Range-Wide Monitoring
of
Black-Tailed Prairie Dogs in the United States:
Pilot Study

Prepared for
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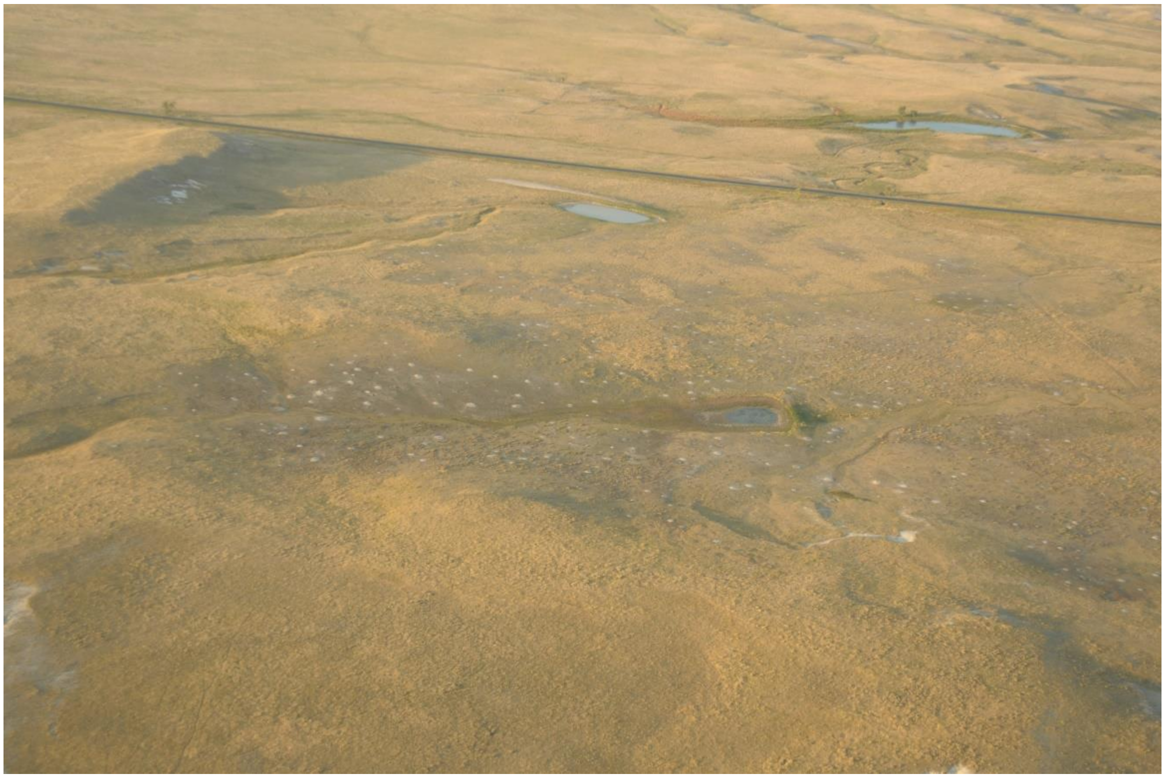

Photo by John Sidle

Glossary of Abbreviations

BAS	Balanced Acceptance Sampling
BLM	Bureau of Land Management
BTPD	Black-tailed prairie dog
GIS	Geographic Information System
NAD	North American datum
NAIP	National Agriculture Imagery Program
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
WAFWA	Western Association of Fish and Wildlife Agencies
WEST	Western EcoSystems Technology Inc.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

We surveyed the latest available National Agriculture Imagery Program (NAIP) images within the current range of black-tailed prairie dog (BTPD, *Cynomys ludovicianus*) colonies in a pilot study to estimate the current extent of apparent BTPD colonies. We estimated the range-wide extent of apparent BTPD colonies on the latest NAIP images for each of 11 states and on lands managed by the Bureau of Land Management (BLM) in Part 1. Western EcoSystems Technology, Inc. (WEST, Inc.) was contracted by the Western Association of Fish and Wildlife Agencies (WAFWA) in a separate project to estimate the extent of apparent BTPD colonies in Wyoming using a census of land units containing BTPD habitat in Wyoming. We gave results for the census in Wyoming and sample surveys for BLM Land and the other 10 states in Part 2. Apparent BTPD colonies that were potential active or inactive BTPD colonies were digitized and delineated in a Graphical Information System (GIS). Apparent BTPD colonies were called "features" for brevity.

Our primary objective was to provide estimates of total acres of all features in the sampling frame of survey units for each state with confidence intervals on estimates. Estimates were corrected for features missed (false negatives) as determined by the use of independent observers on a subset of survey units. Objectives also included estimation of the number of features in each state, the number that were greater than 1,000 acres and the number that were greater than 5,000 acres. In Wyoming, we digitized features on a census of BTPD habitat units in the state and corrected the estimates of total acreage for false negatives. In addition, aerial and ground surveys were conducted in Wyoming to correct estimates for false positives (i.e., digitized features that were not active or inactive BTPD colonies).

We estimated sample sizes necessary to achieve acceptable levels of precision (for example, coefficients of variation less than 15 %) and recommended long term monitoring methods for acreage and abundance of potential BTPD colonies in each state, on BLM managed lands, and range-wide in 11 states based on sample surveys of habitat units.

Objectives included preparation of GIS shapefiles and digital map products showing digitized features, representing potential back-tailed prairie dog (BTPD) colonies associated with 2 mile by 2 mile grid cells in a probabilistic sample of at least 1,000 cells from each state and for BLM managed lands. Data were summarized in spreadsheets and/or data bases giving abundances, locations, and sizes of digitized images in the sample survey of cells. In Wyoming, census values were given.

Objectives on BLM managed lands differed somewhat in that we estimated total acres of features that were on BLM managed lands with confidence intervals. We also, estimated total acres of features that were associated with BLM managed lands in the sense that at least part of the feature was on BLM managed lands.

METHODS

We conducted a desktop survey of BTPD colonies using the latest National Agriculture Imagery Program (NAIP) imagery to identify potential BTPD colonies. NAIP images have at least one square meter resolution, were inexpensive and easy to obtain. Plans exist to update images every 3 years or more often, facilitating a long term monitoring program. The study area was defined as the current known range of BTPD as established by the State wildlife agencies or historic surveys of BTPD colonies (Figure 1.1), see Part 2 for the state study areas and sampling frames.

We created a contiguous 2-mile square grid feature class over all 11 Western U.S. states in our study area, using the projection USA_Contiguous_Albers_Equal_Area_Conic_USGS_version. Each grid cell was given a unique identifier (grid ID) that included the name of one and only one state; grid cells that overlapped multiple states were assigned to the state that had the greatest amount of area within the cell. State-by-state and BLM sample frames were then created by sub setting the grid by state and those grid cells containing BLM managed lands. NAIP imagery was unavailable for areas including and surrounding White Sands Missile Range in New Mexico. Further modifications were described in the section presented for each state.

We used 2 by 2 mile viewing units to facilitate complete coverage of the BTPD habitat and defined a sampling frame within each state and for BLM managed lands. This allowed implementation of the multiple interpreter approach in McDonald et al. (2011) and provided analysis units that were compatible with units being used in the other 11 states containing BTPD (e.g., Kempema et al. 2015). We selected a sample of 2 by 2 mile grid cells within each state and for BLM managed lands. In addition, a sub-sample of the grid cells were also surveyed by two interpreters to make it possible to construct a "capture history" or "double sample" for features in survey units. The double sampling methods enabled estimation of the number of features not detected by either interpreter using logistic regression statistical models (Zar 2009).

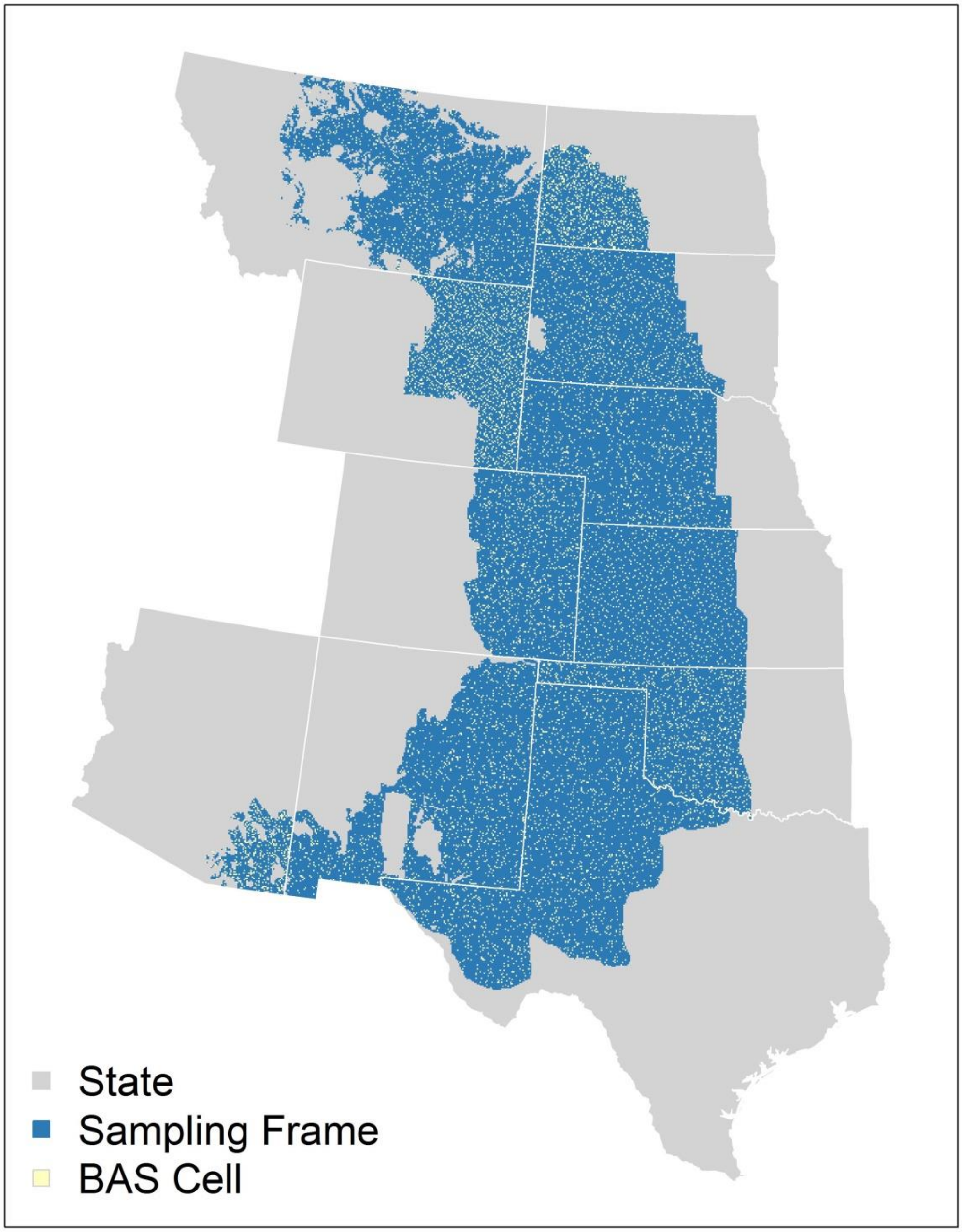

Figure 1.1. Study areas and sampling frames of 2 mi by 2 mi grid cells in 11 states. See the results section for each state for detailed descriptions of the sampling frames for each state and for BLM managed lands within the states.

Digitizing Methods

The digitizers used the latest version of ArcGIS (ArcMap10.2.2) to conduct the GIS work in this study. Using ArcMap, we generated an MXD file for digitizers to use as a template throughout the entire project. In each state and for BLM lands, we constructed a sampling frame consisting of 2 mile by 2 mile grid cells to overlay the NAIP imagery so that observers could systematically search selected cells. To make the process of searching easier and more efficient, we created a smaller mini-grid system within each 2 by 2 mile grid cell. Each 2 by 2 mile cell contains 5 rows and 5 columns for a sum of 25 smaller cells for digitizers to search. The smaller grid system allows full coverage of selected 2 by 2 mile cells and assured that no area was overlooked by observers. Observers viewed the cells of the mini-grid at a scale of approximately 1:4,000.

The observers searched each selected 2 mile by 2 mile cell starting in the northwest corner and worked their way to the southeast corner scanning the cells of the mini-grid one at a time. When an observer found a potential prairie dog colony, they digitized the feature's perimeter at their discretion. Observers zoomed in and out on the images depending on the geographic area and the feature to be digitized. Digitizing was done at a scale no larger than 1:4,000. The interpreters used a "connect the dots" method to connect the outermost burrows that could be identified on the NAIP imagery (Sidle et al. 2002). For some colonies, visible clip lines of vegetation were observable to help identify the outer most burrows. Digitizers were instructed not to digitize colony perimeter by following the clip line in an effort to provide consistency across years with variable vegetation growth and to produce the most comparable results through time. Further details on digitizing methods and methods for the double sampling procedure were given in Appendix A.

Sampling Methods

Observers digitized detected features on a sample of at least 20% of grid cells in the Arizona sampling frame, at least 1,000 grid cells from each of the other states, and more than 10% of grid cells in the sampling frame for BLM managed lands (Table 1. 1). We selected grid cells for sampling from the sample frame by an equal probability sampling procedure known as Balanced Acceptance Sampling (BAS, Robertson et al. 2013). This selection procedure resulted in essentially a stratified random sample from each state and a separate random sample from units containing BLM managed lands. Grid cells were ranked by the BAS procedure and sampling of grid cells proceeded through the ranked order of grid cells. The BAS sample was a spatially balanced sample of grid cells such that any contiguous subset, when taken in order, was an equal probability sample of the target population. We digitized detected features on a census of grid cells in Wyoming.

Table 1.1. Total number of 2 mi by 2 mi grid cells in each state or overlapping BLM managed land, number of grid cells sampled (sample size) and date of National Agriculture Imagery Program (NAIP) imagery.

State	Sample size	Total number of cells	Date of NAIP Images
Arizona	477	2,361	2013
BLM	2,422	21,790	2012, 2013, 2014
Colorado	1,122	11,101	2013
Kansas	1,034	12,785	2014
Montana	1,318	16,302	2013
Nebraska	1,128	13,960	2014
New Mexico	1,362	16,852	2014
North Dakota	1,012	5,011	2014
Oklahoma	1,078	8,888	2013
South Dakota	1,230	12,165	2014
Texas	1,982	24,539	2014
Wyoming	1,722	8,790	2012

Observers visually inspected each sampled grid cell and digitized those areas judged to be potential black-tailed prairie dog colonies. BTPD burrows were usually surrounded by mounds of bare soil one to three meters in diameter. Mounds were often of different color than color of surrounding surface soil. Vegetation was typically reduced in height with different texture that contrasts with vegetation outside the "clip line." The size of mounds, color contrasts, presence of clip lines, and distances between mounds combined to form the search image which triggered the detection of a potential BTPD colony, e.g., Figure 1.2.

Figure 1.2. Black-tailed prairie dog colony with burrow opening visible in a Google earth image at high level of resolution.

For each sample from each state and BLM lands, we digitized features detected and computed their acreage. We estimated total acreage of digitized features and abundance of features on or partly on each surveyed grid cell. Total acreage and abundance of features digitized in the state and BLM sample frames were estimated (see estimation methods below). The precision of these estimates were evaluated to make recommendations on adequate samples sizes required for future work. Details on the digitizing methods for the double sampling procedure were given in Appendix A.

In Wyoming, we completed a census of grid cells under a separate contract with WAFWA, however, we recorded the Wyoming data to enable simulation of the results of a sample size approximately 10% of the cells. Using these sampled cells, we computed estimates of total acreage of digitized features with confidence intervals. These estimates were compared to the census values in Wyoming in order to make recommendations on adequate samples sizes required for future work should a decision be made to monitor acreages based on digitizing features in a sample of cells rather than conducting a census of the entire state.

Estimation Methods

We used three fundamental methods for estimation of the total number (N) and total acreage (S) of features in each state and on BLM managed lands. We called the three methods the clipping, centroiding, and transecting methods. Probabilistic estimates underlie the three methods utilized here, for which small-sample statistical theory allows estimates of both total number (N) of features present and areal extent (S) expressed in acreage. Within Wyoming, we compared these estimates to the estimates made from a census of the entire study area.

The delineation of features with centroids that reside in a selected cell frequently leads to features that spill outside a sample survey grid cell of interest. Concurrently, other features, whose centroids fail to reside in the cell of interest, have extents that reach into a sampled cell. The resulting ambiguous dichotomy that results from the failure of features to reside completely in any one cell suggests the use of multiple estimation approaches, with the aim that concordance resulting from differing approaches will increase confidence in results.

The clipping method involved determination of areal extent (S) of acreage of digitized features within each sampled cell and could be obtained without digitizing the entire perimeter of features when they extend outside the cell. The resulting data analysis involves straight forward methods for estimation of the total areal extent of features in a state or on BLM land, however estimation of abundance and size of large features would not be possible. The centroiding and transecting methods were developed to potentially improve the precision of estimates of the abundance and sizes of features greater than 1,000 acres or features greater than 5,000 acres. Such features were extremely rare or do not exist in some states.

The centroiding method assigns each feature to one and only one grid cell in a sampling frame based on the location of the centroid. Each cell in the sample frame was assigned the number and sizes of features whose centroids were in the cell. Total areal extent of features can be estimated as well as the number and sizes of features using standard statistical estimation methods.

The transecting method was developed based on methods used for Russian snow surveys of animal tracks (Stephens et al. 2006). Animal tracks were detected by crossing the track while following straight line transects. In our application, features were detected by the sample of grid cells when the perimeters of features were intersected by the sides of our sample cells. We used the sides of the 2 mi by 2 mi sample grid cells as "transects" to "capture" features. The objective was to improve the detection of large, rare features and to evaluate the precision of estimates of the size and abundance of rare, large features, e.g., number of features greater than 5,000 acres in size.

Features whose perimeter were intersected by the transects were "in the sample" with probability, P, given by the following formula (Stephens et al. 2006)

$$P = \frac{2LM}{\pi A},$$

where L was the length of the transects, A was the total area of the sampling frame, and M was the perimeter of the digitized feature. Given the probability of detection of features digitized in the sample, it was possible to estimate the total areal extent of features in a sampling frame and the abundance and sizes of features. Further details on the formulas and their derivation were given below and in Appendix B.

Probability of Detection

We developed models to estimate the probability of an observer detecting a feature given the size of the feature. The double-observer approach, when applied to BTPD feature delineation, involved two observers who reconciled the presence of features in a grid cell following the methods described in Appendix A. Differences in feature delineation between the two observers suggest that their probabilities of detection of a feature differ. We utilized logistic regression to estimate the probability that at least digitizer A or B detects a given feature, assuming independence between observers, and allowing adjustment for covariates such as size of the features. We investigated the effects of several covariates in the models including feature size, log of feature size, digitizer pairings, and a measure of convolutedness. Appendix A contains detailed methods for this analysis.

The Horvitz-Thompson Estimator

The estimation of the probability of detection for a feature enables us to utilize the Horvitz-Thompson estimator (Horvitz and Thompson 1952) to estimate both total number of features present and areal extent. The estimate of total number (N) of features was written as

$$\widehat{N} = \sum_{j=1}^{G} \frac{1}{p_j}$$

where p_j was the probability of detection of feature j, and G was the number of features detected. The estimate of areal extent (S) of features was written as

$$\hat{S} = \sum_{j=1}^{G} \frac{s_j}{p_j}$$

where s_j was the size, in acres, of the j^{th} feature.

Clipping Method

The clipping method involves computation of the acreage of features inside a given sampled cell. Areal extents of the j^{th} feature only retain those portions of the feature that falls within the cell of interest. The Horvitz-Thompson estimator of aerial extent, S, incorporates the probability of detection of a feature. Using this method, we averaged the digitized acreage per cell and multiplied the average by the number of cells in the sample frame to estimate total acreage. We used bootstrapping methods to estimate percentile confidence intervals (Manly 1997) for the total.

Note this method was only used to estimate the areal extent S, not the number of features N since one delineated colony may clip to several smaller distinct regions artificially inflating the observed total number of features. Additionally, this method cannot be used for estimation of the number of features greater than 1,000 acres or the number of features greater than 5,000 acres.

Centroiding Method

In the centroiding method, each digitized feature was uniquely assigned to one grid cell, namely the cell to which the centroid of the digitized polygon resides. The Horwitz-Thompson estimators were applied to estimate S and N, based on the numbers and sizes captured in a given sample. By using the acreage of features whose centroids belong to the sample of grid cells, we also estimated the total acreage of features in Wyoming. When estimating the number of features greater than 1,000 acres, we only used digitized features greater than 1,000 acres whose centroids belong to one of the grid cells in the sample.

The centroiding method allowed us to estimate the number of features present when only sample data were available. One pitfall to using this method arose when the centroid of a digitized feature belonged to a grid cell outside of the sample of cells. This may be a particular problem for "large" features, i.e., those greater than 5,000 acres, because there may not be many such large features in the state and fewer in the sample of grid cells.

Transect Method

The third estimation method, known as the Formozov-Malyshev-Pereleshin formula (Stephens et al. 2006), was used to potentially provide better estimates of the number of large features greater than 1,000 acres and the number greater than 5,000 acres. This method depends on identifying those features that intersect the boundary of a sample grid cell. The probability that a feature will intersect with one side of a sampled grid cell was given by $P = 2LM/\pi R$, where M was the length of the perimeter of the feature in miles, L was the sum of the lengths of the sides of all sample grid cells in miles, and R was the area of the study area in a state in square miles (Stephens et al. 2006). Using features that intersect one side of a grid cell and knowing the probability that a feature with perimeter M intersected one side of the gird cell, we estimated the total number of features and total acreage of features in a state using a Horwitz-Thompson estimator for unequal probability sampling. Similarly, using features > 1,000 acres (or > 5,000) acres that intersect one side of the grid cell, we can estimate the number of features > 1,000 acres (or > 5,000) acres in a state. By applying the procedure four times, once for each side of the grid cell, we can compute 4 estimates and average them. We used bootstrapping methods to estimate the confidence interval on estimates of N and S (Manly 1997). See Appendix B for more details of the transect analysis method.

Adjustment for False Negatives

Observers were required to participate in training exercises where images of known BTPD colonies on NAIP images were shown and the observers were to work through the instructions in the Standard Operating Procedure (Appendix A). Images of ant colonies, rocks, patches of bare ground, etc. were included in the training exercises in initial attempts to help the observers develop a "search image" for active or inactive BTPB colonies.

It was expected that observers will miss some active or inactive BTPD colonies (false negatives) as well as include some features that resemble BTPD colonies and trigger the "search image" (false positives). Images of mounds which triggered the search image for BTPD colonies were digitized by connecting the outermost mounds visible on the latest NAIP images available in each state and were referred to as "features" for brevity. For example, if a small feature was digitized by an observer and probability of detection was 0.70 then the acreage of the feature was multiplied by (1/0.70) = 1.43 to account for features of that size that were missed (false negatives). Similarly, the estimate of the number of such small features was increased by 1.43.

Estimation Methods for Features on and Associated with BLM Managed Lands

Estimation of acreage of features on BLM managed land required that a detected feature be clipped to both the selected 2 mi by 2 mi grid cell and BLM land (Figure 1.3). Acreages of detected features on BLM lands and in selected grid cells in the sample survey were averaged and expanded to the number of cells in the BLM sampling frame. We also estimated the number and acreage of features "associated" with BLM managed land in the sense that features overlapped at least partially with BLM land. This required that a feature overlapped BLM managed land and the centroid of the feature belonged to the sampled cell, otherwise associated features could belong to more than one grid cell. For example, the top feature in Figure 1.3 would be counted as associated with BLM managed land because it overlaps BLM managed land and the centroid was in the sampled cell. The feature in the bottom left of the cell would not be counted because its centroid was in the neighboring cell. If the centroid of the bottom left feature had been in the sample cell it would have been counted as associated with BLM managed land and the entire acreage would have been "associated" with BLM land even though some of the feature was on non-BLM land.

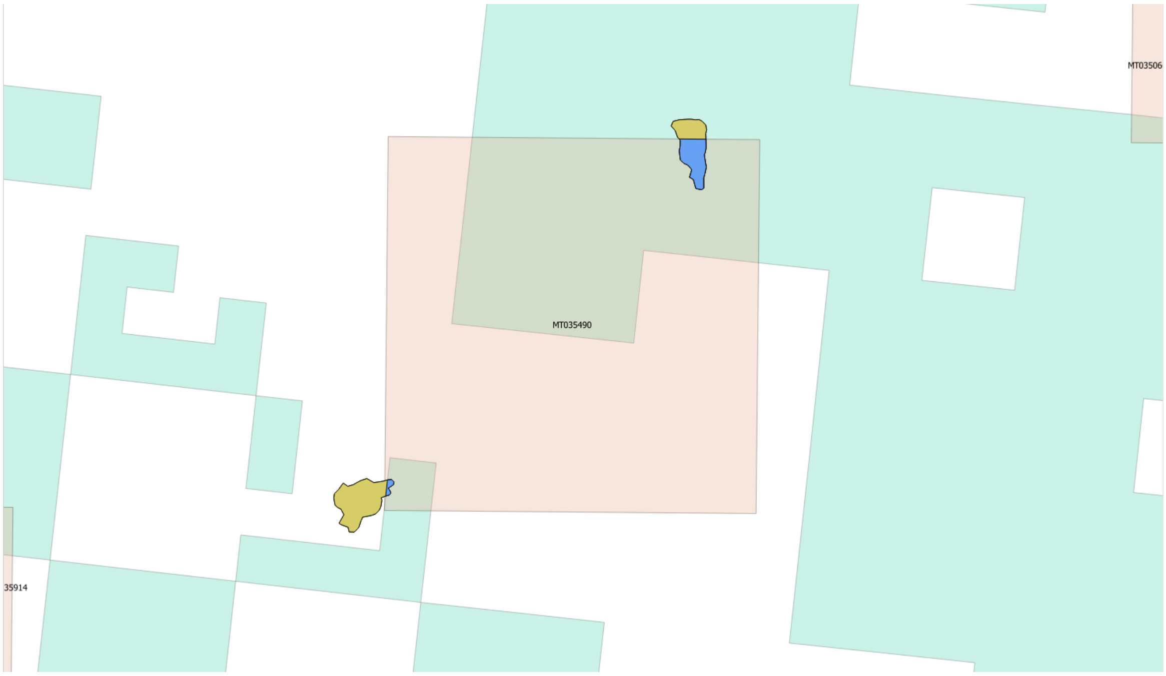

Figure 1.3. Example of features overlapping BLM managed lands (green). The sampled cell (beige) had two digitized features. The centroid of the top feature was in the sampled cell while the centroid of the bottom left feature was in the neighboring cell. The acreage on BLM land and in the sampled cell (blue) was averaged over sampled cells. The top feature was counted as "associated with BLM managed land" because it overlaps BLM managed land and its centroid was in the sampled cell.

PART 1: RANGE-WIDE RESULTS

Range-Wide Estimates of Acreage and Abundance of Potential BTPD Colonies

As part of the training exercises to help observers develop a search image for colonies, and to allow development of models to adjust for probability of detection we required that teams of two observers independently digitize features detected on a sample of grid cells. Composition of the teams varied from state to state and more than one team worked simultaneously in a state. One of the team members was designated as primary observer (A) and the other as secondary observer (B). Each team member was the primary observer on approximately 50% of the team's survey units.

We used features detected by one observer as a "test" set and determined whether the second observer detected those features or not, fitting logistic regression models to the data. Representative graphs of these models for Kansas, South Dakota and Wyoming were contained in Figures 1.4, 1. 5 and 1.6 respectively. The estimated probability of detection by individual observers was 0.70 to 0.80 for small features and increased to 0.9 or more for features greater than 1,000 acres, with the exception of viewing 2012 NAIP images of Wyoming. In all states, the probability of detection of small features by at least one of two independent observers was estimated to be greater than 0.90. The probability of detection by at least one member of a team was greater than 0.95 for relatively large features.

The most difficult NAIP images that we worked with were the 2012 images for the State of Wyoming. Many of the Great Plains States, including Wyoming, experienced a severe drought during spring 2012. Unfortunately, the 2012 images for Wyoming indicated the presence of very little green vegetation. Identification of BTPD colonies was much more difficult in Wyoming than in the other states where NAIP images were taken in 2013 or 2014. Detection of features on 2013 and 2014 images were more reliable due to vegetative vigor and height at the time the images were taken. While it was possible to identify potential prairie dog colonies in Wyoming with 2012 imagery, the probability of detection varied among observers and the probability of detection of large colonies was estimated to be less than 1.00 for some observers (Figure 1.6). For example, observer A was estimated to have probability of detection of about 0.70 for all size features when viewing the 2012 NAIP images of Wyoming. When only observer A searched a grid cell and detected a feature, the inflation factor was about (1/0.70) = 1.43, i.e. for every feature detected by observer A, another 0.43 feature was estimated to have been missed to adjust for false negatives. Also seen in Figure 1.6, observer B's estimated probability of detection in Wyoming was higher, ranging from about 0.90 to 0.95, but exhibited high variation and a negative slope with increasing size. Despite the difficulties experienced with the Wyoming imagery, the probability of detection by at least 1 observer was quite high across the range of colony sizes.

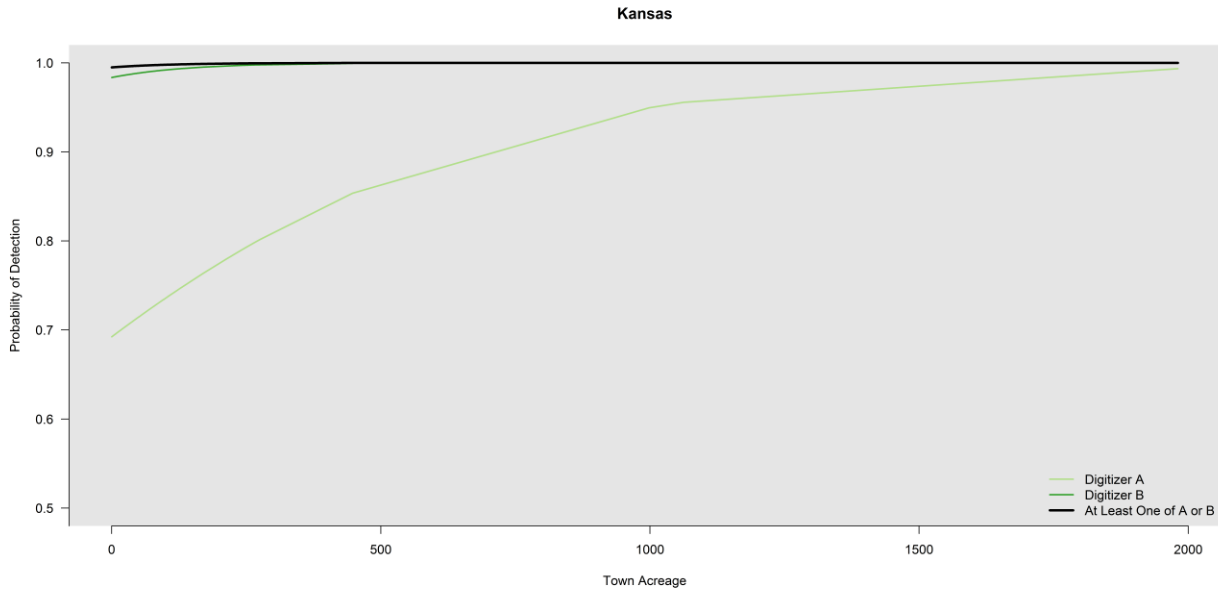

Figure 1.4. Estimated average probability of detection of potential BTPD colonies as a function of size by two observers labeled A and B when searching 2014 NAIP images of Kansas. The black curve was the estimated average probability of detection by at least one of the two observers on grid cells independently searched by observers A and B.

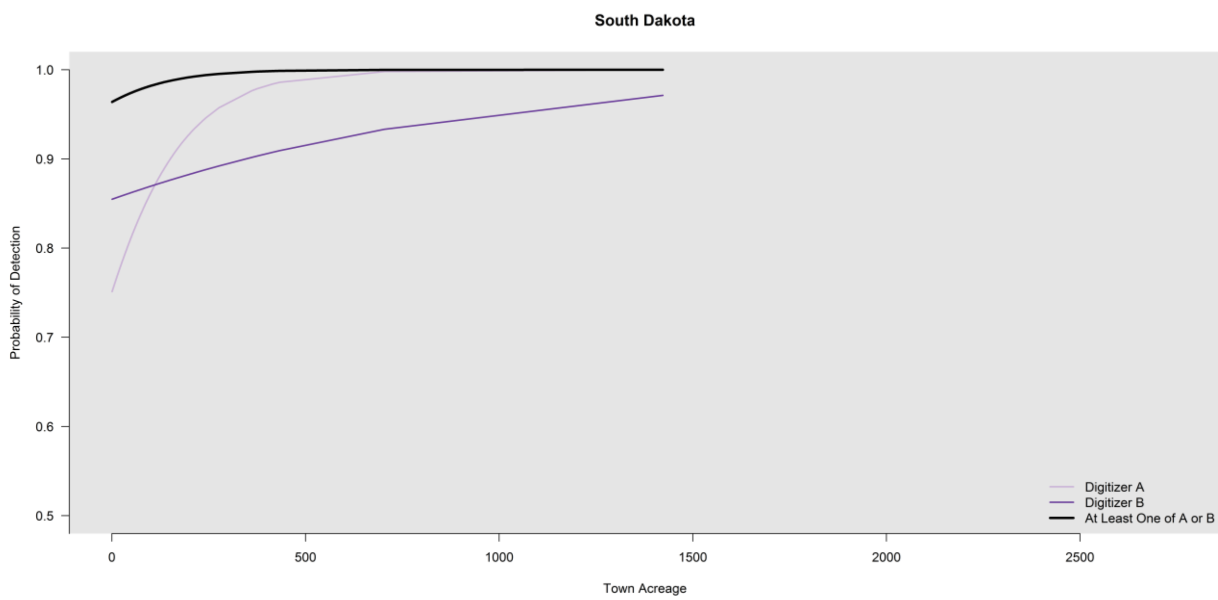

Figure 1.5. Estimated average probability of detection of potential BTPD colonies as a function of size by two observers labeled A and B when searching 2014 NAIP images of South Dakota. The black curve was the estimated average probability of detection by at least one of the two observers on grid cells independently searched by observers A and B.

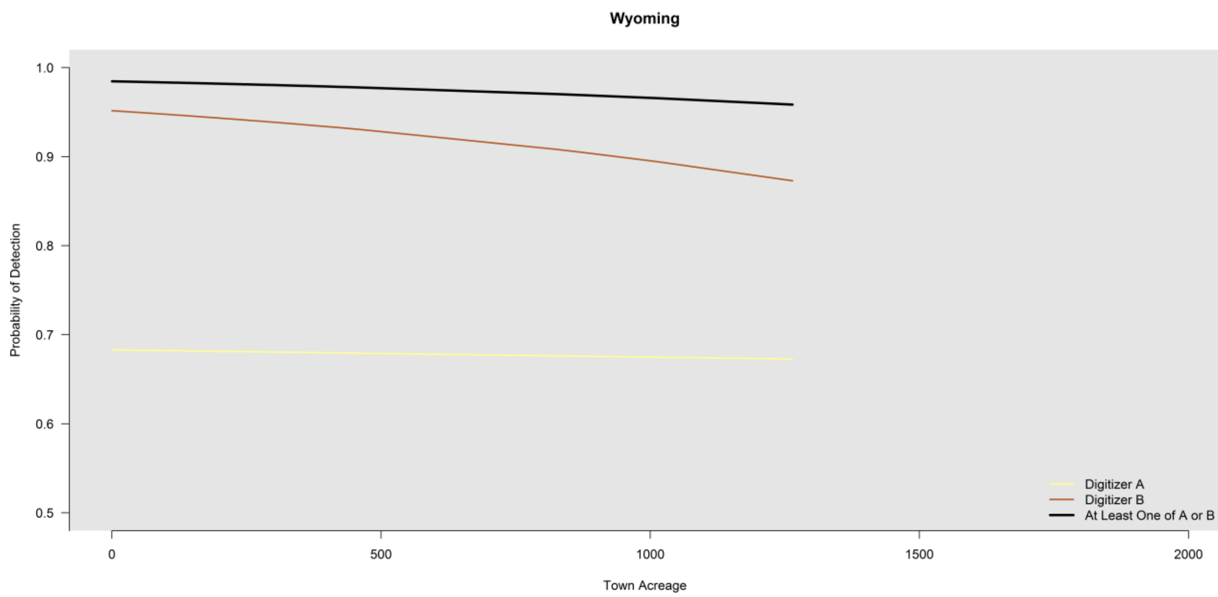

Figure 1.6. Estimated average probability of detection of potential BTPD colonies as a function of size by two observers labeled A and B when searching 2012 NAIP images of Wyoming. The black curve was the estimated average probability of detection by at least one of the two observers on grid cells independently searched by observers A and B.

Estimated Total Acreage of Features in Each State and for BLM Managed Lands

We digitized all features detected on a sample survey of grid cells in 10 states and for BLM managed lands. We digitized all features detected on all grid cells in Wyoming. We also recorded results for the first 1,722 grid cells digitized in the BAS randomized list of 8,790 cells from Wyoming to mimic a probabilistic sample.

We estimated the total acreage of features by the clipping method. The clipping and centroid methods gave unbiased estimates of total acreage of features, however we reported only estimates for acreage of digitized features by the clipping method. The clipping method was simpler to understand, simpler to compute, and there was a 13.5% mean increase in the coefficient of variation (CV) of the centroid method relative to the clipping method.

<u>Eleven states</u>

We estimated the total acreage of all potential BTPD colonies in each state using our digitizing methods and correcting for false negatives (features missed during digitizing) using the double observer methods (Table 1.2). These estimates likely contain an unknown proportion of false positives, i.e., digitized features which were neither active nor inactive BTPD colonies.

Using these methods, total acreage of potential BTPD colonies in these 11 states corrected for false negatives was estimated to 1,932,792 acres uncorrected for false positives (90% Confidence Interval (CI) [1,810,089 to 2,130,030], Coefficient of Variation (CV) 4.9%). Colorado had the largest estimate of total acreage with 532,251 acres while North Dakota had the smallest estimate at 15,561 acres. Coefficients of variation ranged from 8.3% in Montana to 33.1% in North Dakota.

Arizona

Observers detected and digitized only 2 potential BTPD colonies in the sample of 524 cells in Arizona. Based on a close examination using Google Earth, one of the two features digitized was very small (0.05 acre) and was judged to not be a potential BTPD colony. For Arizona, we reported the acreage of three "known" BTPD colonies (17.4 acres, Holly Hicks, Arizona Department of Game and Fish) plus the one feature (16.1 acre) judged to be a potential BTPD colony for a total of 34 acres. It was not meaningful to report confidence intervals, standard errors and coefficients of variation for estimates in Arizona.

Wyoming

The estimated acreage for Wyoming was 288,606 acres (CV = 12.9%; Table 1.2) based on a probabilistic random sample of 1,722 digitized cells and not corrected for false positives. These estimates were reported to be comparable to values reported in the other states and to be comparable to future sample survey monitoring results for trend, should a census of cells not be digitized. Census values for Wyoming, corrected for false positives using aerial survey "truthing," were reported in Part 2 of this report.

Table 1.2. Estimated acreage of potential black-tailed prairie dog colonies in 11 states corrected for false negatives. Standard errors, coefficients of variation (CV), and bounds of 90% confidence intervals were reported.

State	Estimated Acreage	90% Confidence Interval Lower Bound	90% Confidence Interval Upper Bound	Standard Error	CV
Arizona	34	-	-	-	-
Colorado	532,251	454,519	621,546	50,511	0.095
Kansas	154,775	102,084	262,123	45,984	0.297
Montana	184,055	166,219	210,408	15,203	0.083
Nebraska	89,208	77,181	107,481	9,501	0.107
New Mexico	124,098	103,228	155,709	16,778	0.135
North Dakota	15,561	9,578	27,760	5,151	0.331
Oklahoma	81,224	63,015	107,187	13,199	0.163
South Dakota	224,145	187,303	270,383	25,059	0.112
Texas	238,871	193,281	304,826	34,015	0.142
Wyoming	288,606*	236,700	361,896	37,201	0.129
Range-wide Total	1,932,826	1,810,089	2,130,030	94,707	0.049

*Estimated acreage in Wyoming was based on the sample of digitized cells and not corrected for false positives (see Part 2, Wyoming).

BLM managed lands

We estimated 77,723 acres of features to be associated with BLM managed lands in the sense that features partly or wholly intersected BLM managed lands and 31,209 acres of features on BLM managed lands (Table 1.3). Coefficients of variation were 18.3% and 18.4%, respectively.

Table 1.3. Estimated acres of potential black-tailed prairie dog colonies associated with BLM managed land and on BLM managed lands corrected for false negatives. Upper and lower bounds were reported for 90% confidence intervals. The standard error of the estimate and its coefficient of variation (CV) were reported.

				90% Confidence Interval			
Area of Inference	Sample size	No. cells in sampling frame	Estimated acreage	Lower Bound	Upper Bound	Standard Error	CV
Associated with BLM lands[1]	2,422	21,790	77,723	60,374	108,572	14223	0.183
On BLM lands[2]	2,422	21,790	31,209	23,933	43,221	5,743	0.184

[1]Centroid method, [2]Clipping method

Estimated Number of Features

Eleven states

Estimation of the number of features present in a state or associated with BLM land was by two methods. The centroid method essentially counted the number of features with centroids located in a sampled cell, adjusted the count to account for probability of detection (i.e., for false negatives), computed the adjusted number for each sampled cell, computed the mean per cell and applied the mean to every cell in a state (Table 1.4). The method used straight forward standard statistics adjusted for false negatives and was an unbiased estimator of the total number of features. We estimated the number of potential BTPD colonies corrected for false negatives in the 11 states (Table 1.4). We estimated a total of 29,467 potential BTPD colonies in the entire sampling frame (90% CI = [28,757; 30,962], CV = 2.4%). Colorado and South Dakota had the largest estimated numbers of features at 5,793 and 5,204, respectively.

Arizona

We report 3 "known" BTPD colonies in Arizona plus one potential colony for a total of 4 features.

Wyoming

We estimated 3,158 features in Wyoming based on a random probabilistic sample of 1,722 grid cells from the total 8,790 cells to mimic results of a probabilistic sample (Table 1.4). These estimates were reported to be comparable to values reported in the other states and to be comparable to future sample survey monitoring results for trend should a census of cells not be digitized. Census values for Wyoming, corrected for false positives using aerial survey "truthing," were reported in Part 2 of this report.

Table 1.4. Estimated number of potential black-tailed prairie dog colonies in 11 states corrected for false negatives. Standard errors, coefficients of variation, and bounds of 90% confidence intervals were reported.

State		90% Confidence Interval			
State	Estimated number of features	Lower Bound	Upper Bound	Standard Error	CV
Arizona	4	-	-	-	-
Colorado	5,793	5,248	6,361	339	0.059
Kansas	2,553	2,141	3,023	268	0.105
Montana	4,006	3,877	4,188	201	0.050
Nebraska	2,317	2,222	2,456	137	0.059
New Mexico	1,964	1,856	2,123	166	0.084
North Dakota	299	219	394	53	0.177
Oklahoma	1,816	1,542	2,115	174	0.096
South Dakota	5,204	4,693	5,763	326	0.063
Texas	2,353	2,256	2,496	146	0.062
Wyoming	3,158	2,872	3,460	179	0.057
Range-wide Total	29,467	28,757	30,962	707	0.024

BLM managed lands

We estimated the number of BTPD colonies associated with BLM managed lands and corrected for false negatives to be 800 features (90% CI = [748; 882], CV = 8.2%.

Table 1.5. Estimated number of potential black-tailed prairie dog colonies associated with BLM managed land corrected for false negatives. Standard error (SE), coefficient of variation (CV), and bounds of 90% confidence interval were reported.

	90% Confidence Interval			
Estimated number features	Lower Bound	Upper Bound	SE	CV
800	748	882	66	0.082

Estimated abundances of potential BTPD colonies greater than 100 acres and 500 acres

We attempted to estimate the abundance of features greater than 1,000 acres and greater than 5,000 acres in size using the transect method (Appendix B). Unfortunately, there remains unresolved controversy in the formula for probability of detection of features based on intersections of the perimeter of the feature with the "transects" (sides of our grid cells). We obtained improbable estimates of probability of detection, i.e. values greater than 1.0 = 100% using the formulas in Appendix B.

The centroid method provided an unbiased estimated of the total number of features (Table 1.4). However, the method did not work well for estimation of the number of features greater than 1,000 acres and greater than 5,000 acres in the individual states, because such features with centroids in the sampled cells were extremely rare or not present. For example, we detected and digitized 4 features greater than 5,000 acres; however, none of the centroids of the four were in sampled cells.

