able to with another method.

Apparent Seasonal Survival

There are a number of different possible explanations to describe the seasonal differences in apparent survival between Fort Larned, Bent's Old Fort, Scotts Bluff, and Sand Creek. At Sand Creek, we expected the seasonal survival rates during at least the winter to be lower than all the other sites as the population dropped to zero by the spring of 2010. This drop in population suggests a low survival rate as it is assumed the prairie dogs did not all disperse.

Females had higher survival rates than males regardless of season at Bent's Old Fort, Fort Larned, and Scotts Bluff. These differences in survival rates were expected as females are reported to be longer-lived than males (Hoogland 1995, 2006). Males are shorter-lived, largely because they need to establish and defend territories and breeding rights to females, which may result in injury or death. Reduced male survivorship is seen in many other species of ground squirrels and marmots (Michener and Locklear 1990; Schwartz et al. 1998; Sherman and Morton 1984).

The higher winter apparent survival rates seen at Scotts Bluff and Bent's Old Fort may be due to one of many factors such as differences in amounts of activity, predation levels, and energy allocation. Prairie dogs are active in the spring due to breeding and territory defense as well as during the summer when they are actively foraging in order to gain weight to survive the winter. This probably results in longer periods spent above ground, which potentially exposes them to more chances for injury and death by predators, thus lowering survival rates (Kenagy et al. 1989; Neuhaus 2001; Neuhaus et al. 1999). Also, the time between mid-May to the end of June is considered to be the peak time period of prairie dog dispersal (Garrett and Franklin 1988; Hoogland 1995, 2006). Summer dispersal would result in lower apparent survival rates in the summer because every time a prairie dog permanently disperses off the colony, it was treated as

dead in analyses, resulting in a lower estimated survival than what may actually be the case. Bent's Old Fort showed the greatest disparity of apparent survival rates between the seasons. The differences between Bent's Old Fort apparent seasonal survival rates could be caused by an increase in shooting, which may have occurred illegally in the Park or if prairie dogs moved onto the state land abutting the colony where shooting was allowed.

Juvenile Return Rates

We expected to see return rates over 50% for both sexes. We hypothesized that our rates would be higher than what Hoogland (1995) reported from his studies because we were calculating return rates for juveniles a few months following their emergence. The period of time after emergence is when juveniles are expected to be the most vulnerable. They are still small enough for snake attacks and most birds of prey. They also are not as coordinated (personal observation) and probably cannot run from potential threats as well. Using return rates, we cannot determine whether lower return rates are due to (1) the probability of surviving from capture to re-capture (apparent survival, ϕ) or (2) the probability of capture, conditioned upon the animal being alive (apparent encounter probability, p), or a combination of the two (Kendall 2010; Sandercock 2006). However, we can say that juvenile return rates, with the exception of some outlier years, is about 60% for both sexes at all field sites other than Sand Creek.

Estimates of Annual Apparent Survival Rate

We expected to see higher female than male survivorship, as Hoogland (1995) documented, that females have yearly survival rates of 76% and the males have rates of 55%. Our estimates from Fort Larned come closest to these numbers (F: 57%, M: 27%), whereas survival rates at the other sites were lower (F: 0 to 35, M: 0 to 19). The similarity between survival rates at Fort Larned and Hoogland's study may have been driven by the similarity of the habitats between our field site at Fort Larned and that at Wind Cave National Park where Hoogland conducted his study. Fort Larned was a mixed-grass prairie site as was the study site at Wind Cave National Park. Fort Larned is also outside of the known range of plague (Cully et al. 2006), which was also true at Wind Cave (Hoogland 1995).

Our initial impression was that Fort Larned had higher estimated apparent yearly survival rates because it had higher quality forage (appeared to have less toxic vegetation like bindweed)

and no known diseases. However, this was not supported by summer estimates of weight. It should be noted that Scotts Bluff weights were collected two weeks after the other sites which allowed for more foraging time and thus higher weights. Also, Fort Larned typically did not receive snowfall on average until October (High Plains Regional Climate Center, http://www.hprcc.unl.edu/cgi-bin/cli_perl_lib/cliMAIN.pl?ks4530). That is a month later than both Bent's Old Fort (Western Regional Climate Center, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?cola20>) and Scotts Bluff (High Plain Regional Climate Center, http://www.hprcc.unl.edu/cgi-bin/cli_perl_lib/cliMAIN.pl?ne7665). This also allows for a longer foraging season and higher weight gain later in the season before grasses become more scarce. Scotts Bluff and Bent's Old Fort have poor quality forage, dominated by exotic forbs such as bindweed, yellow sweet-clover, and summer cyprus, with low cover of palatable grasses. At Scotts Bluff, a large portion of the colony was avoided by prairie dogs, presumably because it was dominated by summer cyprus, which grows very tall and it appears that the prairie dogs are not able to clip it fast enough to maintain open visual fields. There was also abundant bindweed on the colony, which black-tailed prairie dogs select not to eat (Lehmer et al. 2006). In 2010, > 25% of the colony was covered by sweet clover which grew to about 1.5 m in height, producing additional large sections of inhospitable ground. Vegetation at Bent's Old Fort was also poor for prairie dogs, not due to vegetation height, but rather due to the lack of palatable forage plants.

If vegetation was not the cause of lower survival rates at both Bent's Old Fort and Scotts Bluff, disease and illegal shooting could be. In the spring of 2011, a dead prairie dog was found at Scotts Bluff and sent to the CDC for testing where it came back positive for tularemia. While tularemia is not known to cause large die-offs like plague, it can contribute to lower survival rates. At Bent's Old Fort, there was also the possibility of disease such as plague. The prairie dog population at Sand Creek was believed to have died out due to plague and was only approximately 100km away and Bent's Old Fort is close to other colonies in Animas County, CO where plague was documented recently (Miller et al. 2005).

Comparisons to Previous Studies

Besides location, previous studies of black-tailed prairie dogs differ in their exposure to plague, which can potentially negatively impact survival rates. In addition to Hoogland's (1995) long-term study at Wind Cave National Park in South Dakota, Biggins et al. (2010) conducted a

five-year study in Montana at colonies both with and without flea control that was used in an effort to stop the spread of plague,. Facka et al. (2010) conducted a three-year study in the Chihuahuan desert of New Mexico, where plague was also not known to occur. Both studies looked at monthly survival rates. When these studies are compared to ours, we can see that sites outside the known plague area (Fort Larned, Chihuahuan desert, Wind Cave at the time of the study, and flea-controlled Montana colonies), appear to have annual survival rates > 0.50 (Fig. 2.4). Those within the known plague area and no flea control have survival rates < 0.50 . It is therefore possible that one of the causes for the lower survival rates at our sites was enzootic plague or perhaps some other disease. Biggins et al. (2010) noted that flea control at colonies within a plague active area doubled the survival rate of prairie dogs compared with colonies without flea control. Simultaneous work at the same colonies with black-footed ferrets treated with plague vaccine (Rocke et al. 2010) provided strong evidence that enzootic plague, and not some other disease, was responsible for the lower survival on the untreated colonies. The presence of enzootic plague is a possibility at our Scotts bluff and Bents Old Fort sites, and may explain the differences in apparent annual survival rates between those sites and Fort Larned.

Moreover, differences in site-fidelity could also cause differences in apparent survival rates among previous research sites and among sites in this study. Research on the occurrence of prairie dog dispersal is limited. If there is a large amount of dispersal, survival rates will be underestimated, because dispersed prairie dogs are indistinguishable from dead prairie dogs in these models. However, our study (see Chapter 4, this thesis) and others have shown low dispersal rates in black-tailed prairie dogs and this suggests that dispersal may not be a driving factor in the differences in apparent survival rates among our sites (Garrett and Franklin 1988; Halpin 1987; Hoogland 1995, 2006; King 1955; Newby 2001).

Conclusions

Hoogland's (1995) long-term study is the most thorough study examining annual survival rates of black-tailed prairie dogs, but it is important to note that it was limited to one colony of prairie dogs at one field site, at a location with no recorded plague at the time. Our results are consistent with Biggins et al. (2010), in that we found lower survivorship in colonies in areas with a history of plague. However, these results could also have resulted due to differences in food quality, site-fidelity, predation pressure, or other factors. Information on the causes of

variability in survivorship of black-tailed prairie dogs is important for the management of prairie dogs as well as that of other dependent species like the black-footed ferret. Prairie dogs only reproduce one time per year and females do not always reproduce as yearlings (Hoogland 1995). Low survivorship may lead to a population declines if fecundity rates are also low. Further work needs to be done on multiple sites to compare the effects of fecundity versus survival on the overall abundance of the prairie dog population. With the use of the robust design model, we were able to make precise estimates of apparent survival at single, small colonies over relatively short periods of time. Hopefully with future work, we will be able to use this model to better ascertain which covariates are leading the differences in apparent survival rates among sites.

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Table 2.1. Number of trapping days for all four field sites in the Midwest, spring 2009 - summer 2011.

	State	spring 2009	days b/t	summer 2009	days b/t	spring 2010	days b/t	summer 2010	days b/t	spring 2011	days b/t	summer 2011
Bent's Old Fort	CO	7	44	5	255	13	88	14	268	13	54	14
Fort Larned	KS	12	70	7	270	13	78	14	255	13	81	12
Scotts Bluff	NE	11	56	4	285	11	78	14	255	14	79	12
Sand Creek	CO	7	38	5	267	14	-	-	-	-	-	-

Table 2.2. Mark-recapture modeling using the robust design model to calculate apparent survival (ϕ), heterogeneity (π) encounter rates (p), and abundance (N) of black-tailed prairie dogs at four small national parks.

Site	Model	Dev	K	AIC _c	Δ AIC _c	w_i
Bent's Old Fort	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3189.0	25	3287.5	0.000	0.123
	$\phi(\text{time}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{ses})$	3176.6	31	3287.6	0.097	0.117
	$\phi(\text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3193.6	23	3287.9	0.367	0.102
	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{m}(\text{bh}) N(\text{ses})$	3202.2	19	3288.3	0.780	0.083
	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3187.9	26	3288.5	0.938	0.077
	$\phi(\text{snl}) \pi(\text{ses}) \text{m}(\text{bh}) N(\text{ses})$	3206.6	17	3288.5	1.011	0.074
	$\phi(\text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3192.4	24	3288.8	1.295	0.064
	$\phi(\text{time}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3188.5	26	3289.0	1.516	0.057
	$\phi(\text{sex} + \text{time}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{ses})$	3176.4	32	3289.5	1.930	0.047
$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3193.1	24	3289.5	1.976	0.046	
Fort Larned	$\phi(\text{sex} + \text{time}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3566.3	28	3359.6	0.000	0.260
	$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3573.3	25	3360.4	0.734	0.180
	$\phi(\text{sex}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3575.5	24	3360.5	0.836	0.171
	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	3572.5	26	3361.7	2.037	0.094
	$\phi(\text{sex} + \text{time}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3570.7	27	3361.9	2.288	0.083
	$\phi(\text{sex}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3579.8	23	3362.6	3.007	0.058
	$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	3577.7	24	3362.7	3.041	0.057
Scotts Bluff	$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	2160.4	24	2152.2	0.000	0.165
	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	2156.4	26	2152.4	0.198	0.150
	$\phi(\text{sex}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	2160.7	24	2152.58	0.334	0.140
	$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{sex})$	2159.0	25	2152.9	0.735	0.114
	$\phi(\text{sex}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	2163.5	23	2153.2	0.964	0.102
	$\phi(\text{sex} + \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\text{ses})$	2151.3	29	2153.79	1.544	0.076
	$\phi(\text{sex} * \text{snl}) \pi(\text{ses}) \text{ses:m}(\text{bh}) N(\cdot)$	2160.0	25	2153.9	1.670	0.072
Sand Creek	$\phi(\cdot) \text{m}(\text{t}) N(\text{ses})$	84.8	11	147.5	0.000	0.126
	$\phi(\cdot) \text{m}(\text{t}) N(\cdot)$	92.0	9	147.7	0.201	0.114

^a Model factors included: \cdot = constant, sex, t = time, snl= variation by season, b = behavioral, h = heterogeneity, bh = additive model of behavior and heterogeneity, sex= different within each primary session, ses = each primary period is different, * = a factorial model, + = additive effects model.