After reviewing these results, we changed our objectives and estimated the number of potential BTPD colonies greater than 100 acres in size and the number greater than 500 acres in size. We believe these estimates were reliable and will be repeatable should a similar design and analysis be conducted in the future. We estimated 4,234 potential BTPD colonies greater than 100 acres and 419 potential BTPD colonies greater than 500 acres in the 11 state study area (Tables 1.6 and 1.7).

Table 1.6. Estimated number of potential black-tailed prairie dog colonies greater than 100 acres in 11 states corrected for false negatives. Standard errors, coefficients of variation, and bounds of 90% confidence intervals were reported.

		90% Confidence Interval			
State	Estimated number greater than 100 acres	Lower Bound	Upper Bound	Standard Error	CV
Arizona	0	NA[1]	NA[1]	NA[1]	NA[1]
Colorado	1,372	1,181	1,578	121	0.088
Kansas	198	111	297	53	0.270
Montana	372	335	434	44	0.118
Nebraska	188	151	250	40	0.215
New Mexico	334	297	409	47	0.141
North Dakota	30	15	59	12	0.409
Oklahoma	218	141	305	49	0.227
South Dakota	458	352	577	68	0.149
Texas	446	409	508	48	0.109
Wyoming	620	518	728	64	0.103
Range-wide Total	4,234	4,023	4,649	195	0.046

[1]NA = Not Applicable; Denotes confidence bounds, standard errors and coefficients of variation were not possible to compute.

Table 1.7. Estimated number of potential black-tailed prairie dog colonies greater than 500 acres in 11 states corrected for false negatives. Standard errors, coefficients of variation, and bounds of 90% confidence intervals were reported.

		90% Confidence Interval			
State	Estimated number greater than 500 acres	Lower Bound	Upper Bound	Standard Error	CV
Arizona	0	NA[2]	NA[2]	NA[2]	NA[2]
Colorado	190	127	269	43	0.23
Kansas	25	12	74	17	0.70
Montana[1]	7	NA[2]	NA[2]	NA[2]	NA[2]
Nebraska	12	12	50	12	0.99
New Mexico	25	25	74	15	0.61
North Dakota	5	5	20	5	1.00
Oklahoma[1]	3	NA[2]	NA[2]	NA[2]	NA[2]
South Dakota	20	10	59	14	0.71
Texas	87	62	124	24	0.28
Wyoming	56	31	87	17	0.31
Range-wide Total	419	349	544	62	0.15

[1]No features greater than 500 acres existed with centroids in sampled cells. The estimated number was a conservative underestimate of the number present.

[2]NA = Not Applicable; Denotes confidence bounds, standard errors and coefficients of variation were not possible to compute.

PART 2: INDIVIDUAL STATE AND BLM RESULTS

State study areas and sampling frames

We created a contiguous 2-mile square grid feature class over all 11 Western U.S. states in our study area, using the projection USA_Contiguous_Albers_Equal_Area_Conic_USGS_version. Each grid cell was given a unique identifier (grid ID) that included the name of one and only one state; grid cells that overlapped multiple states were assigned to the state that had the greatest amount of area within the cell. State-by-state sample frames were then created by subsetting the grid by state and making further modifications as described below.

We searched a sample of grid cells in each state and digitized features on the latest available NAIP images judged to be potential BTPD colonies. Shapefiles of the digitized features in each state will be made available to WAFWA, representatives of the wildlife agencies in each state, and the Bureau of Land Management. In addition, high resolution county maps showing the sample of cells searched and features digitized will be distributed. Example low resolution county maps were given below for each of the states and BLM managed lands below. Figures of digitized features were included on the state and county maps to establish the general distribution of potential BTPD colonies. However; clearly, colonies that we missed were not included in the county maps. Also, we did not know which of the individual polygons in the county maps were active or inactive BTPD colonies; that is, some of the individual polygons on the county maps were false positives.

Estimated acreages and numbers of features were given for each state and for BLM lands. Estimated total acreages and numbers of potential BTPD colonies were adjusted for false negatives.

ARIZONA

We started with the shapefile of potential BTPD habitat in Arizona (Holly Hicks, Arizona Game and Fish Department, personal communication, Feb. 18, 2015) to develop a sampling frame consisting of grid cells that met the following criteria (Figure 2.1):

1) the cell contained any portion of area within the 6 county area of interest (Cochise, Graham, Greenlee, Pima, Pinal, and Santa Cruz),
2) the cell had <50% of the land area within the grid cell overlapping US Forest Service designated land,
3) the cell had >25% of the land area within the grid cell designated as “Black-Tailed Prairie Dog Habitat” according to the model layer provided by the Arizona Game and Fish Department, and
4) an exception to criterion 3 above was applied to Cochise, Graham, and Greenlee counties from the eastern edge of the modeled BTPD habitat east to the New Mexico border.

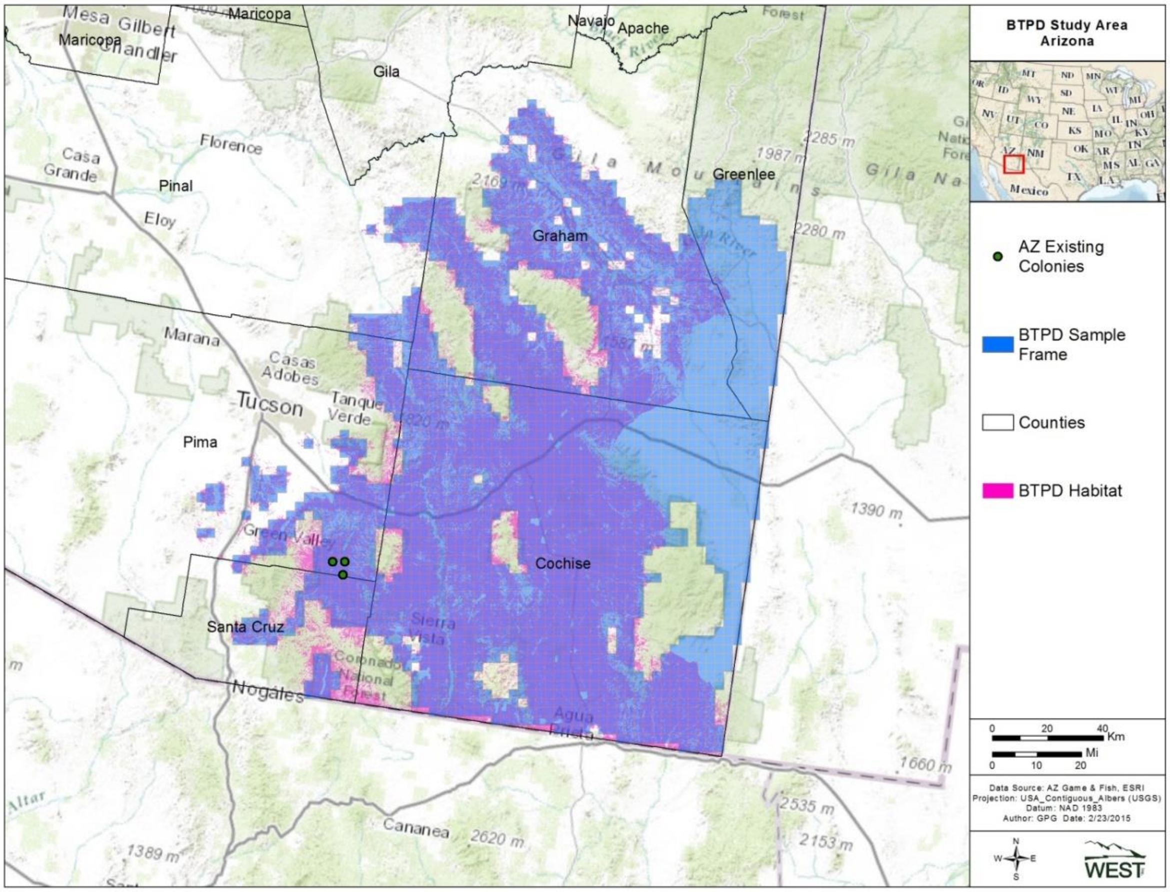

Figure 2.1. Sampling frame of 2,361 grid cells each 2 mi by 2 mi in Arizona for black-tailed prairie dog sample survey, 2015.

We detected and digitized two features on our sample of 477 units (Figure 2.2 and 2.3). After checking on Google earth it appeared the feature detected in Cochise County was unlikely to be a BTPD colony. Figure 2.4 from Google Earth at very high resolution indicates a possible BTPD colony.

There were 3 small “known” BTPD colonies in Pima County, Arizona (Figure 2.5). Two of these colonies were in grid cells searched by our observers on 2013 NAIP images. Neither of the colonies were detected by our observers. Total acreage of 3 known BTPD colonies and the potential colony was 34 acres.

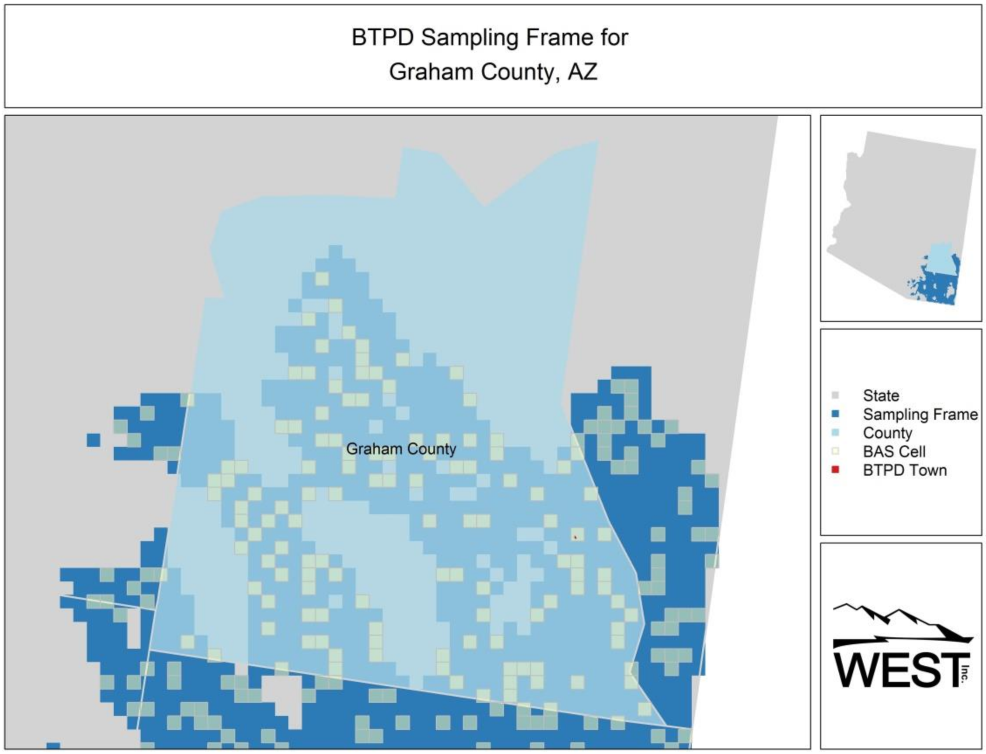

Figure 2.2. Sampling frame and selected grid cells in Graham County with one digitized potential black-tailed prairie dog colony.

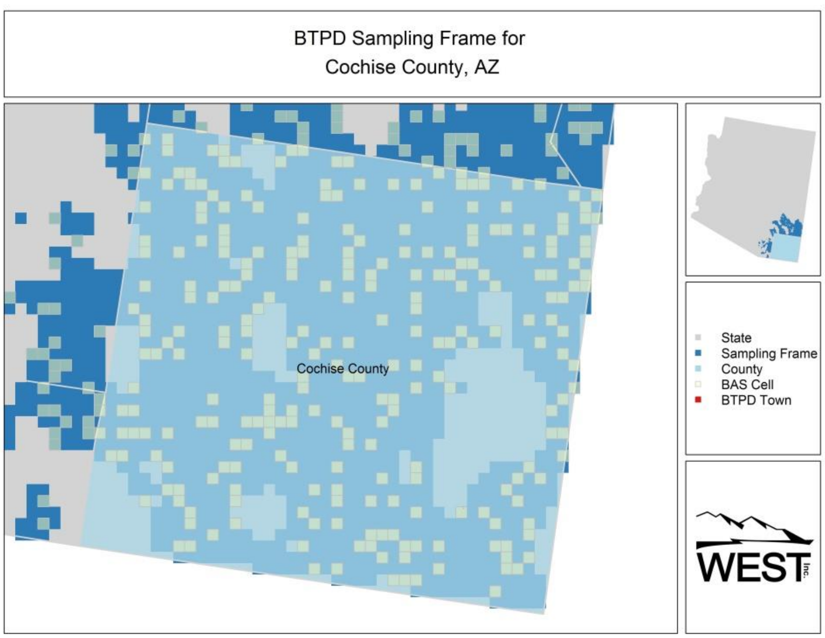

Figure 2.3. Sampling frame and selected grid cells in Cochise County with one very small digitized feature judged to not be a potential black-tailed prairie dog colony.

Figure 2.4. Digitized feature in Arizona. The digitized polygon was shown on this Google Earth screen shot. There appear to be burrow openings in the centers of mounds.

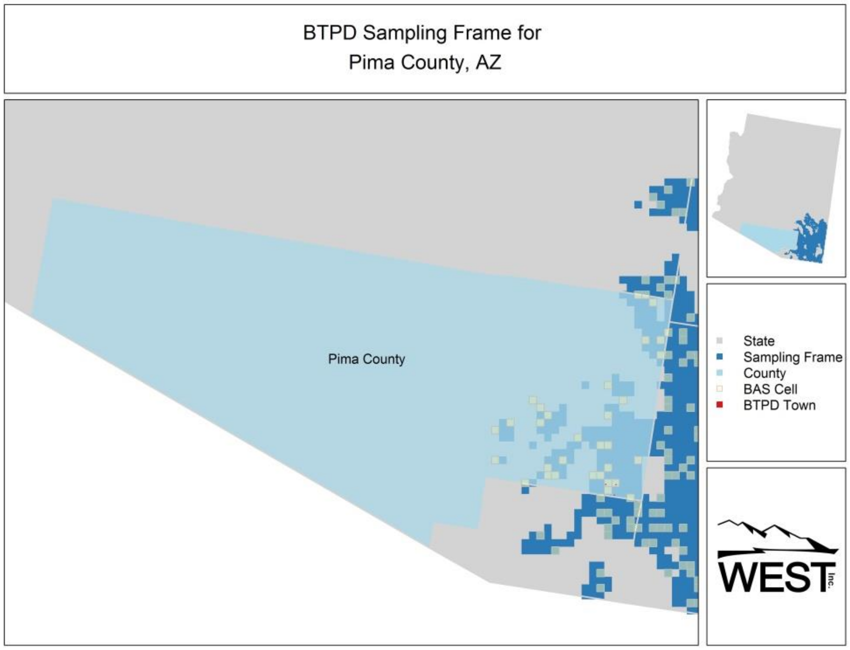

Figure 2.5. Pima County, AZ, with locations of 3 known black-tailed prairie dog colonies.

BUREAU OF LAND MANAGEMENT (BLM)

The sample frames created for the 11 states in the Range-wide BTPD survey were intersected with existing federal lands managed by the Bureau of Land Management, according to the Surface Management Agency GIS dataset compiled and maintained by BLM and updated Jan 1, 2015. Once intersected, we computed the portion of each overlapping grid cell in the sample frame that was managed by the BLM. All cells in which over 0.1% of the grid cell's area (1.28 acres) was BLM land were included in the BLM sample frame (Figure 2.6).

After adjusting for false negatives (missed features) we estimated 31,209 acres of features (90% CI = [23,933; 43,221] with CV = 18.4%) on BLM managed lands (Part 1, Table 1.3). We also estimated the acreage of features that were associated with BLM lands in the sense that the features overlapped totally or partly with BLM land. We estimated 77,723 acres of features (90% CI = [60,373; 108,572], CV = 18.3 %) to be associated with BLM managed lands consisting of an estimated 800 potential BTPD colonies (90% CI = [748; 882], CV = 8.2%) (Part 1, Table 1.5).

There were 21,790 grid cells in the sampling frame for BLM managed lands, of which we searched 2,422 cells. Coefficients of variation for estimated acreage of potential BTPD colonies on BLM land and acreage associated with BLM land were about 18%.

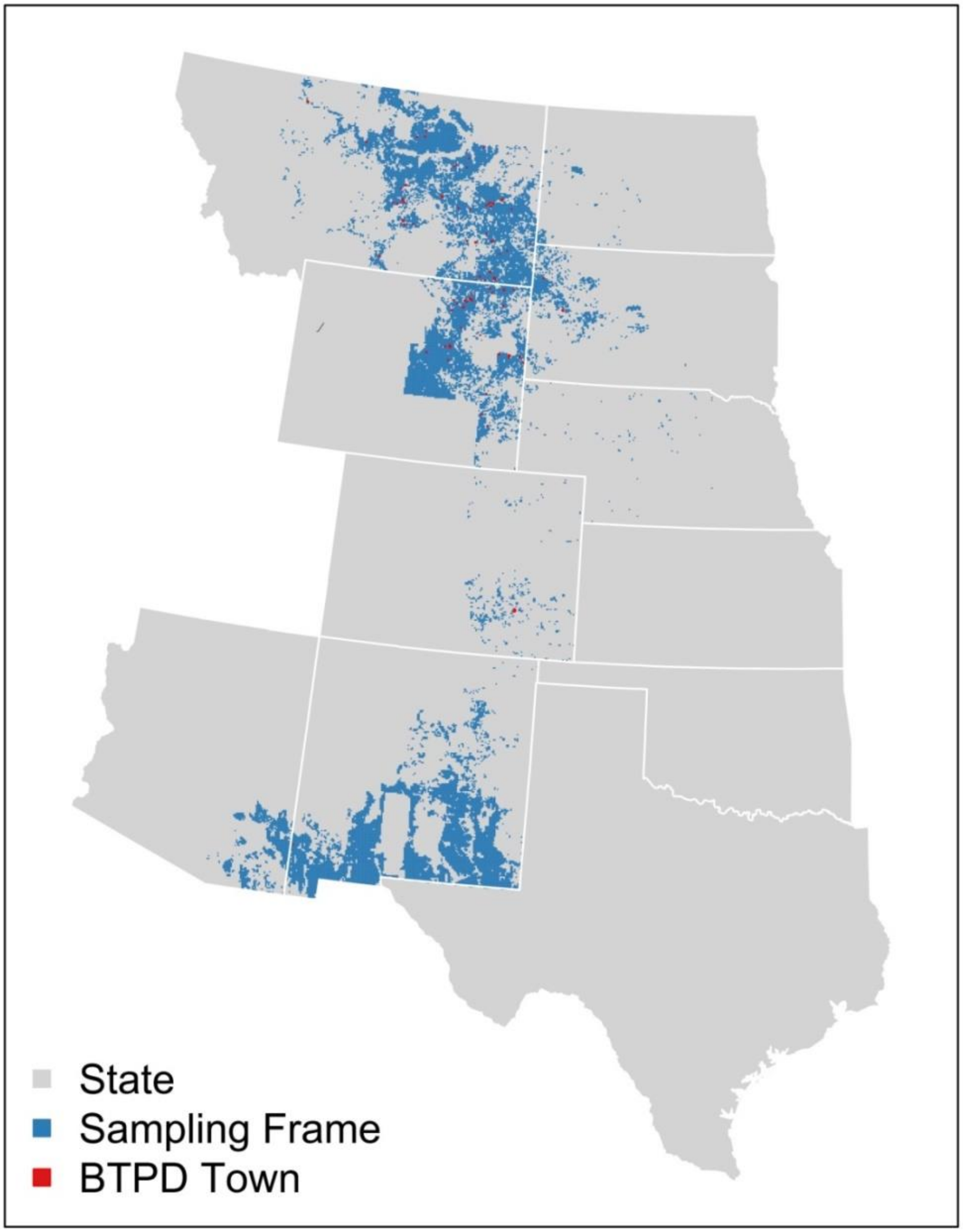

Figure 2.6. Sampling frame for BLM managed lands with 21,790 grid cells each 2 mi. by 2 mi and digitized potential black-tailed prairie dog colonies.

COLORADO

We started with the shapefile of the overall range for BTPD in Colorado (Tina Jackson, Colorado Parks and Wildlife, personal communication, February 4, 2015) to develop a sampling frame consisting of grid cells that contained any portion of the overall range (Figure 2.7). We digitized the perimeters of all features detected on 1,122 sampled grid cells selected from the universe of 11,101 cells in the sampling frame for Colorado (Figure 2.8). We estimated a total of 532,251 acres of potential BTPD colonies in Colorado (90% CI = [454,519; 621,546], CV = 9.5%) (Part1, Table 1.2) and that a total of 5,793 features exist in the state (90% CI = [5,248; 6,361], CV = 5.9%) (Part 1, Table 1.4). We estimated 1,372 features greater than 100 acres (90% CI = [1,181; 1,578], CV = 8.9%) and 190 greater than 500 acres in Colorado (90% CI = [127; 269], CV = 23%) (Part 1, Tables 1.6 and 1.7).

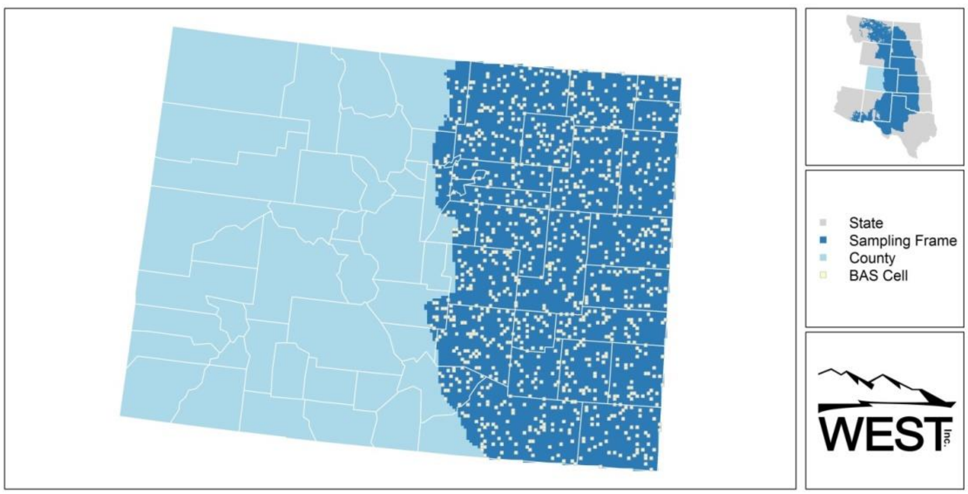

Figure 2.7. Sampling frame for Colorado with 11,101 grid cells each 2 mi. by 2 mi. The 1,122 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

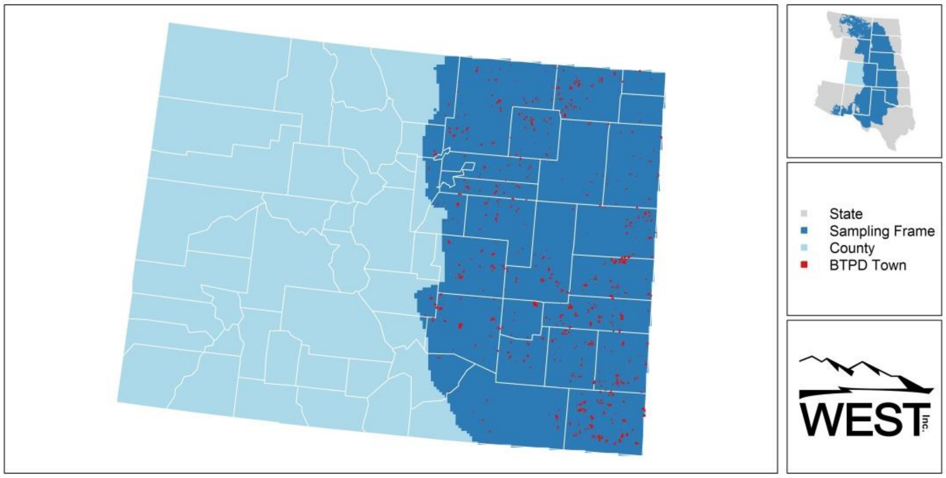

Figure 2.8. Map of features digitized in a sample survey of grid cells in Colorado.

We plotted the estimates of total number of features and acreage of features as a function of the sample size (Figures 2.9 and 2.10). The estimated total acreage and number of features begins to converge to final estimates (horozontal line) at a sample size of about 1,000 (Figure 2.10). Increasing the sample size to 1,100 grid cells did not change the estimated total number of features appreciably. The effect of detecting rare relatively large features on estimated total acreage of features was evident in Figure 2.9. As the sample size was increased and a rare large feature detected, relatively large jumps occurred in the estimated total acreage.

The estimated total acreage and number of colonies began to converge to final estimates at a sample size of about 1,000 grid cells yielding coefficients of variation of 9.5% for total acreage and 5.9 for total number of potential BTPD colonies with a sample of 1,122 cells.

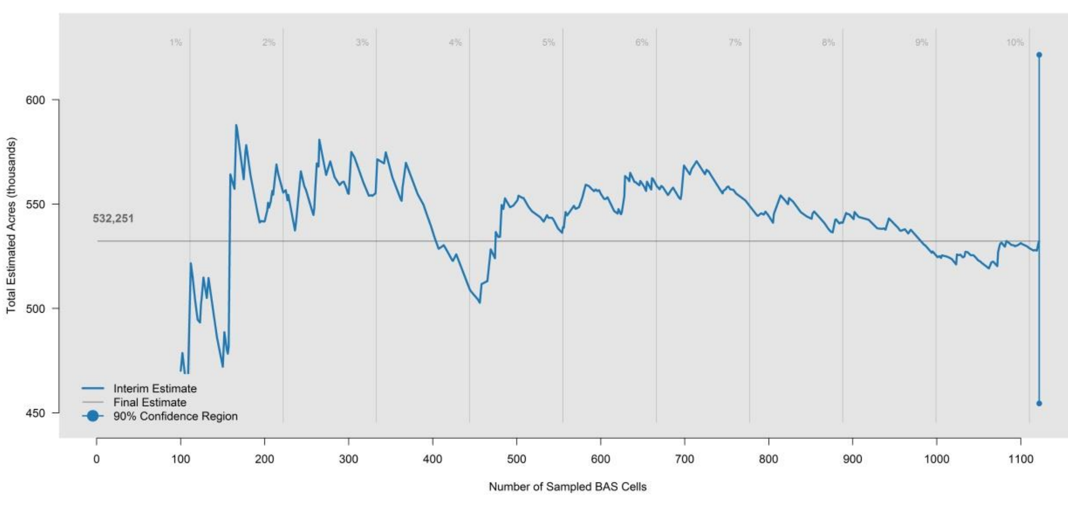

Figure 2.9. Estimated acreage of potential black-tailed prairie dog colonies in Colorado as a function of the sample size.

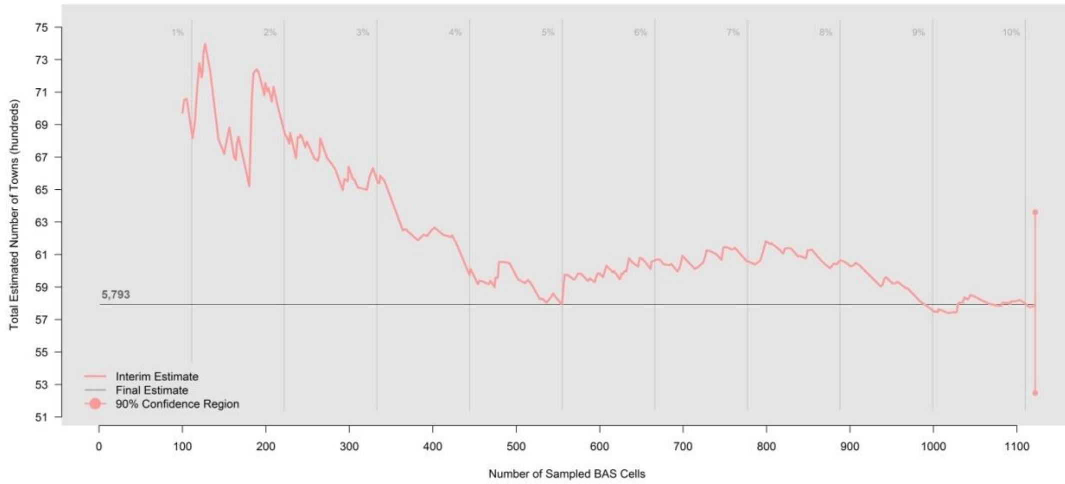

Figure 2.10. Estimated number of potential black-tailed prairie dog colonies in Colorado as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of Colorado with the digitized features in the state and in each county. For example, figure 2.11 depicts the location of features detected and digitized in Pueblo County, CO. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

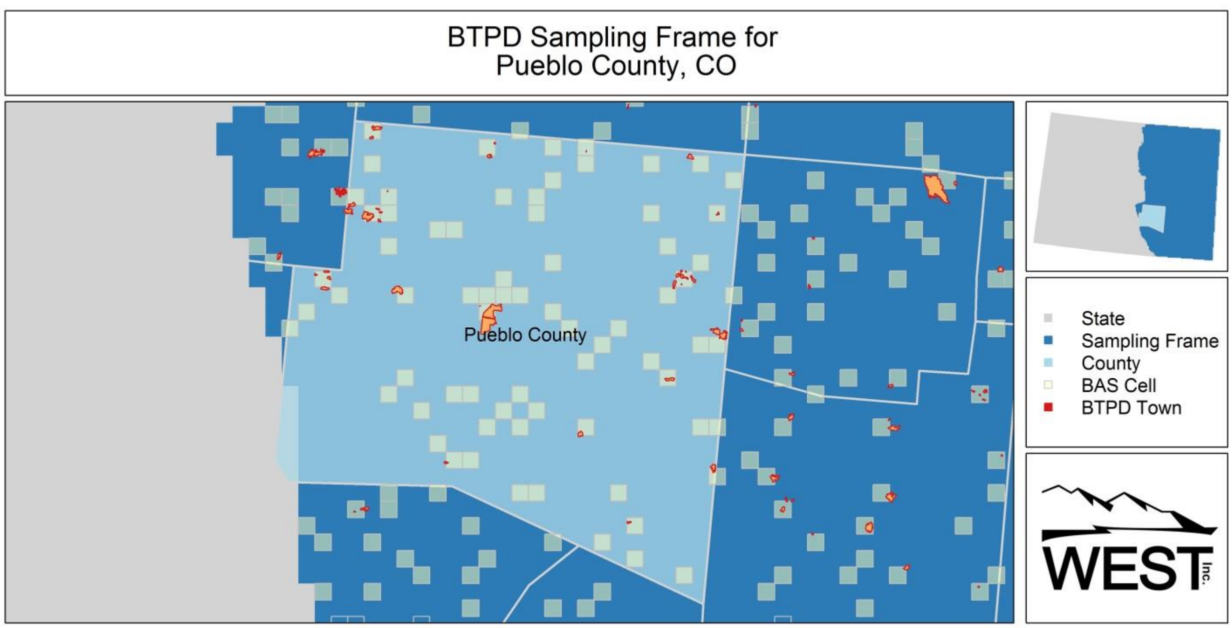

Figure 2.11. Digitized features on a sample survey of grid cells in Pueblo County, Colorado.

KANSAS

We used the shapefile of potential BTPD habitat provided by the Kansas Department of Wildlife and Parks (Matt Peek, personal communication, January 13, 2015) to develop a sampling frame consisting of grid cells that contained any portion of the overall range (Figure 2.12. We digitized the perimeters of all features detected on 1,034 sampled grid cells selected from the universe of 12,785 cells in the sampling frame for Kansas (Figure 2.13). We estimated a total of 154,775 acres of potential BTPD colonies in Kansas (90% CI = [102,084; 262,123], CV = 29.7%) (Part1, Table 1.2). We estimated that a total of 2,553 features exist in the state (90% CI = [2,141; 3,023], CV = 10.5%) (Part 1, Table 1.4). We estimated 198 features greater than 100 acres (90% CI = [111; 297], CV = 27%) and 25 greater than 500 acres in Kansas (90% CI = [12; 74], CV = 70%) (Part 1, Tables 1.6 and 1.7).

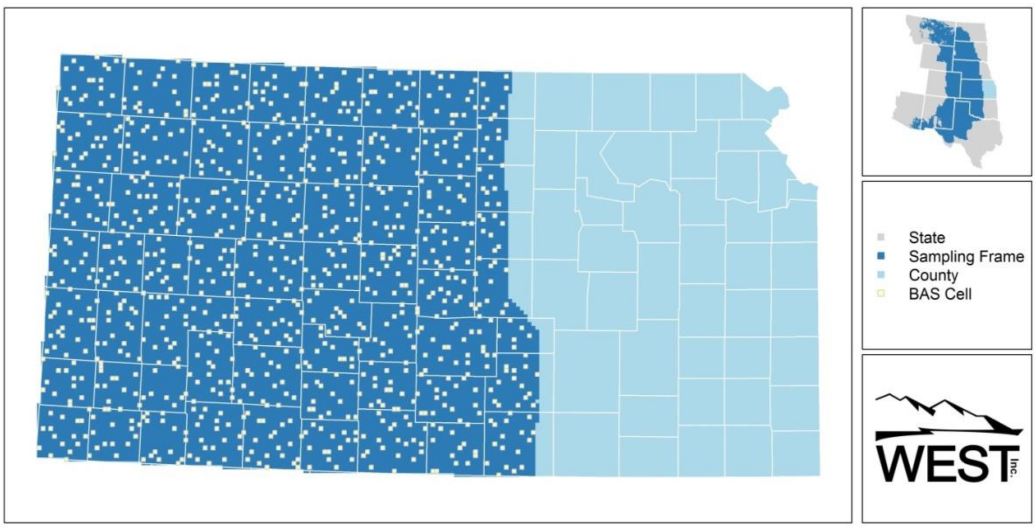

Figure 2.12. Sampling frame for Kansas with 12,785 grid cells each 2 mi. by 2 mi. The 1,034 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

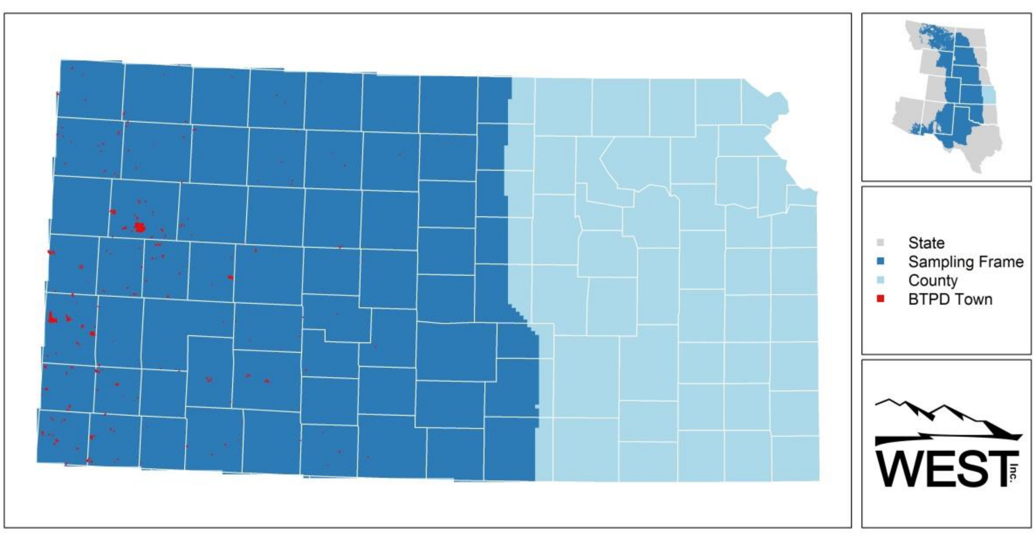

Figure 2.13. Map of features digitized in a sample survey of grid cells in Kansas.

We plotted the estimates of total acreage of features and the total number of features as functions of the BAS sample size (Figures 2.14 and 2.15). The estimated number of features began to converge to final estimates at a sample size of about 800 (Figure 2.15). Increasing the sample size to 1,100 grid cells did not change the estimated total number of features appreciably. The effect of detecting relatively large, but rare, features on estimated total acreage of features was evident in Figure 2.14. As the sample size was increased and rare large features detected, relatively large jumps occurred in the estimated total acreage.

The estimated total acreage was more variable (CV = 29.7%) than the estimated number of colonies (CV = 10.5%), because many cells had no features and one very large feature was detected. However the averaged values began to converge to final estimates at a sample size of about 1,000 grid cells (Figures 2.14 and 2.15).

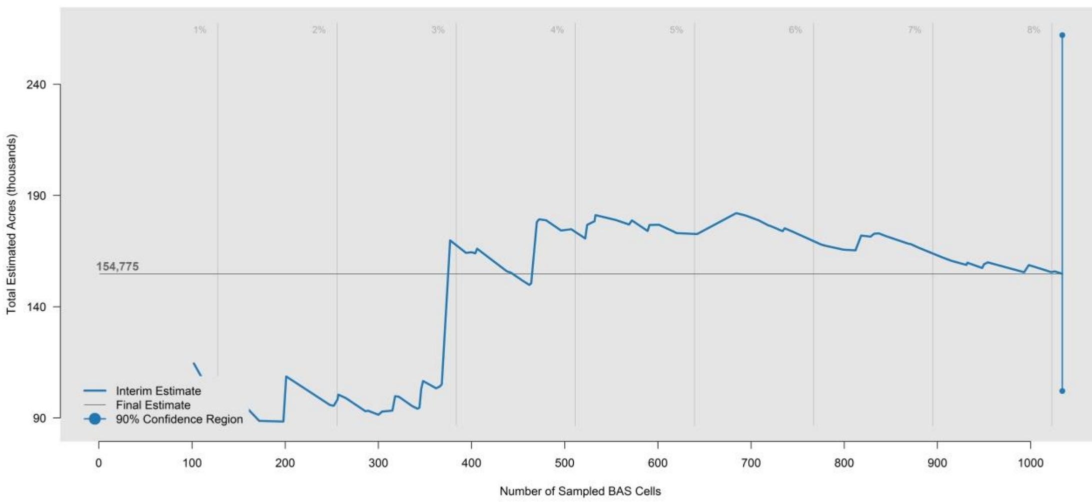

Figure 2.14. Estimated acreage of potential black-tailed prairie dog colonies in Kansas as a function of the size of the probabilistic sample of cells. One relatively large feature was detected at about the 390th cell, resulting in a relatively large increase in the estimated total acreage in Kansas.

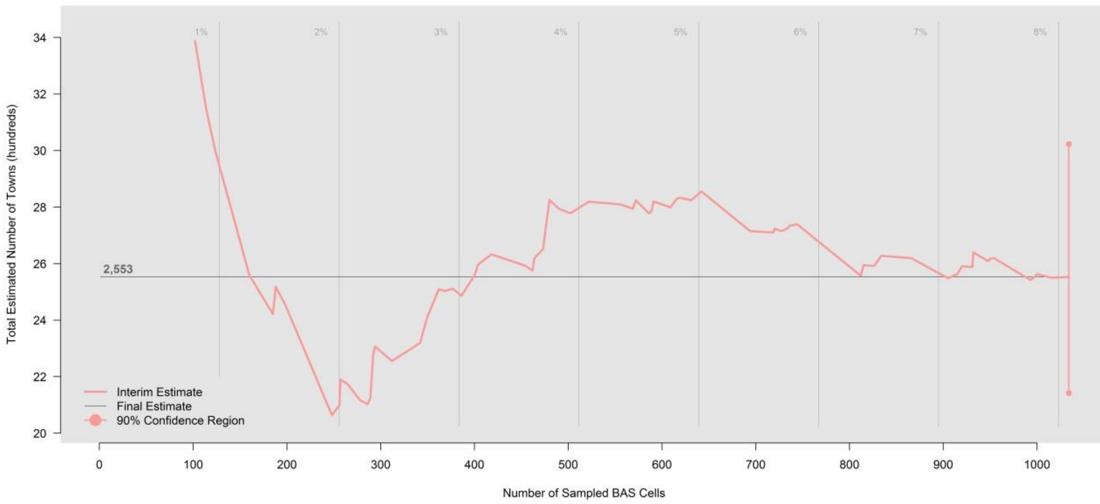

Figure 2.15. Estimated number of potential black-tailed prairie dog colonies in Kansas as a function of the sample size. The estimate begins to converge to final estimates at a sample size of about 800.

GIS shapefiles and electronic maps will be made available to the State of Kansas with the digitized features in the state and in each county. For example, figure 2.16, depicts the location of features detected and digitized in Logan County, KS. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

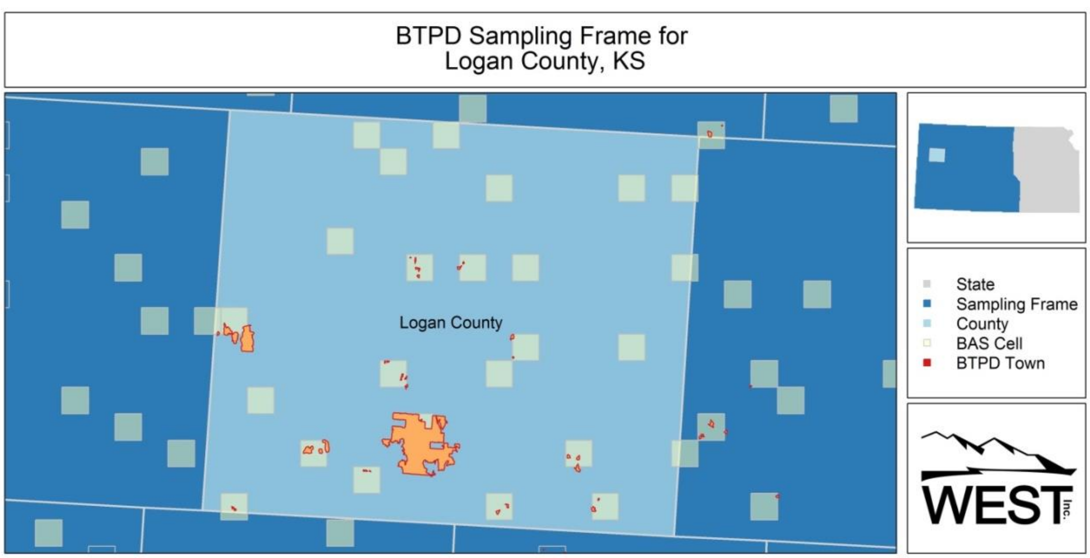

Figure 2.16. Digitized features on a sample survey of grid cells in Logan County, Kansas.

MONTANA

We used the shapefile of potential BTPD habitat provided by the Montana Natural Heritage Program (Dave Ratz, personal communication, February 19, 2015) to develop a sampling frame consisting of 16,302 grid cells that met the following criteria (Figure 2.17):

1) the cell contained any portion of area within the BTPD range according to the layer provided by the Montana National Heritage Program,
2) the cell had >50% of the land area within the grid cell designated as "Suitable Black-Tailed Prairie Dog Habitat" according to a predictive raster model provided by the Montana National Heritage Program (not shown), and
3) the cell had >50% of the land area within the grid cell situated at less than 5500 feet in elevation, using intersections with 1-arcsecond Digital Elevation Model layers from the National Elevation Dataset (USGS).

We digitized the perimeters of all features detected on 1,318 sampled grid cells selected from the universe of 16,302 cells in the sampling frame for Montana (Figure 2.18). We estimated a total of 184,055 acres of potential BTPD colonies in Montana (90% CI = [166,219; 210,408], CV = 8.3%) (Part1, Table 1.2). We estimated that a total of 4,006 features exist in the state (90% CI = [3,877; 4,188], CV = 5%) (Part 1, Table 1.4). We estimated 372 features greater than 100 acres (90% CI = [335; 434], CV = 11.8%) and 7 greater than 500 acres in Montana (Part 1, Tables 1.6 and 1.7).

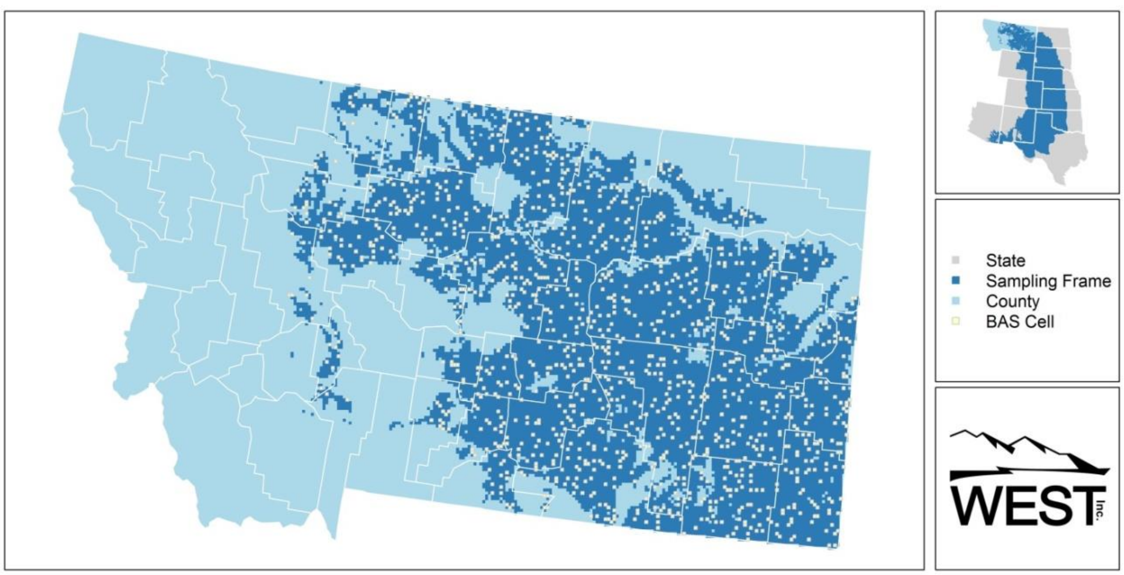

Figure 2.17. Sampling frame for Montana with 16,302 grid cells. The 1,318 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure was shown.

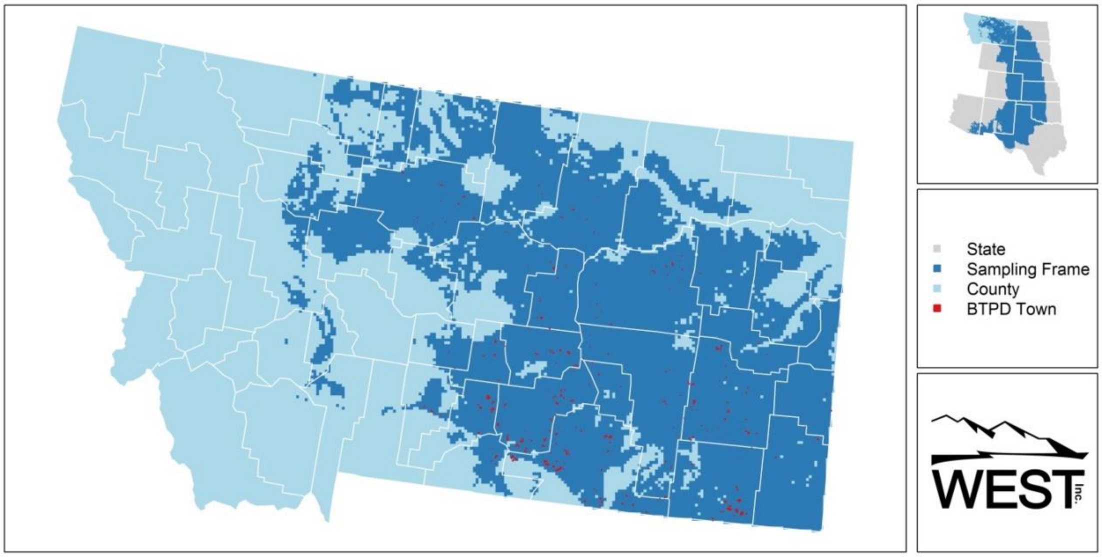

Figure 2.18. Map of features digitized in a sample survey of grid cells in Montana.

We plotted the estimates of total acreage of features and the total number of features as functions of the sample size (Figures 2.19 and 2.20). The estimated acreage and number of features began to converge to final estimates at a sample size of about 1,000 (Figure 2.19 and 2.20). Increasing the sample size to 1,318 grid cells yielded coefficients of variation less than 10%, values adequate for detecting important trends in long term monitoring projects. Estimates had adequate CVs of 8.3% and 5% for total acreage and number of features respectively at the sample size of 1,012.

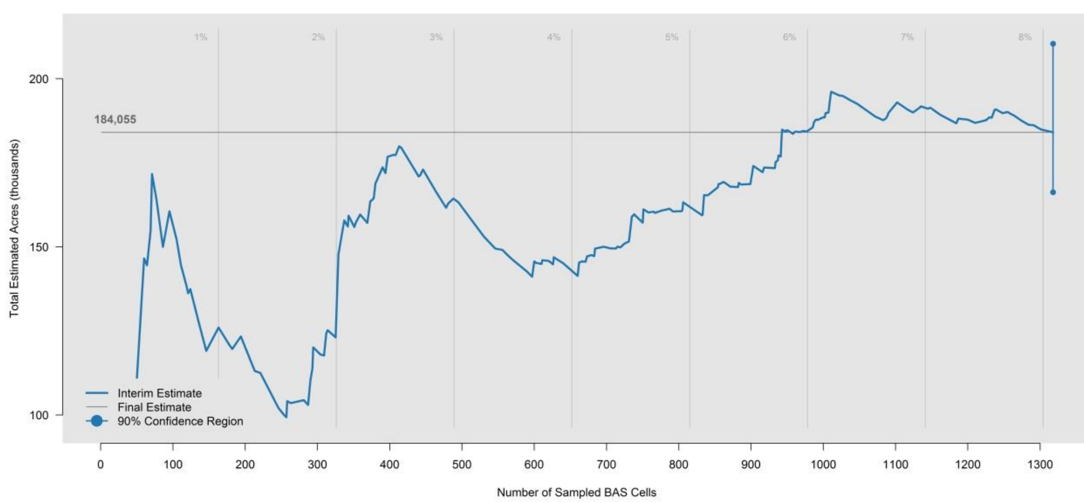

Figure 2.19. Estimated acreage of potential black-tailed prairie dog colonies in Montana as a function of the sample size. Sample size of approximately 1,000 was required for the estimate of total acreage to begin to converge to final estimates.

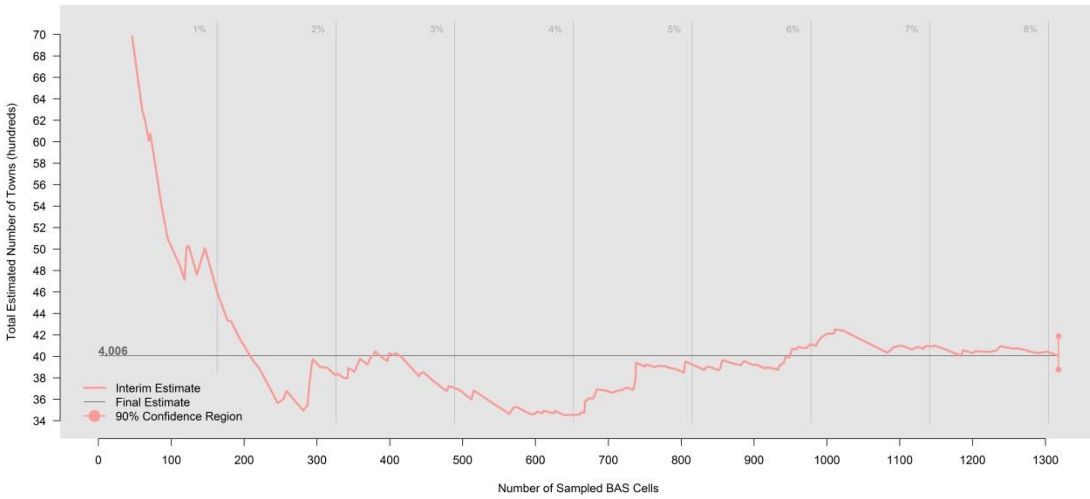

Figure 2.20. Estimated number of potential black-tailed prairie dog colonies in Montana as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of Montana with the digitized features in the state and in each county. For example, figure 2.21 depicts the location of features detected and digitized in Powder River County, MT. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

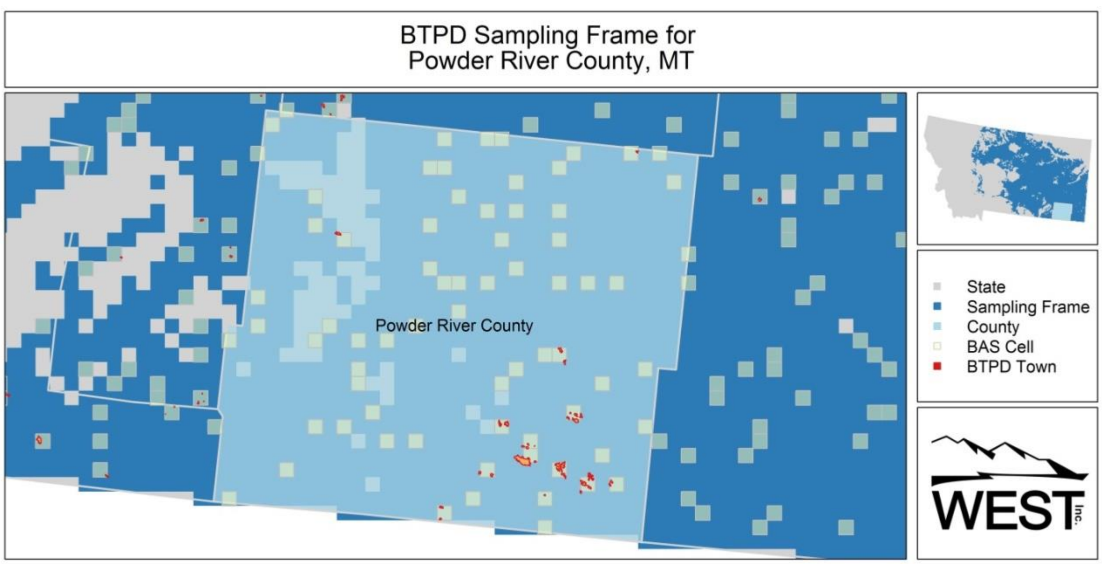

Figure 2.21. Digitized features on a sample survey of grid cells in Powder River County, Montana.

NEBRASKA

We used the shapefile of potential BTPD habitat provided by the Nebraska Game and Parks Division (Mike Fritz, personal communication, April 30, 2015) to develop a sampling frame consisting of grid cells that contained any portion of area within the 54 county area of interest (Adams, Arthur, Banner, Blaine, Box Butte, Boyd, Brown, Buffalo, Chase, Cherry, Cheyenne, Clay, Custer, Dawes, Dawson, Deuel, Dundy, Franklin, Frontier, Furnas, Garden, Garfield, Gosper, Grant, Greeley, Hall, Harlan, Hayes, Hitchcock, Holt, Hooker, Howard, Kearney, Keith, Keya Paha, Kimball, Lincoln, Logan, Loup, McPherson, Morrill, Nuckolls, Perkins, Phelps, Red Willow, Rock, Scotts Bluff, Sheridan, Sherman, Sioux, Thomas, Valley, Webster, Wheeler; Figure 2.22).

We digitized the perimeters of all features detected on 1,128 sampled grid cells selected from the universe of 13,960 cells in the sampling frame for Nebraska (Figure 2.23). We estimated a total of 89,208 acres of potential BTPD colonies in Nebraska (90% CI = [77,181; 107,481], CV = 10.7%) (Part1, Table 1.2). We estimated that a total of 2,317 features exist in the state (90% CI = [2,222; 2,456], CV = 5.9%) (Part 1, Table 1.4). We estimated 188 features greater than 100 acres (90% CI = [151; 250], CV = 21.5%) and 12 greater than 500 acres in Nebraska (90% CI = [12; 50], CV = 99%) (Part 1, Tables 1.6 and 1.7).

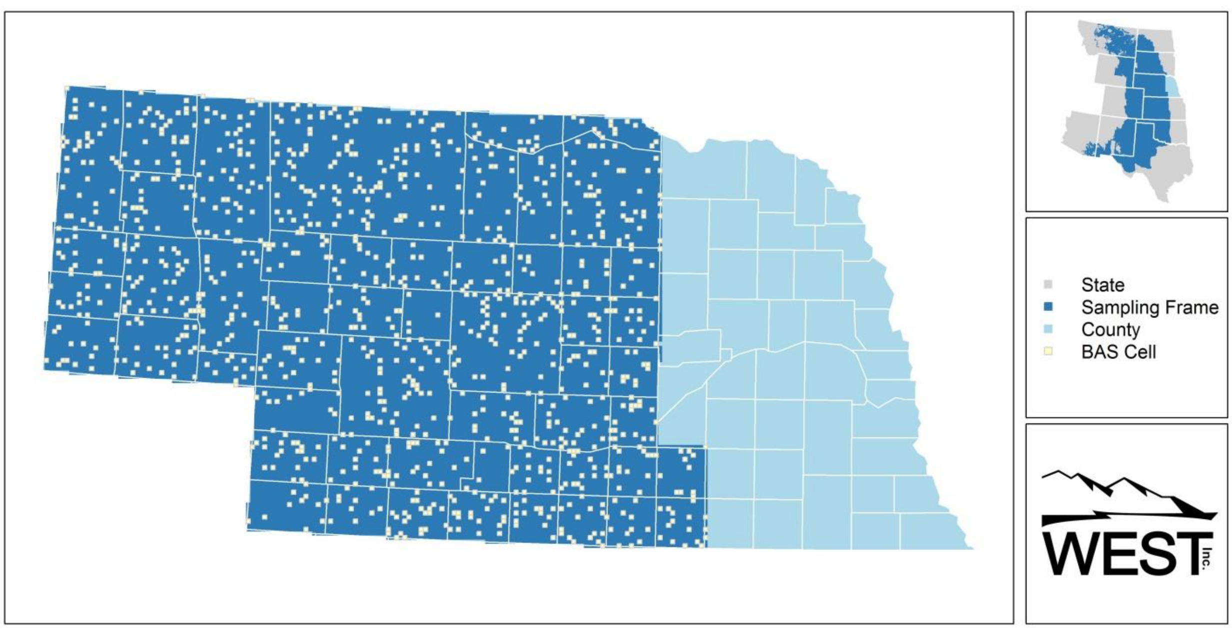

Figure 2.22. Sampling frame for Nebraska with 13,960 grid cells each 2 mi. by 2 mi. The 1,128 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

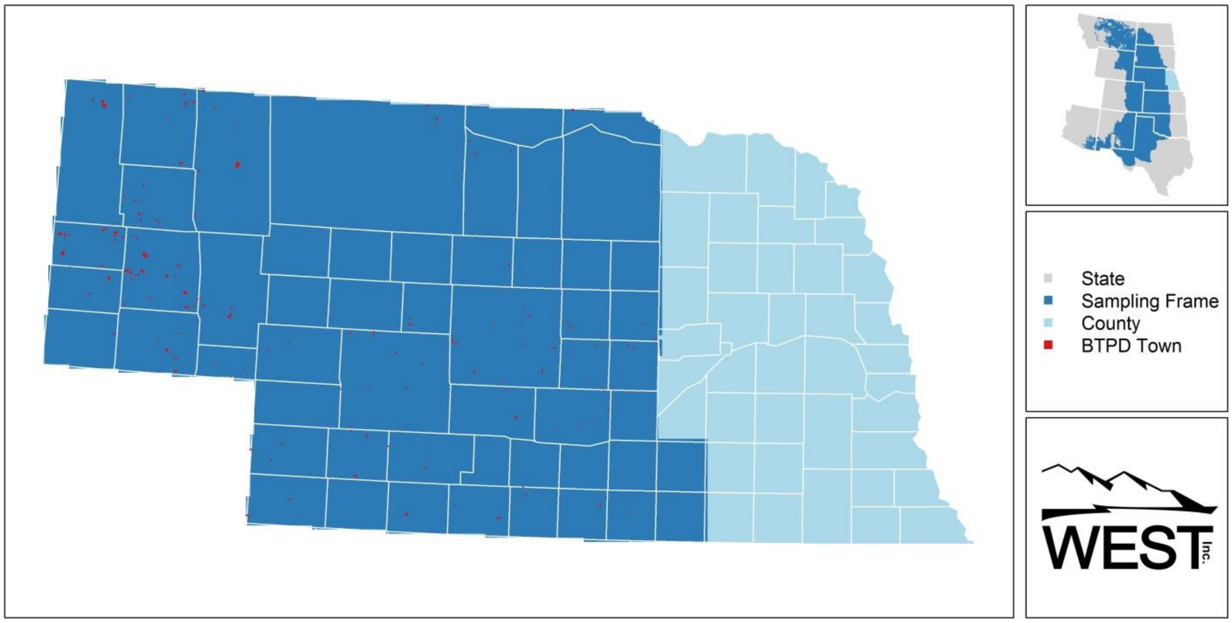

Figure 2.23. Map of features digitized in a sample survey of grid cells in Nebraska.

We plotted the estimates of total acreage of features and the total number of features as functions of the BAS sample size (Figures 2.24 and 2.25). The estimated number of features began to converge to final estimates at a sample size of about 800 (Figure 2.25). Increasing the sample size to 1,128 grid cells did not change the estimated total number of features appreciably. The effect of detecting relatively large, but rare, features on estimated total acreage of features was evident in figure 2.24. As the sample size was increased and rare large features detected, relatively large jumps occurred in the estimated total acreage. The estimated total acreage was more variable than the estimated total number of features; however it began converge to final estimates at a sample size of about 900 grid cells. Estimates had adequate CVs of 10.7% and 5.9% for total acreage and number of features respectively at the sample size of 1,128.

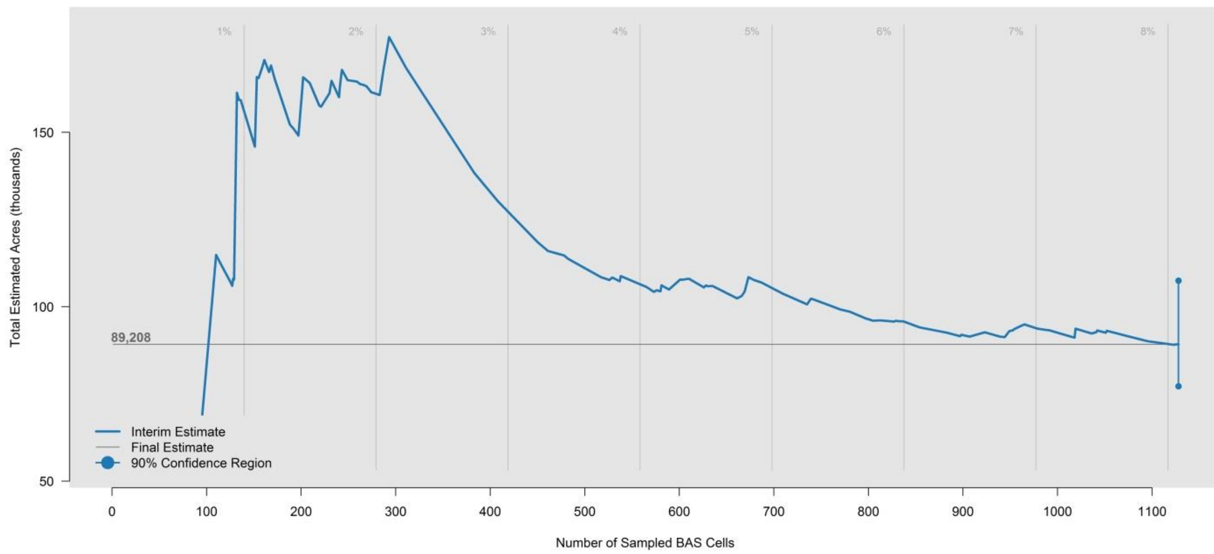

Figure 2.24. Estimated acreage of potential black-tailed prairie dog colonies in Nebraska as a function of the sample size. One or more relatively large features were detected early in the sample.

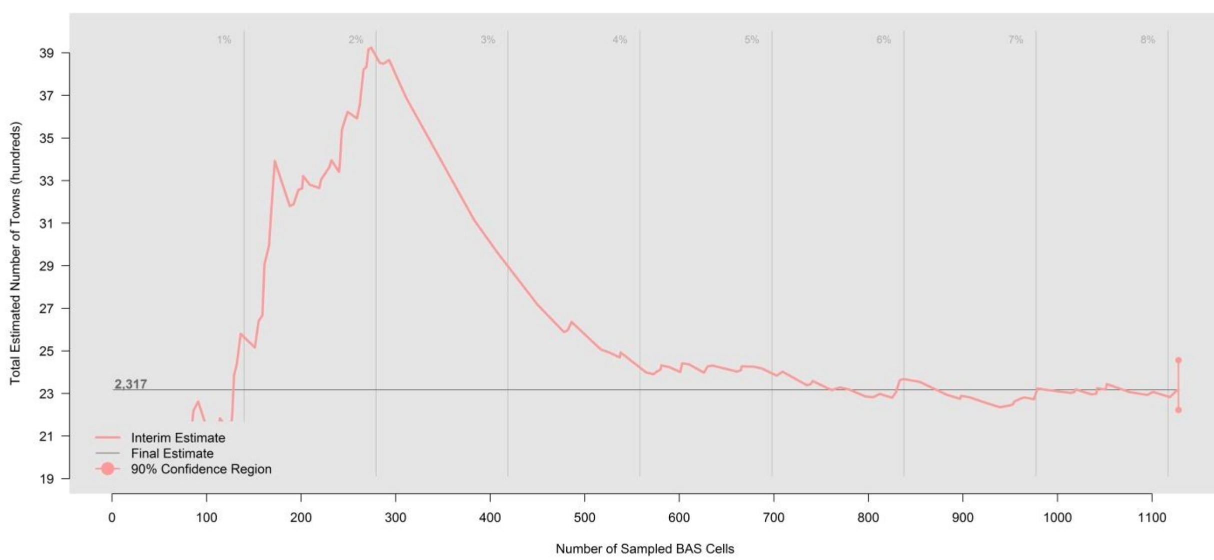

Figure 2.25. Estimated number of potential black-tailed prairie dog colonies in Nebraska as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of Nebraska with the digitized features in the state and in each county. For example, figure 2.26 depicts the location of features detected and digitized in Morrill County, Nebraska. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

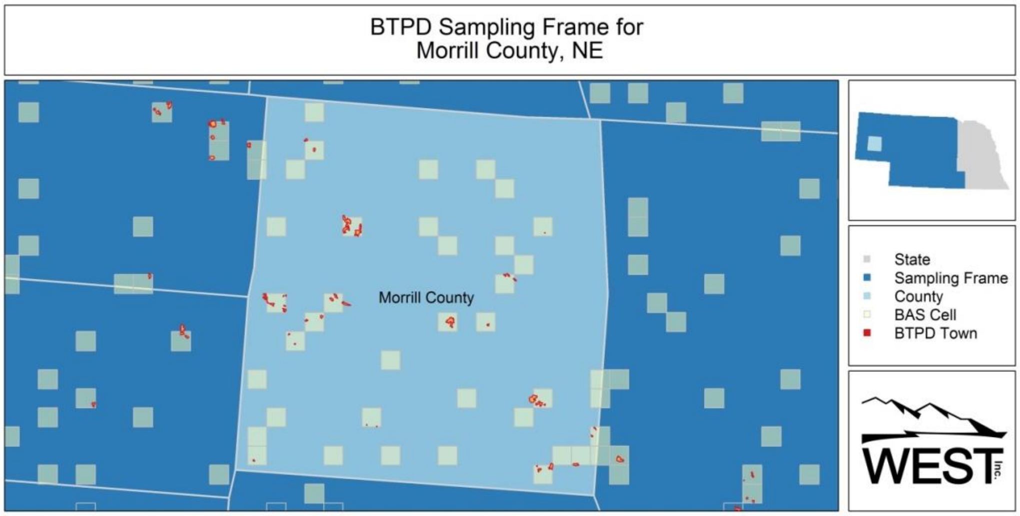

Figure 2.26. Digitized features on a sample survey of grid cells in Morrill County, Nebraska.

The Rainwater Basin Joint Venture (Grosse 2015) conducted a black-tail prairie dog colony inventory of Nebraska using 1-meter National Agriculture Imagery Program (NAIP, 2010) aerial imagery. They estimated the extent of each colony by placing polygon vertices on the furthest visible burrows, the same method implemented in this report. Burrows were then re-evaluated using 2013 sub-meter resolution imagery (Google earth images, 2013). They estimated 97,438 acres of BTPD colonies across the state of Nebraska. This estimate compares favorably with our estimate of 89,308 acres of features in Nebraska based on digitizing on a sample of cells on 1-meter resolution NAIP images taken in 2014.

NEW MEXICO

We used the shapefile of potential BTPD habitat provided by Natural Heritage New Mexico (Teri Brotman Neville, personal communication, March 11, 2015) to develop a sampling frame consisting of grid cells that met the following criteria (Figure 2.27):

1) the cell contained any portion of area within the "historic range for Black-Tailed Prairie Dogs" according to the layer provided by Natural Heritage New Mexico, and
2) did not contain any portion of area with unavailable NAIP imagery (imagery unavailable over area including and surrounding White Sands Missile Range).

We digitized the perimeters of all features detected on 1,362 sampled grid cells selected from the universe of 16,852 cells in the sampling frame for New Mexico (Figure 2.28). We estimated a total of 124,098 acres of potential BTPD colonies in New Mexico (90% CI = [103,228; 155,709], CV = 13.5%) (Part1, Table 1.2). We estimated that a total of 1,964 features exist in the state (90% CI = [1,856; 2,123], CV = 8.4%) (Part 1, Table 1.4). We estimated 334 features greater than 100 acres (90% CI = [297; 409], CV = 14.1%) and 25 greater than 500 acres in New Mexico (90% CI = [25; 74], CV = 61%) (Part 1, Tables 1.6 and 1.7).

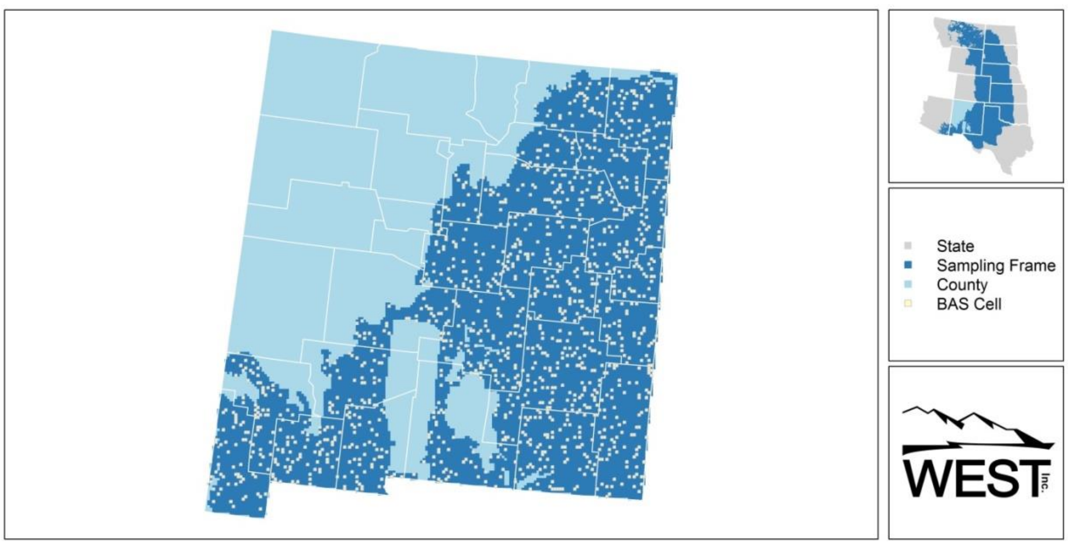

Figure 2.27. Sampling frame for New Mexico with 16,852 grid cells each 2 mi. by 2 mi. The 1,362 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

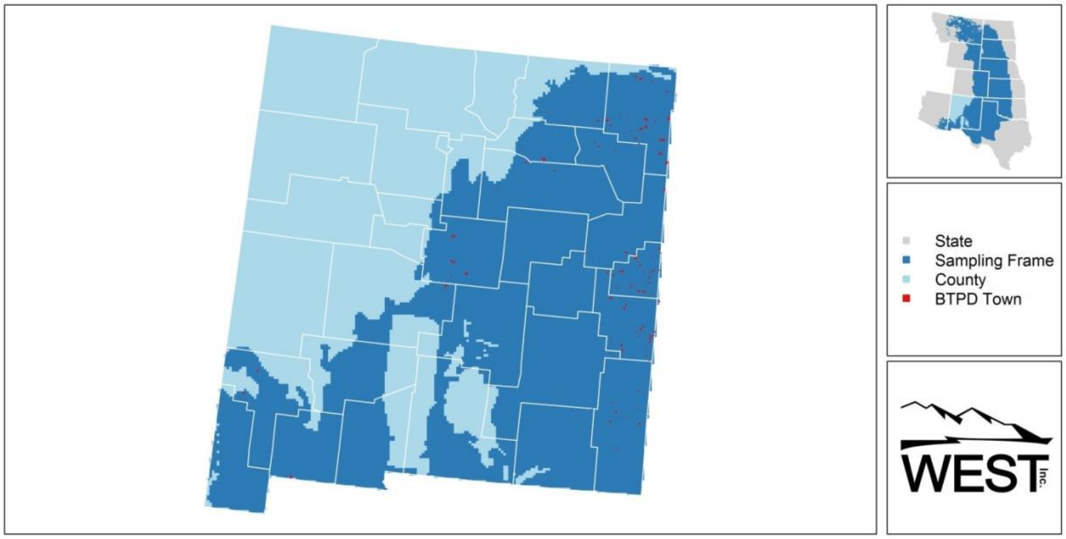

Figure 2.28. Map of features digitized in a sample survey of grid cells in New Mexico.

We plotted the estimates of total number of features and acreage of features as a function of the BAS sample size (Figures 2.29 and 2.30). The estimated number of features began to converge to final estimates at a sample size of about 700 (Figure 2.30). Increasing the sample size to 1,362 grid cells did not change the estimated total number of features appreciably. The effect of detecting rare relatively large features on estimated total acreage of features was evident in Figure 2.29. As the sample size was increased and a rare large feature detected, relatively large jumps occurred in the estimated total acreage. The estimated total acreage began to converge to final estimates at a sample size of about 1,000 grid cells. Estimates had adequate CVs of 13.5% and 8.4% for total acreage and number of features respectively at the sample size of 1, 362.

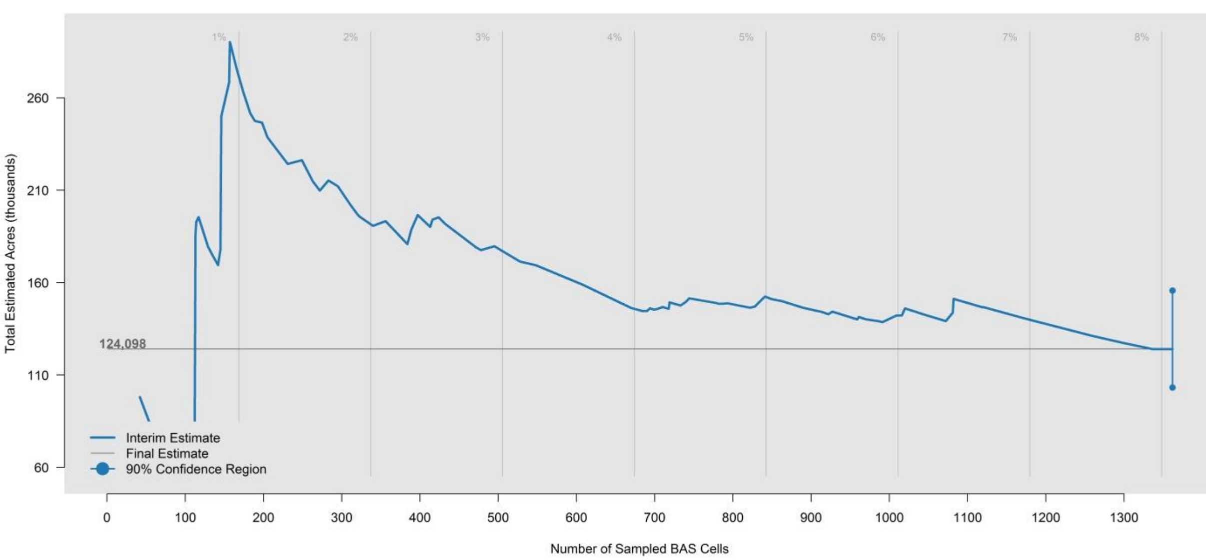

Figure 2.29. Estimated acreage of potential black-tailed prairie dog colonies in New Mexico as a function of the sample size.

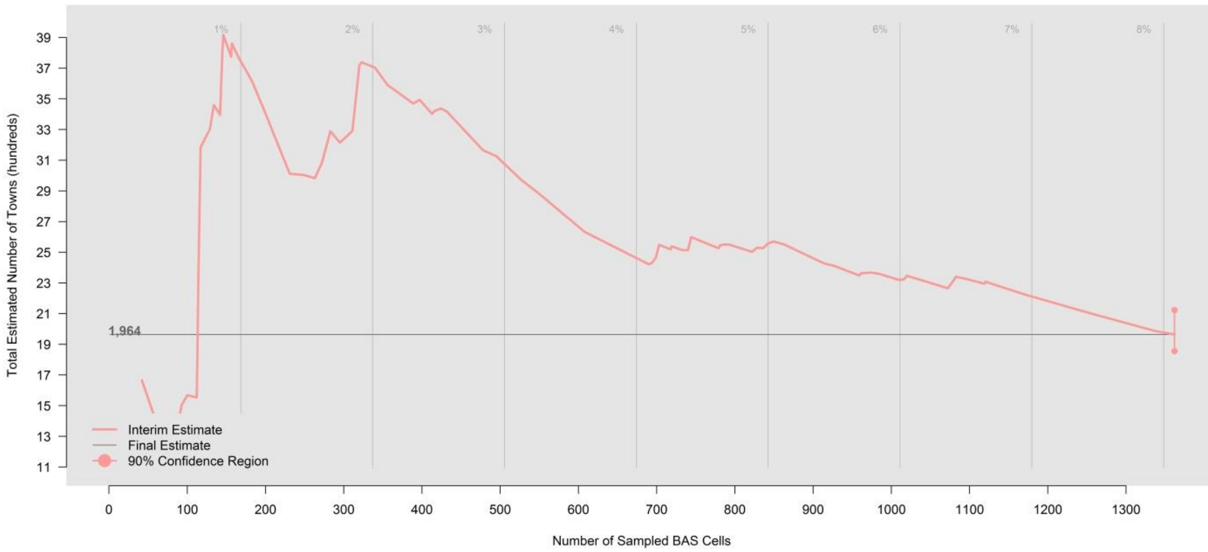

Figure 2.30. Estimated number of potential black-tailed prairie dog colonies in New Mexico as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of New Mexico with the digitized features in the state and in each county. For example, figure 2.31, depicts the location of features detected and digitized in Curry County, New Mexico. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

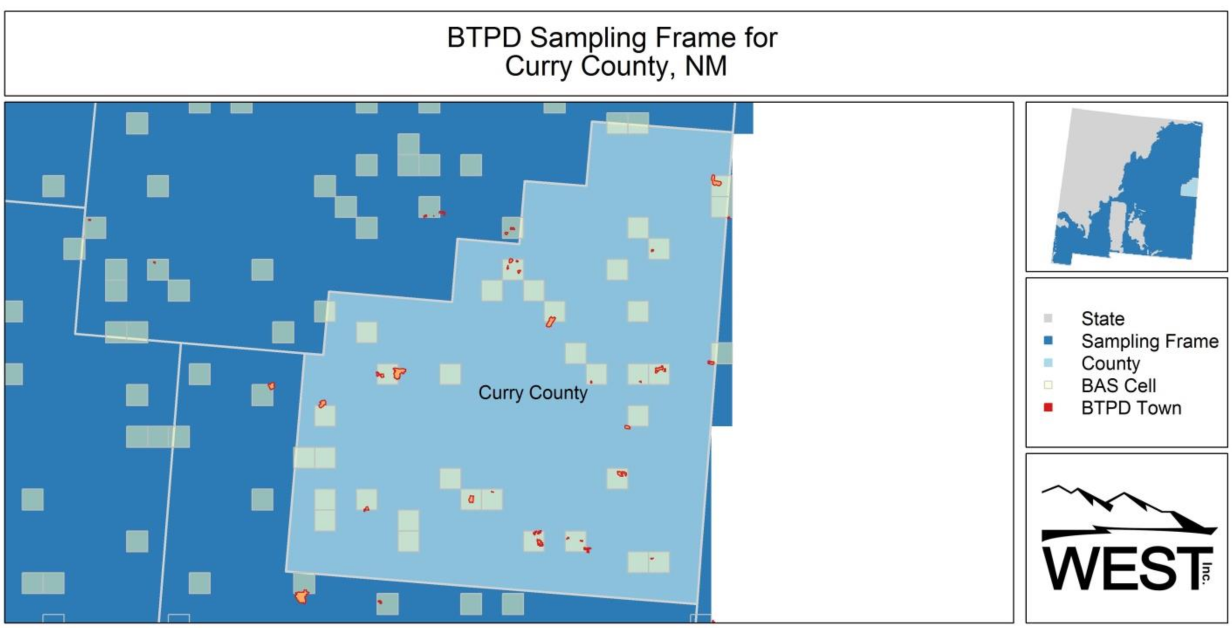

Figure 2.31. Digitized features on a sample survey of grid cells in Curry County, New Mexico.

NORTH DAKOTA

We used the shapefile of potential BTPD habitat provided by the North Dakota Game and Fish Department (Patrick Isakson, personal communication, March 9, 2015) to develop a sampling frame consisting of grid cells that contained any portion of the overall range (Figure 2.32).

We digitized the perimeters of all features detected on 1,012 sampled grid cells selected from the universe of 5,011 cells in the sampling frame for North Dakota (Figures 2.33). We estimated a total of 15,561 acres of potential BTPD colonies in North Dakota (90% CI = [9,578; 27,760], CV = 33.1% (Part 1, Table 1.2) and that a total of 299 features exist in the state (90% CI = [219; 394], CV = 17.7%) (Part 1, Table 1.4). We estimated 30 features greater than 100 acres (90% CI = [15; 59], CV = 40.9%) and 5 greater than 500 acres in North Dakota (90% CI = [5; 20], CV = 100%) (Part 1, Tables 1.6 and 1.7).

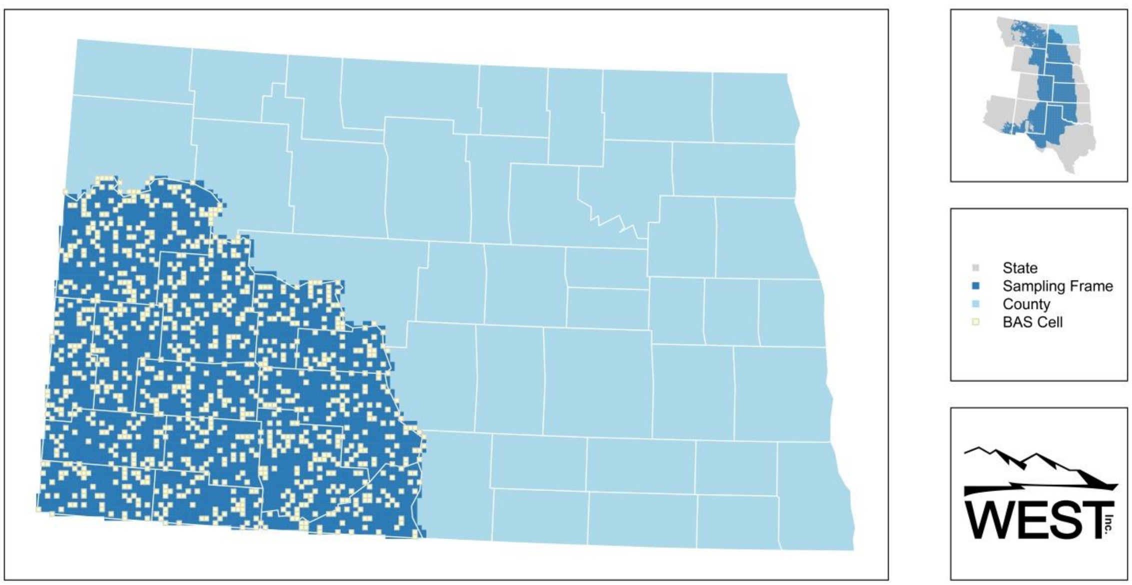

Figure 2.32. Sampling frame for North Dakota with 5,011 grid cells each 2 mi. by 2 mi. The 1,012 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

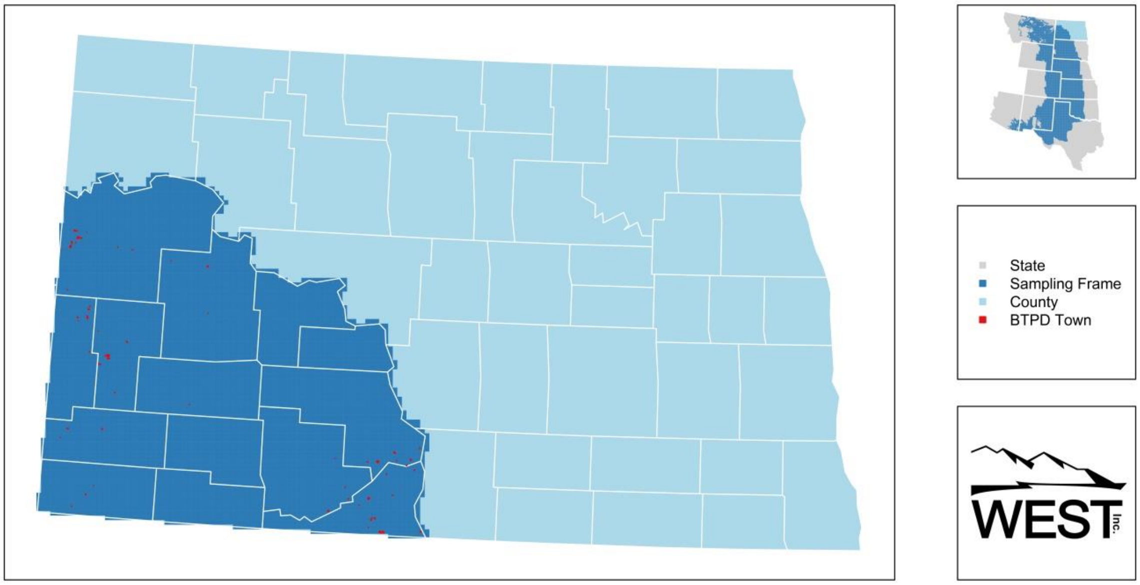

Figure 2.33. Map of features digitized in a sample survey of grid cells in North Dakota.

We plotted the estimates of total number of features and acreage of features as a function of the BAS sample size (Figures 2.34 and 2.35). The estimated number of features began to converge to the final estimate at a sample size of about 300 (Figure 2.35). Increasing the sample size to 1,012 grid cells did not change the estimated total number of features appreciably. The effect of detecting rare relatively large features on estimated total acreage of features was evident in Figure 2.34. As the sample size was increased and a rare large feature detected, relatively large jumps occurred in the estimated total acreage. The estimated total acreage began to converge to final estimates at a sample size of about 1,000 grid cells. Estimates had CVs of 33.1% and 17.7% for total acreage and number of features respectively at the sample size of 1,012. Estimates with CV greater than 30% were marginally adequate for detection of important trends in long term monitoring programs, indicating that the sample size should be increased in North Dakota.

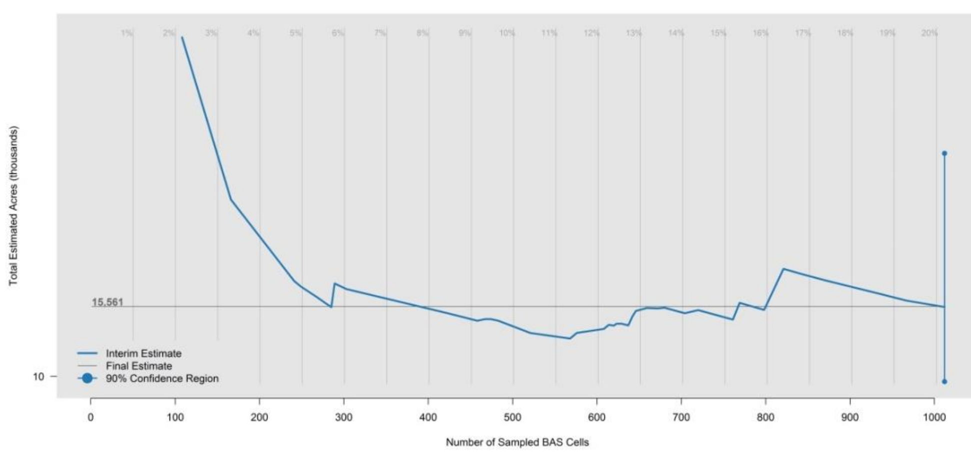

Figure 2.34. Estimated acreage of potential black-tailed prairie dog colonies in North Dakota as a function of the sample size.