^b Model fit is described by the Deviance (Dev), number of parameters (K), and the difference in the Akaike Information Criterion from the best-fit model (ΔAIC_c). Models are presented that had moderate support (Akaike weight (w_i) >.04)

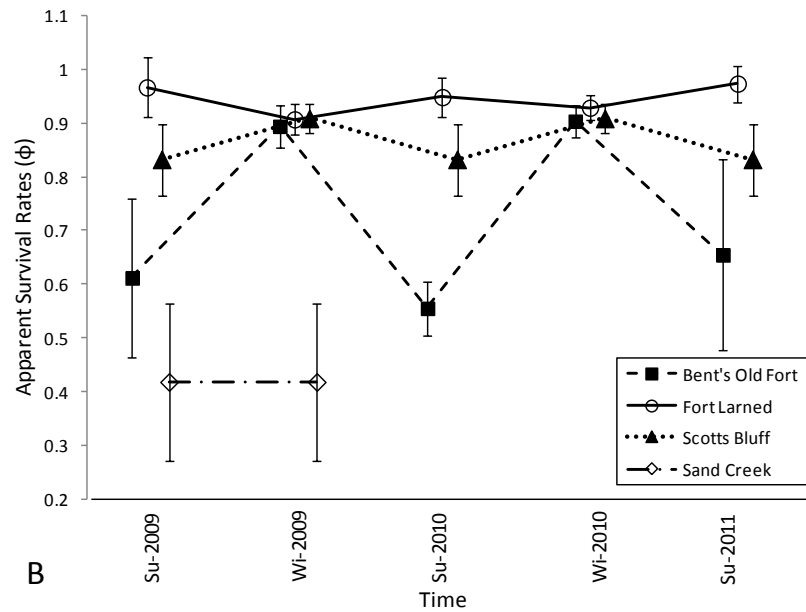
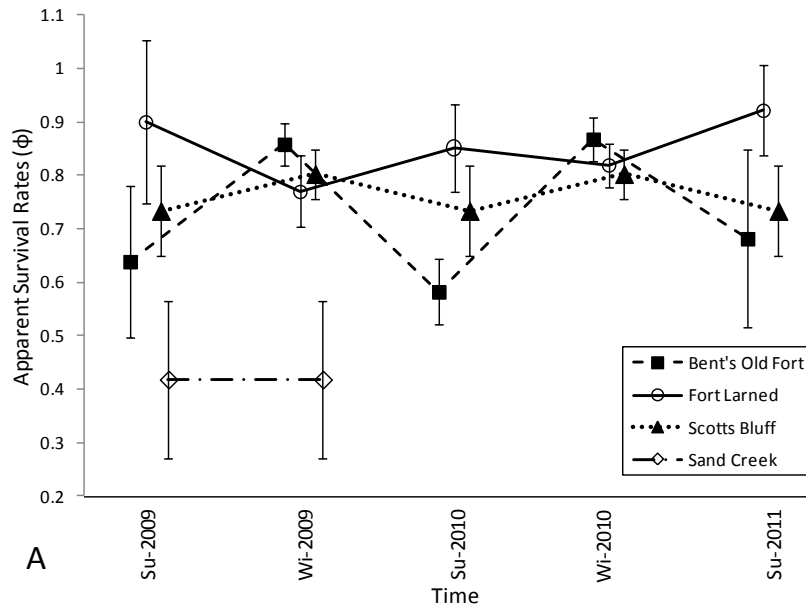


Figure 2.1. (A) Apparent seasonal survival rate (\pm SE) of male black-tailed prairie dogs. (B) Apparent seasonal survival rate (\pm SE) of female black-tailed prairie dogs. Bent's Old Fort is the only site that showed significantly different rates between the seasons with higher rates during the winter than the summer ($\chi^2 = 10.3, P < .01$). Apparent survival rates are based on a 60-day time step. Summer (Su) represents the 2 time steps between the spring and summer trapping periods and the winter (Wi) represents the 4 time steps between the summer and spring trapping periods.

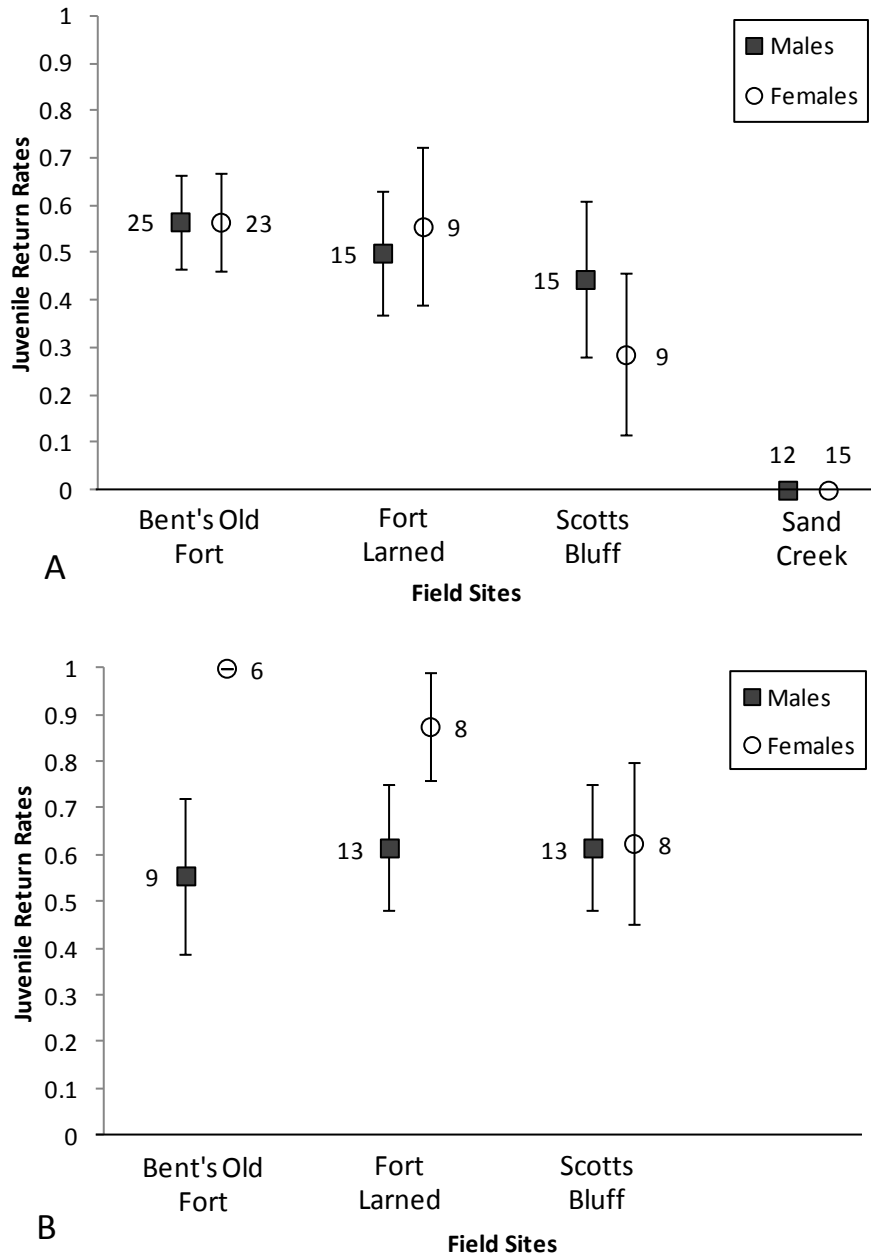


Figure 2.2. Juvenile return rates between summer and spring trapping sessions. (A) Juvenile return rates (\pm SE) at all four National Parks between the summer of 2009 and the spring of 2010. (B) Juvenile return rates (\pm SE) at three National Parks between the summer of 2010 and the spring of 2011. Sample size (n) is included next to each point.

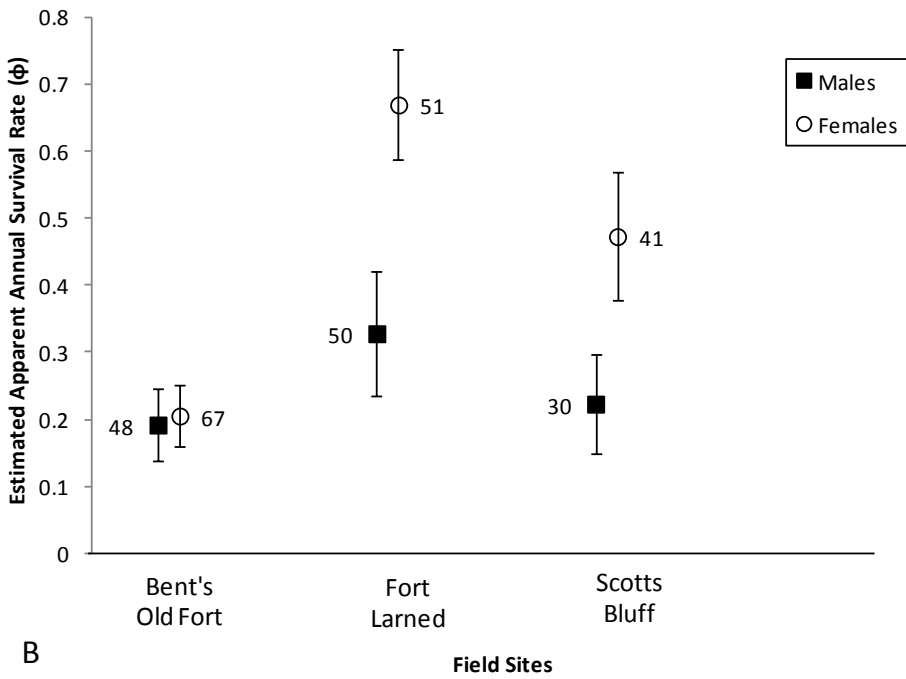
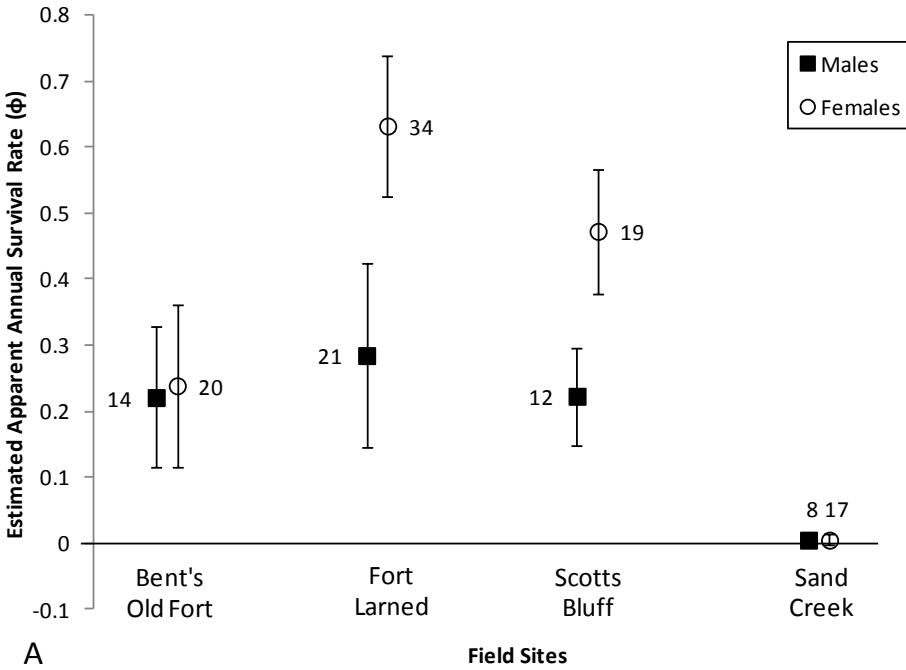


Figure 2.3. (A) Estimated apparent annual survival rate (\pm SE) of black-tailed prairie dogs from spring of 2009 to the spring of 2010. (B) Estimated apparent annual survival rate (\pm SE) of black-tailed prairie dogs from spring of 2010 to the spring of 2011. Standard error bars are included and survival rates are based on a 60-day time-step.