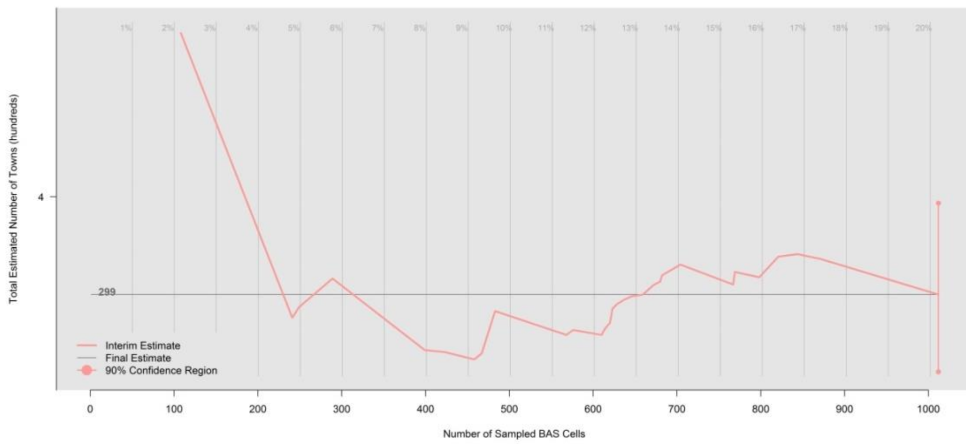

Figure 2.35. Estimated number of potential black-tailed prairie dog colonies in North Dakota as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of North Dakota with the digitized features in the state and in each county. For example, figure 2.36, depicts the location of features detected and digitized in Billings County, North Dakota. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

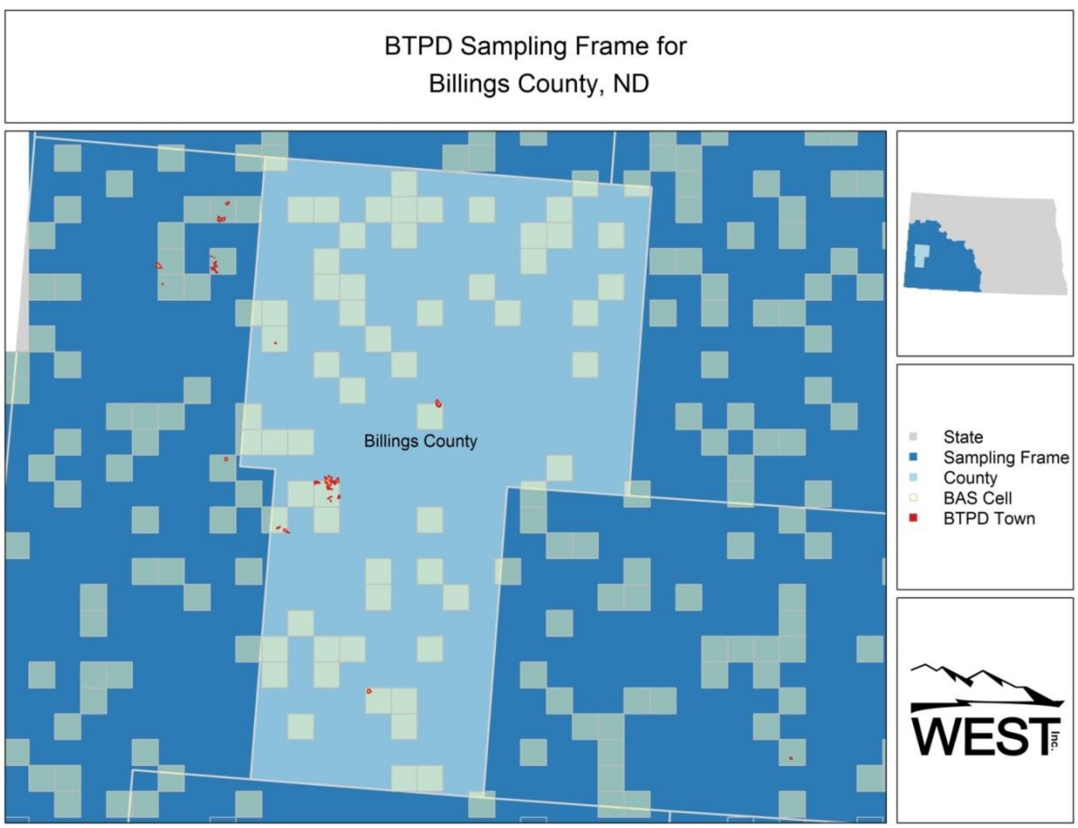

Figure 2.36. Digitized features on a sample survey of grid cells in Billings County, North Dakota.

OKLAHOMA

We used the shapefile of potential BTPD habitat provided by the Oklahoma Department of Wildlife Conservation (Kara M. Caricato-Michalke, personal communication, February 11, 2015) to develop a sampling frame that consisted of grid cells that contained any portion of the overall range (Figure 2.37). We digitized the perimeters of all features detected on 1,078 sampled grid cells selected from the universe of 8,888 cells in the sampling frame for Oklahoma (Figure 2.38). We estimated a total of 81,224 acres of potential BTPD colonies in Oklahoma (90% CI = [63,015; 107,187], CV = 16.3%) (Part 1, Table 1.2). We estimated that a total of 1,816 features exist in the state (90% CI = [1,542; 2,115], CV = 9.6%) (Part 1, Table 1.4). We estimated 218 features greater than 100 acres (90% CI = [141; 305], CV = 22.7%) and 3 greater than 500 acres in Oklahoma (Part 1, Tables 1.6 and 1.7).

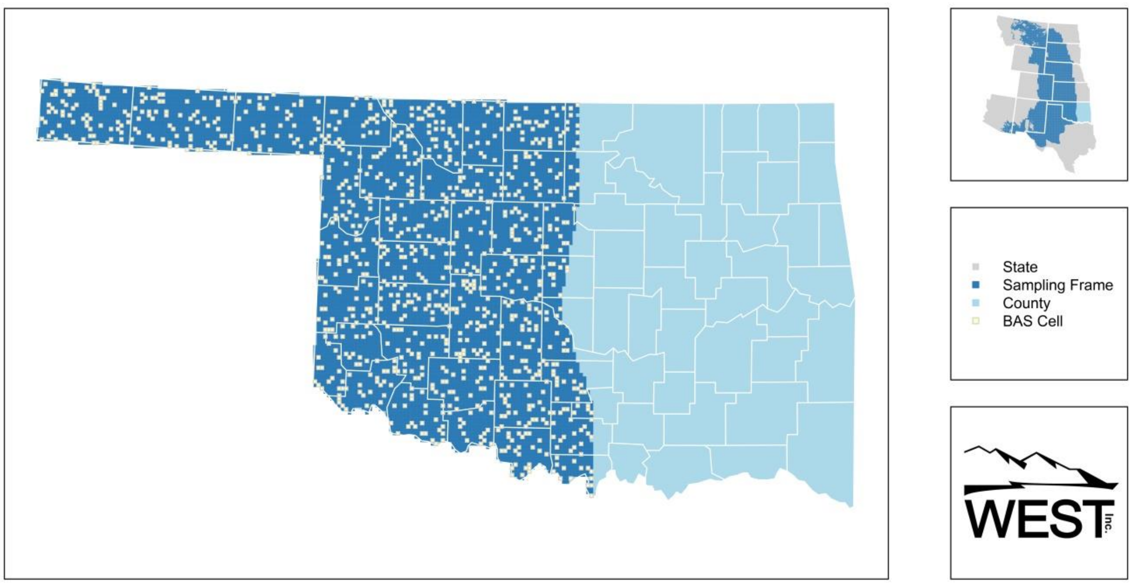

Figure 2.37. Sampling frame for Oklahoma with 8,888 grid cells each 2 mi. by 2 mi. The 1,078 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

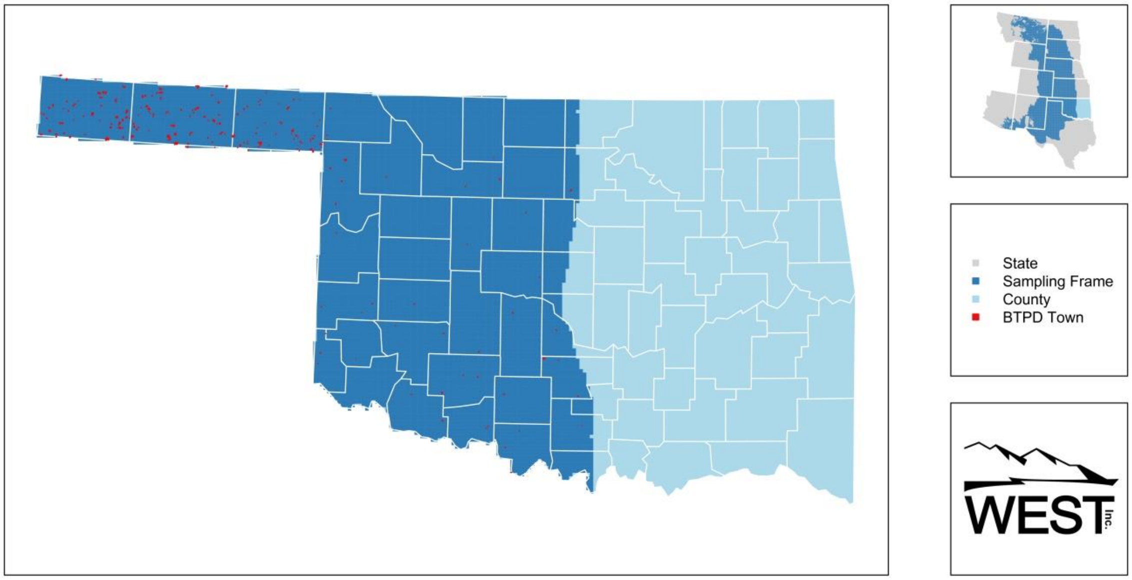

Figure 2.38. Map of features digitized in a sample survey of grid cells in Oklahoma.

We plotted the estimates of total acreage of features and the total number of features as functions of the BAS sample size (Figures 2.39 and 2.40). The estimated total acreage of features began to converge to final estimates at a sample size of about 500 (Figure 2.39). Increasing the sample size to 1,078 grid cells did not change the estimated total acreage appreciably. The estimated total number of features was more variable than the estimated total acreage (Figure 2.40). Estimates had adequate CVs of 16.3% and 9.6% for total acreage and number of features respectively at the sample size of 1,078.

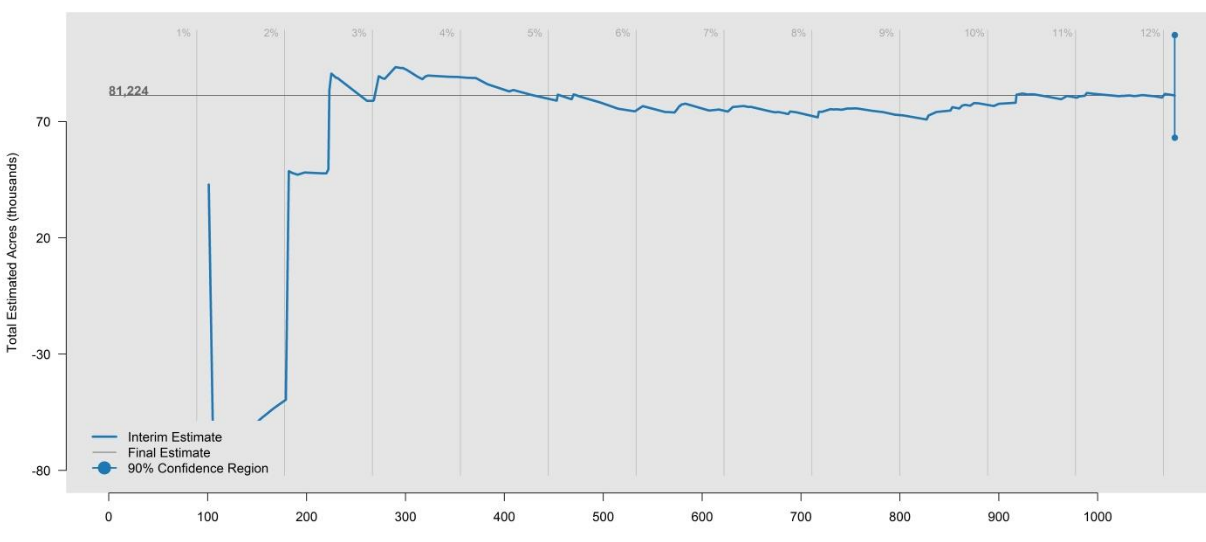

Figure 2.39. Estimated acreage of potential black-tailed prairie dog colonies in Oklahoma as a function of the sample size.

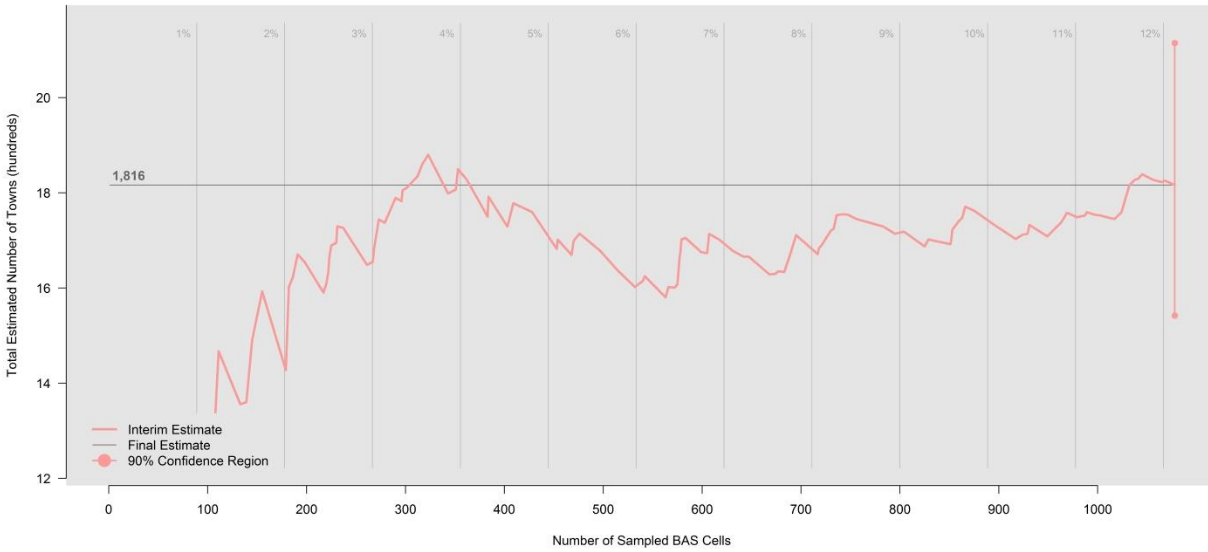

Figure 2.40. Estimated number of potential black-tailed prairie dog colonies in Oklahoma as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of Oklahoma with the digitized features in the state and in each county. For example, figure 2.41, depicts the location of features detected and digitized in Texas County, Oklahoma. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

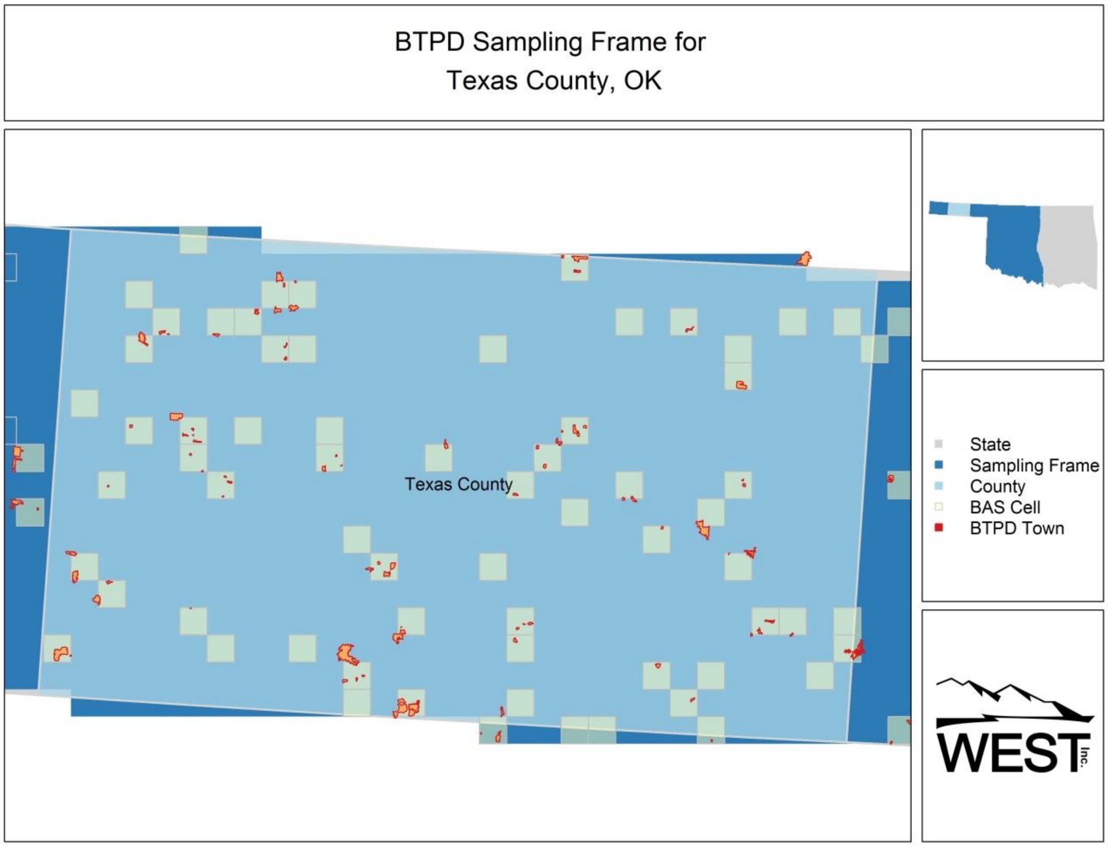

Figure 2.41. Digitized features on a sample survey of grid cells in Texas County, Oklahoma.

SOUTH DAKOTA

We used the shapefile of potential BTPD habitat provided by the South Dakota Department of Game, Fish and Parks (Silka L. F. Kempema, personal communication, January 28, 2015) to develop a sampling frame that consisted of grid cells that contained any portion of the overall range (Figure 2.42). We digitized the perimeters of all features detected on 1,230 sampled grid cells selected from the universe of 12,165 cells in the sampling frame for South Dakota (Figure 2.43). We estimated a total of 224,145 acres of potential BTPD colonies in South Dakota (90% CI = [187,303; 270,383], CV = 11.2%) (Part 1, Table 1.2) and that a total of 5,204 features exist in the state (90% CI = [4,693; 5,763], CV = 6.3 %) (Part 1, Table 1.4). We estimated 458 features greater than 100 acres (90% CI = [352; 577], CV = 14.9%) and 20 greater than 500 acres in South Dakota (90% CI = [10; 59], CV = 71%) (Part 1, Tables 1.6 and 1.7).

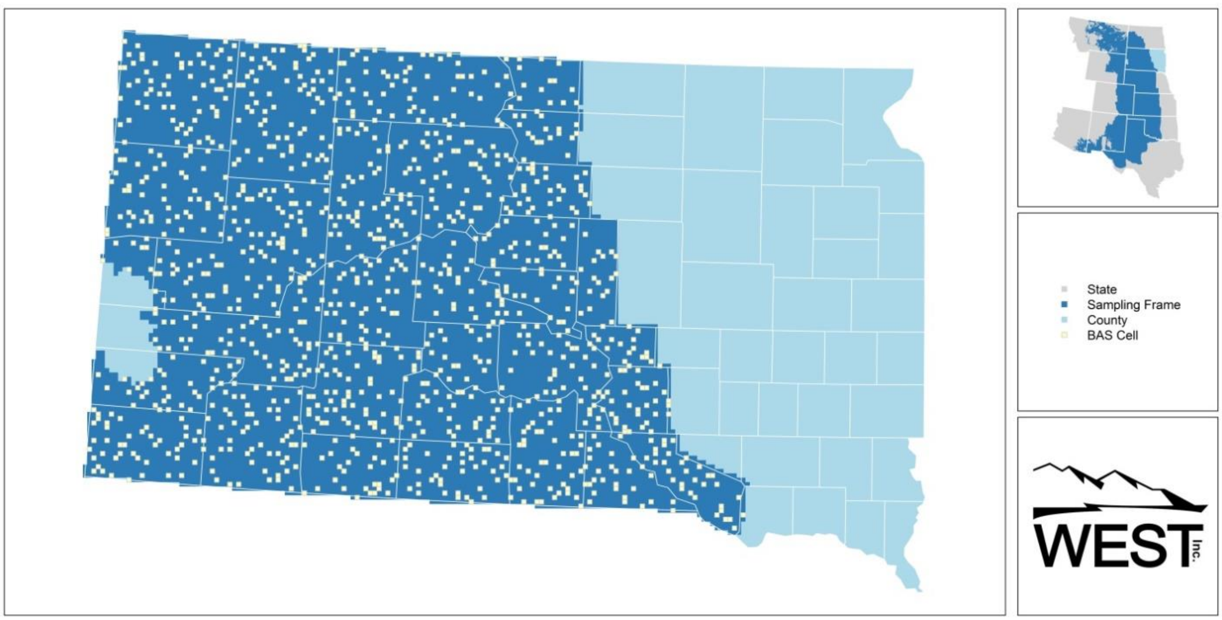

Figure 2.42. Sampling frame for South Dakota with 12,165 grid cells each 2 mi. by 2 mi. The 1,230 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

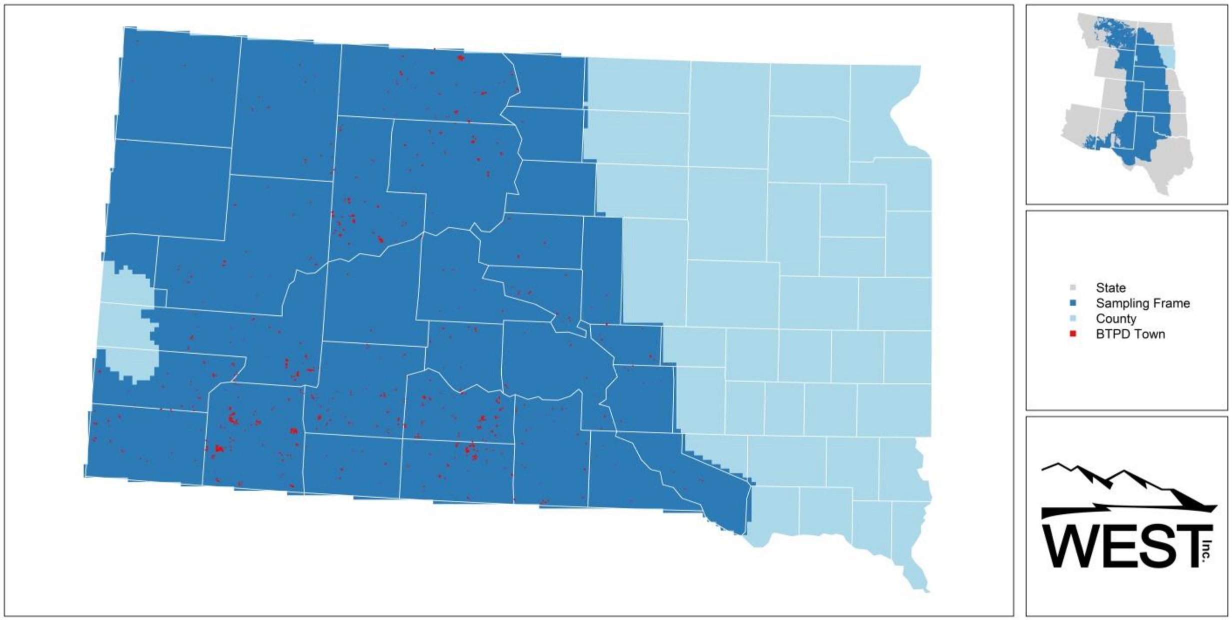

Figure 2.43. Map of features digitized in a sample survey of grid cells in South Dakota.

We plotted the estimates of total acreage of features and the total number of features as a function of the BAS sample size (Figures 2.44 and 2.45). The estimated total acreage of features began to converge to final estimates at a sample size of about 700 (Figure 2.44). The estimated number of features began to converge to final estimates at a sample size of about 1100 (Figure 2.45). Estimates had adequate CVs of 11.2% and 6.3% for total acreage and number of features respectively at the sample size of 1,230.

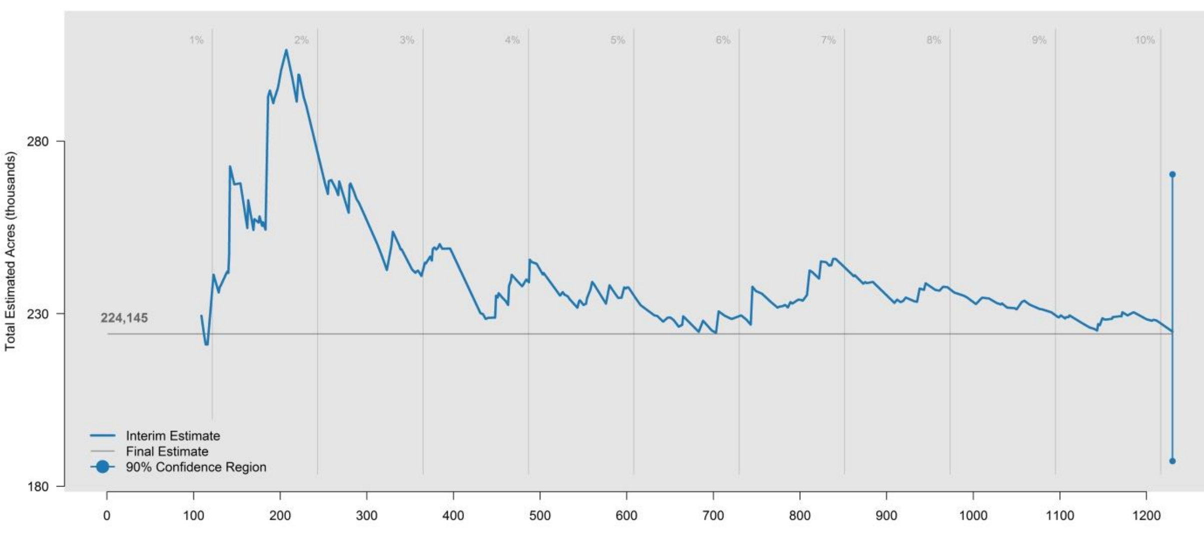

Figure 2.44. Estimated acreage of potential black-tailed prairie dog colonies in South Dakota as a function of the sample size.

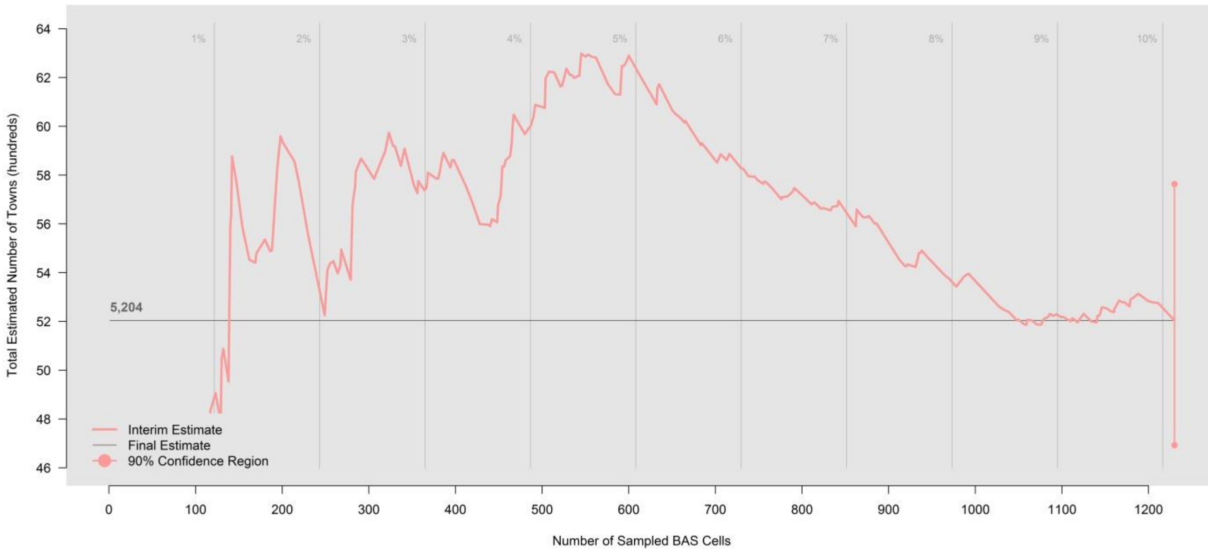

Figure 2.45. Estimated number of potential black-tailed prairie dog colonies in South Dakota as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of South Dakota with the digitized features in the state and in each county. For example, figure 2.46, depicts the location of features detected and digitized in Oglala Lakota County (Shannon County), South Dakota. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

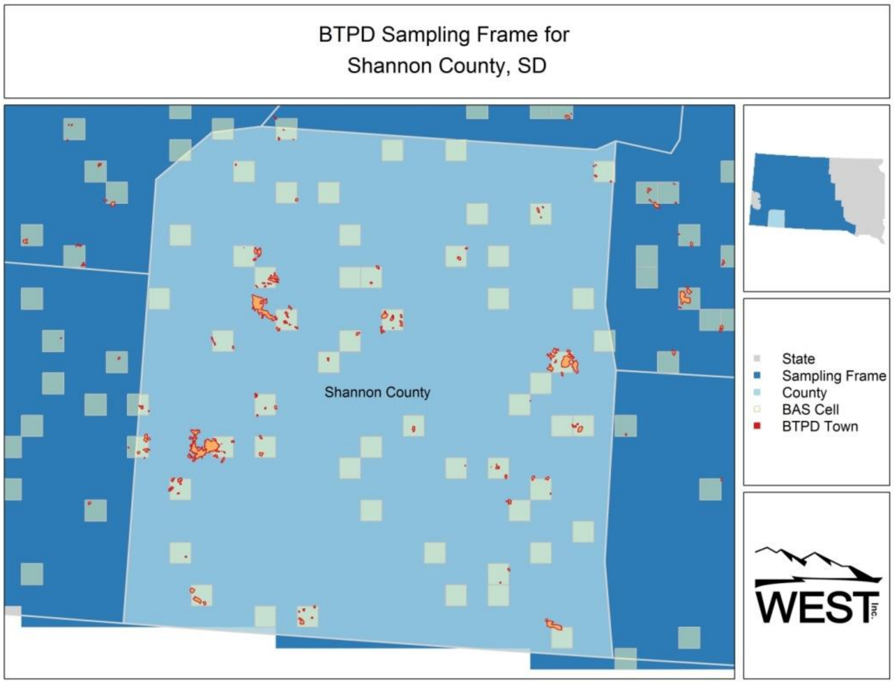

Figure 2.46. Digitized features on a sample survey of grid cells in Oglala Lakota County (Shannon County), South Dakota.

Analysis of Features Digitized by South Dakota Department of Game, Fish and Parks' Personnel

Employees of the South Dakota Department of Game, Fish and Parks independently digitized features on the same sample survey of 1,230 grid cells selected by the BAS probabilistic sampling procedure (Silka L. F. Kempema, personal communication). Training and experience of observers differed; however, the primary difference in methods was that South Dakota employees attempted to digitize polygons that "followed the clip line." We analyzed the features digitized by the South Dakota Department of Game, Fish and Parks using the same analysis methods as used by WEST, Inc. We adjusted for probability of detection (false negatives) using the average probability of detection curve for WEST observers. The estimated acreage of potential BTPD colonies in South Dakota as a function of the sample size was plotted in Figure 2.47 where the estimated acreage converged to 285,318 acres.

Our estimate of 224,145 acres (Figure 2.44) was 79% of the estimate that we derived using the shapefile provided by the South Dakota Department of Game, Fish and Parks (Figure 2.47). The estimated acreage derived from the South Dakota effort was 21% larger than our estimate for two reasons. First, the South Dakota observers detected and digitized many more small features than our observers. The histogram in Figure 2.48 showed that South Dakota observers digitized more features of less than 20 acres than WEST observers. However, an enlarged Figure 2.49 of Oglala Lakota County (Shannon County) indicated that WEST observers also digitized features that were not detected by South Dakota observers. Second, South Dakota observers digitized the outer most "clip line" of detected features resulting in larger acreages in each colony and a larger overall estimate.

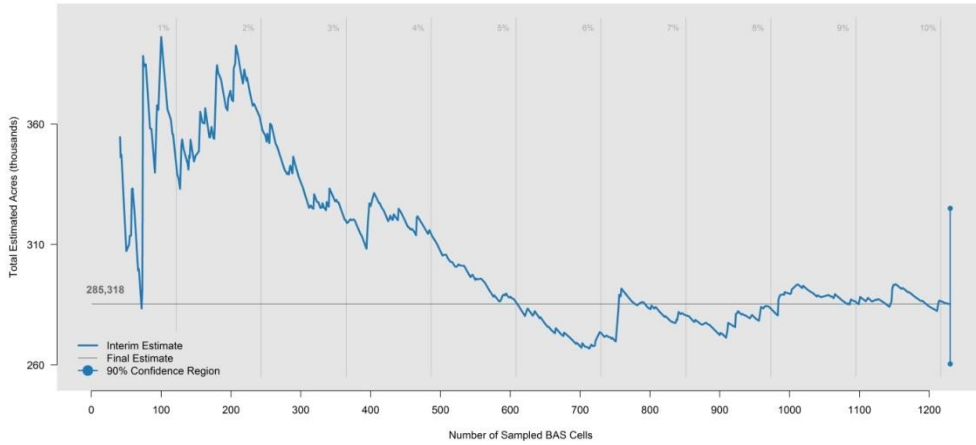

Figure 2.47. Estimated acreage of potential black-tailed prairie dog colonies in South Dakota as a function of the sample size, based on features digitized by South Dakota Department of Game, Fish and Parks employees.

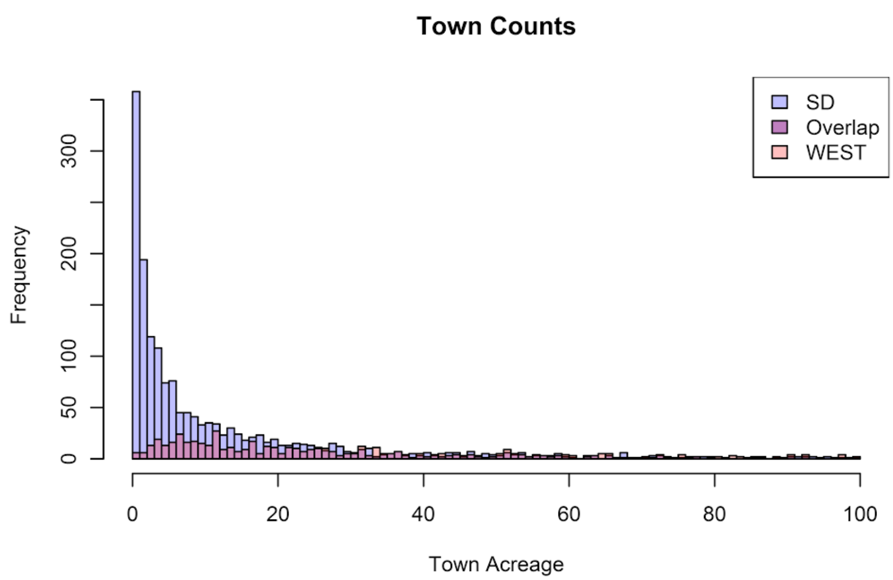

Figure 2.48. Frequency of features by size category digitized by: South Dakota observers and not detected by WEST observers, WEST observers and not detected by South Dakota observers, and overlap of the two sets of observers. Frequencies were shown for features less than 100 acres in size.

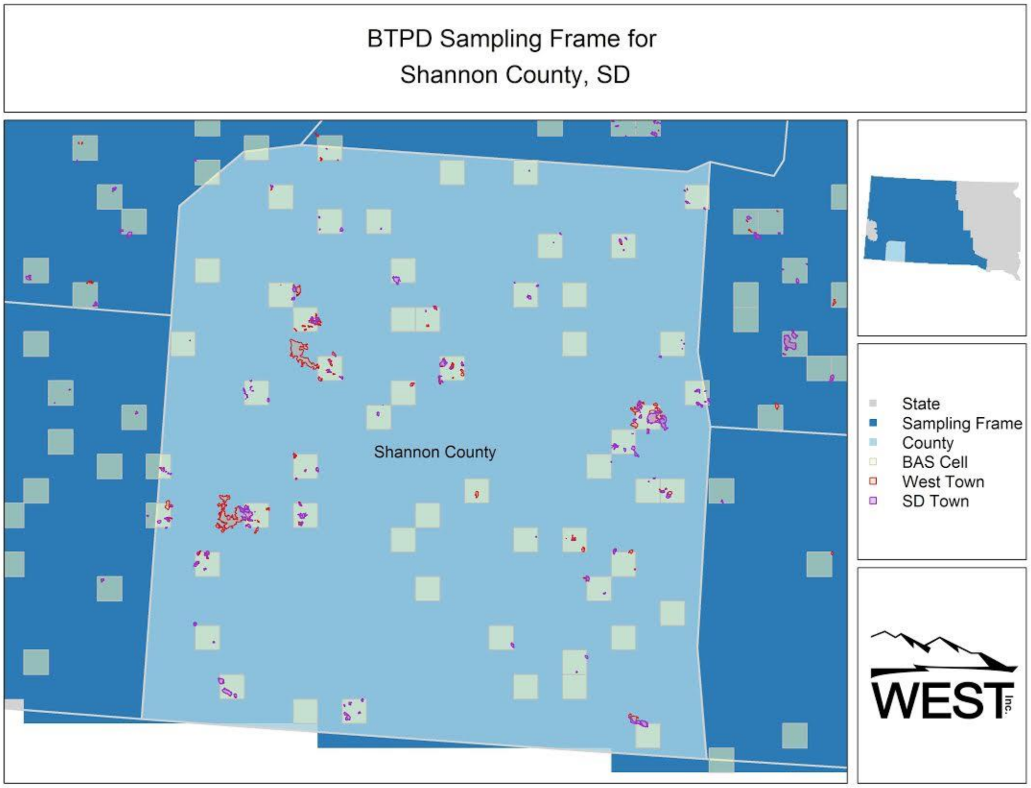

Figure 2.49. Digitized features on a sample survey of grid cells in Shannon County (recently renamed Oglala Lakota County), South Dakota by WEST observers and by South Dakota observers.

TEXAS

We started with two shapefiles of potential BTPD habitat in Texas provided by the Texas Parks and Wildlife (Bob Gottfried, personal communication, Texas Natural Diversity Database Administrator, March 10, 2015). We included grid cells in the sampling frame which met the following criteria (Figure 2.50):

1) cells contained any portion of area within the “Verified BTPD records within 7.5 minute quads” layer provided by Texas Parks and Wildlife (verified through 2008),
2) cells contained any portion of area within the “Texas range of Black-tailed Prairie Dogs,” digitized from Figure 2 in the “Texas Black-tailed Prairie Dog Conservation and Management Plan,” prepared by the Texas Black-tailed Prairie Dog Working Group (2004),
3) cells contained any portion of area within the “Estimated current (2002-2004) distribution of the black-tailed prairie dog in Texas,” digitized from Figure 4 in the article “Estimating black-tailed prairie dog (*Cynomys ludovicianus*) distribution in Texas” (Singhurst, J.R., J.H. Young, G. Kerouae, and H.A. Whitlaw. 2010. Texas J. of Sci. 62: 243-262.),
4) cells contained any portion of area within the “Estimated historical (pre-2000) distribution of the black-tailed prairie dog in Texas” from where it intersects the east border of Brewster County west to the New Mexico border, digitized from Figure 3 in the article “Estimating black-tailed prairie dog (*Cynomys ludovicianus*) distribution in Texas” (Singhurst, J.R., J.H. Young, G. Kerouae, and H.A. Whitlaw. 2010. Texas J. of Sci. 62: 243-262.),
5) cells did not contain any portion of area with unavailable NAIP imagery (imagery unavailable over a small area of Hudspeth County, and
6) the southern boundary was “smoothed” to fill in jagged gaps between component layers as listed above.

We digitized the perimeters of all features detected on 1,982 sampled grid cells selected from the universe of 24,539 cells in the sampling frame for Texas (Figure 2.51). We estimated a total of 238,871 acres of potential BTPD colonies in Texas (90% CI = [193,281; 304,826], CV = 14.2 %) (Part1, Table 1.2) and that a total of 2,353 features exist in the state (90% CI = [2,256; 2,496], CV = 6.2%)(Part 1,Table 1.4). We estimated 446 features greater than 100 acres (90% CI = [409; 508], CV = 10.9%) and 87 greater than 500 acres in Texas (90% CI = [62; 124], CV = 28%) (Part 1, Tables 1.6 and 1.7).

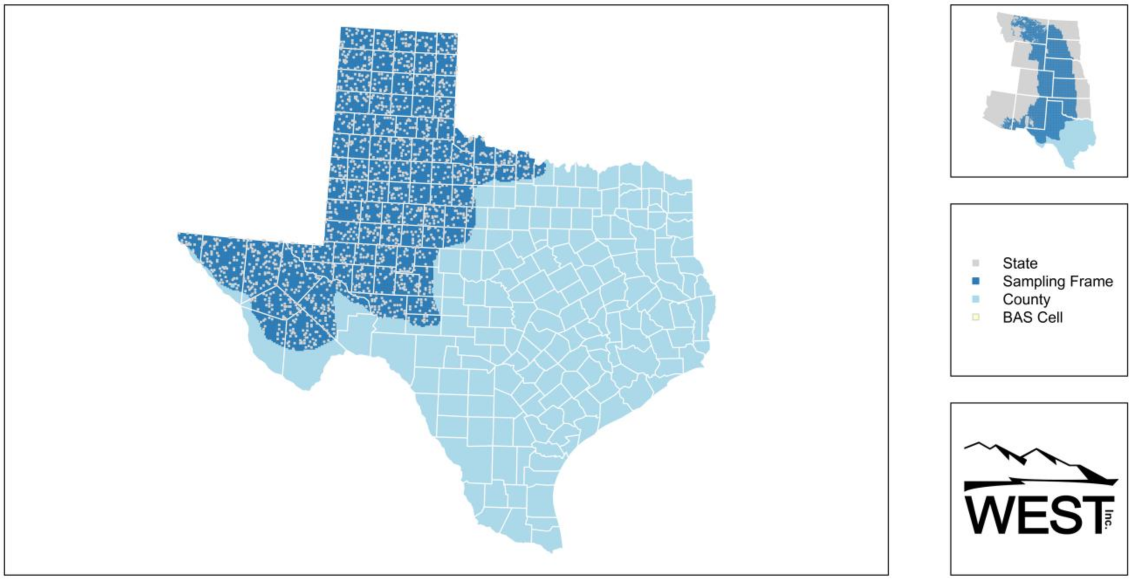

Figure 2.50. Sampling frame for Texas with 24,539 grid cells each 2 mi. by 2 mi. The 1,982 grid cells selected by the Balanced Acceptance Sampling (BAS) probabilistic sampling procedure were shown.

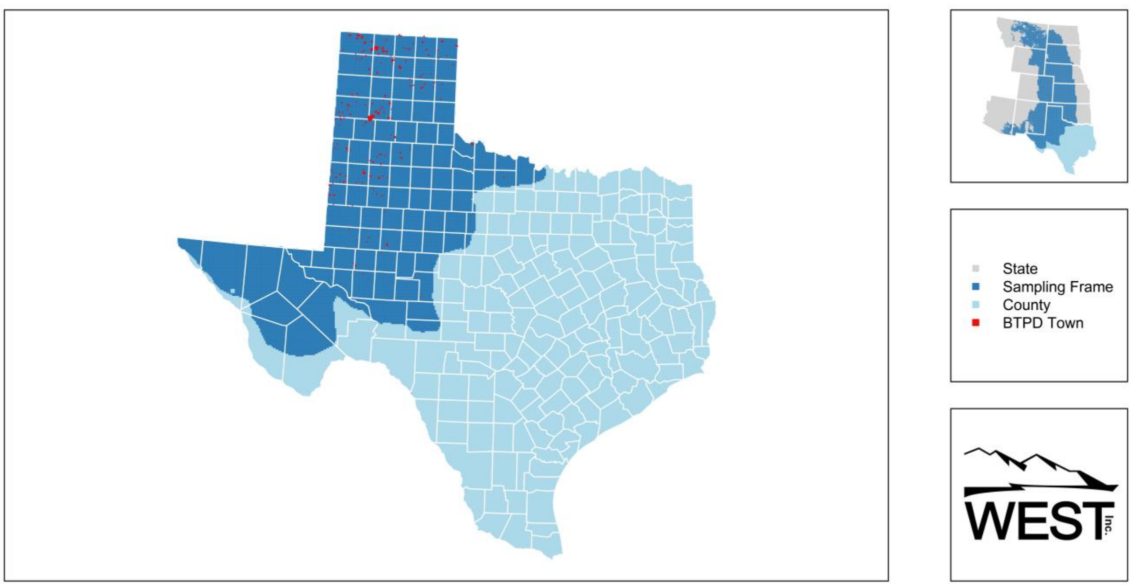

Figure 2.51. Map of features digitized in a sample survey of grid cells in Texas.