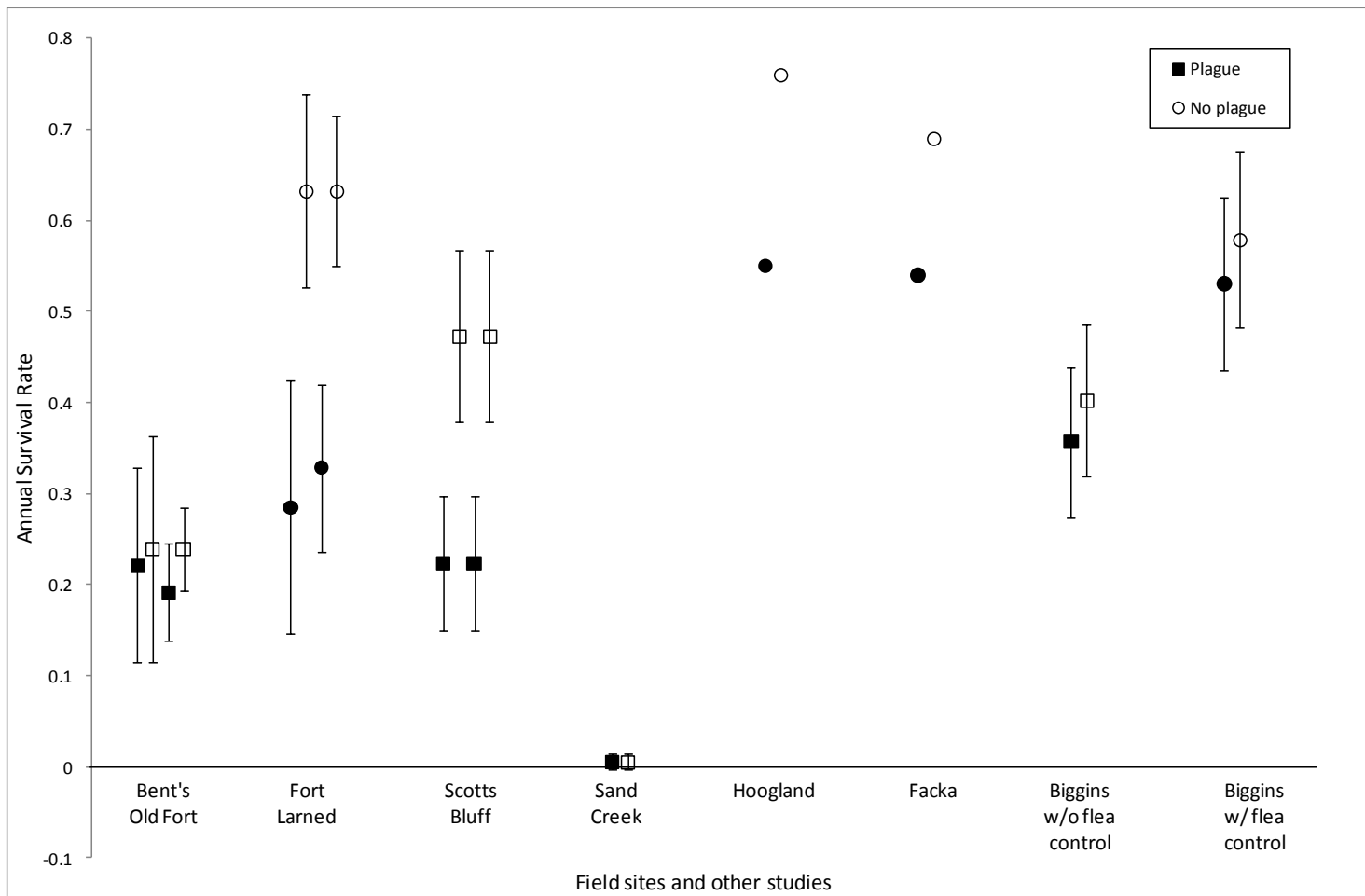


Figure 2.4. Comparison of the estimated apparent annual survival rates (\pm SE except for Hoogland and Facka) of black-tailed prairie dogs at four small national parks to published data of apparent annual survival rates from three other studies conducted by Hoogland (2005), Facka et al. (2010), and Biggins et al. (2010). Closed points represent males and open points represent females. Squares represent sites that potentially have plague and circles are sites without known plague in the area at the time of the study.

Chapter 3 - Comparison of methods for estimating abundance for prairie dogs

Abstract

Precise and cost-effective methods to estimate abundance of black-tailed prairie dogs (*Cynomys ludovicianus*) are important owing to the species overall decline due to disease, loss of habitat, and pest-control measures. A number of different methods have been employed such as mark-resight, mark-recapture, aerial photography, visual counts, and burrow counting. Here, we assessed four methods, minimum known number alive (MNKA), visual counts, mark-recapture, and mark-resight, to estimate abundance of prairie dogs at three small National Parks where there is need to manage populations for both conservation of the prairie and to limit contact with neighboring agricultural land. We compared the methods to see which was most precise and cost-effective to use when working on smaller colony systems, such as at the parks where we worked. Mark-resight produced the most precise estimates the majority of the time. Although it costs more to conduct a mark-resight estimate than visual counts, the methods produced significantly different results from one another 75% of the time, which was especially apparent on sites with visual barriers such as tall vegetation and uneven ground. Whereas mark-recapture differed from visual counts only 33% of the time and from mark-resight only 25% of the time. Our results demonstrate that for managers who need abundance estimates of prairie dogs in smaller colonies, mark-resight will produce the most precise results.

Introduction

In the field of wildlife management, there is a need for effective and precise ways of assessing population abundance. Black-tailed prairie dogs (*Cynomys ludovicianus*) are considered to be both a keystone species and a wildlife pest, and thus requires careful management. While black-tailed prairie dogs are the most abundant of the five prairie dog species, it is estimated that they occupy only 3% of their historic range (USDI, 2009). Reasons for this decline include pest control, habitat conversion from grassland to cropland, and the introduction of the exotic disease, sylvatic plague, caused by *Yersinia pestis* (Miller and Cully, 2001).

Assessment of prairie dog abundances at a broad scale is usually conducted using aerial surveys to assess occupied habitat. Using these methods, the U.S. Fish and Wildlife Service (USDI, 2009) announced that the black-tailed prairie dog did not warrant protection under the Endangered Species Act because the species appeared to be sufficiently abundant. However, this method is not entirely precise, as density varies across a colony and some areas may look like habitat (have visible burrows) but may not be occupied by any prairie dogs (McDonald *et al.*, 2011; Biggins *et al.*, 2006; Miller *et al.*, 2005).

Furthermore, a more detailed evaluation of population abundance at a finer scale is sometimes required such as in areas that are being assessed for reintroduction of black footed ferrets (*Mustela nigripes*) (Biggins *et al.*, 2006; Fagerstone and Biggins, 1986). Beyond that, prairie dogs play an important role for many of the other prairie species such as burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*) whose numbers have been documented as decreasing in areas where prairie dog numbers have also decreased (Kotliar, 2000). Therefore, if the goal of a management plan is to have a diverse community of obligate prairie vertebrates including mountain plovers and burrowing owls, it is important to maintain large and stable populations of prairie dogs.

In order to assess population levels of prairie dogs, there needs to be a reliable and cost-effective way to monitor them. There are a number of different methods that have been developed to meet these needs including: (1) visual counts (Plumb *et al.*, 2001; Severson and Plumb 1998), (2) mark-resight (Magle *et al.*, 2007; McClintock, 2010; White, 1996), (3) mark-recapture using program MARK (Biggins *et al.*, 2006; Fagerstone and Biggins, 1986; Magle *et al.*, 2007; Facka *et al.*, 2008), (4) aerial photography (Biggins *et al.*, 2006; Dalsted *et al.*, 1981; Sidle *et al.*, 2002), and (5) burrow density (Biggins *et al.*, 2006; Plumb *et al.*, 2001; Severson and Plumb, 1998; Morrison and Peitz, 2011) and (6) minimum known number alive (MNKA). Here, we will compare MNKA, visual counts, mark-resight, and mark-recapture methods to assess estimates of population abundance from three small National Park sites. All of these parks need the best method to estimate the number of prairie dogs located on their small colonies in order to manage them for conservation and to minimize conflict with adjoining private landowners.

We hypothesized that no one method will prove best at all three colonies because of differences in: (1) landscape structure and visual barrier to visual counts, (2) the time of year counts are conducted, and (3) the funds available for monitoring protocol for future assessment

at the study sites. Our aim was to evaluate these three methods and identify reasons why a manager might want to employ one of the three methods over another at a specific colony.

Methods

Study Site

Our study was conducted at three small National Parks: (1) Fort Larned National Historic Site, KS; (2) Scotts Bluff National Monument, NE; and (3) Bent's Old Fort National Historic Site, CO. The study began in April of 2010 and concluded in August of 2011. Recreational shooting is banned at all three National Park sites and all are surrounded by agricultural land. None of the parks allow grazing by domestic livestock. Within each park's colony, a four hectare (ha) study area was established and used for these comparisons. Bent's Old Fort is in short grass prairie whereas Scotts Bluff and Fort Larned are in mixed grass prairie. Vegetation on the colony at Bent's Old Fort was dominated by bindweed (*Convolvulus arvensis*), which is a low growing plant, and the terrain of the colony was very flat. Scotts Bluff is located on hilly terrain with the highest point located on the southern end and approximately 40% of the four hectare study site was used by black-tailed prairie dogs whereas the rest was dominated by tall vegetation of summer cyprus (*Kochia scoparia*), sweet clover (*Melilotus officinalis*), and smaller amounts of other forbes. Fort Larned had the highest plant diversity of the three sites. Both bindweed and summer cypress were found there but there were also many grasses such as western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), big bluestem (*Andropogon gerardii*), three-awn (*Aristida oligantha*), and buffalo grass (*Buchloe dactyloides*). Precipitation varied between years and study sites, resulting in variation of vegetation height and composition. All three sites in 2010 received a good amount of precipitation in the spring and summer, resulting in taller vegetation which was most apparent at Fort Larned and Scotts Bluff. In 2011, Fort Larned received very little rainfall, and by August, most of the vegetation was short and brown. Scotts Bluff on the other hand, received large amounts of rainfall in the spring and summer resulting in dense and tall vegetation in 2011.

Capture and Marking

We counted and trapped prairie dogs in 2010 and 2011. Two trapping periods were conducted each year, one in April or May and another in July or August. Each trapping session

lasted between 11 and 14 days. We trapped in the spring before the juveniles emerged (Apr/May), but in the summer (July/Aug) juveniles were included in the abundance estimates. Prairie dogs were live-trapped using single door collapsible Tomahawk live traps (either 16-in x 5-in x 5-in or 19-in x 6-in x 6-in; Hazelhurst, WI) that were placed on a 2.25-hectare plot with a 10 by 10 staked grid with 15 m between traps, in the middle of the four-hectare study area. Each grid contained at least 100 traps, each of which was placed at one stake. During each trapping session, up to 40 traps were added in areas saturated with prairie dogs (containing high densities of prairie dogs). By adding extra traps, we hoped to eliminate the chance that some prairie dogs were being excluded from traps by trap-happy individuals who always entered traps first and often.

Prairie dogs were permanently marked using 12.50mm X 2.07mm pit tags (Biomark Inc, Boise, ID) and uniquely dye marked for visual observations using blue-black Clairol hair dye. The hair dye only lasted for a single trapping occasion (about two weeks), while the pit tag was used as a double-marking for retention. Each animal was identified to sex, and aged as either an adult or a juvenile based on size.