We plotted the estimates of total number of features and acreage of features as a function of the sample size (Figures 2.52 and 2.53). The estimated number of features began to converse to our final estimate at a sample size of 700 (Figure 2.53). Increasing the sample size to 1100 grid cells did not change the estimated total number of features appreciably. The effect of detecting rare relatively large features on estimated total acreage of features was evident in Figure 2.52. As the sample size was increased and a rare large feature detected, relatively large jumps occurred in the estimated total acreage. The estimated total acreage began to converge to final estimates at a sample size of about 1,000 grid cells. Estimates had adequate CVs of 14.2% and 6.2% for total acreage and number of features respectively at the sample size of 1,982.

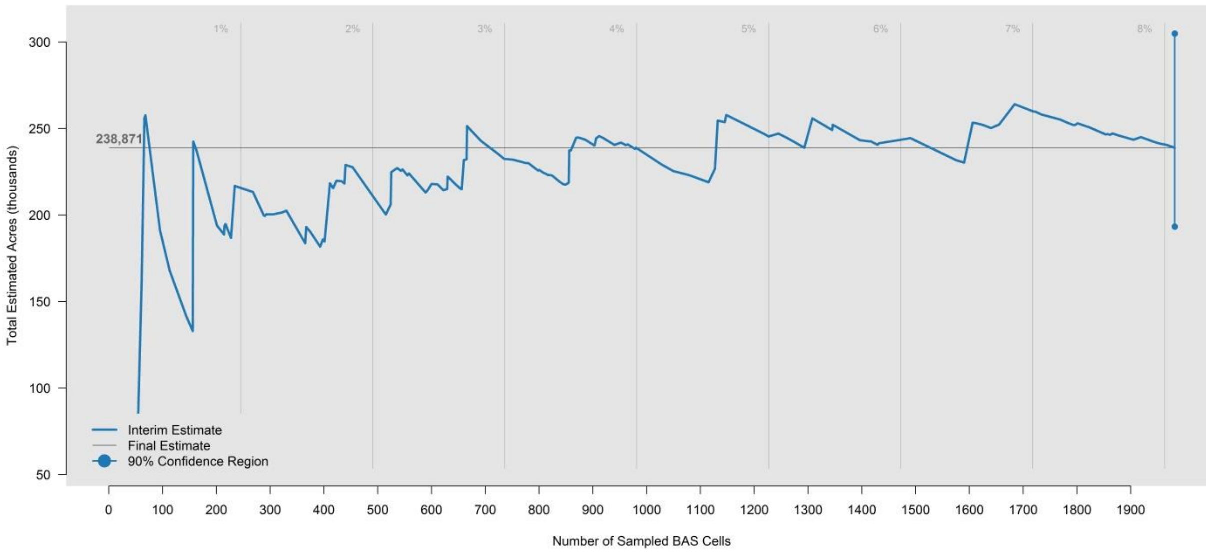

Figure 2.52. Estimated acreage of potential black-tailed prairie dog colonies in Texas as a function of the sample size.

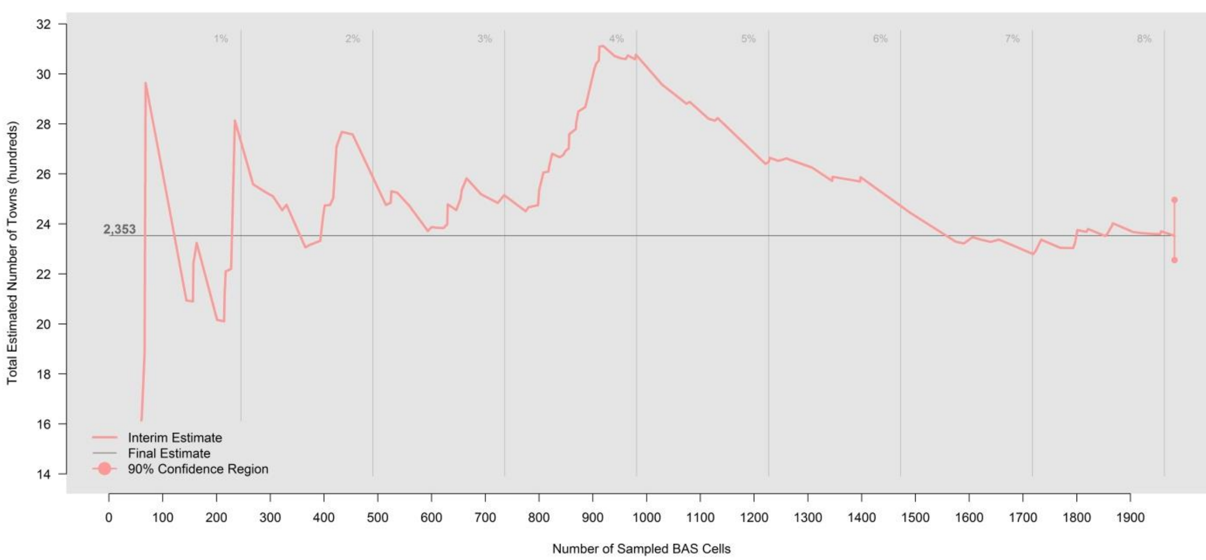

Figure 2.53. Estimated number of potential black-tailed prairie dog colonies in Texas as a function of the sample size.

GIS shapefiles and electronic maps will be made available to the State of Texas with the digitized features in the state and in each county. For example, figure 2.54, depicts the location of features detected and digitized in Randall County, Texas. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.

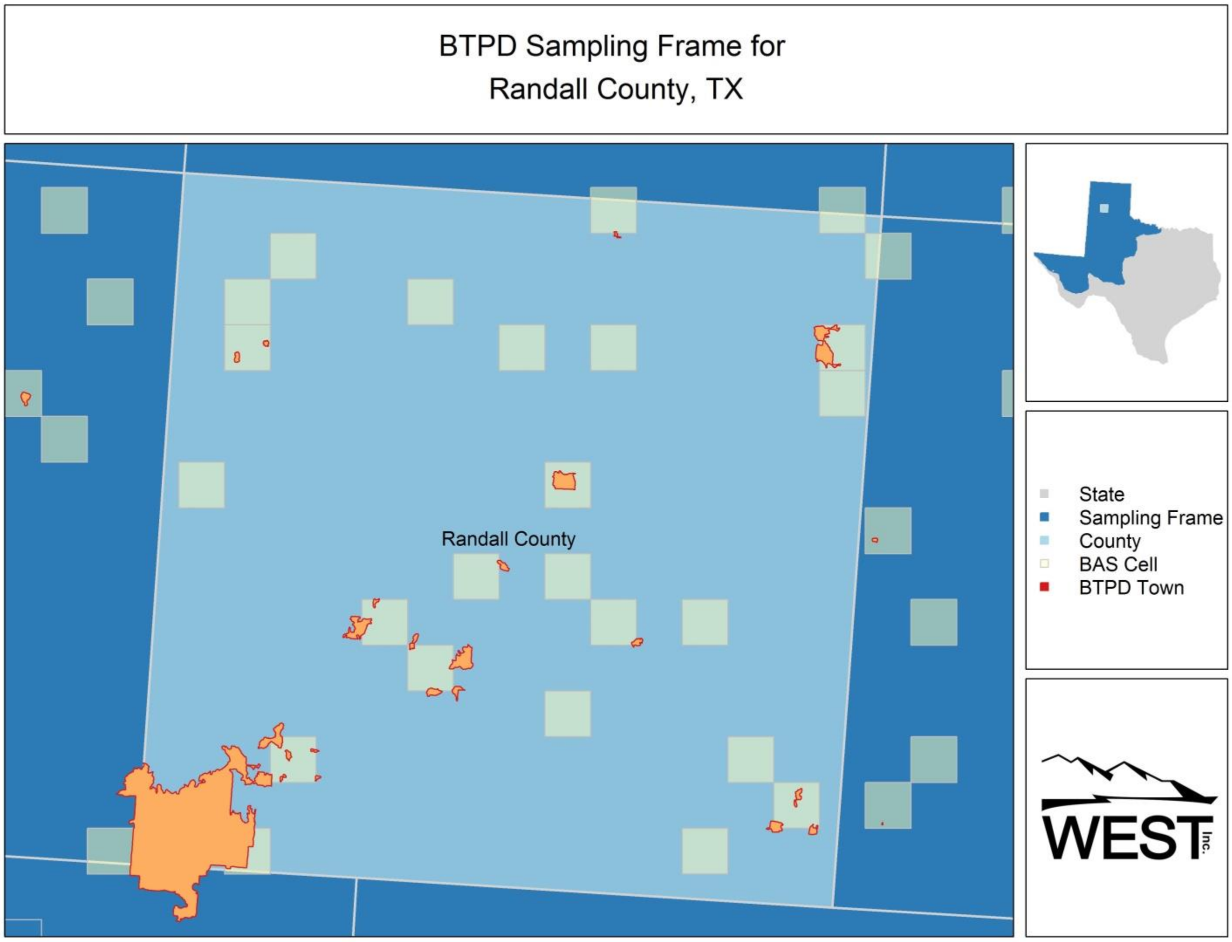

Figure 2.54. Digitized features on a sample survey of grid cells in Randall County, Texas.

WYOMING

The sample frame consisted of 8,790 grid cells that met the following criteria: 1) identified as a Wyoming cell with >50% of the land area in Wyoming, 2) containing any portion of area within the 11 county area of interest (Campbell, Converse, Crook, Goshen, Johnson, Laramie, Natrona, Niobrara, Platte, Sheridan, and Weston Counties), and 3) having >50% of the land area within the grid cell situated at less than 2377 meters (7,800 feet, NRCS 2004) in elevation, using intersections with 1-arcsecond Digital Elevation Model layers from the National Elevation Dataset (USGS). We surveyed a census of (2 mile by 2 mile) grid cells in the 11 county area in Wyoming (Figure 2.55). Figure 2.55 also displayed the sample of 1,722 grid cells, the results of which we reported as a "sample survey" in Part 1. We digitized all features detected in all grid cells and corrected for less than 100% probability of detection, i.e., for missed features called "false negatives."

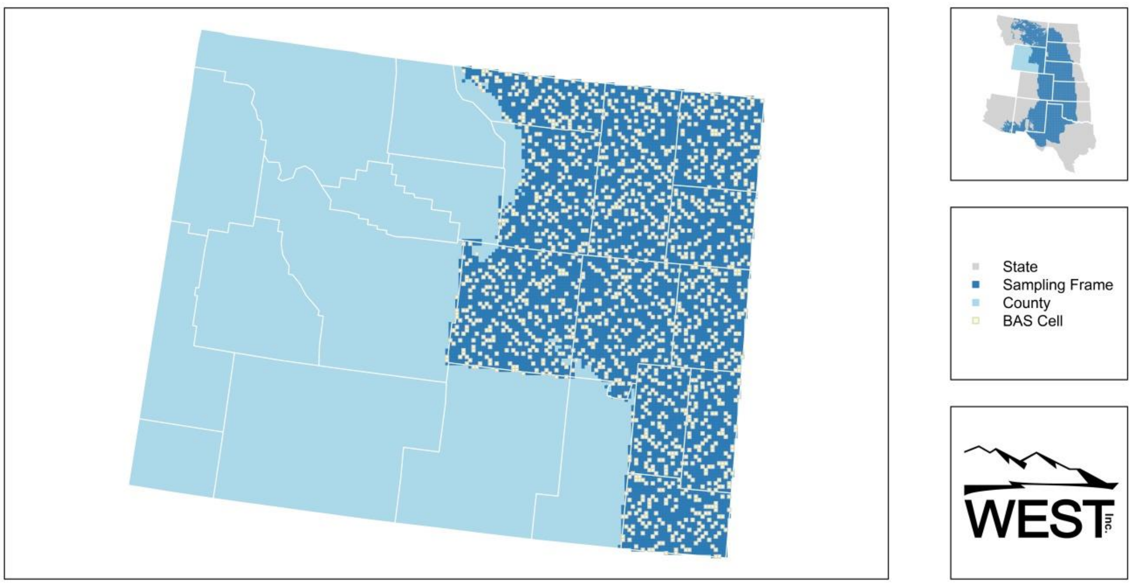

Figure 2.55. Sampling frame for the State of Wyoming showing 1,722 grid cells selected by Balanced Acceptance Sampling (BAS).

<u>Wyoming Black-tailed Prairie Dog Aerial and Ground Truthing Results 2015</u>

<u>Aerial Surveys</u>

Aerial surveys were conducted from July 20 to August 4, 2015 at 400 features digitized on the census of grid cells ("targets"). The targets were selected from the population of digitized potential BTPD prairie dog colonies using a BAS sample to ensure spatial representativeness across the habitat in the state. A probabilistic sample of 377 digitized features less than 1,000 acres was selected for aerial survey (n=377). In addition 23 features greater than 1,000 acres were selected for aerial surveyed (n=23) from the set of 27 features present. Targets were visited and identified as either an active black-tailed prairie dog colony, inactive black-tailed prairie dog colony, or null (not a black-tailed prairie dog colony) (Table 2.1) .

Table 2.1. Classification of aerial surveyed features in Wyoming.

Classification	Features less than 1,000 acres	Features greater than 1,000 acres
Active BTPD[1] colony	311 (82.5%)	16 (69.6%)
Inactive BTPD[1] colony	9 (2.4%)	0
Null (not a BTPD[1] colony	57 (15.1%)	7 (30.4%)
Total	377	23

[1] BTPD = black-tailed prairie dog

Of the 23 large features (greater than 1,000 acres), 69.6% (n=16) were found to be active prairie dogs colonies and 30.4% (n=7) were found to not be prairie dog colonies. Of the 377 small features, 82.5% (n=311) were found to be active prairie dogs colonies, 2.4% (n=9) were found to be inactive prairie dog colonies and 15.1% (n=57) were found to not be prairie dog colonies. The targets that were found to not be prairie dog colonies were generally anthills (88%; n=59), ground squirrels (8%; n=5), or a combination of old holes and bare patches of dirt.

Ground Surveys

Ground surveys were conducted from August 6 to August 11, 2015 at 87 digitized prairie dog colonies ("targets"). The ground truthing targets were selected from the 336 colonies visited by the aerial truthing and found to be prairie dog colonies (active or inactive). The site selection was also limited to targets near a public road based on the TIGER dataset published in 2014 (2014 TIGER/Line Shapefiles (machine readable data files) / prepared by the U.S. Census Bureau, 2014). We visited the first 100 targets that met these criteria following the BAS ranked order of grid cells. In addition, we visited 16 colonies greater than 1,000 acres. For the 116 colonies selected, 87 colonies were successfully accessed for ground truthing.

Eighty four (84) colonies classified as active in the aerial surveys and 3 classified as inactive were selected and visited for ground truthing subject to the requirement that they were accessible from public roads. Four of the colonies classified as active during aerial surveys did not have good access from roads and no mounds or live prairie dogs were detected. Of the 83 colonies with good access, there was agreement with the classification made during aerial flights. The 4 targets with no evidence of prairie dog colonies were found to have tall grasses present in the part of the feature that could be viewed from the ground.

Potential BTPD colonies on all 8,790 grid cells in Wyoming

In our census of grid cells, there was no “sampling error”; however, there was variance due to measurement errors, detection errors, and error in modeling the probability of detection. We accounted for these non-sampling errors by bootstrap sampling the entire census of 8,790 grid cells without replacement, as if we were to backup time and repeat the entire census effort. For each bootstrap sample we computed the estimated number and acreage of potential colonies corrected for false positives. We estimated the confidence intervals by the percentile method and the standard errors by computing the standard deviations of the sets of bootstrapped values for number and acreage of potential colonies (Table 2.2).

Table 2.2. Estimated acreage of total potential colonies, adjusted for false negatives, in the census of grid cells in Wyoming black-tailed prairie dog habitat were reported. Digitized potential colonies have been adjusted for false negatives and false positives.

	Features < 1,000 acres	Features > 1,000 acres	Total
Acreage of Potential Colonies	221,547	47,973	269,520
90% Conf. Intervals	[209,605; 240,131]	[31,830; 70,762]	[250,713; 300,125]
Standard Error	15,021	11,795	9,303
Coefficient Variation	6.8%	24.6%	3.5%
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Number of Potential Colonies	3,015	26	3,041
90% Conf. Intervals	[2,881; 3,154]	[18; 35]	[2,905; 3,181]
Standard Error	84	5	84
Coefficient Variation	2.8%	19.2%	2.8%

The sample survey of 1,722 grid cells from the total of 8,790 cells in Wyoming resulted in an estimate of 3,158 potential BTPD colonies totaling 288,606 acres with CV = 12.9% (Part 1, Tables 1.2 and 1.4), which compared favorably to the census value of 269,520 acres.

<u>Active BTPD colonies on all 8,790 grid cells in Wyoming</u>

Each time we selected a bootstrap resample of the 8,790 grid cells, we selected a bootstrap resample of the aerially surveyed 377 features less than 1,000 acres and of the 23 features greater than 1,000 acres, to generate bootstrapped values for the estimates of the total number and acreage of active colonies in Wyoming. We estimated the confidence intervals for number and acreage of active colonies by the percentile method and the standard errors by computing the standard deviations of the sets of bootstrapped values for number and acreage of potential colonies (Table 2.3)

We stratified and estimated the acreage and number of features less than 1,000 acres and features greater than 1,000 acres in the census of grid cells in Wyoming. Adjusting for less than 100% probability of detection, measurement errors and detection errors, we estimated 3,041 (90% CL = [2,905; 3,181], CV = 2.8%) potential BTPD colonies totaling 269,520 acres (90% CL = [250,713; 300,125], CV = 3.5%) in Wyoming (Table 2.2).

We adjusted the number and acreage of estimated potential BTPD colonies based on the aerial survey of 400 features. We estimated 2,505 active BTPD colonies (90% CL = [2,356; 2,656], CV = 3.6%) in Wyoming totaling 216,166 acres (90% CL = [199,776; 242,419], CV = 4.1%) (Table 2.3).

Table 2.3. Estimated total numbers and acreage of active colonies in the census of grid cells in Wyoming black-tailed prairie dog habitat were reported.

	Features < 1,000 acres	Features > 1,000 acres	Total
Acreage of Active Colonies	182,777	33,389	216,166
90% Conf. Intervals	[170,975; 199,936]	[20,826; 52,051]	[199,776; 242,419]
Standard Error	13,107	9,584	8,798
Coefficient Variation	7.2%	28.7%	4.1%
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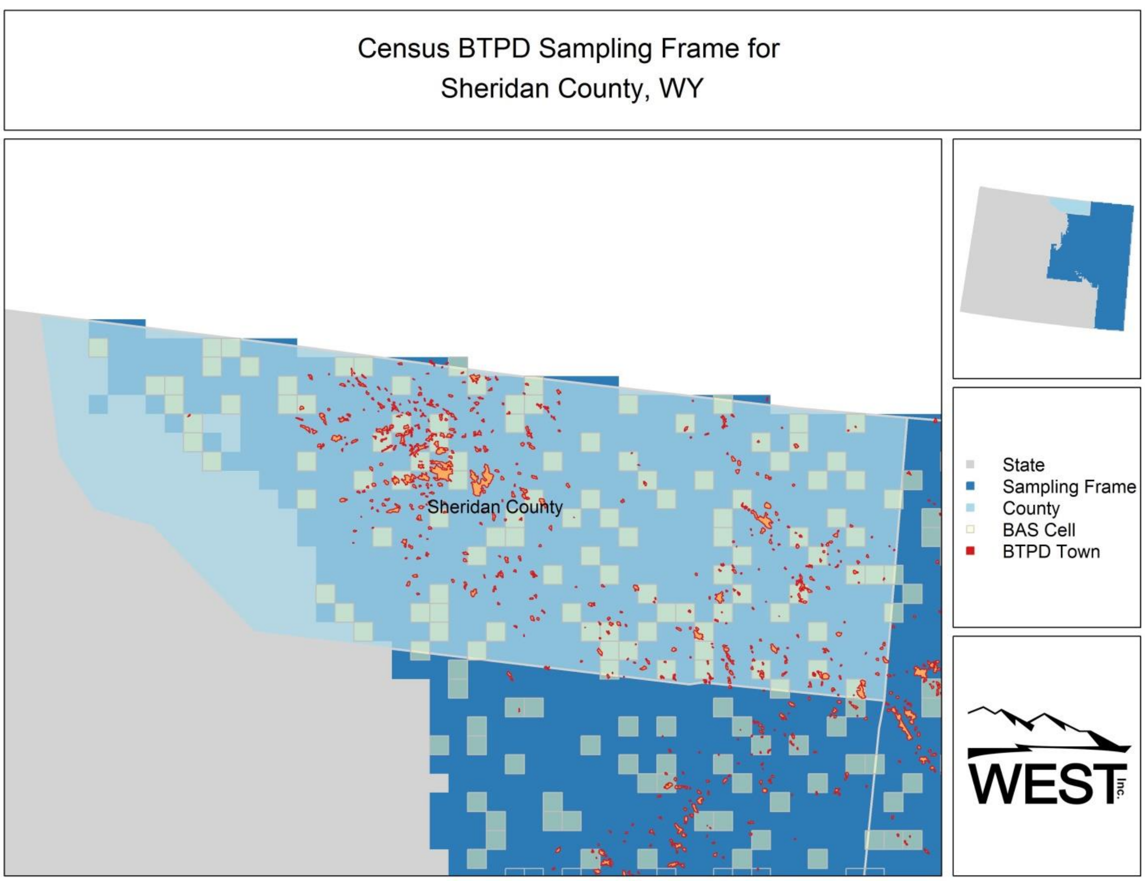
Number of Active Colonies	2,487	18	2,505
90% Conf. Intervals	[2,337; 2,637]	[11; 26]	[2,356; 2,656]
Standard Error	91	5	90
Coefficient Variaton	3.7%	27.8%	3.6%

Electronic maps will be made available to the State of Wyoming with the digitized features in each county. For example, figure 2.56, depicts the location of features detected and digitized in Sheridan County, Wyoming. These maps were created with sufficient resolution to be viewed in detail on a computer monitor.



DISCUSSION AND SUMMARY

Our objective was to develop an economical long term sample survey monitoring procedure for assessment of current status and future trends in range-wide numbers and acreage of black-tailed prairie dog colonies. The procedures included a sample survey of colonies on BLM managed lands and a census of black-tailed prairie dog habitat in Wyoming with aerial and ground surveys in Wyoming for "truthing" results. The census of cell in Wyoming was to serve as a pilot for potential future census work in the other states and for BLM lands.

Part 1 of the report contains the results of our sample surveys of 2 mile by 2 mile grid cells in each state, on BLM managed lands, and included a sample survey of cells in Wyoming that was compared to census results in Wyoming (Part 2). We searched sampled cells and digitized polygons around "features" judged to be potential colonies on the newest National Agriculture Image Program (NAIP) images available in each state. We adjusted our estimates for missed colonies (i.e., false negatives) by using two independent observers on a sample of grid cells and modeling the probability of detection of potential colonies. Our range-wide estimate based strictly on the sample surveys was 29,467 potential colonies totaling 1,932,826 acres. We estimated a total of 4,234 potential colonies greater than 100 acres in size and 419 greater than 500 acres in size.

Precision of the estimates for the entire range-wide 11 state totals were excellent with coefficients of variation of 2.4% and 4.9% for total acreage and number of potential colonies, respectively. The 90% confidence interval for acreage was [1,810,000 to 2,130,000 acres] and the 90% confidence interval for total number of potential colonies was [28,800 to 31,000 potential colonies] range-wide.

Precision of the range-wide estimated number of potential colonies greater than 100 acres was also excellent with coefficient of variation = 4.6% (90% confidence interval [4,000 to 4,650 potential colonies]). Precision of the range-wide estimated number of potential colonies greater than 500 acres in size was very good with coefficient of variation = 15% (90% confidence interval [349 to 544 potential colonies]). Unfortunately, our methods and sample sizes did not provide reliable estimates of the numbers of relatively rare potential colonies greater than 1,000 acres or the number greater than 5,000 acres, because detection of these large colonies within individual states were very rare events.

We conducted a sample survey of grid cells from each state and for BLM lands. The bottom line was that searching about 1,000 grid cells produced statistical estimates that were stable and precise (coefficients of variation < 15%) for number and acreage of potential colonies adjusted for missed features, except for Kansas and North Dakota. In those cases, a large number of cells had no detected potential colonies with the occasional cells containing large acreage or numbers resulting in high variance relative to the other states. We searched 1,078 cells in Oklahoma and 2,422 cells containing BLM lands and to achieve marginally acceptable coefficients of variation of 16% and 18%, respectively.

The estimates of abundance and acreage of potential colonies were most likely biased underestimates of the population totals. We base this conclusion on four observations. First, WEST's observers and South Dakota Department of Game, Fish and Parks' observers independently searched the same sample of grid cells in South Dakota. South Dakota's observers also consulted maps of features from previous NAIP images and detected more small features than WEST observers did. The estimated acreage derived from South Dakota's effort was 21% larger than the WEST estimate. Second, our corrections for the proportion of small potential colonies missed depended on the assumption that each member of the team of independent observers obtained a random sample of features present, specifically a random sample of small features. There were likely small features that were essentially invisible in the sense that they did not trigger the observer's search image for a colony. Third, the first author (McDonald) participated in the spring 2015 range-wide lesser prairie-chicken survey in Texas County, Oklahoma, flying in a helicopter at 25 meters elevation. Groups of 3 to 5 mounds with live prairie dogs were observed. Such "colonies" would be difficult to detect on NAIP one-meter resolution images. Fourth, two of the small known colonies in Arizona were in the sampled cells. We miss both of them. We estimated that an individual WEST observer detected 70% to 80% of small features in each state and corrected for missing features; however, these estimated detection rates were likely too high for small features resulting in a biased underestimate of the total acreage and numbers of potential colonies.

The first time that a long-term sample survey monitoring program is implemented, interest is primarily on accuracy and elimination of bias in survey methods. If the program is repeated in the future using the same methods and biases on the same sampled units, interest switches to changes and trends in the population estimates. We believe our sample survey estimates in Part 1 were biased underestimates of the numbers and acreage of potential colonies; however, if repeated with the same methods and training of observers, correct conclusions would be drawn regarding changes and trends in population statistics.

There was interest not only in estimation of the total numbers and acreage of potential colonies present, but also the numbers and acreage of large potential colonies (e.g., colonies greater than 1,000 acres and greater than 5,000 acres). This introduced a major problem within the individual states, because large potential colonies were very rare. The detection of even one 5,000 acre feature in, for example, Kansas increased the total estimated number and acreage of 5,000 acre features in Kansas by a multiplication factor of about 10, because we searched about 10% of the grid cells in Kansas. That is, the estimated total number and acreage of all features greater than 5,000 in Kansas would jump by as much as 50,000 acres, depending on the statistical method used.

We detected 4 potential colonies that were greater than 5,000 acres in size in the sample surveys of 11 states. We detected 42 potential colonies that were greater than 1,000 acres (including the 4 greater than 5,000 acres). However, none of the centroids of the 5,000 acre potential colonies were in a sampled cell and several of the centroids of the 1,000 acre potential colonies were not in a sampled cell. Consequently, the centroid method would estimate no potential colonies greater than 5,000 acres exist in the 11 states when in fact we detected 4. The centroid method was not reliable for estimation of the number of these large potential colonies.

Because of interest in acreage of large, rare potential colonies, this was the most difficult estimation problem that the first author (McDonald) had encountered in his practice of designing and analyzing environmental studies for rare events. We judged that the state and range-wide estimates of numbers and acreage of features greater than 1,000 and greater than 5,000 acres were unreliable and we did not report them. We reported estimates of the abundance of potential colonies greater than 100 acres and greater than 500 acres within each state. The precision of the estimates of features greater than 100 acres were in an acceptable range within the individual states, however the estimated numbers of potential colonies greater than 500 acres had coefficients of variation too large to be useful in some states.

The sample survey results for number and acreage of potential colonies include "false positives," i.e., some digitized features were not prairie dog colonies. We searched all grid cells in Wyoming and corrected for false negatives using the same methods as in the other states. We conducted aerial and ground surveys of digitized features and corrected our estimates for false positives to estimate the number and acreage of active colonies in Wyoming. There was perfect agreement between aerial and ground surveys for classification of prairie cog colonies as active or inactive on colonies that had good access on the ground.

The flagship for our pilot monitoring program was to be the census of grid cells in Wyoming with: 1) double sampling on a sample of cells to develop correction factors for false negatives, and 2) aerial and ground surveys to "truth" the results and correct for false positives. Results of the census (Part 2) were compared to results of a sample survey (Part 1) and the estimates of potential colonies, corrected for false negatives, were very close. Unfortunately, the latest NAIP images for Wyoming were from the early summer of 2012, taken during one of the worst droughts on record. While it was possible to correct for missed potential colonies, the images were very poor quality with little vegetation to help detect potential colonies. Correction factors from the aerial surveys were large. In hindsight, we should have stopped work on the 2012 images, saved WAFWA and Wyoming's funds and waited for 2015 images. Better products would have been obtained.

RECOMMENDATIONS

Recommendation. Methods and training of observers should be standardized as much as possible in future sample or census surveys. If results of future surveys are to be compared to results in this report, methods and training of observers should be as consistent as possible with our methods and training. Training of observers should include "blind" observation of grid cells containing known small colonies to improve search images for small features.

Recommendation. Future sample surveys for monitoring long-term trends should use two independent observers on all cells in a sample of at least 1,000 grid cells from each state and from the cells containing BLM lands. The probability that potential colonies will be missed by two independent observers was very small and the corrections for missed features were small providing robust estimates of statistics.

Recommendation. Sample sizes used in this pilot study were adequate except for Kansas, Oklahoma, North Dakota and BLM managed lands. In those cases, simulation exercises using data from this study should be conducted to estimate sample sizes necessary to achieve coefficients of variation below 15%.

Recommendation. If the objective in future sample surveys is to detect statistically significant trends or abrupt changes as early as possible; then, the same probabilistic sample of grid cells should be searched. After sample surveys are conducted two or three times, WAFWA or state wildlife agencies might consider implementing rotating panel designs where some cells are dropped and new ones are added each time a survey is conducted.

Recommendation. Viewing features using very high resolution Google earth images should be implemented as an aid in judging whether a feature detected on NAIP images was a potential colony. Burrow openings were clearly detected using very high resolution 2013 and 2014 Google earth images of features judged to be active or inactive colonies during 2015 aerial surveys of features in Wyoming. Unfortunately, some mounds in ant colonies have a dark spot which can be confused with prairie dog burrow openings when viewed on Google earth in Wyoming.

Recommendation. If aerial surveys are conducted to observe a sample of digitized potential colonies, the same sample of potential colonies should be searched by different observers using Google Earth without knowledge of the aerial results, i.e. searched "blind." Aerial and Google Earth search results should be compared to determine if "Google Earth truthing" can be substituted for "aerial truthing" in some states.

Recommendation. Implement aerial survey of a sample of digitized potential colonies regardless of sample survey or census of grid cells in a state. Classify colonies as active, inactive or null (not black-tailed prairie dogs) and estimate the number and acreage of colonies classified as active, regardless of whether the study is a census or sample survey of grid cells.

Recommendation. For study of trend in numbers of large potential colonies within the states use the number of potential colonies greater than 100 acres. The estimated number of potential colonies greater than 500 acres was a reliable statistic for study of trend in range-wide abundance.

Recommendation. Establish a baseline for long-term monitoring of abundance and acreage of potential colonies by searching all grid cells in a state one time. After the first census wide survey for distribution of colonies and large features, increasing or decreasing trends can be based on sample survey results. If a census of cells is conducted, a sample of at least 1,000 grid cells should be searched by two independent observers and the results reconciled to train observers, establish or "re-calibrate" search images on new NAIP images, and allow estimation of the probability that features will be missed by a single observer on the rest of the cells.

Recommendation. Include all potential colonies greater than 1,000 acres in aerial truthing exercises. In our census of grid cells in Wyoming, we stratified the features into potential colonies less than 1,000 acres and potential colonies greater than 1,000 acres. We surveyed 23 of the 27 features greater than 1000 acres from the air. In retrospect, we should have flown to all 27, because survey of only 23 introduced a small sample of 27 and relatively high variance into the procedures for estimation of the number and acreage of active colonies.

Recommendation. Future sample or census surveys using our methods should not be conducted on NAIP images collected during severe drought.

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APPENDIX A

Standard Operating Procedure:

Digitizing potential black-tailed prairie colonies using NAIP imagery

National Agriculture Imagery Program (NAIP) Images and Sampling Grid

The study area consisted of the estimated current range for black-tailed prairie dogs (BTPD) as defined by the Wildlife Departments in the 11 states containing BTPD habitat (Figure C.1, repeated from Part 1). We clipped the latest NAIP imagery available for each state to the study area. For example, the estimated current range for BTPD covered the 12 most eastern counties in Wyoming. National Agriculture Imagery Program (NAIP) images were the choice for the study area because they were at least one square meter resolution, inexpensive, and were replicated on a three year or more often rotation.

The digitizers used the latest version of ArcGIS (ArcMap10.2.2) to conduct the GIS work in this study. In order to keep a consistent geometry across the western United States, we chose to apply the continental projection. The USGS version of this projection, USA Contiguous Albers Equal Area Conic, sets the projection of the entire project.

Using ArcMap, we generated an MXD file for digitizers to use as a template throughout the entire study area. In each state, we constructed a sampling frame that consisted of 2 mile by 2 mile grid cells to overlay the NAIP imagery. Observers systematically searched selected cells to detect potential BTPD colonies, dubbed “features” for brevity. We created a smaller mini-grid system within each 2 by 2 mile grid cell. Each 2 by 2 mile cell contained 5 rows and 5 columns for a sum of 25 smaller cells for digitizers to search. The smaller grid system allowed full coverage of selected 2 by 2 mile cells and helped assure that no area was overlooked in selected grid cells. Observers viewed the cells of the mini-grid at a scale of approximately 1:4000.

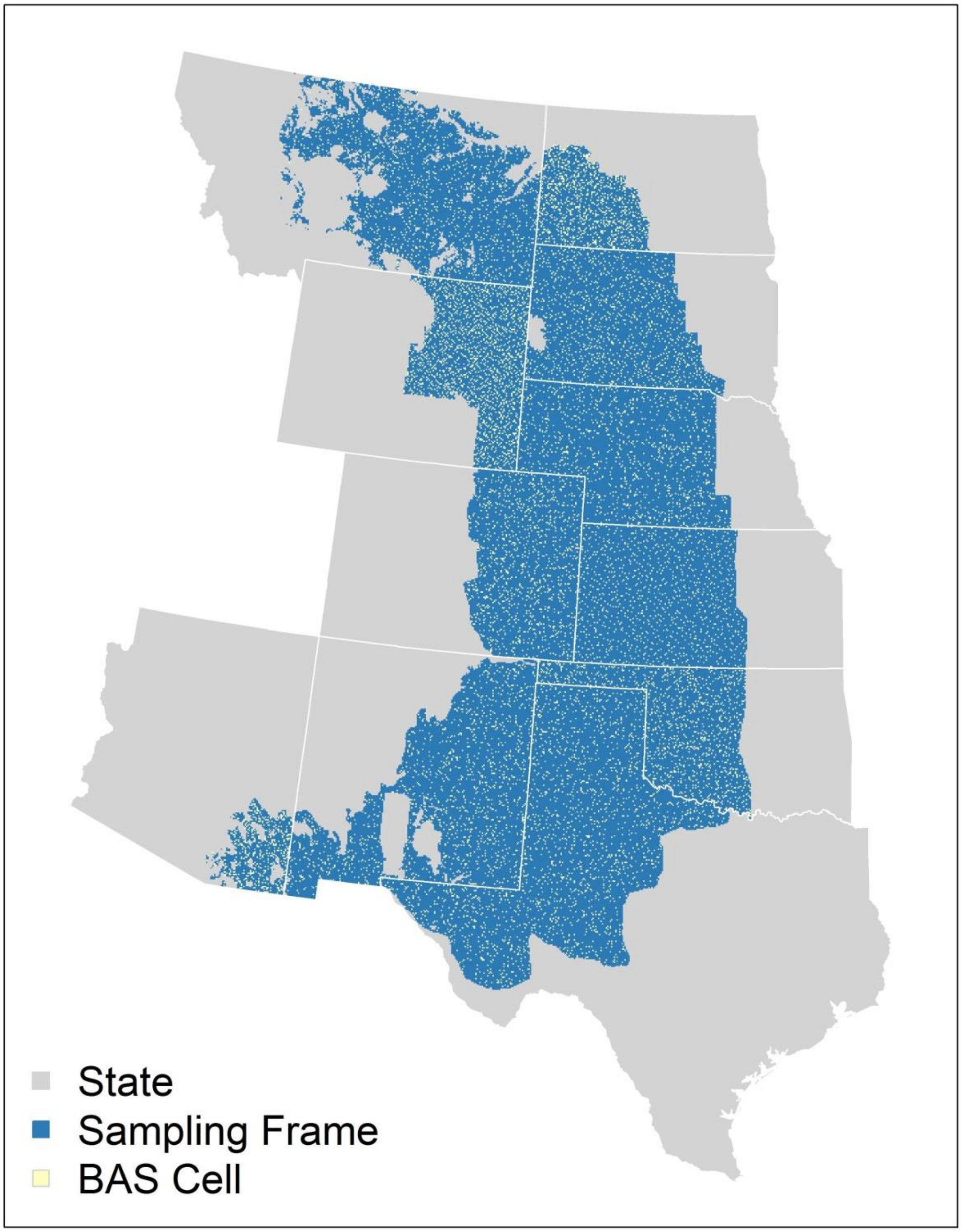

Figure 1 (Part 1). Study area for the range-wide monitoring of black-tailed prairie dogs using NAIP imagery. Sample grid cells were selected by a probabilistic random procedure known as Balanced Acceptance Sampling (BAS).

Methods for Selection of a Sample of Grid Cells

We ranked the grid cells in the study areas for each state by an equal probability sampling procedure known as Balanced Acceptance Sampling (BAS, Robertson et al. 2013). Cells selected by the BAS procedure represent a spatially balanced sample of grid cells such that any contiguous subset, when taken in order, was an equal probability sample of the target population.

We digitized potential BTPD colonies that overlapped a sample of grid cells in each state. Features were digitized by "connecting the dots", i.e., connecting the outer most mounds and burrows in a potential colony. Using two independent observers on a sub-sample of cells, we were able to model and estimate the probability that an observer will miss a potential colony of a given size (see Methods, Part 1). All grid cells were selected with equal probability by following the rank order in the original BAS list for a state.

Observer Training

Possibly the most difficult aspect of training new observers was helping them to develop their search image of prairie dog colonies on NAIP imagery. In many of the areas searched by WEST, Inc., prairie dogs were likely to occur in the same areas as ants or ground squirrels and could easily blend in with the surrounding landscape. As ant colonies can be quite large, it was important that observers learn to distinguish between them. During training, prairie dog colonies were described as small, raised, white mounds in the landscape. The observers then learned to refine that general image with help from example images, other observers, contextual cues, and other imagery sources.

As part of training, observers were required to participate in reconciliation of their independently digitized results with a partner. Observers were assigned the same cells as their partner, but they searched and digitized those cells independently. When completed, they met, compared polygons, and finalized how the feature would be digitized (see section, Double Sampling with Independent Observers).

One important objective in reconciling results was to help observers develop "search images" for features by communicating why they decided to digitize or not digitize a feature as well as observe features others choose to digitize. By explaining their process, observers refined their search images. The objective was for observers to develop consistent and similar search images.

Images of confirmed prairie dog colonies, ant colonies, and ground squirrel colonies were used in the training (see section, Images used in Training). Observers were given images to reference while conducting their searches. While prairie dog colonies vary in appearance, there were a few key features that observers checked for. Such features included mounds, burrow openings, trails between mounds, and a clip line in the surrounding vegetation.

Digitizing in Kansas, South Dakota, Colorado, Oklahoma, North Dakota and Wyoming was completed using two observers and independent double sampling and reconciliation. After those states were completed and observers had obtained consistent search images, digitizing in Montana, Arizona, New Mexico, Texas, and Nebraska was completed using only single sampling. The survey on BLM managed lands was also completed using one observer.

Double Sampling with Independent Observers

Sub-samples of grid cells were selected and interpreted by two independent observers. The observers searched the same set of randomly generated cells and digitized "features" defined as potential prairie dog colonies. The observers searched each selected 2 mile by 2 mile cell starting in the northwest corner and worked their way to the southeast corner scanning the cells of the mini-grid one at a time. For approximately half of the units that each team interpreted, one observer (1-A) was designated as the primary observer. For the other half of the units, the other observer (1-B) was designated as the primary observer.

When an observer found a potential prairie dog colony, they digitized the feature perimeter at their discretion. Observers zoomed in and out depending on the area that they were in and the feature to be digitized. Digitizing was done at a scale no larger than 1:4,000, It was suggested to digitize features at a scale of 1:3,000 to achieve the most accurate values for acreage. The observers used a “connect the dots” method to connect the outermost burrows that could be identified on the NAIP imagery (Sidle et al. 2002). For some colonies, visible clip lines were observable to help identify the outer most burrows. However, in order to be consistent and to produce the most comparable results through time, digitizers were instructed to not digitize a colony perimeter by following the clip line.

Original features digitized by an observer were recorded in an original shapefile and post-reconciliation features were recorded in a reconciliation shapefile. With these different sets of shapefiles, we were capable of comparing the sizes of original and reconciled features.

Observers were instructed to digitize the entire perimeter of the potential colony that overlapped the assigned grid cell. Even in situations where the centroid of the polygon did not belong to the cell assigned, the observer still digitized the entire potential colony. The same protocol applied when an observer found a potential colony with a centroid that lies within another state in which they were not working in at the time.

During the process of digitizing, observers within each team were also responsible for recording unique identification names for detected features in a spreadsheet and syncing information from those spreadsheets to the values in the attribute table for each of their shapefiles. After an observer digitized a potential colony, they recorded the appropriate values in the spreadsheet. In ArcMap, they also edited the attribute table for each feature that they digitized. The observer assigned a town ID to potential colonies when the centroid of that colony fell within an assigned cell. For example, if an observer found two potential colonies within the grid cell WY078456 and assigned each a town ID. They assigned the first colony the town ID of 1 and the second colony the town ID of 2. For each cell, the town ID reset and starts at 1 while the grid ID remains constant as a unique identifier for each of the 2 by 2 mile cells. Observers also recorded other data such as which observer found which colonies and which observer failed to find a given colony. Observers used the centroid finder function in the Arc toolbox to identify the unique cell containing the centroid of a feature.

Positive and negative outcomes arose during the reconciliation period. The optimal scenario occurred when both observers found and digitized the same feature in an assigned cell or when they agreed that no features were present. If features were present, the primary observer placed the shapefiles into the MXD file. Together, the two observers discussed each feature and made decisions about the size and shape of the potential colony in question. To obtain the “reconciled” feature, the primary observer re-digitized the feature while the secondary observer was present.

Another scenario occurred when one observer found and digitized a feature missed by the other team member. In this case, the observers discussed the feature in question and made the decision whether it was a potential colony or not. When observers decided it was a potential colony, the primary observer was responsible for “re-digitizing” the reconciled feature while the secondary observer was present. The observers deleted features they decided were not potential colonies.

Bureau of Land Management Survey

In addition to the Wyoming and range-wide surveys, WEST, Inc. also conducted a survey of Bureau of Land Management (BLM) land in Arizona, Colorado, Montana, North Dakota, Nebraska, New Mexico, South Dakota, Texas, and Wyoming (see Methods, Part 1). Observers digitized features that intersected BLM managed land and continued to digitize the entire feature regardless of how far it expanded.

Google Earth Use

Google Earth was a useful tool for digitizers while they were searching and developing their search images. It was also helpful in resolving disagreements during reconciliation of survey results collected by two independent observers.

Use of Google Earth remained an option for use when questionable features were detected on the NAIP images and observers were encouraged to use Google Earth imagery throughout the surveys. When an observer found a potential colony in NAIP imagery while digitizing, they could optionally look for the feature in Google Earth to confirm their decision to digitize the potential colony. With Google Earth, observers were usually able to zoom in on the questionable feature to look for distinct burrow openings, paths between burrows, and clip lines, which may not have been visible on NAIP imagery.