Visual Counts

Counts were conducted by two observers from elevated platforms (approximately 4 m high) established in two adjacent corners of the study plot. Scans were conducted from the same locations in both years. Platforms were established on a particular corner, which maximized the total area visible and avoided looking directly into the rising sun. Observers used a 45 x 60 spotting scope mounted on a window mount stand on each platform to increase stability. Scan sessions followed protocol established by Plumb *et al.* (2001). Ideally, scans were conducted for three consecutive days. However, some sessions only had two due to bad weather. Each day, scans began one hour after sunrise. Within each day, there were a minimum of 8 scans over a 2 hour or longer period of time. Each new scan began 15 minutes after the previous. We tried to conduct visual counts at all sites on three days each trapping session, but due to high winds or precipitation sometimes only two could be completed. Each marked animal was tallied in a separate column from unmarked animals. Scans moved across the terrain only once each 15-minute period so that no prairie dog was counted more than once.

Abundance Estimates

MNKA.– The MNKA was determined from either the known number of marked prairie dogs or the highest total visual count from one scan. Whichever of the two methods produced the highest number of prairie dogs known alive on the study area was used.

Visual Counts.– Abundance estimates were estimated from visual count data using the equation created by Plumb *et al.* (2001). This is the technique currently used at Scotts Bluff National Monument (Morrison and Peitz 2011). While originally developed for prairie dogs in Conata Basin, South Dakota (Severson and Plumb 1998), Morrison and Peitz believed it could be applied in Scotts Bluff as well. Subsequently, we have also applied it at Fort Larned and Bent's Old Fort National Monuments. We followed the equation created by Plumb *et al.* exactly for estimation of abundance. Standard errors were calculated using the following equation adapted from Plumb *et al.* (2001)

$$\text{Variance (P)} = \text{SE(P)}/(.4)^2 ((1 + 1/n + [P - \bar{x}]^2) / \sum [x_i - \bar{x}]^2)$$

where P is the estimated density of prairie dogs in the total area sampled, n is the total number of counts (total number of scans each trapping session), \bar{x} is the average count, x_i is the maximum count.

In 2010, traps were left open during the visual counts which forced some prairie dogs to stay above ground. In 2011, we stopped opening traps during counts. We combined counts of marked and unmarked individuals together for the visual counts. Due to the fact that we had two observers for each park, we used only the observer who had the highest maximum count any of the days that counts were conducted. We did this because typically one visual count stand was in a better position than the other and could observe a larger percentage of the study area and thus provide a more complete count.

Mark-resight.– We used the same data from our visual counts for our mark-resight analysis with counts of marked and unmarked prairie dogs. We used the same observer's data as we did for the visual count. We used the mixed logit-normal mark-resight model without individually identifiable mark within program MARK for our analyses. We sampled without replacement in the secondary sampling periods (each of the eight counts per day). We also assumed that no individuals' marks were lost, because we used a permanent hair dye, and prairie dogs do not molt until mid-August at which time we were finished with our counts. Each day of visual counts, the total number of marked individuals on the study site was known. We modeled

the following parameters: abundance during primary interval j (N_j) and the mean resighting probability (p_{ij}). Support for each model was assessed using Akaike's Information Criterion which was corrected for small sample size (AIC_c). Models with a ΔAIC_c of 2.0 or less were used for parameter estimation. If there was more than one top model, all those with at least 5% AIC_c weight were used in model averaging to calculate the parameter values. The sin link function was used to run all the models. We chose a set of 8 models a priori for analysis. These models included the following for the mean resighting probability: changes over time between secondary occasions but not primary $p(t)$, changes over time both between primary and secondary occasions $p(ts)$, constant between secondary occasions but time effect between primary occasions $p(s)$, and constant between both primary and secondary occasions $p(\cdot)$. Abundance (N) was modeled as the same for all primary occasions $N(\cdot)$ to obtain one overall estimate for the resighting session.

Mark-recapture. – We used the package RMark (Laake and Rexstad 2009) within Program R ver. 2.14.0 (R Development Core Team 2010) to construct closed capture models with full heterogeneity for Program MARK (White and Burnham 1999). During each trapping period the population was considered closed. Closure means that no individuals were considered to have died, been born, emigrated, or immigrated. We believe closure was met as the time of year we trapped was either before juvenile emergence or after they had all emerged (Hoogland, 1995). Further, trapping periods were conducted before or after what is considered to be the most active time of dispersal for prairie dogs (Hoogland, 1995; Garrett and Franklin, 1988).

We modeled encounter or initial capture (p), re-encounter or recapture (c), and population size (N) parameters. We grouped all the prairie dogs together in one group regardless of age or sex. This was done to increase our sample size and allow for more parameters to be tested. We ran models for each National Park separately.

Support for each model was assessed using Akaike's Information Criterion which was corrected for small sample size (AIC_c). Models with a ΔAIC_c of ≤ 2.0 were used for parameter estimation. If there was more than one top model, all those with at least 5% AIC_c weight were used in model averaging to calculate the parameter values. No goodness-of-fit test was run because at this time there is none for closed population models (Lukacs, 2009). We modeled the nuisance parameters of encounter (p) and re-encounter rates (c) using the eight models established by Otis *et al.* (1978).

Comparison of tests.— Each test was compared to another for each trapping session. Abundance estimates were compared using Program Contrast (Hines and Sauer 1989). All the chi-square tests had 1 degree of freedom. The percentage of total percentage of instances the tests differed significantly was used to compare the tests (the number of times they differed/12 (the total number of trapping sessions))

Results

A total of 157 days of trapping at Bent's Old Fort, Fort Larned, and Scotts Bluff yielded 521 marked individuals. Average number of days spent capturing and marking prairie dogs during each trapping session was 13.1 days (SD = 1.0 days, $n = 12$). Total number of scans (counts of prairie dogs which was a minimum of 8 per day), was 287 for 21 primary periods of which three trapping periods consisted of only two primary periods instead of three due to weather conditions (one during the spring of 2010 at Fort Larned and the other two during the spring of 2010 and 2011 at Scotts Bluff). With the exception of the three sessions with only two days, the average number of scans per trapping session was 25.89 (SD = 2.03 scans/trapping session, $n = 9$).

Top models for mark-recapture all included the additive model of behavior, heterogeneity, and time for encounter and re-encounter rates except for Bent's Old Fort during the summer of 2011 (Table 3.1). Mark-resight showed a range in model structure depending on the primary period and location (Table 3.2). The most common model was $p(ts)$ (66.7% of the visual count sessions had this as the top model, $n = 12$) showing a difference in time both between primary and secondary occasions. This was the only top-rated model for all seasons at Bent's Old Fort. Fort Larned had one top model of $p(s)$ indicating that resighting rates were constant throughout secondary periods but different between primary sessions. Two trapping sessions at Fort Larned and one at Scotts Bluff had top models of $p(\cdot)$ indicates that resighting rates were the same for all primary and secondary occasions.

Comparison of Population Estimates

Abundance estimates were above the minimum number known alive (MNKA) for all instances with mark-resight. However, using visual counts, the estimate fell under the MNKA two times (16.7%, Figure 3.1) and using mark-recapture one time (8.3%, Figure 3.1). Mark-recapture estimates had the largest standard errors in all instances with visual counts having the

second largest six times (50%, Table 3) and visual counts having the smallest six time (50%, Figure 3.1). In terms of abundance estimates, mark-recapture's estimates were significantly different ($P < 0.05$) than mark-resight 25% of the time for each site and season comparison. Mark-recapture estimates were also significantly different from visual counts 33.3% of the time. Mark-resight was significantly different than visual counts 75% of the time. This resulted in very few abundance estimates that were similar between mark-resight and visual count methods. Visual counts and mark-resight most often differed from the other two methods when grouped together 58.3% of the time. Mark-recapture significantly differed from the other two methods when grouped together 41.7% of the time.

Discussion

We compared four different techniques for assessing abundance of black-tailed prairie dogs at three small National Parks. We did not use burrow density counts as this is the most contested index in the literature (Biggins *et al.*, 2006; Morrison and Peitz, 2011; Hoogland, 1995; King, 1955). Overall, estimates of abundance from mark-resight were the most precise and never underestimated the population below the MNKA. Mark-resight benefits from its ability to control for encounter rate (resight rate) as well as being the only method of the four, to estimate abundance for both unmarked and marked prairie dogs (Table 3.3).

Total work-hours

Based on visual estimates, we marked more than 75% of the population in our study area within each trapping session. In order to accomplish this task, prairie dogs needed to be trapped for approximately 8 – 14 days depending on weather conditions, time of year, and food availability. For a 4 ha field site (and no more than two trapping sessions a day), trapping takes about three to six hours a day of effort if one excludes waiting time between opening and checking traps. In total, time required for trapping would be 24 to 84 hours of work per person with a minimum of two people. For mark-resight studies, it is believed that only 25% of the population needs to be marked to obtain precise estimates of N (Magle *et al.*, 2007; McClintock, 2010; Facka *et al.*, 2008). Trapping for mark-resight would have taken approximately three or four days to accomplish, or 9 to 24 hours per person. We then conducted counts for another three days leading to a total time commitment of six or seven days or 15 to 30 hours per person in total. Visual counts required the least amount of time to conduct with just three days required

for counting, or 6 hours of work. Time can be an important factor in choosing a method as all techniques require at least two people to conduct the study. Large time commitments can lead to high labor costs and less time to work on other projects.

Prairie dog health and safety

Besides time, one of the biggest concerns when conducting a mark-recapture study is the stress it can put on prairie dogs. There is always the chance of mortality within traps from teeth getting stuck, heat exhaustion, and predator attacks. While stresses are minimized as much as possible during trapping, stress is still a factor that needs to be addressed when choosing the best method to be used. Stress or mortality can be a much more important consideration if working in an area with low abundance or with a different species of prairie dog that is threatened or endangered, such as the Utah (*Cynomys parvidens*) or Mexican prairie dogs (*Cynomys mexicanus*). Visual counts require no handling of animals and thus have the least amount of impact on populations.

Accuracy of estimates

One of the most serious problems with visual counts was that they depend on the observers' ability to see the prairie dogs. The Plumb *et al.* in the linear model (2001) helps to mitigate the issue that some prairie dogs are above ground while some may be below for reasons such as feeding young, burrow maintenance, and so forth (Biggins *et al.*, 2006). However, the same number may not work for all prairie dog populations (Severson and Plumb, 1998) during all years (Facka *et al.*, 2008). For instance, during the summer of both years of the study at Scotts Bluff, the visual count estimates less than the MNKA (Figure 3.1). The underestimation of the visual counts most likely occurred because the landscape is not flat and the vegetation gets very high and dense by late summer. Tall vegetation leads to large sections of the study area not being visible, and extremely small maximum abundance counts that underestimates the population size.

Underestimation below the MNKA is not a factor with mark-resight because the estimate will always be higher than both the total number of marked animals and the highest total counted in one scan. Mark-resight uses the total number of marked animals along with a ratio of seen marked and unmarked animals to estimate the abundance of the population. The mixed logit-normal model that we ran in program MARK is comparable to the joint hypergeometric

estimator (JHE) of Program NOREMARK (White, 1996). Mark-resight models in Program MARK are considered to be more precise than NOREMARK because they can use information about resighting probability across the primary periods (McClintock, 2010).

Mark-recapture is considered to become more precise as the percentage of captured animals increases (Biggins *et al.*, 2006). However, it is difficult to capture all the animals on the study plot and requires large numbers of traps and days. Some prairie dogs are more likely than others to enter a trap and a few may never go into one (Biggins *et al.*, 2006, Hoogland, 1995). Because we were unable to trap all the prairie dogs on the study sites, we needed to use program MARK to accommodate unequal capture probabilities to estimate abundance (Biggins *et al.*, 2006; Otis *et al.*, 1978). The estimates from mark-recapture resulted in the largest confidence interval of the three techniques. Estimates occasionally were much higher than expected, such as seen at Scotts Bluff during the summer of 2010 (Figure 3.1).

Overall impressions

Mark-resight produces the most precise estimates that are never below the MNKA. Standard errors for mark-resight were smaller than mark-recapture and were always within the range of expected values based on personal observation from the field. Visual counts using the Plumb *et al.* linear equation (Plumb *et al.*, 2001) is the simplest and quickest technique. However, it was not found to be highly precise which may be due to the fact that not every field site is the same and may need a different correction equation. Keep in mind that this equation may not just need to be changed by individual site, but also due to changing weather conditions, which may make it difficult to establish precise protocols for its use.