Images used in training

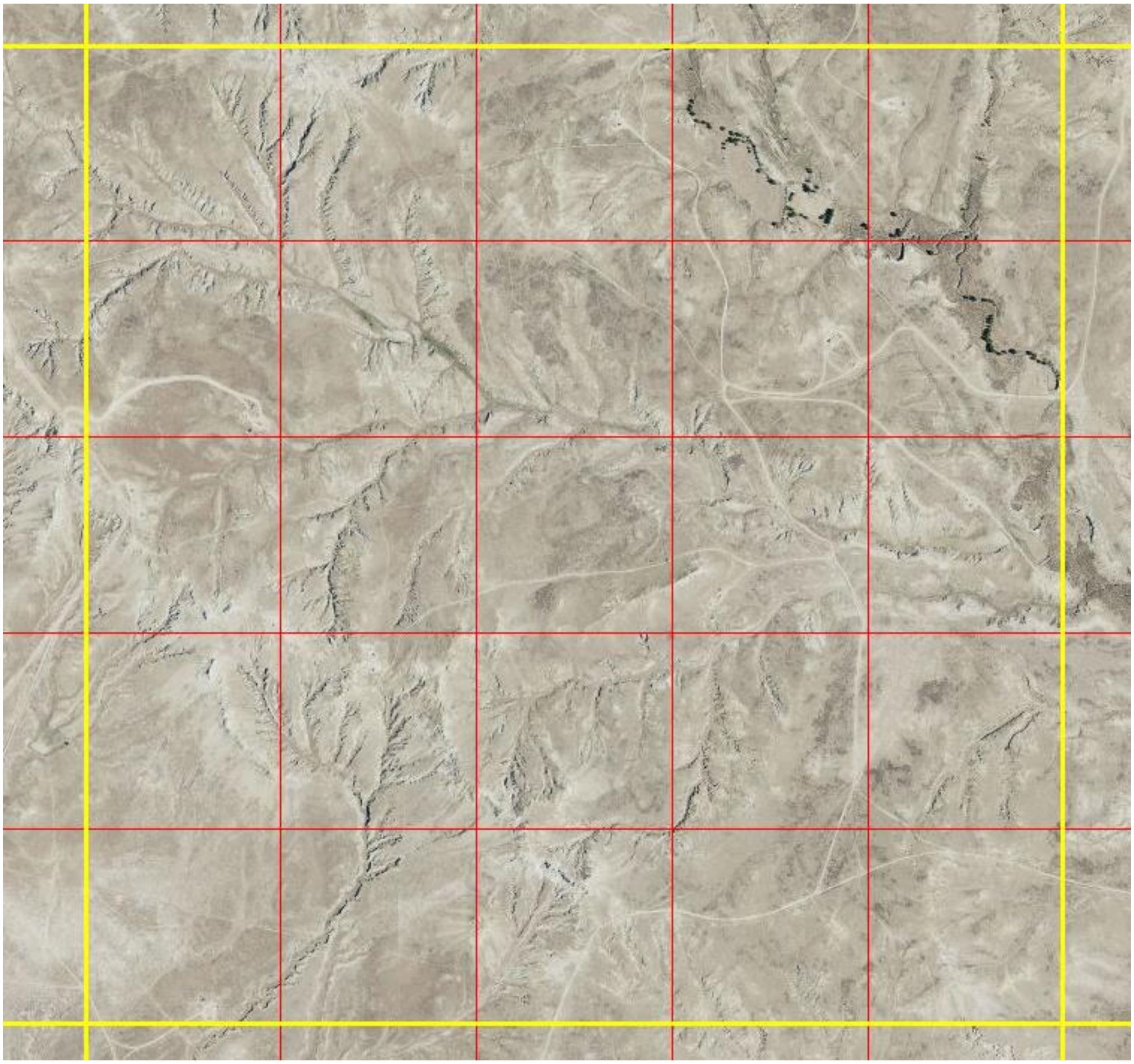

Figure A1. In all surveys, observers used a combination of 2 x 2 mile grid cells (yellow) and smaller mini-grid cells (red) to search for potential prairie dog colonies. Grid cells had unique identification names and were searched for features. Digitized features were given unique names identifying the grid cell and features associated with the cell. Mini-grid cells were used for navigation within the grid cell and to help insure that all parts of the cell were searched. Observers digitized an entire prairie dog colony, even if it extended beyond their assigned grid cell.

Figure A2. A digitized potential black-tailed prairie dog colony. Identifying mounds was difficult in this landscape. The observer was able to use the “connect-the-dots” method on this 2012 NAIP image in Wyoming. When using this method, the observer digitized the outline of the colony by connecting the outer most mounds, rather than following a clip line. Aerial truthing confirmed this feature to be a black-tailed prairie dog colony.

Figure A3. Observers were able to confirm digitized colonies using Google Earth. The above image was the same colony as Fig. A2. Due to a much higher resolution, mounds, burrows, and trails between mounds were more frequently visible in Google Earth than in the 2012 NAIP imagery.

Figure A4. Though some small, white dots were visible on this 2012 NAIP image of Wyoming, there were no visible wear patterns or clip lines so it was judged that this was not a potential black-tailed prairie dog colony.

Figure A5. This figure shows a small segment of the area in Figure A4 viewed in Google Earth. In this image, it was more apparent that paths between burrows and clip lines were not present. This feature was judged to be a colony of ants or a very old prairie dog colony. Unfortunately, as was the case in this image, dark spots appear on Google Earth images of ant mounds and can be confused with black-tailed prairie dog burrow openings.

Figure A6. Google Earth image of a large ant colony in central Wyoming. Although dark spots were visible on the mounds, the mounds were judged to be too small for a black-tailed prairie dog colony and there was no other evidence of the presence prairie dogs.

Figure A7. In areas with developed land and rectangular property lines, prairie dog colonies can also take on rectangular shapes. The owner of this property in Kansas may allow black-tailed prairie dog to remain on selected areas.

Figure A8. In developed agricultural areas, ants will often colonize old cultivated fields and between pivot-irrigated fields. Though they had a similar appearance to prairie dog colonies, anthills often had much smaller mounds. Unfortunately, anthills often have a dark spot on the mound when viewed using Google Earth. The above image was not included as a feature, as it was most likely an ant colony.

Figure A9. Roads often intersect prairie dog colonies and potentially split a large colony. Depending on the size of the colony, the type of road and how close the mounds were to the road, digitizers may break up the colony into smaller colonies. In this image, the observer digitized the mounds as one entire prairie dog colony. This was due to mounds present right up to the road and immediately on the other side which indicates that prairie dogs were moving across these roads. Large roads such as interstate highways were considered to be barriers to significant black-tailed prairie dog movement.

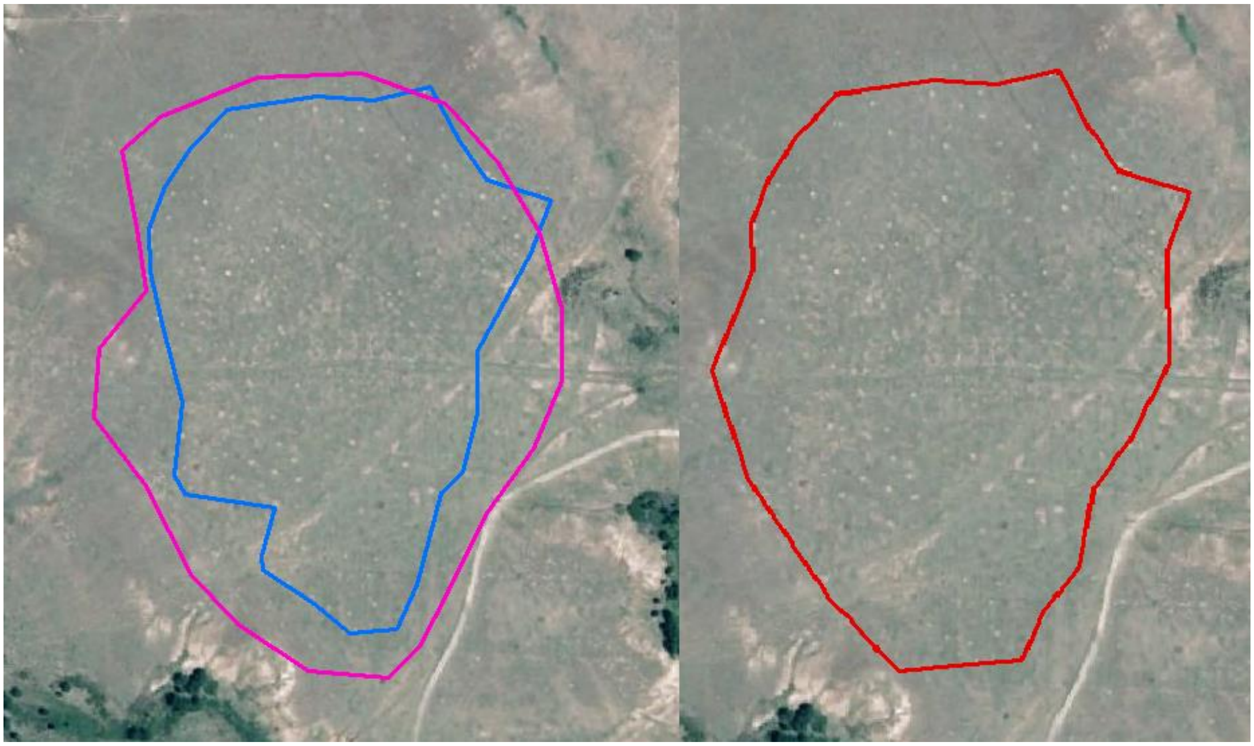

Figure A10. During training and independently digitizing features, observers compared their digitized features and reached an agreement on how the feature should be enclosed. When digitizer pairings were consistent with each other, only minor changes needed to be made. In the above images, the independently digitized features were shown on the left and the post-reconciled feature on the right.

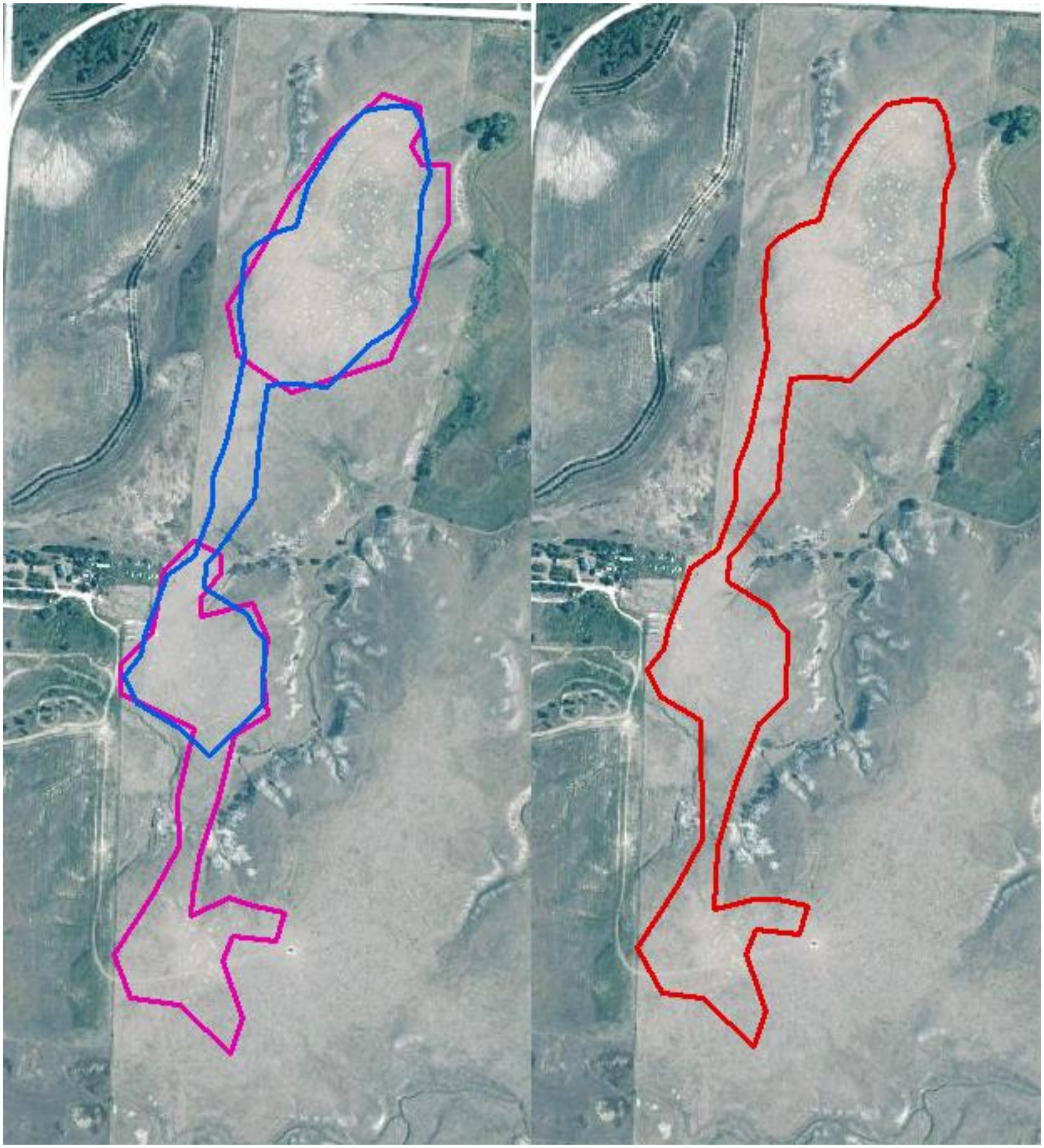

Figure A11. When observers were not consistent with each other, they needed to make modifications to their features to come to an agreement. While the observers digitized the same areas in this image, one drew it as a single feature while the other split it into separate ones. The post-reconciling image on the right reflects the decision to connect them into a single feature.

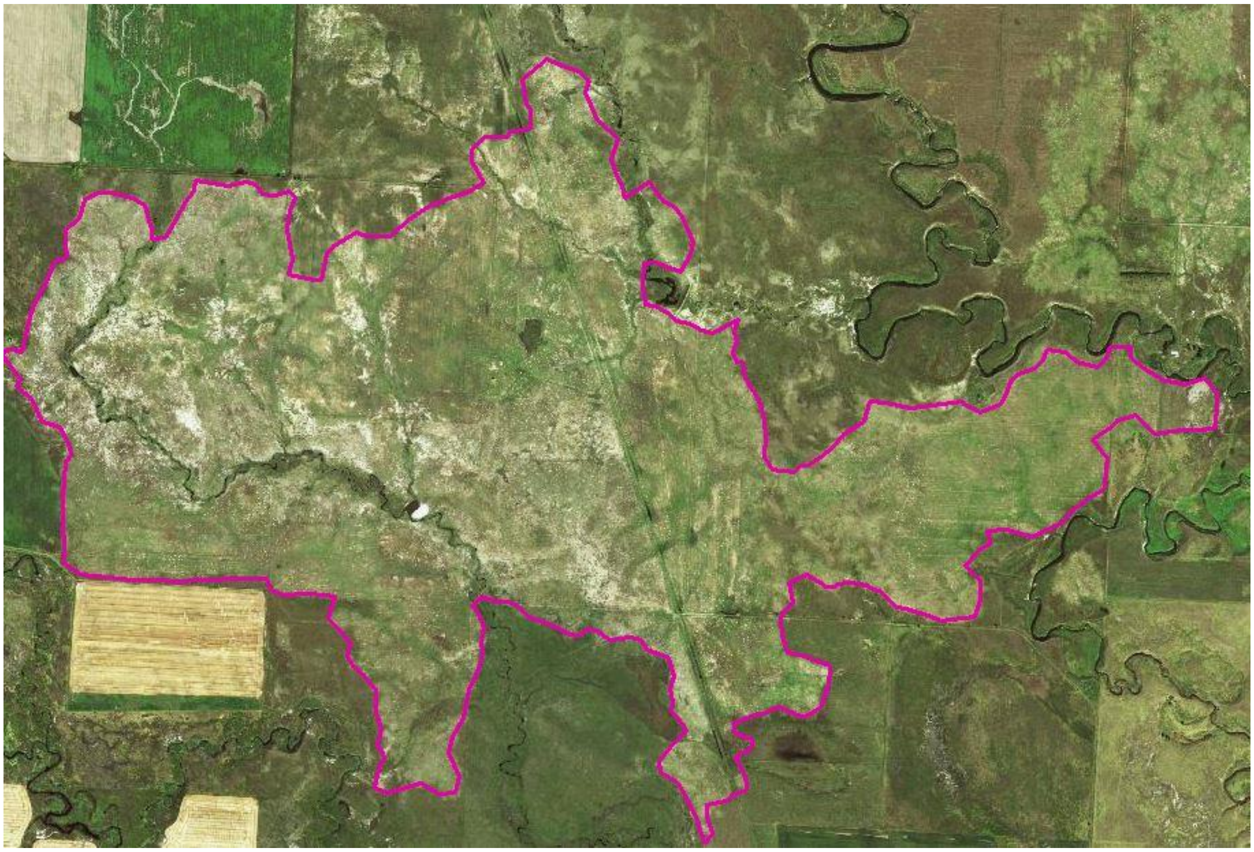

Figure A12. For this large potential colony in South Dakota, the presence of a prairie dog town was evident by the difference in vegetation color. Compared to the imagery available in Wyoming, South Dakota towns were easier to identify. Observers were required to keep in mind regional differences and drought conditions as they digitized.

Figure A13. A close up of an area in the previous image (Fig. A12). Mounds, burrows, and some trails were visible in Google Earth. This image was from a different date than the NAIP imagery. It was captured in September 2011 while the NAIP imagery was captured during the summer of 2014. Such a difference in time can yield discrepancies in what was visible, but the images also often corroborated each other. In this example, because it was later in the season and it was drier, less vegetation was present.

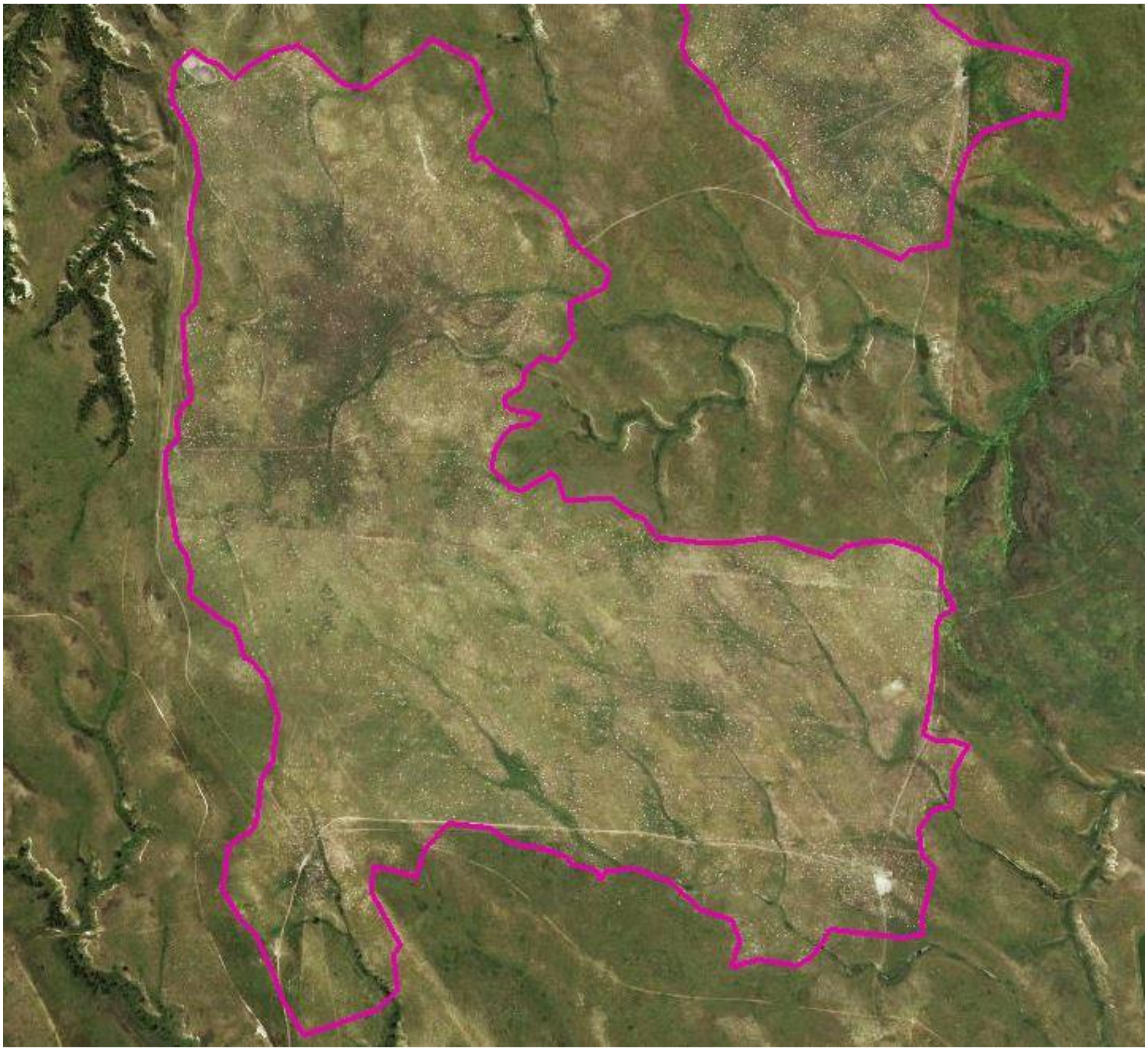

Figure A14. While the protocol for observers was to draw the colony by connecting the outermost mounds, a clip line was useful in identifying a potential black-tailed prairie dog colony. Mounds, a wear pattern, and a clip line were visible in this image from South Dakota. Wear patterns were created by prairie dogs moving between burrows; often creating paths in between them and were often visible when using Google Earth.

Figure A15. Another regional difference that observers needed to be aware of was the presence of agricultural land. Hay bales, as in this image, looked like mounds but will often cast a shadow and follow systematic patterns.

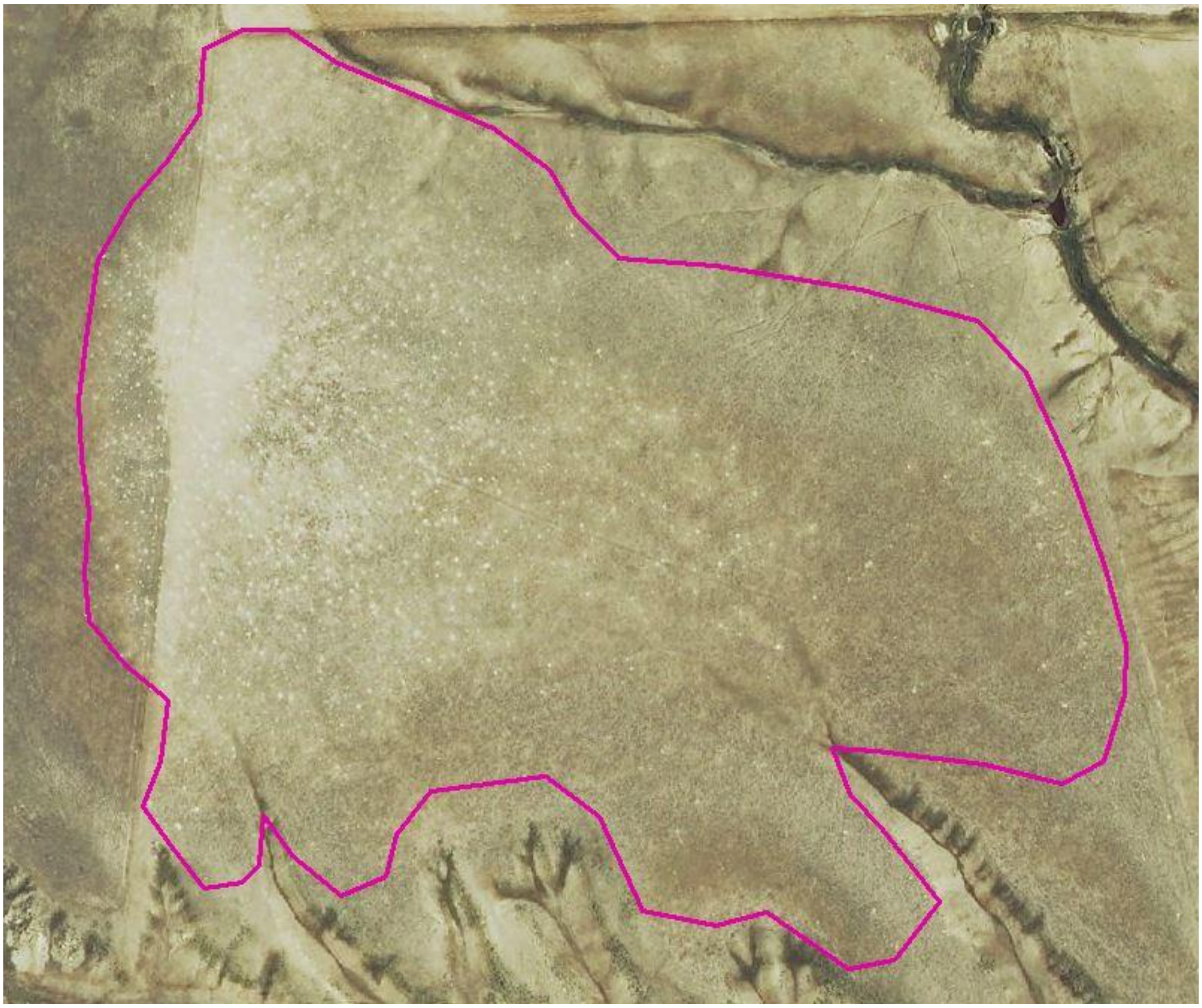

Figure A16. Prairie dog colonies often had similar patterns such as a concentrated area of mounds near the center with more dispersed mounds in the surrounding area. The wear patterns and trails between mounds were more visible near the center in this Colorado image. Ant colonies did not exhibit this pattern.

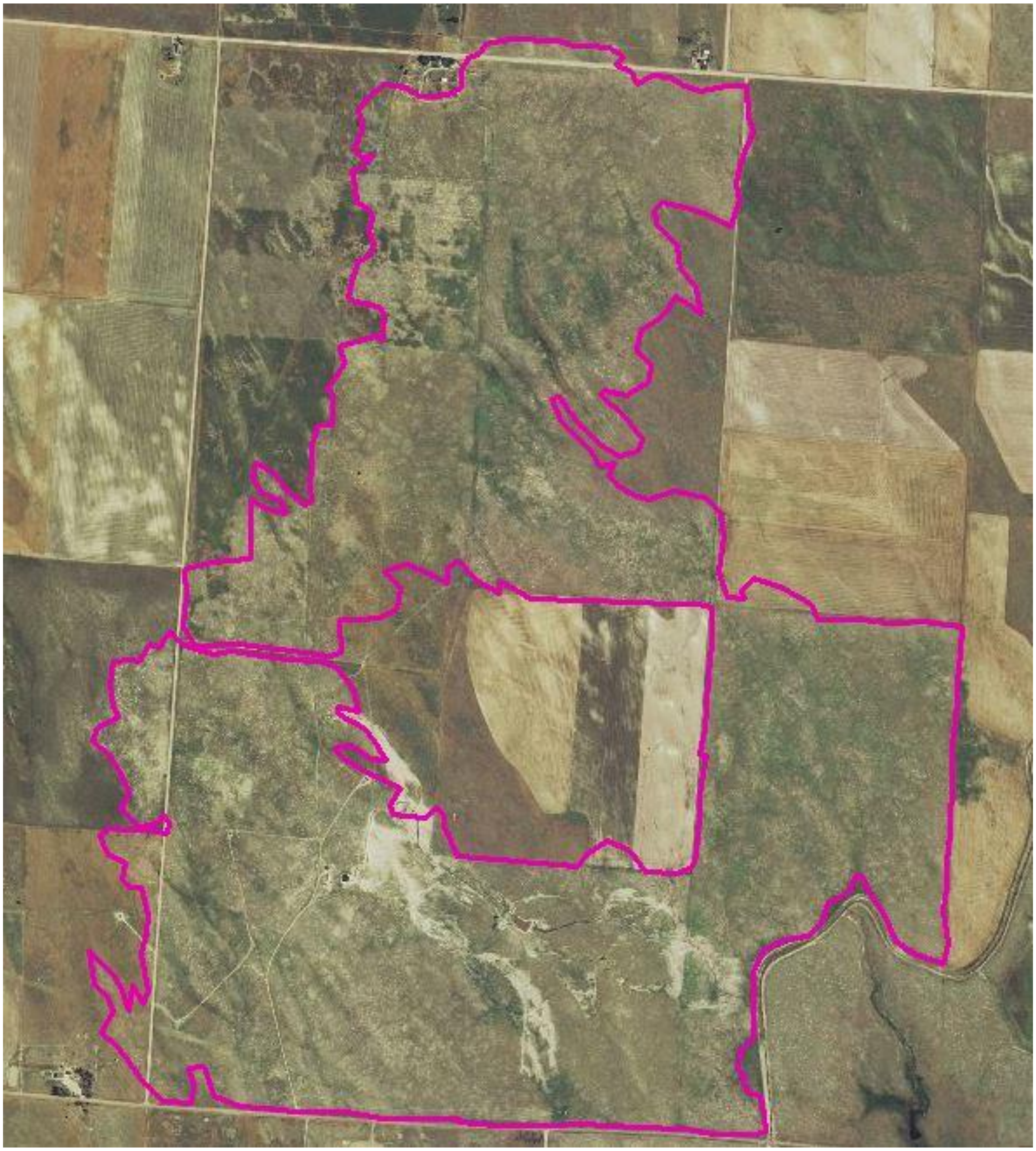

Figure A17. Odd, large shaped colonies often appear around areas of developed agricultural land. In this Colorado image, the observer digitized a feature that surrounds a smaller plot of farmland. These instances can occur due to land owners differences and whether or not they choose to remove prairie dogs from their land.

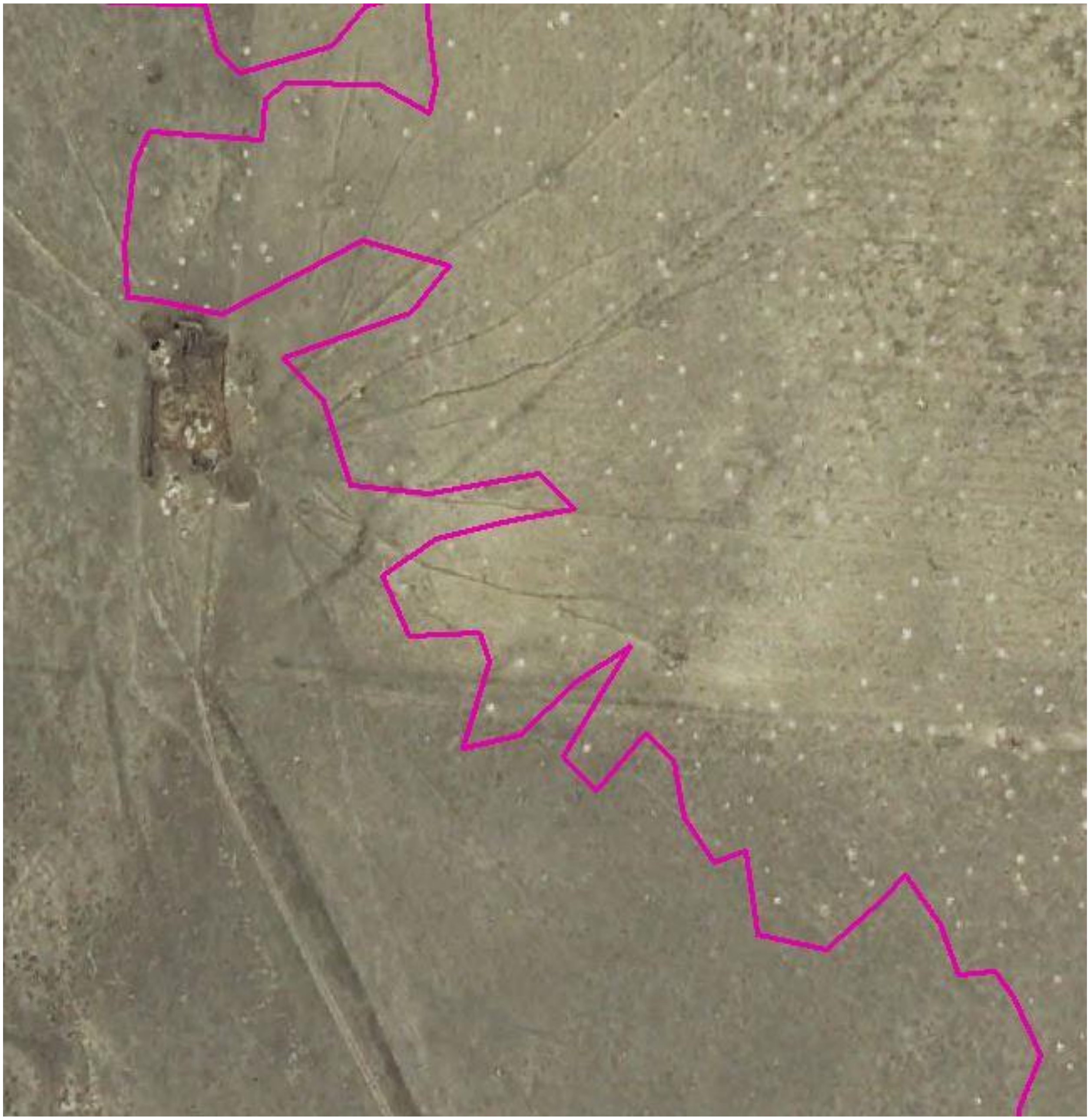

Figure A18. When digitizing, observers were instructed to connect the outermost mounds visible on the NAIP images, regardless of what might be visible using Google Earth.

Figure A19. Drought and landscape made digitizing difficult in some areas. In this image, observers used their best judgement to determine where the outermost burrows were on the NAIP imagery. Although observers were to digitize on the NAIP imagery, Google Earth helped determine the extent of the potential colony.

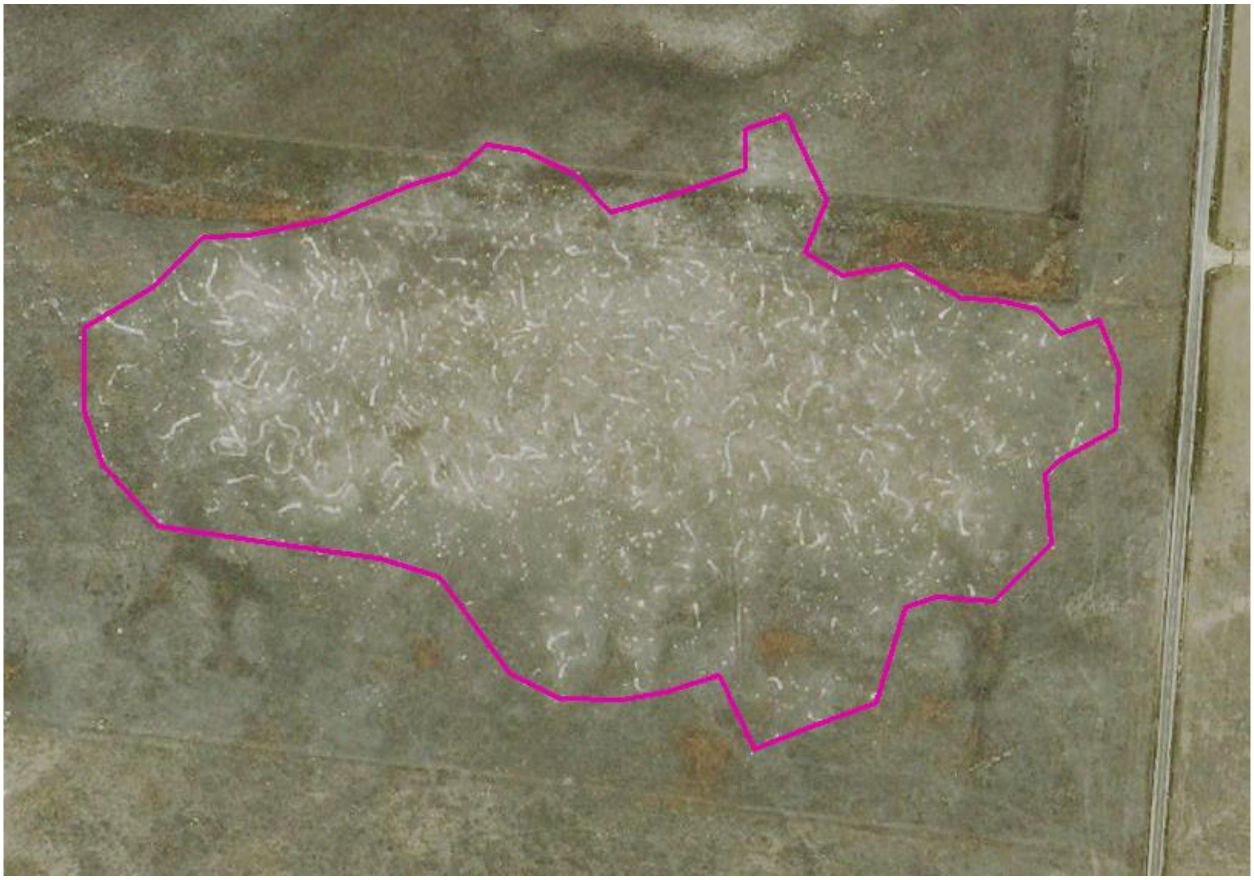

Figure A20. Unusual features were sometimes encountered. This feature was judged to be a potential black-tailed prairie dog colony, perhaps inhabited by black-footed ferrets with visible trenches.

Figure A21. This image shows a close-up in Google Earth of the potential black-footed ferret colony from the previous image, A20. Both images were from 2013.

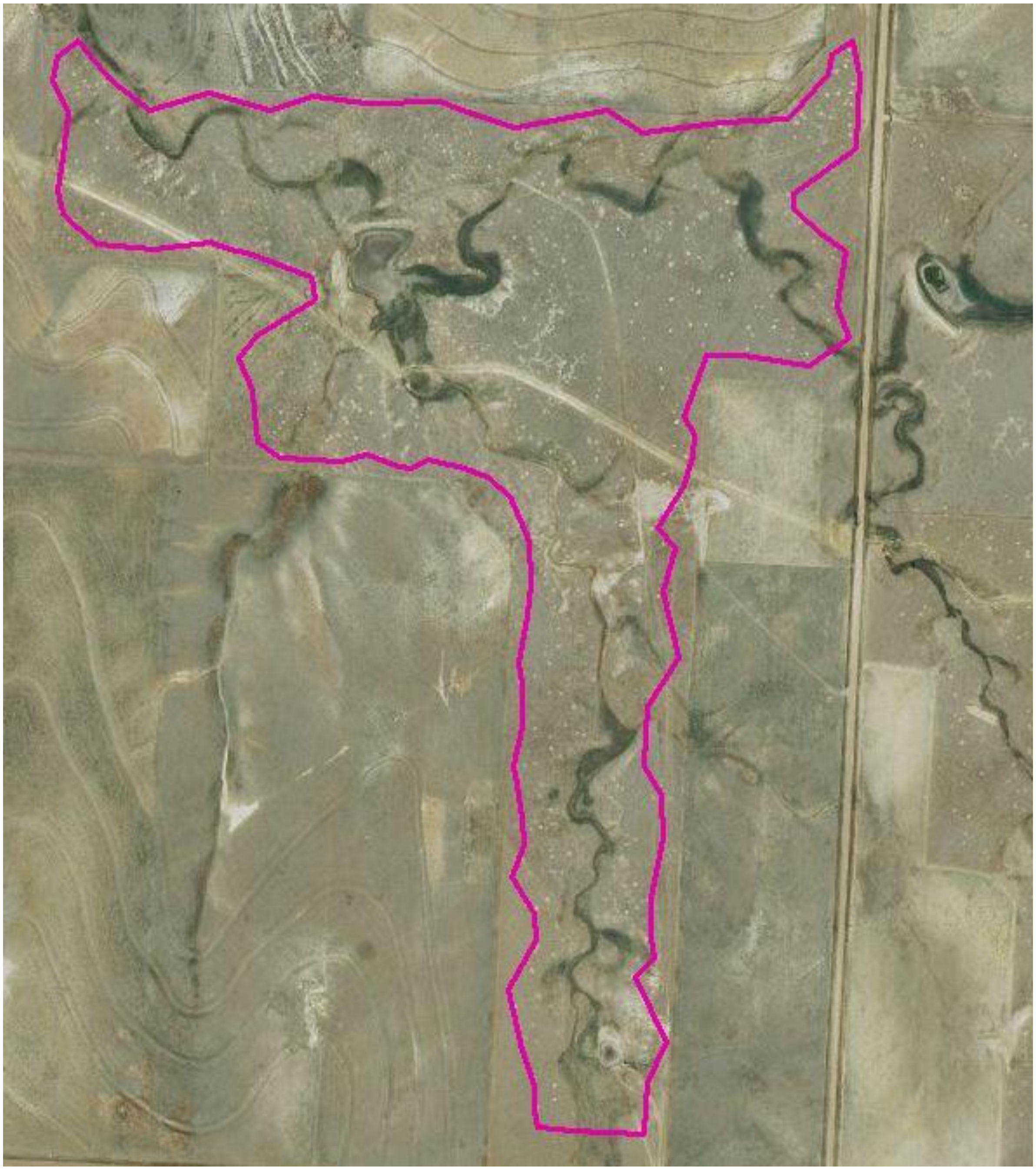

Figure A22. While digitizing colonies near riparian areas or bodies of water, observers were instructed not to include areas in the feature that prairie dogs would not use. In this image, the observer digitized this relatively large feature although it included some riparian areas probably not used by black-tailed prairie dog. To avoid over estimating the acreage of potential black-tailed prairie dog colonies, several smaller or more convoluted features of approximately the same area could have been digitized.

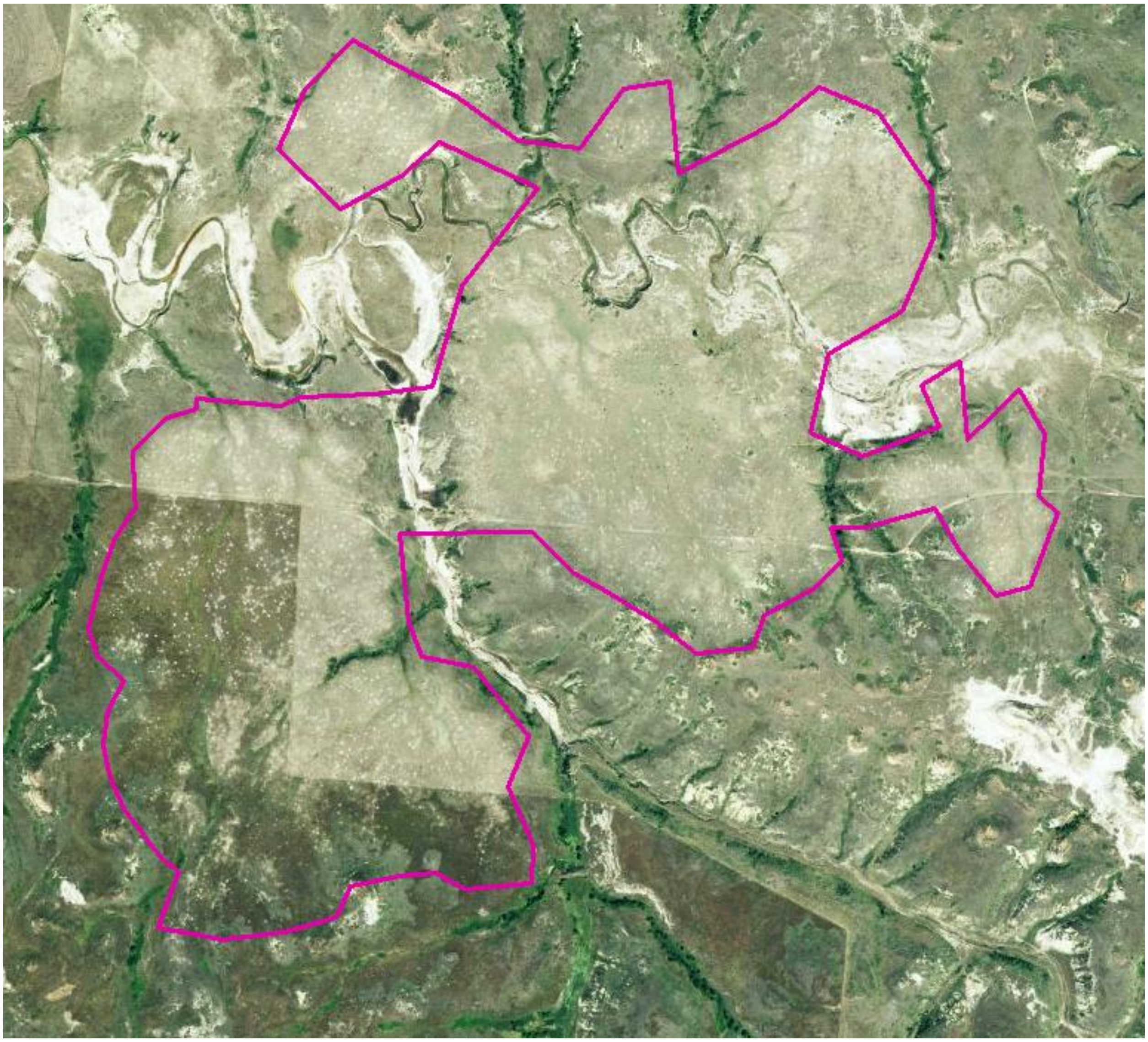

Figure A23. For difficult landscape features as here and in Figure A22, observers could consider splitting the colony into multiple parts. While prairie dogs may not feed or dig burrows in some parts of a feature, they may move across them. The above image contains a river and a ravine. Because the mounds go up to the feature and begin immediately again on the other side, the observer digitized this as a single colony.