Furthermore, in mark-resight we did not use individually identifiable marks on our marked prairie dogs. As a result, we could not account for heterogeneity in individual resighting. Using individually identifiable marks may have made our estimates more precise. Making consistent individual identifications is difficult and may not be possible in areas with tall vegetation due to the difficulty in clearly reading numbers, but is something to consider for future work where visibility is adequate. Also, we only marked the sides of prairie dogs. There is always the possibility that a mark was missed because of vegetation covering their sides. It may prove helpful for future studies to also mark the head since that is the easiest part of the animal to see, and then individually mark the sides.

It should be noted, that if the objective of the study is to look at factors other than just abundance, mark-recapture may be the better option. While we felt that mark-resight was the overall best technique for counting prairie dogs, it does not allow us to count males and females separately (Table 3.3). Nor are we able to count juveniles and adults separately as by August, their body sizes appear similar and it is hard to discern between the two age-classes.

Use for other sites

The three field sites in this study have the advantage of being relatively small colonies. If a manager was interested in total population abundance of large colonies, mark-recapture would probably not be a good technique to consider. Even if a small area was still trapped, it would be hard to use those estimates for the larger area because the density of prairie dogs changes across a colony (Biggins *et al.*, 2006; Hoogland, 1995; King, 1955). Visual counts would be the easiest logistically, as one can break up the colony and conduct counts on different days at different quadrants around the colony to get a total abundance estimate. However, due to problems with the correction equation, the results may lead to over-or-under estimating the population. The bias in these estimates, may be reduced by conducting a mark-recapture or a mark-resight count at the same time in a small section and then use that information to adjust the Plumb *et al.* equation to better represent the area being studied. The corrected equation could then be applied to visual counts across the larger colony area.

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Table 3.1. Mark-recapture modeling using the closed capture with full heterogeneity model to estimate abundance.

Site	Season, Year	Model	Dev	K	AIC _c	Δ AIC _c	w_i
Bent's Old Fort	Sp 2010	m(bth) N	574.4	17	772.2	0.000	1.000
	Su 2010	m(bth) N	474.6	18	617.0	0.000	1.000
	Sp 2011	m(bth) N	416.3	17	549.8	0.000	0.867
		m(th) N	422.9	16	554.2	4.449	0.094
	Su 2011	m(bh)N	498.7	5	608.4	0.000	0.927
		m(bth) N	477.1	18	613.5	5.082	0.073
Fort Larned	Sp 2010	m(bth) N	270.5	16	383.7	0.000	0.930
		m(th) N	277.7	15	388.9	5.171	0.070
	Su 2010	m(bth) N	584.1	18	738.5	0.000	0.995
	Sp 2011	m(bth) N	277.1	16	389.1	0.000	0.941
		m(th) N	284.7	15	394.7	5.557	0.058
	Su 2011	m(bh)N	438.3	5	486.1	0.000	0.555
		m(bth) N	417.1	16	487.2	1.132	0.315
		m(th) N	421.0	15	489.0	2.914	0.129
	Scotts Bluff	Sp 2010	m(th) N	220.1	14	313.3	0.000
m(bth) N			219.2	15	314.5	1.196	0.352
Su 2010		m(bth) N	371.6	18	494.6	0.000	0.991
Sp 2011		m(bth) N	312.7	18	409.8	0.000	0.995
Su 2011		m(bth) N	207.6	16	307.3	0.000	0.909

^a Model factors included: . = constant, t = time, b = behavioral, h = heterogeneity, bh = additive model of behavior and heterogeneity

^b Model fit is described by the Deviance (Dev), number of parameters (K), and the difference in the Akaike Information Criterion from the best-fit model (Δ AIC_c). Models are presented that had moderate support (Akaike weight (w_i) >.05)

Table 3.2. Mark-resight modeling using the mark-resight model with logit-link to estimate abundance.

Site	Season, Year	Model	Dev	K	AIC _c	Δ AIC _c	w _i
Bent's Old Fort	Sp 2010	p(t) N(.)	3822.2	28	3878.8	0.000	1.000
	Su 2010	p(t) N(.)	1615.1	25	1666.1	0.000	1.000
	Sp 2011	p(t) N(.)	1452.4	28	1509.6	0.000	1.000
	Su 2011	p(t) N(.)	2395.8	28	2452.7	0.000	1.000
Fort Larned	Sp 2010	p(.t) N(.)	1737.9	4	1746.0	0.000	0.943
		p(t) N(.)	1700.8	25	1751.6	5.612	0.057
	Su 2010	p(.) N(.)	1738.0	2	1742.0	0.000	0.744
		p(.t) N(.)	1736.3	4	1744.3	2.355	0.229
	Sp 2011	p(t) N(.)	1560.5	25	1611.1	0.000	1.000
	Su 2011	p(.) N(.)	4125.9	2	4129.9	0.000	1.000
Scotts Bluff	Sp 2010	p(t) N(.)	1396.1	20	1436.8	0.000	1.000
	Su 2010	p(.) N(.)	1965.5	2	1969.5	0.000	0.848
		p(.t) N(.)	1965.0	4	1973.0	3.452	0.151
	Sp 2011	p(t) N(.)	634.5	18	671.2	0.000	1.000
	Su 2011	p(t) N(.)	1069.1	25	1119.9	0.000	0.954

^a Model factors included: . = constant, t = time, $.t$ = same between primary period but changes with time within primary periods,

^b Model fit is described by the Deviance (Dev), number of parameters (K), and the difference in the Akaike Information Criterion from the best-fit model (ΔAIC_c). Models are presented that had moderate support (Akaike weight (w_i) >.002)

Table 3.3. Comparison between four methods: minimum known number alive (MNKA), visual counts (VC), mark-recapture (MR) and mark-resight (MS) to estimate abundance of black-tailed prairie dogs.

	age/sex info	Cost (both financial and mortality risk)	Control for encounter rate (p)	Estimate using both marked and unmarked	Model Selection
MNKA	Y	\$	N	N	N
VC	N	\$	N	N	N
MR	Y	\$\$\$	Y	N	Y
MS	N	\$\$	Y	Y	Y

MNKA = minimum known number alive, VC = visual counts, MR = mark-recapture, MS = mark-resight

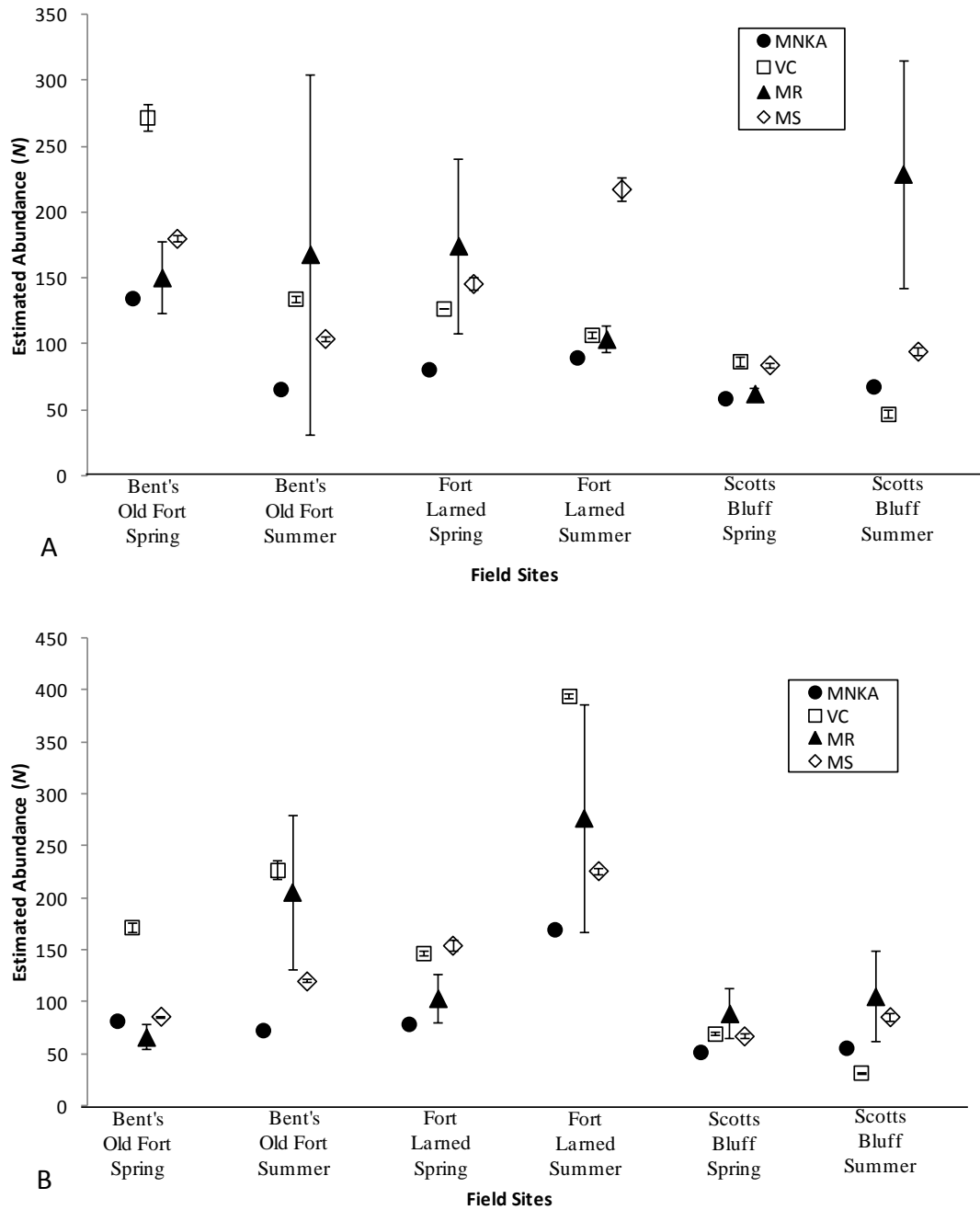


Figure 3.1. A comparison of estimated abundance (\pm SE) for black-tailed prairie dogs in 2010 (A) and 2011 (B) using four different methods: minimum number known alive (MNKA), visual counts with Severson and Plumb (2001) correction (VC), mark-recapture (MR), and mark-resight (MS) for each of the 4 ha study areas.

Chapter 4 - Intercolony and intracolony dispersal by black-tailed prairie dogs

Abstract

Little is known about dispersal in black-tailed prairie dog (*Cynomys ludovicianus*), which is both a keystone species and an agricultural pest. Dispersal may play an important role in stabilizing prairie dogs metapopulations through recolonization following poisoning or plague epizootics. Dispersal may also transmit plague from one colony to another through transfer of fleas infected with *Yersinia pestis*. Dispersal may result in establishment of prairie dogs onto private property where they are not welcome. We placed 149 VHF collars and 6 GPS collars on prairie dogs to document dispersal rates between 2009 and 2011 on three small National Parks. Collars were placed on a variety of age and sex classes to determine which groups were the most likely to disperse and to determine the frequency of dispersal. Prairie dogs were also trapped and observed on each of the three sites to study frequency of intracolony dispersal. We found 23 intracolony and eight intercolony dispersal events. The GPS collars documented extra-coterie movements by all of the collared individuals. Young males were the most likely intracolony. Yearling males and females and adult females were the most likely to disperse off the colony (intercolony dispersal).

Introduction

Dispersal has been defined in two major categories: (1) natal dispersal - movement by an individual from its natal site to another area permanently (Bekoff 1977; Gaines and McClenaghan 1980; Garrett et al. 1982) and (2) breeding dispersal – movement between two breeding areas (Bekoff 1977; Clobert et al. 2001). It is also possible to have a combination of the two (Stenseth and Lidicker 1992a). There are a number of reasons that an animal may choose to disperse, such as to avoid inbreeding and increase heterozygosity (Gaines and McClenaghan 1980; Gandon and Michalakis 2001; Lidicker 1962; Stenseth and Lidicker 1992b); to gain diplomatic advantage – animals that avoid involvement in a population crash by dispersing from a congested area to another where they have a higher chance of survival than those who do not disperse (Lidicker 1962); in response to density (Gaines and McClenaghan 1980; Knowles 1985; Lidicker 1962; Stenseth and Lidicker 1992b), change in body mass (Nunes

and Holekamp 1996), and/or due to genetic predisposition to disperse (Gaines and McClenaghan 1980; Garrett and Franklin 1988). All of these reasons have previously been used to explain why sciurids, in particular, disperse (Dobson and Jones 1985; Garrett and Franklin 1988; Halpin 1987; Sherman and Morton 1984). However, there is still little known about the causes and frequency of dispersal in black-tailed prairie dogs (*Cynomys ludovicianus*).

Black-tailed prairie dogs are diurnal, colonial, ground-dwelling sciurids (Hoogland 1995; Manno et al. 2007). Within colonies, prairie dogs live in territorial family groups called coterie (Dobson et al. 1997; Hoogland 1995; King 1955). A coterie can contain between 1 and 26 yearlings and adults (Hoogland 1995, 2006; King 1955). The physical area of a coterie can range in size and usually more members, the larger the area of the coterie. Most coterie contain one breeding adult male, three or four adult females, and several nonbreeding yearlings and juveniles (Hoogland 1995).

Black-tailed prairie dog dispersal is of great interest because the species is considered both a keystone species and an agricultural pest (Cully and Williams 2001; Hansen and Gold 1977; Hanson et al. 2007; Kotliar et al. 2006). Furthermore, the percent of occupied habitat has decreased from a historical high of 31.85 million hectares of habitat to today's estimate of 0.97 million hectares (USFWS 2009) which is a loss of approximately 97%. The loss of occupied habitat is thought to be due to an increase in pest control, habitat conversion from grassland to cropland, and the introduction of the exotic disease, sylvatic plague, caused by *Yersinia pestis* (Cully and Williams 2001; Miller and Cully Jr. 2001). Plague, which was introduced into North America around 1900 from Asia (Adjemian et al. 2007; Gage and Kosoy 2005) causes nearly 100% mortality in black-tailed prairie dogs during an epizootic (Collinge et al. 2005; Cully and Williams 2001; Seery et al. 2003). *Yersinia pestis* is spread to prairie dogs through fleas (Cully and Williams 2001; Gage and Kosoy 2005; Wilder et al. 2008). Dispersal may play a role in the movement of plague infected fleas from colony to colony (Collinge et al. 2005; Gage and Kosoy 2005; Hoogland 2006; Jones et al. 2011; Slobodchikoff et al. 2009). Plague-positive colonies tend to be closer to other plague-positive colonies whereas more isolated colonies, were plague free (Augustine et al. 2008; Collinge et al. 2005; Cully and Williams 2001; Johnson and Collinge 2004). Plagues potential effects on isolation of colonies suggests that the plague positive fleas were not being dispersed to the more isolated colonies (Jones et al. 2011).

Prairie dog dispersal also needs to be better understood to manage populations adjacent to private land, where prairie dogs are often considered pests. The more we know about where prairie dogs are most likely to go, why they disperse, and the frequency with which dispersal occurs, the more likely we will be able to control prairie dog movement and colonization. It might be possible to control movement through the use of visual barriers such as straw bales and vinyl sheeting (Gray 2009). At the same time, dispersal might be facilitated towards a singular direction by mowing or burning (Augustine et al. 2007; Northcott et al. 2008).

For the remainder of this paper, dispersal is defined as movement of a prairie dog from its natal home range to establish a new permanent home range. A new home range can be either intracolony dispersal, which is movement from the natal coterie to another coterie within the colony, or intercolony dispersal, which is movement to another colony (Halpin 1987). Previous studies have shown that both males and females of different age classes disperse (Garrett and Franklin 1988; Halpin 1987; Knowles 1985). Genetic studies also show that colonies close together exchange individuals regularly (Antolin et al. 2006; Jones et al. 2011; Roach et al. 2001).

The objectives of this study were: (1) to determine the frequency of dispersal, (2) to identify which age and sex classes were most likely to disperse, (3) to compare frequency of intracolony versus intercolony dispersal, and (4) to identify characteristics of sites to which prairie dogs disperse.

Materials and Methods

Study area

Our study was conducted at three small National Parks: (1) Fort Larned National Historic Site, KS; (2) Scotts Bluff National Monument, NE; and (3) Bent's Old Fort National Historic Site, CO. Recreational shooting of prairie dogs was banned at all three National Park sites and all lie within an agricultural matrix. Within each park's colony, a four hectare (ha) study area was established and used for these comparisons. See below for a description of trapping and handling protocols. The colony at Bent's Old Fort was in short-grass prairie whereas Scotts Bluff and Fort Larned were each in mixed-grass prairie. The terrain of the colony at Bent's Old Fort was flat, and the vegetation was dominated by bindweed (*Convolvulus arvensis*) which is a low growing plant. The Scotts Bluff colony was located on hilly terrain with the highest point

located on the southern end. Approximately 40% of the study area was used by black-tailed prairie dogs. The remaining 60% was dominated by tall vegetation of summer cyprus (*Kochia scoparia*), sweet clover (*Melilotus officinalis*), and smaller amount of other forbs. The colony at Fort Larned was on relatively flat topography with small dips throughout the colony caused by historical Santa Fe Trail ruts. Based on observation, the Fort Larned site had the highest plant species diversity of the three sites. Both bindweed and summer cypress were found there, but there were also many grasses such as western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), big bluestem (*Andropogon gerardii*), three-awn (*Aristida oligantha*), and buffalo grass (*Buchloe dactyloides*).

Trapping

The study was conducted from 2009 to 2011 with two trapping occasions conducted each year, one during the spring (April/May) and the other during the summer (July/August). Each trapping occasion lasted between 4 and 14 days. We trapped in the spring in attempt to capture yearlings before the juveniles emerged for the year, but this was not always possible. Prairie dogs were live-trapped using single door collapsible Tomahawk live traps (either 16-in x 5-in x 5-in or 19-in x 6-in x 6-in; Hazelhurst, WI) that were placed on a 2.25 ha plot with a 10 by 10 staked grid in the middle of a 4 ha boundary. Each grid contained 100 traps, each of which was placed at one stake. Up to an extra 40 traps were added during the 2010 and 2011 trapping season in areas saturated with prairie dogs. By adding extra traps, we hoped to reduce the chance that some prairie dogs were being excluded from traps by trap-happy individuals who always entered traps soon after they were set.

Prairie dogs were permanently marked using 12.50mm X 2.07mm pit tags (Biomark Inc, Boise, ID) and dye-marked using blue-black Clairol hair dye. The hair dye only lasted as a marking for a single trapping occasion (about two weeks), whereas the pit tag was expected to last for the duration of the study. Each animal was sexed (male or female) based on external genitalia and aged as either an adult or a juvenile based on body size. After an animal was pit-tagged and dye-marked with a unique number and released, the burrow that it ran to was also marked in an effort to identify coterie boundaries. Each subsequent time a prairie dog was captured, the location was noted and the animal was released.

Radio telemetry

For three years of the study, 149 VHF collars (Wildlife Materials, IL) and six GPS collars (Telemetry Solutions, CA) were put out on prairie dogs. Wildlife Materials collars weighed approximately 22 grams whereas the Telemetry Solutions collars weighed approximately 35 grams which is less than 5% of the body weight of the selected yearling males, and should not have interfered with their normal activities (Corner and Pearson 1972). Collars were put out during the spring trapping season before what was thought to be the most likely period of the year for dispersal, following juvenile emergence (Garrett and Franklin 1988, Hoogland 1995). In 2009, our goal was to put collars on an equal number of male and female adults that weighed at least 500 grams. Starting in 2010, we added a second age class of known yearlings (those trapped as juveniles in 2009) and again collared equal numbers of males and females across the two age classes of adults and yearlings. In 2011, we added a third age class of known two-year olds. We tried to distributed collars equally among the age and sex classes as well as increase the number of collars distributed at each colony. However, due to a limited number of two-year olds, this was not always possible (Table 4.1). Two GPS collars were put out in 2010, and four in 2011, at Scotts Bluff. GPS collars were only deployed at Scotts Bluff because the soil type there appeared to contain more sand which allowed signals to be heard when the collars were underground. The ability to receive a signal from collars underground, increased our chances of retrieving collars if the animals died underground.

Throughout the period between trapping sessions, collared prairie dogs were monitored using a three-element folding Yagi antenna at least once every two weeks in 2010 and 2011. Due to a smaller number of personnel in 2009, collars were not monitored as frequently. Starting in 2010, prairie dogs were triangulated to determine their relative location on the colony and to monitor them to identify permanent shifts in home range. Dead or dispersed prairie dogs were searched for both on foot and from a vehicle throughout a 12 km buffer. The buffer distance was established based on the literature, This distance was the farthest that a prairie dog would disperse (Garrett and Franklin 1988). Collars were retrieved from dead prairie dogs and GPS coordinates were recorded. Dispersed prairie dogs were trapped and collars removed during the summer trapping session and GPS coordinates were also recorded.

We attempted to remove all collars during the summer trapping session. There were a few instances when we made visual sightings of collared prairie dogs on the colony but were

unable to re-trap the animals and remove their collars. Occasionally, they were trapped the following year and the collars were then removed. GPS collars were removed and the data were then uploaded to a computer. Our trapping protocol was approved (Approval No. 2994) by the Institutional Animal Care and Use Committee at Kansas State University. We also followed the guidelines of the American Society of Mammalogists for the use of live mammals in research (Sikes et al. 2010).

Coterie boundaries were estimated using minimum convex polygons (MCPs) (Mohr 1947) generated by Home Range Tools for ArcGIS (Rodger et al. 2007). We chose to use 95% MCPs to exclude any exploratory movements (forays into other coterie) by prairie dogs.

Observations

During the trapping sessions beginning in 2010, we observed prairie dogs from 4 m tall deer stands that were located just outside the four hectare study area. Two observers with a variable power 15-45 X 60 spotting scope mounted with a window mount to the stand frame watched dye-marked prairie dogs and noted their location on the grid using the marked stakes as locations. We were able to distinguish relative boundaries of the coterie within the colony and watch for intracolony dispersal using a similar method to Newby (2005). We kept records of both aggressive (fighting, bluff charges, and so forth) and amicable (kissing, grooming, and so forth) interactions between prairie dogs to further help establish coterie boundaries. Amicable interactions were a good indicator that both animals were located within the coterie boundaries whereas aggressive behavior could indicate a border area or an intrusion. By combining both observational data and trapping data, we were able to document intracolony dispersal of marked prairie dogs that were not collared both during the summer (April – August) and winter (August – April).

Results

Of 155 prairie dogs with either GPS or VHF collars, 8 were documented as intercolony dispersers, 4 as intracolony dispersers, 28 were missing, 12 were found dead, and the remaining 103 did not disperse (Table 4.1). All intercolony dispersal that we documented occurred in the months of May and June. Yearling males had the highest rate of intercolony dispersal followed by adult females. The highest number of dispersing collared prairie dogs at all three sites occurred in 2010 (Table 4.2). Scotts Bluff was the only site where the collars of dead prairie

dogs could be heard underground and thus it had the highest percentage of dead prairie dogs. However, when dead prairie dogs are combined with missing both Bent's Old Fort in 2010 and Scotts Bluff in 2011 had higher percentages (Table 4.3).