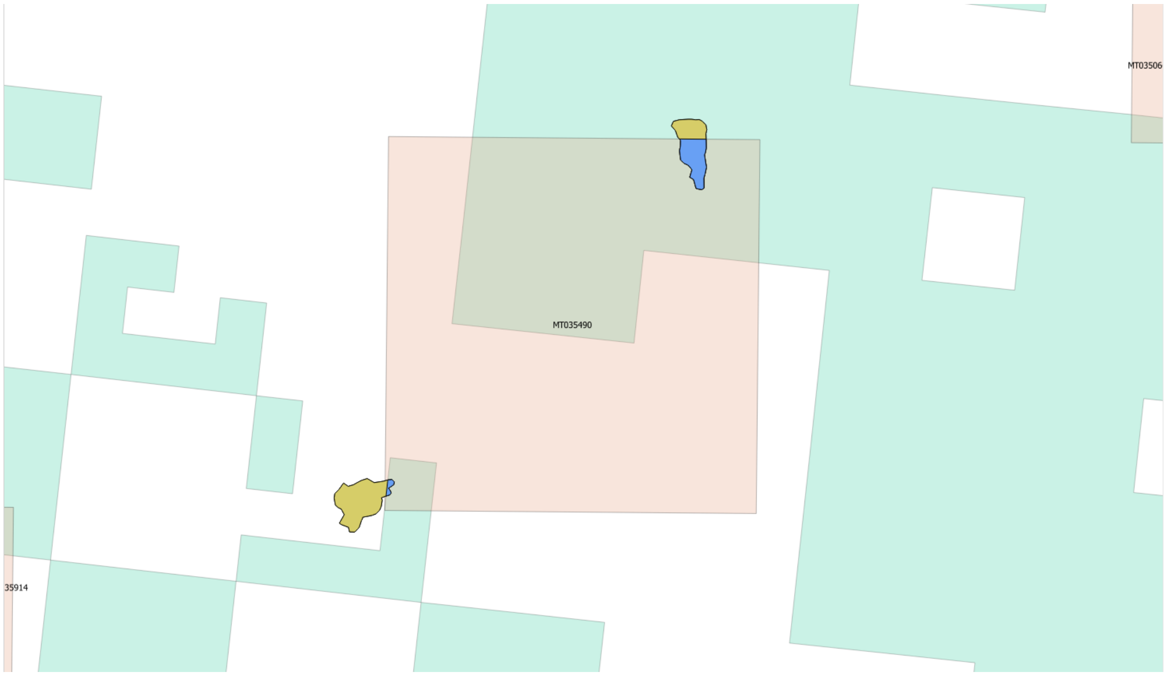

Figure A24. These two features overlapped BLM managed lands (green). The sampled cell (beige) had two digitized features with the centroid of the top feature in the sampled cell while the centroid of the bottom left feature was in a neighboring cell. The acreage on BLM land and in the sampled cell (blue) was averaged over sampled cells from the sampling frame for BLM land. The top feature was counted as associated with BLM land because it overlaps BLM land and its centroid was in the sampled cell.

APPENDIX B

Formozov-Malyshev-Pereleshin Analysis Methods

Formozov-Malyshev-Pereleshin formula for the transecting method

The Formozov-Malyshev-Pereleshin (FMP) formula estimates the probability P that a delineated feature boundary intersects with a grid-cell, or defined transect of interest based on simple probabilistic arguments (Stephens et al. 2006). Given a state containing T grid cells each 4 square miles in size and a total areal extent of $A = 4T$ square miles, the process of digitizing features results in two spatially related datasets. The first was the BAS sampling grid, consisting of t cells with four sides of equal length l, each oriented in one of the cardinal directions. For example, for all t western transects, with length l_w, the total length L_w over all western sides was $L_w = tl_w$.

The second spatial dataset contains the G digitized features. In practice, K_j line segments of length m_{jk} form the closed border of each jth feature, where the number of segments in each feature may vary. The perimeter of the jth feature was of length $M_j = \Sigma_k m_{jk}$, with M_j varying over the G features.

Suppose that one of the western transects of length l_{wi} of the ith cell, and a feature segment of length m_{jk}, were examined together. Given that all t cell transects were the same length l_w, the use of the cell index i is unnecessary. Now, assuming the two segments intersect, they either cross or connect in a "V," via their endpoints. Assuming the latter, the resulting parallelogram with sides of length l_w and m_{jk}, with internal angles α and $\pi - \alpha$, forms the largest possible area these two intersecting segments could form, of extent $l_w m_{jk} \sin\alpha$. This area, when compared to the total study area $A = 4T$, was then the maximum probability $P(i, j, k, \alpha)$ that the two segments l_w and m_{jk} intersect. Specifically, let

$$P(i, j, k, \alpha) = \frac{l_w m_{jk} \sin\alpha}{A}$$

represent this angular-dependent probability. In reality, the angle α could vary, taking on any value between 0 and 2π, due to random orientation of the line segment m_{jk}. Assuming that α was distributed uniformly on [0, 2π], then the probability of intersection $P(i, j, k)$ of l_w and m_{jk}, averaged over angle α, is

$$P(i, j, k) = \frac{1}{2\pi} \int_0^{2\pi} \frac{l_w m_{jk} \sin\alpha}{A} d\alpha$$

$$= \frac{2l_w m_{jk}}{\pi A}.$$

Now, sum over all t western borders of length l_w and all K_j constituent segments m_{jk}, of the jth feature, to see that the probability P_j that the jth feature intersects any of the t western transects, equals

$$P_j = \sum_{i=1}^{t} \sum_{k=1}^{Kj} P(i, j, k)$$

$$= \sum_{i=1}^{t} \sum_{k=1}^{Kj} \frac{2l_w m_{jk}}{\pi A}$$

$$= \frac{2}{\pi A} \sum_{i=1}^{t} l_w \sum_{k=1}^{Kj} m_{jk}$$

$$= \frac{2}{\pi A} t l_w M_j$$

$$= \frac{2(2t)\ M_j}{\pi A},$$

after recalling that the sum of all t western transects of length $l_w = 2mile$ must equal L_w. The probability P_j of intersection of the jth feature and the entire western transects, with total length L_w, was proportional to L_w, the perimeter of the jth feature M_j, and the total study area A. The total transect length associated with each cardinal direction was equal for all four directions, i.e., P_j was the same in all four cardinal directions.

The study design suggests further simplification of P_j; recalling that each cell was 2×2 miles in size, and noting that $L_w = tl_w,\ A = 4T$ miles ^{2}, and that l_w = 2 miles, conclude that

$$P_j = \frac{2L_w M_j}{\pi A}$$

$$= \frac{2tM_j l_w miles^2}{4\pi T miles^2}$$

$$= \frac{tM_j}{T\pi}.$$

Note that P_j represents the probability that the jth feature intersects the western transects in all t sampled cells only *once*.

Given a probabilistic estimate, P_j, that the jth feature, b_j, crosses at least one of the individual T western transects, an estimate of both the total number of features N in the study region of area A, and total feature areal extent S, can be made via a Horvitz-Thompson estimator. The summation was over features, which cross the set of western transects. Consider the set of all western transects in a sample of the C grid cells.

Define G to be the number of digitized features that intersect the set of all western transects in a sample of the t grid cells. Finally then, to estimate the total number of features N_w, based on west-transect feature-extent crossings in a sample of grid cells, use a Horvitz-Thompson estimator to form

$$\hat{N}_w = \sum_{j=1}^{G} \frac{1}{P_j}$$

$$= \sum_{j=1}^{G} \frac{T\pi}{tM_j}$$

$$= \pi(T/t) \sum_{j=1}^{G} \frac{1}{M_j}$$

where the G indicates the summation was over all features which intersect the western transects in a sample of the C grid cells.

Similar calculations to estimate the total areal extent S suggest that

$$\hat{S}_w = \sum_{j=1}^{G} \frac{s_j}{P_j}$$

$$= \sum_{j=1}^{G} \frac{\pi T s_j}{tM_j}$$

$$= \pi(T/t)\sum_{j=1}^{G}\frac{s_j}{M_j}.$$

Intuitively, if the ratio of total number of grid cells (T) to the sampled number of grid cells (t) was increased by, for example, factor or 2 then P_j will decrease by a factor of 2 and the number of features (G) intersecting the western transects will increase by 2. In the long run,

$$\hat{S}_w = \sum_{j=1}^{2G}\frac{s_j}{2P_j}$$

will remain approximately the same.

Finally, this process was then repeated for the other three directions, so as to obtain, for both N and S, four directional estimates for each of the four cardinal directions. Sets of features with more of an east-west extent, rather than north-south, can expect to cross in higher numbers with respect to either the eastern or western transect, thus inflating N_e and N_w more readily than N_s and N_w. The estimation with respect to the four cardinal directions thus provides a guard against any feature anisotropy, or preferential alignment of features to one direction over all others. Given the resulting four estimates for each of N and S, we took the average over all four directions to obtain a final estimate for each, i.e., calculate

$$\hat{N} = \frac{\hat{N}_w + \hat{N}_e + \hat{N}_n + \hat{N}_s}{4}$$

and

$$\hat{S} = \frac{\hat{S}_w + \hat{S}_e + \hat{S}_n + \hat{S}_s}{4}.$$

Hyperglycemia in acute aluminum phosphide poisoning as a potential prognostic factor

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Hyperglycemia in acute aluminum phosphide poisoning as a potential prognostic factor

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Aluminum phosphide (AlP) is a solid fumigant widely used in Iran as a grain preservative. When reacted with water or acids, AlP produces phosphine gas, a mitochondrial poison that interferes with oxidative phosphorylation and protein synthesis. Poisoning by AIP is one of the most important causes of fatal chemical toxicity in Iran. There are few studies in the medical literature addressing prognostic factors associated with AlP poisoning. In this prospective study conducted across a 14-month period commencing on 21st March 2006, we enrolled all patients admitted to the ICU of Loghman–Hakim Hospital Poison Center (Tehran, Iran) with AIP poisoning, no history of diabetes mellitus diagnosed before hospitalization, and normal body mass index. We recorded patient-specific demographic information, blood glucose level on presentation (before treatment), arterial blood gas (ABG) analysis, time elapsed between ingestion and presentation, ingested dose, duration of intensive care admission, and outcome data related to each presentation. We enrolled the group of patients who survived the intoxication as a control group and compared their blood glucose levels with those who died because of AlP poisoning. Data were analyzed by Statistical Product and Service Solutions (SPSS) software (Version 12; Chicago, Ilinois, USA) using logistic regression, Pearson correlation coefficient and Student's *t*-test. *P* values of 0.05 or less were considered as the statistical significant levels. Forty-five patients (21 women and 24 men) with acute AlP poisoning were included in the study. The mean age was 27.3 ± 11.5 years (range: 14–62 years). Thirteen patients survived (29%) and 32 expired (71%). AlP poisoning followed deliberate ingestion in all patients. The time elapsed between ingestion and arrival at the hospital was 3.2 ± 0.4 h. There was no significant difference between survived and non-survived groups according to age, gender, and time to treatment. However, the difference between mean blood glucose levels in survived (143.4 ± 13.7 mg/dL) and non-survived (222.6 ± 20 mg/dL) cases was statistically significant ($P = 0.021$). There was no significant correlation between blood glucose level and time to treatment, age, gender, pH, HCO_3 concentration, and ingested dose. Twenty-three (71.9%) of non-survived and four (30.8%) of survived patients had a blood glucose level greater than 140 mg/dL. After adjusting according to age, gender, ingested dose, pH and HCO_3 concentration The odds ratio for hyperglycemia as a risk factor for death was 5.7 (CI of 1.4–23.4). In our study, patients who succumbed to AIP poisoning had significantly higher mean blood glucose levels than those who survived. This correlation of hyperglycemic effect and mortality suggests that it may be useful in guiding risk assessment and treatment of AIP poisoning. Management of hyperglycemia may have a useful role in treatment of these patients by allowing increased entrance of glucose into cells and reducing oxygen consumption.

Key words: aluminum phosphide; hyperglycemia; mortality

Introduction

Aluminum phosphide (AlP) is a commonly used pesticide and is used as a fumigant in grain storage facilities.[1–3] In Iran, AlP is available as 3 g tablets; each consists of 56% AlP (total 1680 mg) and 44% ammonium carbonate. Following ingestion, AlP reacts with water and hydrochloric acid in the stomach, liberating phosphine (PH_3) gas. Phosphine gas is colorless, flammable, and highly toxic, with an odor of garlic or decaying fish. Phosphine is a mitochondrial poison and interferes in enzyme and protein synthesis[2,3] via mechanisms that are poorly understood. Experimental studies show that

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interruption of mitochondrial oxidative phosphorylation may lead to multi-organ dysfunction, and therapeutic strategies aiming to maintain enzyme activity may help in managing patients who are intoxicated with AlP.[4] There has also been evidence presented suggesting direct damage to blood vessels and erythrocyte membranes.[5]

AlP is one of the most frequently reported acute chemical poisonings in Asia.[6,7] Human exposure to AlP is rarely accidental and it often occurs following ingestions with suicidal intent. It is cheap, easily available in developing countries (e.g., India and Iran), and highly toxic.[8]

Presenting features of AlP intoxication include rapid onset of shock, severe metabolic acidosis, cardiac arrhythmias, and adult respiratory distress syndrome (ARDS). Animal studies have shown that phosphine causes fluctuations in glucose levels.[9] AlP poisoning has been postulated to stimulate cortisol, glucagon, and adrenaline secretion, or inhibit insulin synthesis.[10] Hyperglycemia in AlP poisoning has been observed in the literature,[1,10] but has not previously been used in risk assessment.

AlP poisoning presents a spectrum of clinical and laboratory findings, with scant historical data on factors predictive of prognosis. The aim of our present study was to evaluate the effects of AlP poisoning on blood glucose levels, and determine its potential utility as a prognostic factor in AIP-poisoned patients.

Methods

We designed a prospective case-control study to include patients admitted with a history of single agent AlP poisoning to the intensive care unit of Loghman–Hakim hospital poison center (Tehran, Iran) during a 14-month period commencing on 21st March, 2006. Forty-five patients with no history of diabetes mellitus diagnosed before hospitalization, and a normal body mass index (BMI) were enrolled. Diagnosis was based on the information provided by the patient or the patient's family about the agent involved in the exposure. Data were recorded on a standardized form, and included demographic information, blood glucose level at presentation (before treatment), ingested dose, arterial blood gas (ABG) results, time elapsed between ingestion and presentation, length of stay in the ICU (intensive care unit), and the clinical outcome.

Upon presentation to the emergency department, all patients received gastrointestinal lavage with potassium permanganate solution of 0.2 g/L, followed by 50 g oral-activated charcoal, and a $NaHCO_3$ (7.5%) infusion based on ABG and pH. All patients then received treatment in ICU guided by the same protocol (oral coconut oil, magnesium sulfate, calcium gluconate, adequate hydration). The physicians and nursing staff delivering care were common to all patients.

We enrolled the group of patients who survived the intoxication as an internal control, and compared their blood glucose levels with those who died because of AlP poisoning as the test group. Data were analyzed by SPSS software (Version 12; Chicago, Illinois, USA) using logistic regression, Pearson correlation coefficient and Student *t*-test. P values ≤0.05 were considered as the statistically significant levels.

Results

Forty-five patients (21 women and 24 men) with AlP poisoning were included in the study. The mean age was 27.3 ± 11.5 years (range: 14–62). Most patients were in their second and third decade of life (Table 1). Thirteen patients survived (29%) and 32 patients expired (71%). AlP poisoning followed deliberate ingestion in all patients. 44.4% of patients were poisoned with only one tablet of AlP, delivering 1680 mg AlP (Table 2). The interval time to treatment between ingestion and arrival at the hospital in survived and non-survived were 4.2 (±0.7) h and 2.8 (±0.3) h, respectively (Table 3).

There were no significant differences between survived and non-survived groups according to age, gender, and time to treatment (Table 3). All patients required endotracheal intubation and mechanical ventilation. Lengths of stay in the ICU for survived and non-survived were 175.3 ± 3.5 h and 15.6 ± 2.1 h, respectively ($P = 0.01$) (Table 3). There was no significant correlation between blood glucose level and time to treatment ($r = 0.083$) (Figure 1), age ($r = 0.078$) (Figure 2), gender ($r = 0.05$), or ingested dose ($r = 0.05$). Additionally, there were no significant correlations between

Table 1 Distribution of age in patients with aluminum phosphide poisoning

Age (year)	*Number*	*Percent (%)*
0–9	0	0
10–19	14	31
20–29	18	40
30–39	5	11
40–49	5	11
50–59	2	5
60–69	1	2
Total	45	100

Table 2 Distribution of dose ingested among patients with aluminum phosphide (AlP) poisoning (one tablet = 1680 mg AlP)

No. tablets ingested	*AlP ingested (mg)*	*Patients (%)*
0.25	420	2
0.33	554	2
0.5	840	13
1	1680	44
1.5	2520	2
2	3360	18
3	5040	9

blood glucose level and blood HCO_3 concentration or pH (Figure 3). The mean blood glucose levels in survived and expired patients were 143.4 ± 13.7 mg/dL and 222.6 ± 20 mg/dL, respectively (Table 3), a difference that reached statistical significance ($P = 0.02$). Twenty-three (72%) of non-survived and 4 (31%) of survived patients had blood glucose levels greater than 140 mg/dL. After adjusting according to age, gender, ingested dose, pH, and HCO_3 concentration, the odds ratio for hyperglycemia as a risk factor for death was 5.7 (CI 95% = 1.4–23.4).

Discussion

Phosphine poisoning following AlP ingestion develops rapidly and the majority of deaths occur within the first 12–24 h, usually because of cardiovascular dysfunction.[2] Mortality rates in AlP poisoning reportedly lie between 60% and 80%,[11,12] figures congruent with our experience in this case series. AlP exposure to moisture liberates highly toxic phosphine gas, the toxicity of which is related to free radical generation and inhibition of metabolic enzymes such as cytochrome-C oxidase.

AlP poisoning may lead to multi-organ dysfunction, and histopathological examination of tissues in a rabbit AlP toxicity model showed profound degenerative changes in liver, heart, and kidney.[13] Animal studies on the effect of AlP on blood glucose levels have shown fluctuations in glucose levels.[9] Elevation, reduction, and lack of effect on blood glucose levels have previously been observed[10]; however no attempts have been made to correlate these observations with clinical toxicity or outcomes. Significant rises in plasma cortisol levels, rennin activity, and mean serum and tissue magnesium and phosphate levels have also been observed in some studies.[14–19] Chugh, *et al.* (1989) reported findings of 50 cases that showed a significant rise in plasma cortisol (>1048 nmol/L) in 40% of cases. Postmortem examination in 10 patients showed mild-to-moderate adrenal cortex changes including congestion, edema, and cellular infiltration.[4] This involvement of the adrenal axis provides a plausible

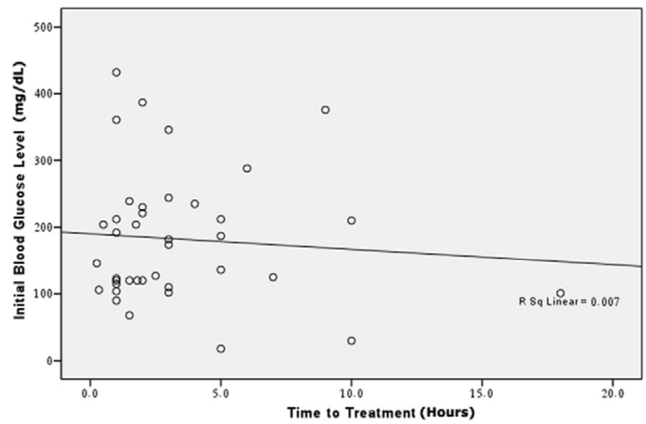

Figure 1 Relationship of time to treatment with initial blood glucose level (not significant).

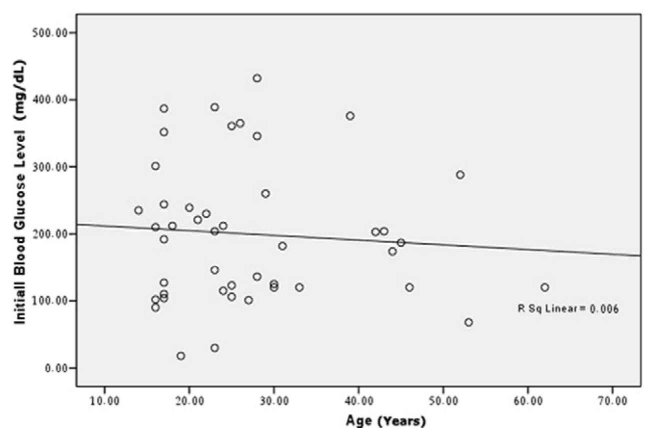

Figure 2 Relationship of age with blood glucose level (not significant).

Table 3 Distribution of age, gender, time interval between ingestion and admission to the hospital and blood glucose levels

Patient group	*Age (years)*	*Gender*	*Length of stay in ICU (h)[a]*	*Blood glucose (mg/dL)[a]*	*Elapsed time to treatment (h)*
Survived	24.2 (±8.8)	6 female, 7 male	175.3 (±3.5)	143.4 (±3.7)	2.8(±0.3)
Non-survived	28.5 (±12.3)	15 female, 17 male	15.6 (±2.1)	222.6 (±20)	4.2(±0.7)

Data are represented as mean ± SE.
[a]Represents significant differences at $P < 0.05$ level.

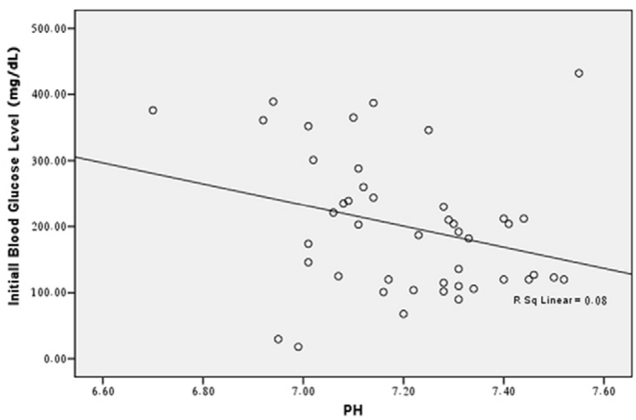

Figure 3 Relationship of pH with blood glucose level (not significant).

explanation for the historically observed derangement of glucose homeostasis underpinning the current study. In addition AlP poisoning has been reported to be associated with acute pancreatitis and hyperglycemia in some cases,[20] suggesting that the effect of AlP on the pancreas may have a role in causing hyperglycemia in this setting. Furthermore, studies of the intragastric administration of AlP in rats showed significant decreases in adenosine triphosphate (ATP), strongly suggesting that the effects outlined above are significant enough to directly impact metabolic energy production.

The results of our study suggest an increased risk of death in those patients with glucose levels greater than 140 mg/dL at Emergency Department (ED) admission. Suggested mechanisms for this elevation include impaired oxidative phosphorylation and glucose utilization, or involvement of the adrenal axis or pancreas. It may be proposed that directly addressing hyperglycemia by administering insulin might result in improved glucose influx into the cells, improved cellular metabolic function, and increased ATP production. Potentially, this simple intervention may prove beneficial in the management of this devastating poisoning, and we are currently conducting an additional study to evaluate this further. Novel therapies such as trimetazidin, which switches myocyte metabolism, to glucose from fatty acid, thus reducing oxygen consumption may also have a potential therapeutic role.[21]

The influence of food relating to a last meal ingested by our patients could not be accurately assessed because of the acute illness of patients due to their toxic condition, and the unreliability of history from family members because of stress. Thus, the effect of a last meal on blood glucose level at the time of admission was not included in our study. The lack of this information was not an exclusion criterion for patient enrollment in the study, and this is a limitation in our study. However, the majority of patients had at least a 3 to 4-h delay between ingestion of AlP and admission to the hospital. During this period, no food was consumed because of the acuteness of the poisoning.

Conclusion

Our study reported that non-survivors of AlP poisoning had a statistically significant tendency towards hyperglycemia when compared with survivors, suggesting that hyperglycemia may be used as a marker of AlP poisoning severity and may be a useful prognostic tool in evaluating and managing this particular poisoning. Further study is required to determine if interventions targeting hyperglycemia may be of therapeutic value in the management of AlP poisoning.

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THE PRAIRIE DOG OF THE GREAT PLAINS.

By C. Hart Merriam,
Chief of Division of Biological Survey.

INTRODUCTION.

In crossing the United States by any of the transcontinental railways the traveler who looks out from the car window on the second day westward from Chicago is sure to have his attention arrested by colonies of small animals about the size of cottontail rabbits. These animals are prairie dogs. Some stand erect at the mouths of their burrows, view-

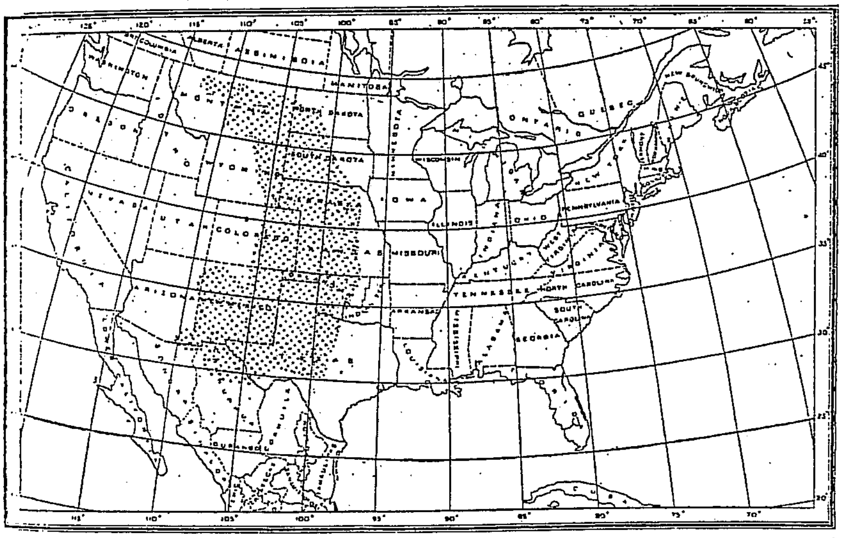


Fig. 24.—Distribution of plains prairie dog (*Cynomys ludovicianus*): The occupied area is marked with dots.

ing the passing train; others are engaged in feeding or running to and fro about the colony. The land they occupy is the broad expanse of level and slightly rolling semidesert country known as the Great Plains, a vast tract which stretches from the Rocky Mountains easterly to the western edge of the Mississippi Valley, and from Montana and North Dakota southward to Texas and Mexico. (See fig. 24.) The plains are treeless, except along the streams, and the ground is sparsely covered with grass and other small plants, which are green in early spring and brown the greater part of the year.

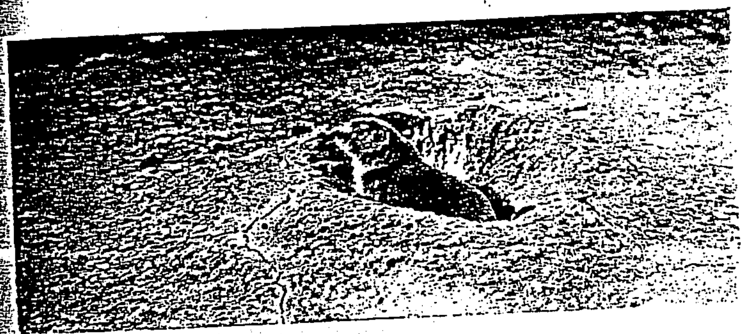
The prairie dog loves sunshine and a dry atmosphere, and in ranging easterly from the arid plains toward the humid prairies of the Mississippi Valley becomes less and less numerous, till between the ninety-seventh and ninety-eighth meridians he disappears altogether. Not even the luxurious vegetation of the prairies is sufficiently attractive to lure him into the humid belt adjoining his chosen home. That he is fond of rich vegetation and prefers it to the dry bunch grass of the plains is shown by his great destructiveness to alfalfa, grain, and other crops grown on irrigated lands within his range. This is an important illustration of the law that in fixing the limits of distribution of animals climatic factors are even more potent than food.

The prairie dog is preeminently a social animal, living in colonies which vary in extent from a few acres to thousands of square miles and inhabited by thousands, and in some cases millions, of animals. Colonies 20 to 30 miles in length are not rare, and in Texas one is known which measures about 250 miles one way by 100 to 150 the other, covering an area of about 25,000 square miles. The number of holes in use on each acre varies from a few to upward of a hundred, and probably averages at least 25. At Alma, Nebr., W. H. Osgood found the number ranging from 35 to 64, and on an alfalfa field near Carlsbad, N. Mex., Vernon Bailey found 1,009 on 20 acres, or 50 to the acre. In old towns many holes are abandoned, or used only as refuges, so that it is difficult to ascertain how many animals live in a stated number of holes. Another difficulty lies in the varying number of animals in the occupied holes, for in winter and early spring the usual number is two (a pair), while after the birth of the young the number is at least quadrupled, and then decreases with the advance of the season, as the young are killed by enemies. It is certainly a conservative estimate to assume the average number of animals per acre to be 25. On this assumption, the number of prairie dogs in the great Texas colony must be at least 400,000,000.

According to the formula for determining the relative quantities of food consumed by animals of different sizes (kindly given me by Prof. W. W. Cooke), 32 prairie dogs consume as much grass as 1 sheep, and 256 prairie dogs as much as 1 cow. On this basis the grass annually eaten by these pests in the great Texas colony would support 1,562,500 head of cattle. Hence, it is no wonder that the annual loss from prairie dogs is said to range from 50 to 75 per cent of the producing capacity of the land and to aggregate millions of dollars.

GENERAL HABITS OF PRAIRIE DOGS.

When a person approaches a dog town the animals see him a long way off and keep a close watch on his movements. As he comes nearer an alarm note is sounded, at which those away from their burrows rush to the entrance mounds, where they sit or stand erect, nervously twitching



PHOTOGRAPHED BY C. HART MERRIAM. HELIOTYPE CO., BOSTON.

THE PLAINS PRAIRIE DOG (CYNOMYS LUDOVICIANUS).

their tails and chattering or barking excitedly. If he continues to move toward them the excitement increases, and most of the animals on the near side of the colony plunge headlong into their burrows. Some withdraw more slowly, and for some time their heads and eyes may be seen peering up from the funnel-shaped openings of the mounds. Those near by are usually silent, while those at a little distance continue to scold and chatter. This chattering or barking, as it is usually called, can often be heard after the animals have gone down out of sight in their holes. (Pl. XXII.)

Along railroads the animals have become so accustomed to the trains that they no longer take fright as the great noisy engine rushes madly by, and they are best observed, perhaps, from the windows of passing trains. Their indifference at such times is amazing. I have often watched them from the "Overland Limited," some standing erect on their mounds; others chasing one another about or quietly feeding within 40 or 50 feet of the roaring, rushing train, without showing the least outward sign that anything unusual was happening. One would think the fury and deafening roar would be too much for their nerves, but they appear to regard it with absolute unconcern. It is extraordinary how soon animals lose their fear of naturally terrifying objects when such objects come and go frequently without doing them bodily violence.

In summer, prairie dogs are most active mornings and evenings, usually remaining in their holes during the hotter part of the day. In fall they become very fat, and apparently sleep a good deal; at least, they are much less regular and are less frequently seen. In winter, in the southern part of their range, they may be seen nearly every day unless it is stormy. Thus, in Texas and New Mexico they are said to come out in good weather shortly after sunrise, even at times when the temperature is below freezing. On the northern plains they hibernate irregularly, but still appear at intervals. The periods of hibernation are probably determined by storms and by the length of time the ground is covered with snow, for in Montana and Wyoming they have been known to appear, in places where the ground was bare, on calm sunshiny days in midwinter when the mercury stood at or below zero.

Prairie dogs, like the desert species of kangaroo rats, pocket mice, ground squirrels, and other rodents of arid regions, are able to live and thrive without drinking. In many places the only moisture they take into their systems is the small quantity contained in the dry grasses, seeds, and roots they eat. In arid western Texas they are abundant in places where the annual rainfall is slight and uncertain and where some years pass without any rain. With respect to the theory that their burrows are deep enough to reach water, it need only be said that in some of the dog towns artesian wells have been sunk to the depth of 1,000 feet without striking water.

TIME OF BIRTH AND NUMBER OF YOUNG.

The time of reproduction varies with the latitude and altitude, but exact information as to the dates of birth and the number of young in a litter in different parts of the plains is not at hand. In Texas the young are usually seen at the mouths of the holes in early May, while in North Dakota and Montana they rarely appear before the latter part of May or first week of June. The usual number of young seems to be four, but the cases in which the number is definitely known are few.

MOUNDS AND BURROWS.

The mouth of each burrow opens in the middle of a mound, which is usually a foot high and 3 or 4 feet in diameter (Pl. XXIII, fig. 1). The mound increases in size with age, those that have been used for many years attaining a height of 1½ or 2 feet and a diameter of 8 or 10 feet. The interior of the mound is funnel-shaped, forming an elevated crater-like rim around the entrance of the hole. This is pressed into form by the nose of the animal, as may be seen in Pl. XXIII, fig. 3, which shows prints of the nose all around the inside. After injury from rains or other causes the rim is repaired by scraping up the ground from outside (Pl. XXIII, fig. 2). Sometimes the repairs are made before rains, and some observers regard the animals as exceptionally clever weather prophets. Thus, Maj. H. W. Merrill states that whenever they are busy scraping the earth up around their burrows and pressing it into place with their noses rain is sure to follow in a very short time. The chief object of the elevated rim is to keep the water out of the burrows when the ground is flooded by sudden rains, as shown in Pl. XXIV, fig. 1. The ground immediately surrounding each burrow is usually cleared of small plants and kept clean and bare, and where burrows are near together the bare areas often join, so that in thickly populated colonies the ground is hard and smooth like a playground, and the animals are obliged to go some distance for food. This they dislike to do, lest they be pounced upon by enemies; hence, when the grass near their burrows has been consumed they dig new holes nearer the supply. It takes a long time for vegetation to regain a foothold on the hard floors of the dog towns, and the sites of old towns remain conspicuous for years after they are abandoned.

The holes go down for some distance at a very steep angle and then turn at nearly a right angle and continue horizontally, rising somewhat toward the end. The nests are in side chambers connecting with the horizontal part of the burrow, and usually, if not always, at a somewhat higher level (fig. 25, *H*). Recently, at Alma, Nebr., W. H. Osgood dug out a burrow, of which he made a careful diagram (fig. 25), accompanied by measurements. In this case the

FIG. 1.—NORMAL MOUND IN NEW GROUND (AN ALFALFA FIELD).

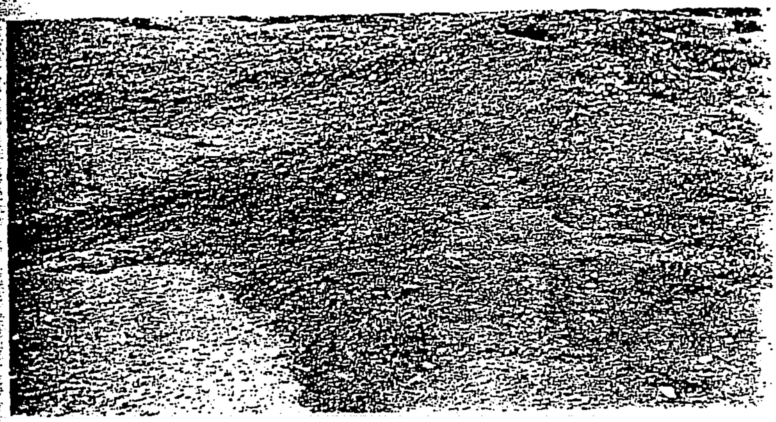
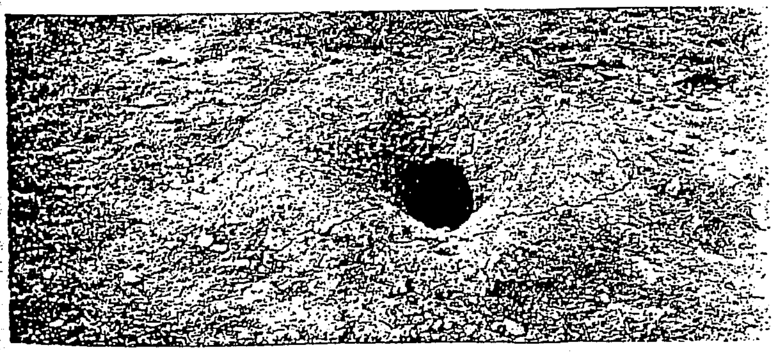


FIG. 2.—MOUND REPAIRED BY SCRAPING UP EARTH FROM THE OUTSIDE.



PHOTOGRAPHED BY VERNON BAILEY. HELIOTYPE CO., BOSTON.

FIG. 3.—INSIDE OF RIM OF MOUND, SHOWING NOSE MARKS.

MOUNDS OF THE PLAINS PRAIRIE DOG.

burrow went down nearly vertically to a depth of 14½ feet below the surface, when it turned abruptly and became horizontal, as shown in the diagram. The horizontal part was 13½ feet in length. One-third of the horizontal part (the terminal 4 feet, *F*) and two old nests and passageways (*E*) were plugged with black earth brought in from

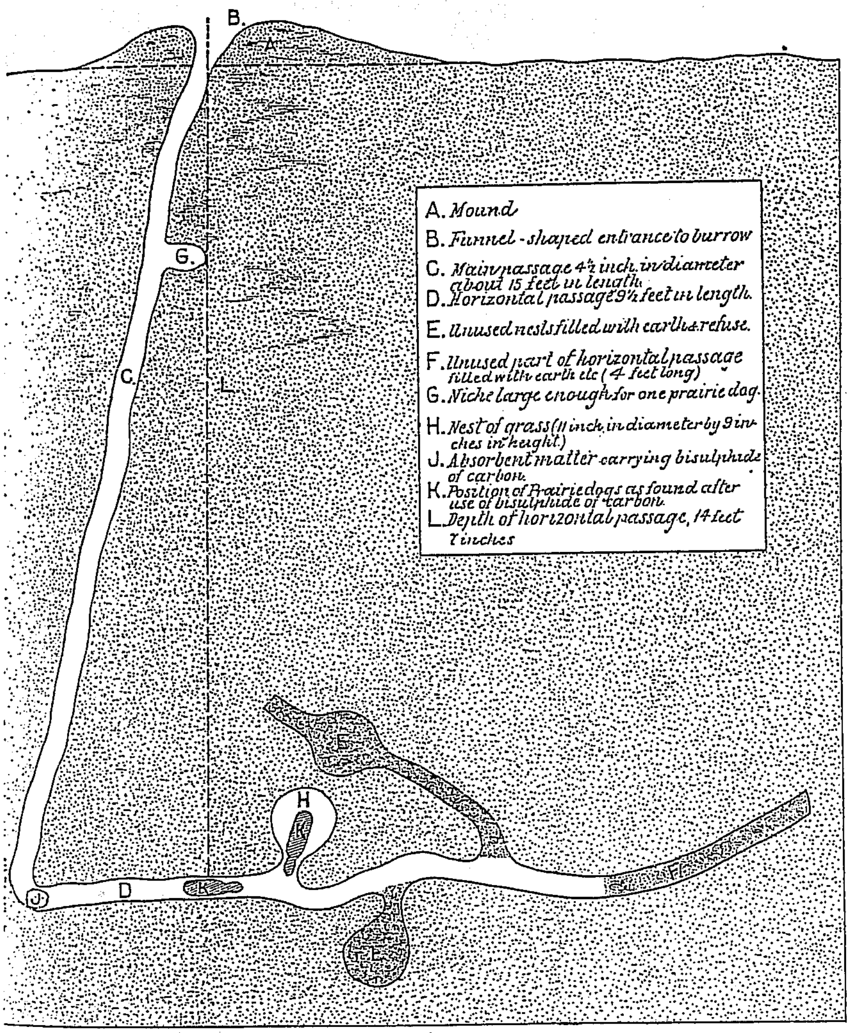


FIG. 25.—Prairie-dog burrow.

the surface layer, which was very different from the light-colored clayey earth in which the greater part of the burrow lay. Four or five feet below the entrance was a diverticulum, or short side passage (*G*), probably used as a place in which to turn around when the animals come back to take a look at the intruder before finally disappearing in the bottoms of their burrows. It is also used, apparently, as a resting place where they bark and scold after retreating from the mouths of the burrows. As elsewhere noted, they are often heard barking after they have gone in. The burrow was opened the day after bisulphide of carbon had been used for destroying the animals, and the material carrying the bisulphide was found at the bottom of the vertical part, just where the horizontal part turns off. Two dead animals were found, one in the horizontal part, the other in the nest, as indicated by the letter *K* in the diagram.

NATURAL ENEMIES.

The prairie dog has several mortal enemies which, when not interfered with by man, usually serve to hold its numbers in check. The most inveterate of these appear to be the coyote, badger, black-footed ferret, and rattlesnake. Their methods of attack differ widely.

The coyote sneaks up to the borders of a colony, hiding behind straggling tufts of vegetation and depending largely on his protective coloration for concealment. He usually approaches when the animals are in their burrows, and strives to reach some object behind which he may hide and lie in wait until some unwary inhabitant comes out to feed, when by a quick rush it may be headed off and caught.

The badger usually drives his prey into its burrow and then deliberately digs it out. He is for his size one of the most powerful animals in the world. His foreclaws are long and strong, and his sense of smell is highly developed. On sniffing a prairie dog or gopher in its burrow, he simply bores down to his victim, which has no possible means of escape.

The black-footed ferret is built like a weasel, and though much larger, is small enough to enter and traverse freely the burrows of prairie dogs, so that he is able to pursue them to the ends of their holes and capture them with absolute certainty. He is, therefore, one of their most relentless and terrible enemies, and if sufficiently abundant would quickly exterminate all the inhabitants of the largest colonies.

The rattlesnake, like the ferret, glides silently into the hole, but is said to confine his attentions to the young, which he takes from the nest or seizes in the passageways. Travelers on the plains, from the time of Lewis and Clark to the present day, speak of finding young prairie dogs in the stomachs of rattlers killed in the dog towns. The usual number so found appears to be one or two, but Dr. J. A. Allen states that he once found three. One author claims that in Texas these reptiles live almost wholly on the young of the prairie dog and do more, perhaps, to keep down the numbers than all other agencies. This writer continues:

A curious thing about the snake and the dog is that each is mortally afraid of the other. The dog is afraid of being eaten by the snake, and the snake is afraid of being entombed by the dog. If the mother of the young dogs, on a return to the home hole, finds that a snake has intruded, she at once sets up a peculiar cry or bark, to which all the citizens of the town at once respond. They gather about the hole, and in a moment all are at work filling it up. The quickness with which they can do this is remarkable. When the hole is filled they butt and pack the dirt in the mouth of the hole till it is almost as hard as the prairie adjacent. There is no chance for an escape of the invader. He is sealed up in his tomb. The snake understands this danger, and is prepared to escape from it on the least warning. A handful of dirt thrown in a hole where the snake is will bring him with all speed out of the hole, because he is under the impression that the dogs are about to seal him up.[1]

There are other enemies also, such as cougars or mountain lions, bobcats, eagles, hawks, and owls, but most of them are not sufficiently abundant on the Great Plains to be regarded as important factors in holding the prairie dog in check. Still, in some localities, hawks and owls kill large numbers of the young. They should be protected and encouraged.

RECENT INCREASE AND SPREAD OF PRAIRIE DOGS.

Formerly the area of available land in proportion to the population was so great that little attention was paid to such pests as prairie dogs and gophers. But in recent years the development of improved methods of farming, including irrigation and artesian water supply, has led ranchmen to push farther and farther westward over the semiarid plains, until agriculture and stock raising have invaded most parts of the prairie dog's domain, the land holdings have decreased in size and increased in value, and the depredations of pests are more keenly felt.

On many parts of the plains prairie dogs are now more abundant than formerly and their colonies have overspread extensive areas previously unoccupied. This is due to the coming of the white man, whose presence favors their multiplication in two ways—(1) by increasing the food supply, and (2) by decreasing the animal's natural enemies. The white man cultivates the soil and thus enables it to support a larger number of animals than formerly; at the same time he wages warfare against the coyotes, badgers, hawks, owls, snakes, and other predatory animals which had previously held the prairie dogs in check. Thus favored, the prairie dogs have multiplied until they have become one of the most pernicious enemies to agriculture. The increase of late years is well known to ranchmen on the plains, but for the information of others a few definite instances recently collected by my assistants may be of interest.