Our longest known dispersal distance was ~ three kilometers. This was accomplished by a yearling male at Scotts Bluff. He was resighted on a small colony on private land, but by the time we returned to trap him in June, the landowner reported that he may have shot him. There were three prairie dogs that dispersed within the Scotts Bluff colony system, which was made up of small colonies distributed in patches. These prairie dogs all dispersed less than 500 meters but had to travel through tall vegetation with no burrows to hide in. In 2011, the park attempted a controlled burn on the colony but only burned small patches of vegetation. A female yearling made the trip to a burned patch, which is a common occurrence for prairie dogs (Augustine et al. 2007; Milne-Laux and Sweitzer 2006; Northcott et al. 2008). However, by the end of July, the prairie dog was missing and presumed dead. An adult female also dispersed about 400 meters, but she too was dead by June when we found her in a burrow. She was also trapped earlier in May on the other side of the trapping grid from her coterie, perhaps scouting out her final dispersal trip. There was one successful dispersal event, which was a yearling male who moved ~415 meters and was trapped there at the end of July. The longest distance that a collar was found was at Fort Larned, where a male yearling's collar was found in the middle of a corn field 6.7 km from the colony. Whether the prairie dog dispersed and then died or was carried there by a predator could not be determined. The two prairie dogs at Fort Larned that dispersed, an adult male and female, were assumed dead at the edge of a wheat field when their collars were found. We suspect they died after harvesting occurred as signals were active during the day but disappeared at night (when they should be in a burrow) prior to harvest. A burrow was located near where we detected their signal. Bent's Old Fort had two dispersers, one in 2010, which was a yearling male and one 2011, which was a yearling female. We were never able to locate them exactly, though they appeared to be on private land on a large colony about five to six km away from the Bent's Old Fort colony. They were both alive until the last week of June, when we heard their collars. However after the July 4th weekend, when we returned to trap them, the signals were gone and we presumed they died.

Of the six GPS collars, five were retrieved and their data recovered. Using 95% MCP estimates of the coterie range, all five of the yearling males had at least one short-distance

movement event outside of their coterie (Figure 4.1). Each time they left the coterie, they returned within a day to their natal coterie. One of these events occurred in early May but the majority occurred between June and August, after the peak of yearling dispersal.

Of the total collared prairie dogs, yearling males (9.38%, $n=3$) and females (9.09%, $n=2$) were the most common intercolony dispersers (Table 4.4). For intracolony dispersal, adult females (3.92%), yearling females (4.55%) and yearling males (3.13%) were the most likely to disperse between April and August. Two-year old males and females were the least likely to disperse either within or between colonies (0.00%). It should be noted, that all the two-year old males collared had undergone intracolony dispersal or fission of their natal coterie prior to being collared.

From trapping and observational data, we identified an additional 23 intracolony dispersal events but we could not determine the time of year when the dispersal event occurred for two of them because individuals were not trapped every session. Of the 21 events where the time of dispersal was known, 55% occurred during the summer between April and July whereas 41% occurred during the winter between August and April (Table 4.5). Both male yearlings and female adults made up the majority of summer intracolony dispersal ($n=9$) whereas male yearling prairie dogs were the majority over the winter ($n=7$). Bent's Old Fort also had the highest percentage of total intracolony dispersal of prairie dogs based on both observation and collar data, regardless of season (43%). However, Scotts Bluff had the highest in the summer (21%) whereas Bent's Old Fort was highest during the winter (26%).

Discussion

Prairie dog dispersal is not well studied and only a few studies have attempted to look at it directly. These studies documented that dispersal usually occurs from May through June or during the winter (Garrett and Franklin 1988; Knowles 1985). These reports suggest that yearling males and adult females are the most likely to disperse (Garrett and Franklin 1988; Jones et al. 2011; Knowles 1985). However, these studies have looked at dispersal either as prairie dogs immigrating into the colony or by finding prairie dogs en route. Both these methods are biased because by only looking at immigration, one still has no idea of the number of prairie dogs that attempt to disperse. By only looking at prairie dogs found en route, one is sure to miss a number of prairie dogs that attempted to disperse or were killed enroute. Our study was

designed to identify the proportion of age and sex classes of prairie dogs on a colony that disperse, where they go, and how successful they are.

Across our three colonies, we found that approximately 5.0% of all collared prairie dogs dispersed between colonies (intercolony dispersal) and 3.0% dispersed within the colony (intracolony dispersal) during summer. There were differences among age and sex classes. For example, none of our two-yr olds dispersed during summer, when our collars were monitored, however, this was based on a small sample size of two-year olds ($n = 11$). We did not expect to see two-year old females dispersing, as they are expected to be breeding in their natal coterie and are strong enough to compete with other females for access to males. Two-year old males on the other hand, are expected to disperse if they are still in their natal coterie, to avoid inbreeding (Hoogland 1982). Based on our trapping data, it appears that all our collared male two-year old prairie dogs at Bent's Old Fort had already undergone intracolony dispersal to a nearby coterie as yearlings, most likely over the previous winter. Our collared two-year old male at Fort Larned appeared to have made a new coterie through territorial fission. In this case, our two-year old males were not expected to have dispersed again because they had already moved away from close female relatives.

Yearlings, both males and females, had the highest rate of dispersal, which would be expected if breeding was the primary motivation for dispersal. Previous studies show that most male black-tailed prairie dogs leave the coterie, undergoing natal dispersal just before they reach sexual maturity (Hoogland 1995). The heterozygosity of a yearling males offspring will increase if they leave their natal coterie. By leaving, the yearling males avoid breeding with their mother and sisters as well as physically compete with their fathers (Foltz and Hoogland 1983). Yearling females that leave their natal coterie, may gain access to a breeding male who is both not their father and will also not have to compete for breeding access and other resources with their mothers.

Adult prairie dogs may also disperse away from their coterie for a number of reasons. With an increase in density, comes an increase in intraspecific competition over resources. This can lead to an increase in aggression and drive dispersal (Gaines and McClenaghan 1980). If the prairie dog disperses to an expanding colony (one with low density), there will be less competition for resources, and fitness may increase over that if he remains at home. Population dynamics tend to be different in expanding colonies with larger litters, faster juvenile growth

rates and a higher likelihood of mating as a yearling (Cully 1997; Hoogland 2006). However, there is little evidence to support that change in density is a cause for dispersal (Newby 2005) but further studies need to be conducted.

Most breeding males do not survive longer than two consecutive years in a coterie. This may be because they die either from predation or fighting with another male over a coterie. Knowles (1985) found that half the male prairie dogs that dispersed long distance had recent bite wounds showing that they were recently in fights with other male or female prairie dogs. Fighting increases the chances for adult male deaths, which we may not have been able to detect due to our inability to find prairie dogs underground.

Other prairie dogs disperse for reasons that are not clear. One possibility is that after two years, a breeding male's daughters will become sexually mature. By leaving as yearlings, females may avoid inbreeding (Hoogland 1995). According to our data, yearling females are just as likely to disperse as yearling males (Table 4.4). We also saw that many adult female prairie dogs disperse (Table 4.1, 4.4). Adult females may leave a coterie because they no longer have as high a reproductive value as younger females and are outcompeted for resources or mates. Especially during the breeding season, when females become pregnant, they become very territorial of their natal burrow, and older females may no longer be able to out-compete younger prairie dogs. This could be a reason for females to disperse to another colony where density is lower.

Knowles (1985) saw many more dispersing black-tailed prairie dogs during 1979, which was a drought year following a record year of precipitation in Montana. He believed that this increase in dispersal could have resulted from a need to balance population numbers with the availability of resources. Nunes and Holekamp (1996) looked at body mass and fat and its influences on timing of natal dispersal in Belding's ground squirrels (*Urocitellus beldingi*). They found that ground squirrels with lighter weights, dispersed later than heavier ones. Intercolonial dispersers are more vulnerable to predation and it takes a lot of energy to move long distances. Thus, a certain level of fat reserves may be needed to stimulate long distance dispersal. Perhaps, this is true for prairie dogs as well and needs to be explored further.

Regardless of age, prairie dogs may choose to disperse to another colony during a plague epizootic (Jones et al. 2011). Jones et al. (2011) suggest that prairie dogs may choose to emigrate from a small declining population to a larger one in order to increase the amount of

social contact. Prairie dogs are social animals and their colonial system aides in the detection of and protection from predators. The dangerous journey to another colony may be worth the risk for the added benefit of breeding access and predator protection.

Whereas a few studies have found large numbers of dispersing animals in one season (Antolin et al. 2006; Knowles 1985), we did not. It should be noted that those studies with higher rates of dispersal (Garrett and Franklin 1988; Halpin 1987; Knowles 1985), used prairie dogs that were already en route or had immigrated onto their study sites. To our knowledge, we collared a larger number of prairie dogs than previous studies. The study that is closest to ours in both size and sampling was conducted by Newby (2005) at Badlands National Park, South Dakota. She collared male yearlings and also found low rates of dispersal. We had an advantage over her study in that we could find most of the prairie dogs that died with collars at Scotts Bluff. This helped us determine whether collars were really lost or just on animals that died in burrows.

Based on our results, we found that most intercolony dispersing prairie dogs moved to other established colonies with the exception of the two prairie dogs at Fort Larned which moved to a wheatfield. Furthermore, Fort Larned is a highly isolated colony, with no close neighboring prairie dog colonies, which may have affected the rate of dispersal there. The nearest prairie dog colony to this one, was approximately 14 km away, which is outside of the documented range of dispersal by black-tailed prairie dogs (Garrett and Franklin 1988).

With GPS collars, we recorded daily movements of 5 yearling male prairie dogs. Almost nothing is known about when a prairie dog decides to disperse or if they partake in exploratory trips to locate destination sites, as do Florida Scrub Jays (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1984). Whereas none of our GPS-collared prairie dogs dispersed, four out of the five collared prairie dogs took short trips for a day outside of their coterie (Figure 4.1). Reasons for these exploratory movements are unknown, but future work using GPS collars could potentially shed light on this behavior. It is interesting to note that one prairie dog (Figure 4.1d), appears to have created a new coterie using fission. As a juvenile, he was observed alongside prairie dogs found on the coterie next to the one established by data from his GPS collar. It appears that over the course of May-August, his coterie expanded eastward while maintaining his boundary on the western side. Perhaps, the other GPS collared prairie dogs will disperse over the fall or winter. Return rates for yearling male prairie dogs over the winter is

quite low and perhaps we have just missed an important period of time for dispersal within this age class.

Genetic studies conducted on black-tailed prairie dogs, have shown that there is movement between colonies (Antolin et al. 2006; Jones et al. 2011; Roach et al. 2001). Whereas mixing is uncommon between distant colonies (more than 80 km), genetics studies have shown that mixing is definitely occurring in colonies that are nearer to one another (less than 80 km). Dispersal can play an important role in management of black-tailed prairie dogs in terms of re-colonization of dead colonies, and spread of *Y. pestis* infected fleas between colonies. Furthermore, understanding when and where dispersal onto private land is most likely to occur may lead to new management insights and implement actions to facilitate movement towards other colonies on public land and away from private land.

During the experiment, we found that less than 10% of each age class with collars dispersed over a long distance. Furthermore, only 62.5% or 5 prairie dogs moved onto private land. Of those 5 prairie dogs, 3 moved onto established colonies and we suspect died from pest management/shooting. The only successful intercolony dispersal event was a prairie dog that stayed on national park land. Consequently, successful movement of prairie dogs from public to private land is very low and most successful movements of prairie dogs are intracolony dispersal events.

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Table 4.1. Number of collared prairie dogs at Fort Larned, Scotts Bluff, and Bent's Old Fort combined from 2009-2011 field seasons.

		intercolony dispersal	intracolony dispersal	dead/missing	stayed on colony	total # collared
yearlings	males	3	1	11	17	32
	females	2	1	6	13	22
two-year olds	males	0	0	0	5	5
	females	0	0	2	4	6
adults	males	1	0	7	31	39
	females	2	2	14	33	51
total		8	4	40	103	155

Table 4.2. Results of collars from all three years of the study. Study sites were all combined.

		2009		2010		2011	
		intercolony dispersal	intracolony dispersal	intercolony dispersal	intracolony dispersal	intercolony dispersal	intracolony dispersal
yearlings	males	0	0	2	0	1	1
	females	0	0	1	1	1	0
two-year olds	males	0	0	0	0	0	0
	females	0	0	0	0	0	0
adults	males	0	0	1	0	0	0
	females	0	0	2	2	0	0
totals	males	0	0	3	0	1	1
	females	0	0	3	3	1	0

Table 4.3. Number of black-tailed prairie dogs at each field site for every year of the study that died before dispersal or went missing.

			2009		2010		2011	
			dead	missing	dead	missing	dead	missing
Fort Larned	yearlings	males	-	-		2	1	
		females	-	-				
	two year olds	males	-	-	-	-		
		females	-	-	-	-		2
	adults	males		1		1		
		females		1				1
	percentage		0.00%	12.50%	0.00%	18.75%	10.53%	10.53%
percentage combined			12.50%		18.75%		21.05%	
Scotts Bluff	yearlings	males		2			2	2
		females	-	-			1	2
	two year olds	males	-	-	-	-		
		females	-	-	-	-		
	adults	males		0			1	1
		females		2			1	
	percentage		0.00%	25.00%	0.00%	0.00%	21.74%	21.74%
percentage combined			25.00%		0.00%		43.48%	
Bent's Old Fort	yearlings	males		2		1		
		females	-	-		2		1
	two year olds	males	-	-	-	-		
		females	-	-	-	-		
	adults	males			1			
		females		3		3	1	1
	percentage		0.00%	31.25%	6.25%	37.50%	5.88%	11.76%
percentage combined			31.25%		43.75%		17.65%	

Table 4.4. Percent of results of collars for each age and sex class for all sites and all years combined.

		% stayed on colony	% dead	% dispersed (intra or inter)	% intercolony dispersal	% intracolony dispersal
yearlings	males	53.1%	37.5%	12.5%	9.4%	3.1%
	females	59.1%	27.3%	13.6%	9.1%	4.6%
two-year olds	males	100.0%	0.0%	0.0%	0.0%	0.0%
	females	66.7%	33.3%	0.0%	0.0%	0.0%
adults	males	79.5%	12.8%	2.6%	2.6%	0.0%
	females	64.7%	25.5%	7.8%	3.9%	3.9%

Table 4.5. Intracolony dispersal of black-tailed prairie dogs at each site for each season. Winter is the time between July/August trapping and April/May trapping. Summer is the time between April/May trapping and July/August trapping. Percentage = seasonal percentage of total intracolony dispersed prairie dogs. One prairie dog season of dispersal could not be determined leaving the total percentage of dispersal less than 100%.

	winter					summer				
	Female Juvenile	Female Adult	Male Juvenile	Male Two-year Old	Male Adult	Female Yearling	Female Adult	Male Yearling	Male Two-year Old	Male Adult
Fort Larned			1	1			1	2		1
Scotts Bluff			5							
Bent's Old Fort			1		1	2	3	3		
Total			7	1	1	2	4	5		1
Percentage			40.91%					54.55%		

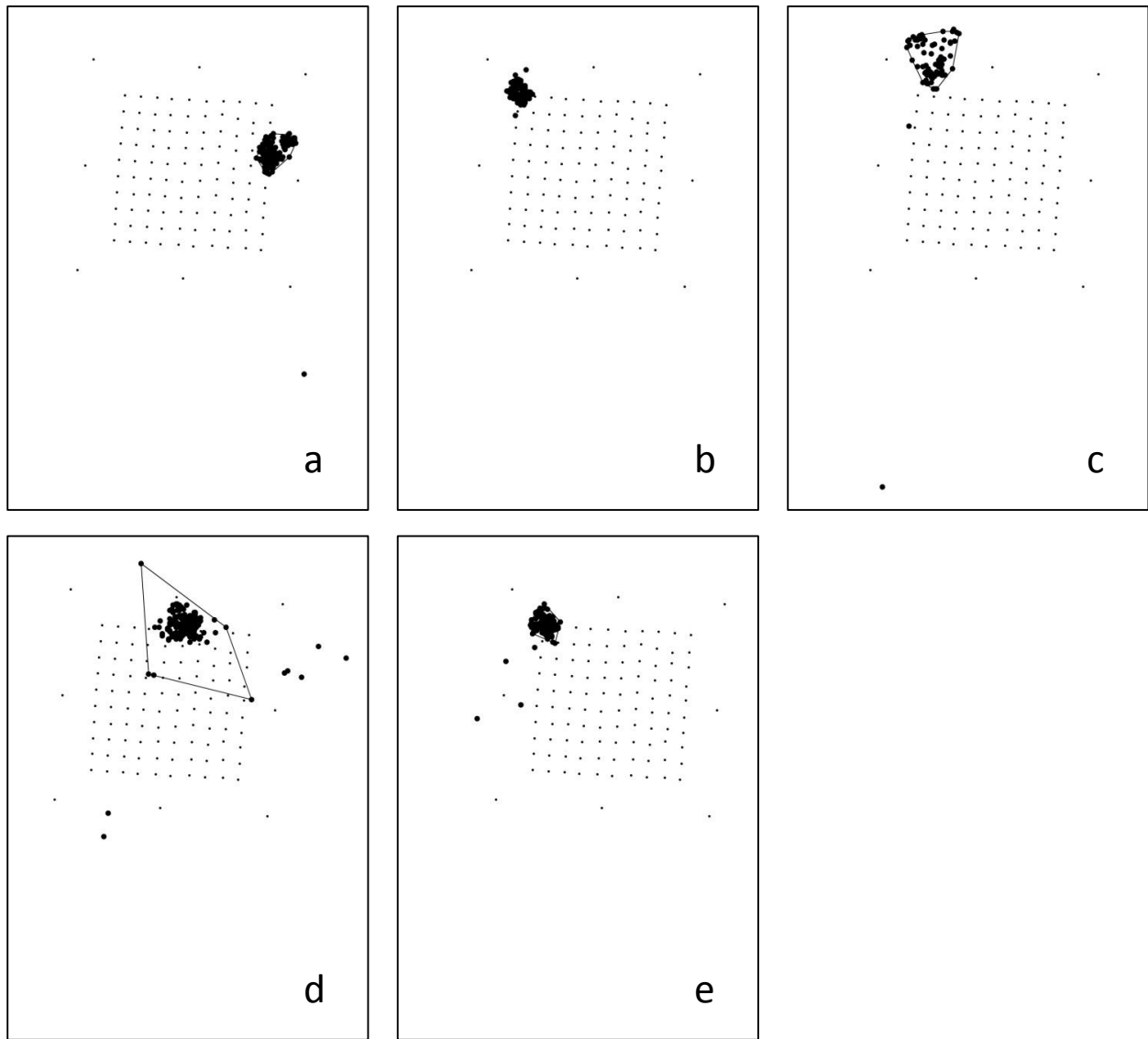


Figure 4.1. GPS collar locations for the five yearling male prairie dogs located at Scotts Bluff National Monument. Outer square of 8 small points represents a 4ha area with the 2.25ha trapping grid (100 points) inside. Collars b and e) were from 2010 and collars a, c and d) were from 2011. MCP (95%) estimates are shown as a polygon around the prairie dog coterie. All points outside the edge of the polygon are considered exploratory movements.

Chapter 5 - Conclusions

Information about black-tailed prairie dog survival, abundance, and dispersal is important in order to manage populations for both conservation and management. Conservation of black-tailed prairie dogs is important as the species is a keystone species in the short and mixed-grass prairie ecosystem (Kotliar et al. 2006). Furthermore, it currently occupies ~3% of its historical habitat (USFWS 2009). There is a strong need to have good information on prairie dog populations so that they can be managed effectively for both conservation and pest-control. Furthermore, prairie dogs are highly susceptible to plague caused by the bacterium *Yersinia pestis*. Little is known about how plague moves between colonies of prairie dogs, so further information about dispersal may aide in our understanding of the disease. Information on survival rates also can aide in management and conservation of prairie dogs through the knowledge of what factors affect prairie dog survival rates. Once these factors are understood, we may be able to better manipulate populations into either higher survival rates or lower depending on the goals of the manager. As we develop better protocols for assessing population abundance it will be easier to identify trends and we will be able to effectively communicate with land managers and decide if abundance is great enough for re-introduction of the black-footed ferret (Biggins 2005) or needs to be culled in order to keep the population at a sustainable size.

Through the use of the robust design model in program MARK (Kendall 2010) and RMark (Laake and Rexstad 2008), we found that apparent survival rates differed between seasons and sites. Estimated apparent yearly survival rates indicate disease may be a factor in lower survival rates at sites where plague is known to occur. Longer survival rates potentially allow prairie dogs to have higher fecundity, which should result in a larger population size. Prairie dogs only reproduce one time per year (Hoogland 1995) and yearling females do not always reproduce, so females need to live multiple years if they are going to reproduce enough to keep the population steady or increase it.

Survival rates are an important measurement to have in order to begin to understand what effects growth of a colony. However, not every colony can be monitored that intensively over a long period of time. Most land managers are interested in estimates of abundance to easily assess whether the population of prairie dogs is stable. We were able to compare four different methods for estimating abundance and found that no one single method is the absolute best. We

encourage land managers who want to track or estimate abundances of prairie dogs over time, think about both the sites topography and height of vegetation on the colony before choosing which technique to incorporate into their management plan. If the colony is on very flat ground with little to no tall vegetation (everything is easily visible), then visual counts using the method describe by Plumb et al. (2001) may be the most cost-and-time effective technique. However, if sight lines are not good, a mark-resight visual count (Magle et al. 2007; McClintock 2010) may return a more consistently precise count. Land managers should also take into account how precise counts need to be before choosing the most appropriate method. Mark resight was the most precise method we studied, however if additional information on demography is needed, mark-recapture provides the most complete information. Also, if change in population size is the only thing that matters, and the vegetation stays the same throughout the years, a visual count may be all that is needed since it will be equally as problematic each year resulting in an precise estimate of change in density over the study period.

In order to know if our estimates of apparent survival are influenced by site-fidelity, we need to increase our knowledge about the rate of prairie dog dispersal. Using both radio-collars and observational data, we found that prairie dogs do disperse. However, the rate of intercolony dispersal appears to be lower than 10% suggesting that site-fidelity is not heavily influencing our estimate of apparent survival. However, we found that intracolony dispersal and exploratory movements occurred throughout the year, which provides a potential mechanism for fleas and plague to be exchanged between coterries. Furthermore, intercolony dispersal also occurs, which is also a potential route for the spread of plague between colonies but also may play an important role in re-colonization of dead colonies after an epizootic.

We hope that future research will be conducted regarding both rates of dispersal and survival of black-tailed prairie dogs. The more we know about prairie dog movement both within and between colonies the more we can learn about potential ways that plague infected fleas are moved among colonies. We can also know whether our survival models are underestimating survival due to dispersed prairie dogs being incorrectly counted as dead. More work could be done comparing towns isolated like the ones in this study to towns located in larger complexes found on many of the National Grasslands and National Parks. Also, through manipulative or long term studies, we could learn more about whether dispersal is density or energy dependent. Still unanswered questions include, do prairie dogs participate in intercolony

dispersal more often during good vegetative growth or when space and access to mates becomes increasingly difficult? More research also needs to be done on seasonal aspects of dispersal, particularly between August and April. We found that many marked yearling males disappeared sometime during this period and we do not know if they died or dispersed. With the use of GPS collars it should also be possible to analyze daily movement patterns of prairie dogs and track their dispersal routes. Through observations and genetic studies we know that prairie dogs disperse between colonies, but we do not know the routes they take to get from point A to point B. With increased knowledge about prairie dogs dispersal routes, we may be better able to facilitate or inhibit prairie dog dispersal between particular colonies. Future studies should also aim to study the causes for differences in survival rate between sites used in this study and others. By measuring forage quality at different sites across years, one would be able to analyze how forage quality affects survival. We also hope that with improved techniques to detect plague, we will be able to know with confidence whether plague occurs in an enzootic fashion on prairie dog towns and whether disease leads to lower survivorship. Another way plague's influence on prairie dog colonies could be studied is by comparing paired sites, one with a form of plague control and the other with nothing. If the control (no treatment) sites have lower survival rates (but no plague epizootics), assuming all other factors are equal, then enzootic plague is a very possible explanation for the difference. Fleas can be controlled using powdered 0.05% deltamethrin formulation (DeltaDust, BayerEnvironmentalScience, Research Triangle Park, NC) which in effect controls for plague (Biggins et al. 2010; Seery et al. 2003). Currently trials are being conducted on a recombinant raccoon poxvirus (RCN) expressing plague antigens (Rocke et al. 2010), which potentially will prevent plague from killing prairie dogs. This vaccine has great potential to be much more easily distributed and may prove to be an excellent tool in understanding the dynamics of plague.

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