Richard Harrison, of Blunt, S. Dak., states that ten years ago there were possibly 25 occupied burrows on his land; the animals increased slowly and six years ago not more than 10 acres were infested. Since then the increase has been so rapid that at present the area they occupy covers about 160 acres.

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[1] American Field, p. 194, March 11, 1899.

O. E. McArthur, also of Blunt, S. Dak., states that about fifteen years ago his children noticed two or three burrows about a mile from his house, and that no particular attention was paid to the inmates, which, during the next few years, increased slowly. A little later, however, they spread over so much land that their multiplication became a matter for serious alarm. At present they occupy a full quarter section (160 acres), having surrounded Mr. McArthur's house and taken possession of all the land near it.

A cattle ranch in Logan County, Kans., which ten years ago pastured a thousand head of cattle, will barely support 500 at present, owing to the great increase in prairie dogs, which have overrun the range. Practically, the whole of the southern half of Logan County is now one continuous dog town, estimated to cover about 300 square miles. In the past decade the population of this area has decreased, a post-office (Elkader) has been abolished, and many homes have been vacated, the result, it is said, of the great increase in prairie dogs.

At Carlsbad, in the Pecos Valley, New Mexico, in September, 1901, Vernon Bailey studied a colony of prairie dogs which completely covered a 20-acre alfalfa field, 4 or 5 acres in each of two adjoining fields, and several acres of prairie. He was told that this large colony had spread in three years from a small one in a corner of the alfalfa field.

E. W. Nelson states that when he and his brother located ranches in a mountain valley in eastern Arizona in 1884, the only prairie dogs in the vicinity were a colony 3 miles distant, inaccessible except by way of a narrow box canyon. About three years later a prairie dog's burrow was found on the ranch, after which the animals multiplied steadily, until in 1895 they occupied a large part of the valley.

Complaints are constantly received of the spread of the pests on farm lands adjoining Government, railroad, school, and other lands, over which the inhabitants have no jurisdiction. This is a very serious evil, and one with which it is exceedingly difficult to cope.

FOOD.

The normal food of the prairie dog is grass, chiefly the bunch grass of the plains. In addition to this, grass roots, other plants, seeds, and sometimes insects are eaten.

DESTRUCTIVENESS.

The damage done by prairie dogs consists in the loss of grass and other crops eaten, or buried under the mounds; in the accidental drainage of irrigation ditches,[1] and in the danger to stock from stum-

[1] In Stillwater Valley, Montana, an irrigating ditch on a side hill was tapped by a prairie dog burrow and the water came out 50 feet lower down on the slope. The hole was twice stopped and the ditch moved a little, but the break recurred, and it was finally necessary to dig a new ditch around the washout.

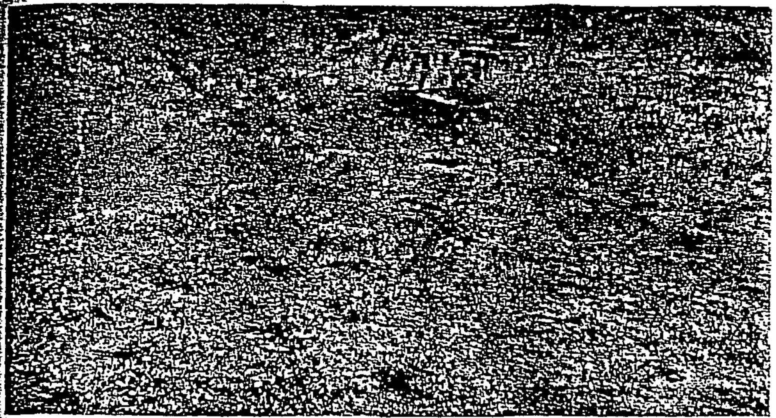


FIG. 1.—MOUND IN FLOODED GROUND, SHOWING PROTECTION FROM RAINS.

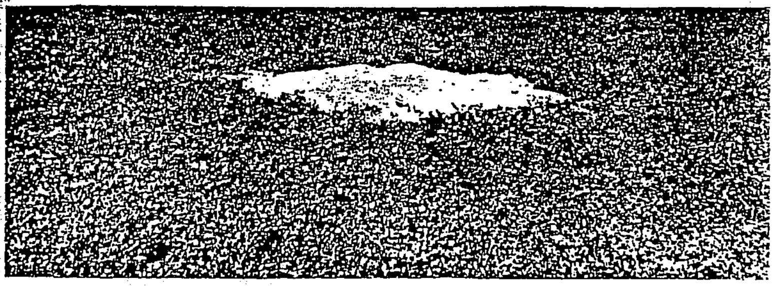
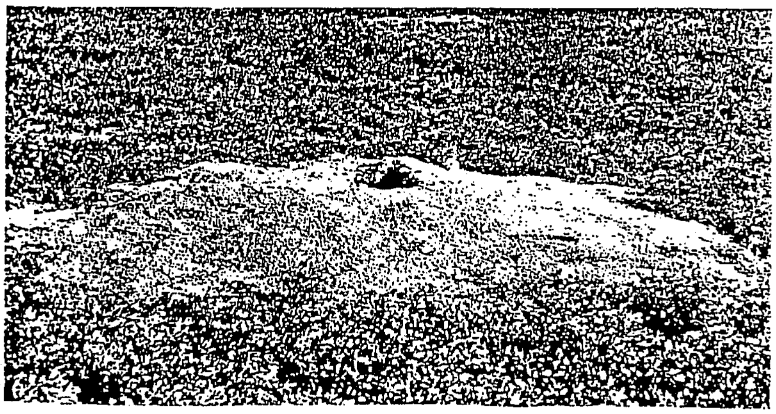


FIG. 2.—NEW MOUND IN ALFALFA FIELD.



PHOTOGRAPHED BY V. BAILEY AND W. H. OSGOOD. HELIOTYPE CO., BOSTON.

FIG. 3.—NEW MOUND IN ALFALFA FIELD.

MOUNDS OF THE PLAINS PRAIRIE DOG.

bling in the holes. Running horses often trip and break their legs, and riders are sometimes injured and even killed.

On ranch lands prairie dogs have proved destructive to a variety of crops, among which are alfalfa (Pl. XXIV, figs. 2 and 3), grain, potatoes, and sugar beets, and on grazing lands they are said to consume, or bury under their mounds, so much grass that the capacity of the land for supporting stock is reduced, as already noted, from 50 to 75 per cent. A prominent Texas newspaper recently published an editorial containing the following:

> No man who has not gone through the portions of Texas infested by prairie dogs can conceive the enormous ravages they have committed. Millions of acres of land once covered with nutritious grasses have been eaten off by these animals, until the land is naked and worthless, and will remain worthless so long as the prairie dog remains. They invade the farms and eat down the growing crops. Here and there individual effort has been made to destroy them, without avail, and their numbers steadily increase, until they are a menace to the prosperity of the land.

POPULAR INTEREST IN THE DESTRUCTION OF PRAIRIE DOGS.

The general apathy of a few years ago, when land was plentiful and of little value, has given place to widespread and active effort to rid the country of the pests. Wherever our field experiments have been made, from the Dakotas to Texas, the inhabitants were found fully awake as to the necessity for immediate action, and hundreds, if not thousands, of them had already expended time and money in single-handed efforts. The recent attempt of the National Government to ascertain the simplest and most efficient means of combating the evil has been received with universal approval. With one or two exceptions, our field men were granted free access to private lands, and in most instances were enthusiastically received and accorded every assistance and courtesy. In some cases, where the animals are rapidly increasing, the actual and prospective losses are so great that ranchmen expressed their willingness to pay for the destruction of the animals at a rate per acre exceeding the actual market value of the land.

METHODS OF DESTRUCTION.

In the case of prairie dogs, as in the case of gophers and ground squirrels, numerous remedies have been suggested and tried, most of which have met with a certain measure of success. Few, however, have proved available on a large scale. It is easy to destroy isolated animals, and to completely exterminate the inhabitants of small isolated colonies, but, as a rule, the problem confronting the sufferer from prairie dogs is one of larger dimensions; to cope with it successfully means the employment of measures and remedies that are simple, easily handled, available on a large scale, and last, but not least, not too costly (either for materials or labor) to be used over areas comprising thousands of acres. The cost on large ranches should not exceed 18 cents per acre, and should fall as far short of this as possible.

Among the measures that succeed well enough on a small scale or under special conditions are trapping, drowning, destruction by domesticated ferrets, and capture in sand barrels and straw barrels placed over the holes. On a large scale, poisoning and fumigating have yielded the best results.

POISONING.

By poisoning is meant the administration of a poison or combination of poisons by means of some article of food which the animals will readily eat. The poisons most in favor are strychnine and cyanide of potassium. Phosphorus also has been used and is an ingredient of many of the poison mixtures sold in the stores. It is efficient, but its use is attended with danger, and it is not recommended by this Department.

CYANIDE OF POTASSIUM.—Cyanide of potassium kills quickly, and is an excellent poison, but it is sometimes difficult to administer, chiefly on account of its odor, which is offensive to most animals. Like phosphorus, it is dangerous to man, and must be handled with great care. It is said to lose its power when wet or exposed to the atmosphere. It has been administered in prunes and raisins, and (in combination with strychnine) is a component of the celebrated Peters mixture for poisoning grain, in which it is disguised by a coating of molasses, flavored with oil of anise.

STRYCHNINE.—Strychnine is probably, all things considered, the best and most satisfactory poison now known for the destruction of prairie dogs. It can be obtained everywhere, usually at a moderate price, and its use is simple. The minimum dose necessary to kill prairie dogs is not known, but it is safe to say that the quantity recommended in the Peters formula (3 ounces to a bushel of wheat) is excessive. Two ounces is doubtless sufficient, and 1½ ounces is probably enough. (For ground squirrels, 1 ounce to the bushel of grain is ample.) The strychnine sulphate should be dissolved in warm water, in which the grain should be soaked for twenty-four or thirty-six hours, until all is absorbed. Some experimenters find this sufficient; others prefer to sweeten the grain by stirring in a quart or two of molasses and sprinkling with enough corn meal to prevent sticking. Some use corn meal alone, made into pellets, without any whole grain. Another way to administer strychnine is to introduce small quantities in prunes or raisins, in pieces of apple, carrot, or turnip, or on bread and butter. In the last case it is said that the strychnine should be sprinkled on buttered bread and then coated lightly with sirup, after which the bread is cut in small squares and placed around the burrows. The cost of strychnine sulphate, as customarily sold in small Western towns, is $1.50 to $2 per ounce. It comes in 1-dram (⅛-ounce) bottles which usually retail for 25 cents. Assuming that 2 ounces is the quantity necessary to poison a bushel of grain, the poisoned grain would cost about $5 per bushel. Allowing a tablespoonful to be the average quantity necessary to scatter about each hole, and allowing 50 holes to the acre,[1] a bushel of grain will poison 40 acres, at a cost of 12½ cents per acre. A man can scatter poisoned grain over 50 acres or more per day; hence, if labor costs $1 per day, the expense per acre of putting out the poison would be 2 cents, which added to the above 12½ cents for materials, makes the total cost 14½ cents per acre. The first application of the poison, if carefully made in late winter or early spring when food is scarce, may be counted on to kill 75 to 80 per cent of the animals (and has been known to kill as high as 95 per cent), and this at a cost per acre of less than 15 cents. The second application, a week or two later, is aimed at the few remaining occupied holes, which should not average more than two or three to the acre, and the cost per acre should not exceed 1, or at most, 2 cents. If any animals remain, they may be killed by bisulphide of carbon, and in many cases it is better to do away with the second poisoning and use bisulphide to kill off those that are left after the first poisoning.

FUMIGATION.

By fumigation is meant the destruction of animals by fumes arising from substances thrown into the burrows, as bisulphide of carbon, or generated outside and forced in by mechanical appliances known as "fumigators." Fumigators are devices by means of which fumes from burning sulphur or other materials are pumped into the burrows. In parts of the West, particularly California, they have been used with success in killing gophers and ground squirrels. They have been successfully used also against prairie dogs, but their employment for this purpose does not appear to be gaining ground.

Bisulphide of carbon.—Bisulphide of carbon is a volatile liquid which rapidly loses its strength on exposure to the air, and should be kept in tightly corked bottles or cans, which, when used, should be immediately recorked. It is inflammable and highly explosive, and should never be opened in the vicinity of a light or fire. Its fumes are heavier than atmospheric air, and when introduced into burrows sink quickly to the bottom.

The method of application is exceedingly simple. The usual dose for prairie dogs is 1 ounce (about a tablespoonful). This quantity should be poured on some absorbent substance, such as a lump of horse manure, a corncob, a handful of rags, or even a clod of earth, which

[1] A large average, but made to include unoccupied holes, as it is much cheaper to put out a little extra grain than to plug the holes to find out which are occupied. Furthermore, grain scattered anywhere in the dog towns is liable to be eaten.

should be immediately dropped into the burrow, the mouth of which should then be closed.

For introducing the bisulphide there is nothing better than dry horse manure—a material which costs nothing and is always at hand. A lump of horse manure wet with the bisulphide and dropped into a hole falls at once to the bottom of the vertical part, as shown in the diagram (fig. 25, *J*), where it is very near the animals. The liquid can be used to best advantage after a rain, when the interspaces in the soil are filled with water, so that the fumes are less readily diffused into the surrounding ground. This, however, is of much less consequence in the case of prairie dogs, which are deep-burrowing animals, than in the case of pocket gophers and ground squirrels, whose burrows and tunnels, as a rule, lie much nearer the surface.

Crude bisulphide, suitable for killing prairie dogs and other burrowing animals, costs about 10 cents per pound in 50-pound carboys or drums. A dollar's worth is enough to poison 100 holes. The cost, therefore, is about 1 cent a hole. The fluid should not be introduced haphazard into the burrows of a colony, but should be used only in those which the animals have been seen to enter immediately before it is applied. In this way none is wasted on unoccupied holes.

GENERAL DIRECTIONS FOR PRAIRIE-DOG DESTRUCTION.

Poisons are of very little use except in winter and early spring, when the ordinary food of the prairie dog is scarce and difficult to obtain. At such times poisoned grain, vegetables, fruit, and bread and butter are freely eaten. In distributing the poisoned grain or other material, it is usually better to scatter it about the holes instead of putting it into the mouths of the burrows, where it gets mixed with the dirt and is trodden down by the animals and lost. An exception to this course is recommended in case of the use of pellets of grain, made by wrapping teaspoonful doses of poisoned grain in greasy tissue paper; these should be dropped into the burrows. The danger to stock is much less when the grain is scattered about the colony than when it is placed in spoonfuls at or near the openings of the burrows. In case any considerable number of animals are left after the first poisoning the ground should be gone over a second time.

It should be clearly understood that the method recommended by this Department consists in two steps, the first of which is to destroy the great bulk of the inhabitants of a colony by poisoning with strychnine, applied in winter or early spring when food is scarce; the second, to kill the remaining animals with bisulphide of carbon. In this way it is believed that colonies of any size may be wiped out at a total cost not to exceed 16 or 17 cents per acre, probably less.

Bisulphide is probably the most efficient single agent known for the destruction of prairie dogs, and can be used, of course, for the extermination of colonies of any size, and at any time of year when the animals are active. If the killing is put off until late spring or early summer, when food is plenty, the animals are not likely to eat enough of the poisoned grain to amount to anything, and bisulphide becomes the best remedy. The only objection to its general use is its cost, which is likely to be about 1 cent per hole.

OBSTACLES AND DIFFICULTIES OF EXTERMINATION.

The chief obstacle to the extermination of prairie dogs on the plains is lack of cooperation among landowners. It is of little use to kill off the animals on ranches adjacent to large colonies in which the pests are allowed to go on multiplying. Many ranchmen who have again and again poisoned those on their own lands have finally given up in despair because of the rapid overflow from adjoining lands, new animals continually taking the places of those killed, until the expense and labor of repeated poisonings were too great to be continued. Complaints from this source are common in the case of ranches adjoining Government, State, or school lands, and railroad lands, and occasionally arise in the case of those adjoining lands owned by nonresidents, corporations, and certain individuals. This phase of the subject requires local legislation. In some States drastic measures have been recommended. Thus, in Texas, during the session of 1899, a bill was introduced making it the duty of every man owning land inhabited by prairie dogs to destroy the animals, under penalty of a fine not exceeding $100 for each section or part of a section on which the pests were allowed to remain. In the case of land owned by corporations or nonresidents, the destruction of the animals was provided for, the expense to be a lien on the land. While this bill failed to become a law, it had many supporters, and goes far to show the real extent of the prairie-dog scourge.

The Kansas legislature has recently appropriated $5,000, to be expended under the supervision of the regents of the State agricultural college, in "experiments for the purpose of determining the most effective and economical method of destroying prairie dogs and gophers," and has also authorized the township auditing boards to expend $100 [or more if requested by two-thirds of the electors of such township] in each township each year for the destruction of these animals (approved February 12, 1901).

PRAIRIE DOGS ON NANTUCKET.

In 1890–1892, one or two pairs of prairie dogs were introduced into Nantucket, where, for several years, they increased slowly and were regarded with interest. After a few years, however, they grew so numerous and spread so rapidly that the inhabitants became greatly alarmed and feared the animals would overrun the whole island. Mr. Outram Bangs wrote in December, 1899, that when on a visit to the island during the summer and fall of the same year he counted 200 prairie dogs visible at one time in one colony, and states that three or four such colonies existed, besides many scattering pairs and small colonies. A specimen sent the Biological Survey by Mr. Bangs proves to be the plains species (*Cynomys ludovicianus*), in rather red pelage, and probably came from some point on the Great Plains between western Kansas and Texas.

W. W. Neifert, writing from Nantucket, under date of February 12, 1900, states that ten years previously two pairs of prairie dogs were brought to the island, where they multiplied so rapidly "that they are now counted by thousands, and are a dangerous pest and nuisance, destroying crops and fields;" also, that "at a recent town meeting a committee was appointed with a view of exterminating them and an appropriation of $350 was made to procure poison." In a subsequent letter, Mr. Neifert writes: "In addition to the $350 raised by the town, about $200 was subscribed by farmers and others interested. The poisoning scheme was adopted, and bisulphide of carbon was the drug. A bunch of old rags was saturated and placed in the mouth of the burrow and the hole closed with dirt or sod. This method was simple and inexpensive but did the work successfully, and now there is not a dog left to tell the tale."

Plague in Colorado and Texas

Part I

Plague In Colorado

Dean H. Ecke, M.S., and Clifford W. Johnson, M.A.

Part II

Rodent Plague

in the Texas South Plains

1947-49

With Ecological Considerations

Virgil I. Miles, B.A., Maxwell J. Wilcomb, Jr., M.S.,
and J. V. Irons, Sc.D.

Public Health Monograph No. 6

Contents

Part II

Rodent Plague in the Texas South Plains 1947-49

With Ecological Considerations

Virgil I. Miles

Maxwell J. Wilcomb, Jr.

J. V. Irons

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Part II

Introduction

Plague was first recorded in Texas during the period June-November 1920 (*1*, *2*), when there were 32 human cases resulting in 18 deaths at Galveston and Beaumont. These infections were apparently acquired from domestic rats or their fleas. The origin of infection of local rats and their fleas was not determined but has been attributed to importation by shipping. Evidently native wild rodents escaped infection since plague was not found in 77,800 wood rats and a small number of other native rodents examined (*1*).

While it has been concluded that the origin of sylvatic or rodent plague in the western United States and Canada is unknown (*6*), there is strong evidence that plague in rodents has spread from California eastward over a vast area since 1900 (*3*). Largely as a result of surveys by the Plague Suppressive Measures Laboratory of the U. S. Public Health Service, by the end of 1945 sylvatic or "campestral"[1] plague was found as far east as western North Dakota, Kansas, Oklahoma, and eastern New Mexico. Prior to 1935, surveys were restricted to ground squirrels almost exclusively, but subsequently, and particularly since 1940, emphasis has been placed on collection of other rodents (*12*). Fortunately, infections in man rarely have occurred even in the midst of remarkable epizootics in wild rodents. No instance of campestral plague transmission to man has been reported in Texas although cases recently have been reported in New Mexico (*9*). The apparent eastward extension of plague has caused fears to be expressed on many occasions that it may result in infection of native rodents and domestic rats in more populous areas.

The possible occurrence of campestral plague in west Texas was suggested by observations of farmers and ranchers who reported finding dead pack rats, prairie dogs, and ground squirrels late in the summer of 1945 in the general vicinity of Brownfield, Tex. Subsequently, campestral plague was found in Texas by the Plague Suppressive Measures Laboratory, San Francisco: in Cochran County in 1946 (*7*), and in Dawson County in 1947 (*8*). That plague had not been present in the area very long before it was found was suggested but not proved by earlier failures to demonstrate its existence (*7*). Subsequently, the Communicable Disease Center and the Texas State Health Department, in conjunction with the South Plains Health Department, created a plague-typhus control unit to investigate plague in the nine-county South Plains area of west Texas (fig. 1). While

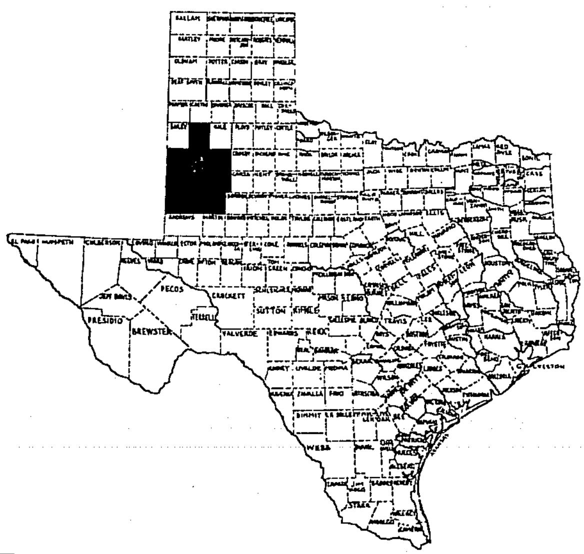

Figure 1. Location of the nine-county area in Texas.

[1] The term "campestral" possibly is more descriptive than "sylvatic" since rodents of the plains, prairies, and fields more often are involved than those of the forests or woods.

the usual practice of the Public Health Service survey units had been to take samples of wild rodents and their fleas in certain designated areas and to move on within a short time, the program of the plague-typhus control unit in the South Plains followed a somewhat different pattern. The project was designed to map out more accurately the location of plague foci, to learn which mammals and ectoparasites were chiefly concerned, to maintain surveillance over them, and to acquire data on the hazard of human infection. The data included in this report were obtained from July 1947 to June 1949.

Methods and Procedures

Field collections were begun in July 1947 by a mobile field laboratory unit of three men; two additional units began work in April 1948. A field supervisor assisted in directing the activities of the crews in the field. Collections were made in areas previously determined by scouting. Areas were not selected for trapping and hunting particular animals except where apparent die-off suggested the presence of plague. At the beginning of the project, considerable attention was given to previously proved foci of plague in Cochran and Dawson Counties.

Since decline in rodent population may indicate occurrence of plague, practical methods of detecting population fluctuations were tried. For estimating fluctuations in activities of prairie dog colonies, all burrows within a 10-yard strip were inspected and the results were recorded on a standard form sheet. Inspections were made by two persons whose estimates, by repeated comparison, did not differ more than 10 percent which was sufficiently accurate for the purpose. Prairie dog colonies in the study area were inspected during each spring, summer, and fall. Similarly, fluctuations of pack rat activity were detected by observing random samples of about 20 dens in each area, and classifying them as active, recently abandoned, or long unused. The relative abundance of the smaller rodents, and also of pack rats, was estimated from comparisons of catches per trap.

During the earlier phase of the study, a variety of traps was employed, including large and small Sherman metal box traps, wooden snap mousetraps and museum traps. Subsequently, the large snap trap was utilized exclusively, except for domestic rats, which were taken alive in steel traps by county-employed rodent control operators. Prairie dogs and rabbits usually were obtained by shooting. Each animal was identified, placed in a cloth bag, and exposed to hydrocyanic acid gas for 10 to 15 minutes. The animals and everted sacks were examined for ectoparasites which promptly were put in vials of 2-percent saline solution.

Fleas and *Ornithodorus* ticks were also obtained by swabbing prairie dog burrows with flannel secured to a length of flexible cable. This method was valuable in places where prairie dogs had been decimated by apparent die-off. The examination of pack rat nest material was a useful procedure during poor trap catches in the winter. Predatory or scavenger birds and their nests were examined, and a number of other less satisfactory methods of collecting ectoparasites were tried.

Ectoparasites on ice were sent by express to Austin where they were identified. Separate pools of fleas, lice, and ticks, according to animal hosts from each area, were tested for plague by animal inoculation and bacteriological procedures. Pools [2] of fleas were prepared in such

[2] A pool of fleas is the total of all fleas of the same species obtained from all of the animals of the same species collected at one hunting area in 1 to 3 days. A pool of tissues is a portion of the tissues of each of several animals of the same species collected at one hunting area in 1 day.

a manner that maximal information was possible. In other words, aliquots of components of many pools were saved for possible reinoculation if plague was found in the over-all pool. Saline suspensions of crushed fleas containing *Pasteurella pestis* were found invariably viable after a 10-day storage at 4° to 10° C. (*3*). When longer storage was desirable, the flea suspensions were mixed with skim milk and were stored under glass seal in the deep freeze box.

Field autopsies were done routinely and tissue was saved from all animals during the earlier phase of the study; tissue specimens were later saved only from animals found dead or with other indication of plague infection. Tissues were frozen and sent to Austin on dry ice where appropriate tests for plague were done. Tissues or tissue pools from 1,006 animals were inoculated into 352 laboratory test animals. No plague bacilli were found in any of the multiple animal-tissue pools.

The usual criteria for recognition of plague in animals at autopsy were utilized (*5*). For all animals dying of suspected plague, direct smears of liver and spleen were stained by Wayson's procedure and were examined for characteristic numerous small, short, plump bipolar stained bacilli. A pure culture was obtained on blood agar and the usual criteria for identification of *P. pestis* were utilized. The characteristic pathogenicity of the suspected organism following culture was determined in the guinea pig before the specimen was reported "positive for plague."

Blood specimens were obtained occasionally and were tested for agglutination of the plague bacillus and for complement fixation.[3] A serologic reaction is believed to be suggestive of past infection or exposure to plague.

[3] Agglutination and complement-fixation antigens were prepared from culture No. 1122, an avirulent culture of *P. pestis* supplied by Dr. K. F. Meyer, Hooper Foundation, University of California, San Francisco, Calif.

The Area and its Fauna

The area surveyed (fig. 2) includes 8,620 square miles, much of which consists of level, treeless plains with gradually increasing elevation, from approximately 3,000 feet in the southeast to 4,000 feet in the northwest. Shallow draws, usually dry, traverse the plains in a southeasterly direction. The soil is principally a sandy loam largely free of rocks except for occasional outcrops of caliche along the draws. An estimated 60 percent of the area is under cultivation. Cotton and grain sorghums are the principal crops. The population of the area approximates 165,000, of which an estimated 40 percent is rural. Wide expanses of ranch land occur principally in the western and southern portions of the area and are sparsely populated except where augmented by resident oil field workers. Winters are not severe, with a monthly mean temperature of 40° F. in January. Summers are warm, with a monthly mean temperature of 80° F. in July. The average annual rainfall measures scarcely 18 inches. The average relative humidity is under 40 percent.

Uncultivated land comprises four principal habitat types in the South Plains; these are designated the shinnery oak, mesquite, mesquite-shinnery oak, and short grass associations (figs. 3–5). While all four vary locally in soil type and relative abundance of the principal plant and animal species, most of the area in the South Plains which is not under cultivation can be classified in one of the above categories.

An estimated 60 to 70 percent of the uncultivated land in the nine-county area is covered predominantly with shinnery oak. The most common species, *Quercus breviloba,* grows to an average height of only 2 feet. The usual understory is of bunch grass and short grass with scattered forbs, much of which is subject

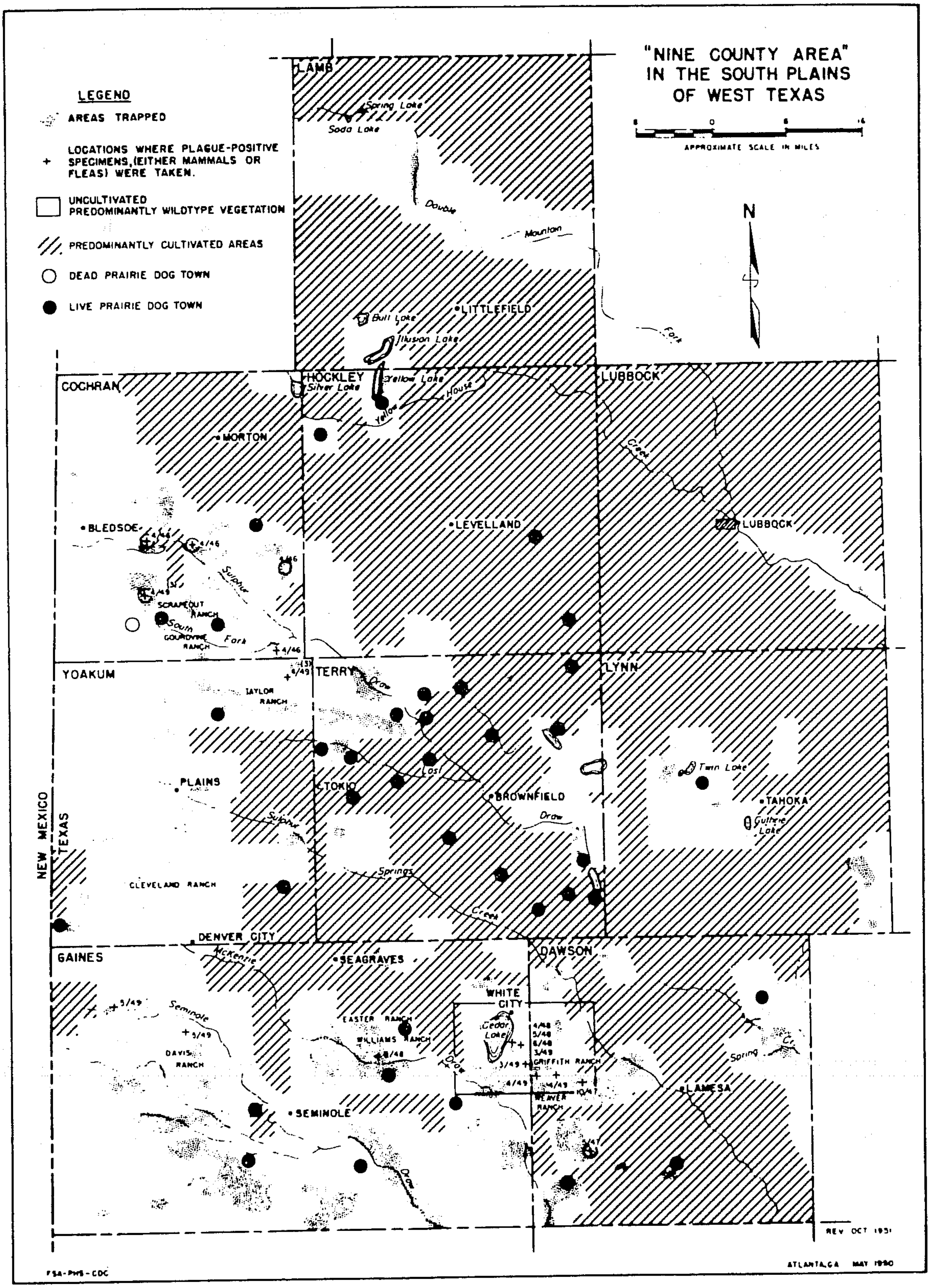

FIGURE 2. Nine-county area.

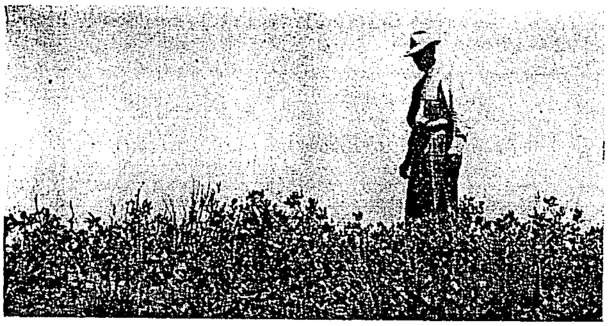

FIGURE 3. Shinnery oak habitat.

to grazing by cattle. Mesquite occurs on an estimated 20 to 30 percent of land not under cultivation in this area. The mixed mesquite-shinnery oak habitat was found to be particularly favorable to supporting populations of the associated small-mammal species. While the soil under the shinnery oak is subject to caving and drifting, and that under mesquite is dark, stable, and hard to dig, the soil of the mixed habitat is much more suitable for burrowing. Areas of the short grass association are covered principally by buffalo grass with no brush overstory, and the soil is typically dark and stable. The shortgrass areas are relatively small and discontinuous and compose scarcely 10 percent of land not under cultivation.

Table 1, based upon trap records and observations, indicates the estimated relative abundance of the small-mammal species for each of the four habitat types. A total of 17,380 animals was taken, principally by trapping or shooting. These animals represent 22 species in 9 families and 4 orders: Rodentia, Carnivora, Lagomorpha, and Marsupialia. In addition to animals listed in tables 1 and 2, a relatively small number of skunks, coyotes, and opossums also were taken.

The pack rat, *Neotoma micropus*, is widely distributed in the mesquite and mesquite-shinnery oak habitats throughout the area of investigation. During the period of investigation, fluctuations in populations of some areas were observed, apparently influenced in part by epizootics of plague. Areas with about 10 active *N. micropus* dens per acre commonly were encountered, but limited concentrations as high as 30 to 40 active dens per acre were

Table 1. Relative abundance of small mammals

Mammals	Associations			
	Shinnery oak	Mesquite Shinnery oak	Mesquite	Short grass
Ground squirrels and prairie dogs:				
Citellus me icanus [1]	?	?	2	2
Citellus spilosoma	3	2	2	2
Citellus tridecemlineatus	1	2	2	3
Cynomys ludovicianus [2]	0	0	1	3
Kangaroo rats and pocket mice:				
Dipodomys ordi	3	5	3	0
Dipodomys spectabilis [3]	0	1	2	0
Perognathus flavus [2]	1	2	1	1
Perognathus hispidus [2]	1	2	1	0
Pocket gophers:				
Cratogeomys castanops	1	1	2	3
Geomys sp	1	1	2	3
Native rats and mice:				
Neotoma micropus [2]	0	4	2	0
Onychomys leucogaster	2	4	3	2
Peromyscus leucopus [2]	0	1	1	0
Reithrodontomys sp.[2]	0	1	1	0
Sigmodon hispidus [2]	0	1	0	1
Rabbits:				
Sylvilagus auduboni	2	4	3	1
Lepus californicus	2	3	4	2

[1] Taken only in Dawson County.
[2] Colonial or spottily distributed.
[3] Taken only in southwestern Yoakum and northern Gaines Counties.

NOTE: The estimated relative abundance of each species is given according to the following scale: (1) Rare; (2) few; (3) intermediate in abundance; (4) common; (5) abundant.

FIGURE 4. Mesquite habitat.

FIGURE 5. Short-grass habitat occupied by prairie dog town.

Table 2. Average number of common species of fleas found on small mammals in the Texas South Plains, all seasons, 1947–49 [1]

Species of flea	Total fleas found	Mammalian host										Average number of fleas on all animals examined
		Sciuridae			Heteromyidae		Cricetidae		Muridae [2]	Leporidae [3]		
		Cynomys ludovicianus[3]	*Citellus spilosoma*	*Citellus tridecemlineatus*	*Perognathus hispidus*	*Dipodomys ordi*	*Onychomys leucogaster*	*Neotoma micropus*	*Rattus norvegicus*	*Lepus californicus*	*Sylvilagus auduboni*	
Echidnophaga gallinacea	62,965	2.1	0.5	0.4	2.8	(4)	0.2	7.1	6.9	(5)	1.0	3.62
Orchopeas sexdentatus	38,496	(4)	(4)	(5)	0	(4)	(4)	5.4	(4)	0	(4)	2.21
Anomiopsyllus hiemalis	6,162	(4)	0	0	0	(4)	(4)	.9	0	0	(5)	.35
Hoplopsyllus affinis	5,800	0	(4)	(4)	0	(5)	(5)	(4)	0	.2	5.0	.33
Monopsyllus exilis	1,755	0	(4)	(4)	0	(5)	1.0	(5)	0	0	(5)	.10
Thrassis fotus	1,200	0	.9	0.3	.3	(4)	.3	(5)	0	(5)	(4)	.07
Pulex irritans	1,740	3.4	(5)	0	0	(5)	(4)	(5)	(5)	(5)	0.1	.10
Opisocrostis hirsutus	997	1.9	0	0	0	0	(4)	0	0	(5)	(4)	.06
Thrassis campestris	546	0	(5)	0	0	(4)	.2	(4)	0	0	(4)	.03
Xenopsylla cheopis	152	0	0	0	0	0	0	0	.1	0	0	.01
Meringis parkeri	120	0	0	0	0	(4)	(4)	(5)	0	0	0	.01
Total number of fleas	119,933	3,571	885	173	97	464	3,062	94,629	10,063	68	6,921	-------
Number of animals examined	17,380	476	612	212	32	4,421	1,645	7,081	1,426	344	1,131	-------
Average number of fleas per animal	6.9	7.5	1.4	0.8	3.0	0.1	1.9	13.3	7.1	0.2	6.1	6.90

[1] Mammals found dead in traps, except where otherwise noted.
[2] Taken alive—examined immediately.
[3] Mostly taken alive—some dead in traps.
[4] 0.005 to 0.05 per animal.
[5] Less than 0.005 per animal.

observed. It appears that each active den was probably occupied by a single individual except during the breeding season, as was observed for *Neotoma albigula* by Vorhies and Taylor (*11*). While single rats almost invariably were taken from dens during late summer, fall, and winter, two or three adults, along with juveniles, were often taken from individual dens in the spring or early summer when most of the findings of plague were made.

The kangaroo rat, principally *Dipodomys ordi,* also is widely distributed throughout the area; it was taken in numbers only somewhat less than pack rats, and it probably was even more numerous than pack rats in the South Plains. In contrast with the pack rat, the kangaroo rat was found to be relatively free of fleas, so that the failure to find plague associated with kangaroo rats was not surprising.

Colonies of the prairie dog, *Cynomys ludovicianus,* occur in localized areas as shown in figure 2. Plague was proved in fleas collected from prairie dogs and their burrows, and in tissues of one of the rodents found dead. Prairie dogs were of particular value as indicators of occurrence of plague because of the visible decimation which usually accompanies the infection of a colony. Activity of prairie dogs in the South Plains was observed on warm days throughout the winter. Prairie dogs also were taken during the winter months, indicating that if hibernation of these rodents occurs in the region, it is limited to individuals or to short periods of unusually cold weather.

Of the three species of ground squirrels taken, *Citellus spilosoma* appeared to be better adapted to the principal habitats of the region. Ground squirrels were widely distributed but were not numerous in any one place. Plague was not found in fleas or tissues of ground squirrels.

The grasshopper mouse, *Onychomys leucogaster,* is common in mesquite-shinnery oak habitats and occurs in fair numbers in shinnery oak, mesquite, and grassland habitats. Fluctuations in populations of the grasshopper mouse usually were evident in the midst of marked fluctuations of prairie dog or pack rat populations. These mice usually were caught in traps set at pack rat dens and were also taken in sets placed at prairie dog burrows.

Over 130,000 ectoparasites, including 119,933 fleas, 11,498 ticks, 1,237 mites, and 2,152 lice, were recovered. With few exceptions, all ectoparasites were identified and tested for plague. A total of 117,240 fleas in 2,821 pools was inoculated into 3,371 test animals. Distribution of the fleas has been recorded by Eads of the division of entomology, bureau of laboratories, Texas State Health Department (*10*).

The total numbers of common species of fleas found on small mammals, arranged in the order of their relative abundance, are shown in table 2. The total numbers of the chief small mammals examined for ectoparasites also are shown. Since practically all of the smaller mammals were found dead in the traps and there was ample opportunity for fleas to desert the host, their calculated flea indices perhaps are low.

Plague Findings

Findings of campestral plague in wild rodents and fleas in the nine-county area are given in table 3. Locations of affected prairie dog colonies are shown in figure 2. The presence of *P. pestis* was demonstrated in the fleas or in the tissues of wild rodents in four of the nine counties surveyed. Most of the trapping was done in these four counties. Gaines County was the source of the major part of the plague-positive specimens; plague findings in Dawson County were near those found in bordering Gaines County. Cochran County proved to have campestral plague in 1946 and was again shown to have plague infection in wild rodent fleas in 1949. Plague was also found in Yoakum County which has limited areas of habitat favorable for obtaining the wild rodent species.

P. pestis was found in the tissues or bones of three rodents: a prairie dog found dead and two pack rats, one of which was found dead in the field. The bacillus was recovered from the marrow of the larger bones of the pack rat found dead. Blood serums from three pack rats showed serologic reactions suggesting that these animals had recovered from previous plague infections. In view of these serologic findings, an occasional pool of pack rat tissues was mixed with a dilute suspension of *P. pestis*, but evidence of protection was not observed.

Plague was found in fleas or tissues in January, March, April, May, June, and October. Most of the findings were recorded from March through May; while this was the period most favorable for trapping kangaroo rats and pack rats, the numbers of pack rats taken during these months were not significantly greater than in February, October, and December. Plague was repeatedly proved in tests of fleas from pack rats. Two of the three findings of plague in tissue or bones were in those of pack rats. Blood serums from an additional three pack rats showed serologic reactions suggesting that these animals had recovered from previous plague infection. One lot of *Anomiopsyllus hiemalis* collected from pack rat nests in January 1949 was found to be plague infected, and a pool of *Orchopeas sexdentatus*, simultaneously collected from the same nests, proved positive.

The numbers of the pack rat fleas, *A. hiemalis* and *O. sexdentatus*, sharply declined both in nests and on the hosts with approach of warmer weather. The prevalence of *O. sexdentatus* increased during the winter to a peak in April and decreased to its lowest level in midsummer. Its greatest abundance generally coincided with that of the plague findings. The numbers of *A. hiemalis* were greatest in February and declined sharply prior to the principal findings of plague in the spring. Since plague was found in this flea in January, its possible importance in the overwintering of plague was suggested.

Of the 13 lots of fleas collected from pack rats and found plague positive, 8 consisted of *O. sexdentatus* only, and the remaining 5 lots contained this species in the majority. Of these 5 mixed lots, 3 contained small numbers of *A. hiemalis*. The number of fleas in pools proved positive for plague varied greatly. The smallest pool found plague positive was that of 5 *Monopsyllus exilis* from 3 grasshopper mice.

Two additional lots of *M. exilis,* the predominant flea found on grasshopper mice, were found infected. Grasshopper mice were also hosts of a rich flea fauna characteristic of other rodents, possibly because of their habit of frequently visiting the burrows of other rodents.

Although both *Echidnophaga gallinacea* and *Pulex irritans* were commonly found on the prairie dog, *P. pestis* was identified from only one unmixed pool of fleas from this rodent—of *Opisocrostis hirsutus* (table 3). In another instance, a pool of 35 of this species and 1 *P. irritans* collected from a prairie dog burrow was proved positive for plague.

E. gallinacea was the most abundant flea collected and was found in considerable numbers on all species of rodents examined. It was the predominant flea found on both *Rattus norvegicus* and the pack rat, *N. micropus.* The seasonal prevalence of *E. gallinacea,* in contrast with that of the other principal fleas, increased during the summer months to a peak in the fall.

Table 3. Findings of plague in wild rodents and fleas in the Texas South Plains, 1946–1949 [1]

County	Date collected	Plague-positive material: Number of fleas in pool: *Anomiopsyllus hiemalis*	*Echidnophaga gallinacea*	*Monopsyllus exilis*	*Opisocrostis hirsutus*	*Orchopeas sexdentatus*	*Pulex irritans*	Fleas (not identified)	Material examined: Tissue	Bones	Blood serum	Number of hosts: *Citellus tridecemlineatus*	*Cynomys* sp.	*C. ludovicianus*	*Dipodomys* sp.	*Neotoma micropus*	*O. leucogaster*	*Onychomys* sp.	Location: nearest town, direction, and airline distance (in miles) from place of collection
	1946																		
Cochran	Apr. 27 [2]							31					26						
								12				8							Morton, SW, 10.
								15										14	
	Apr. 27 [2]							50					31						Morton, WSW, 15.
	Apr. 30 [2]							85					30						Morton, SE, 20.
								15										17	
	Apr. 30 [2]							25					11						Morton, SSE, 25.
								5							x				
	1949																		
	Apr. 5					31										2			Morton, SSW, 16.
	Apr. 6–8			52													9		
	Apr. 8				6									1					Morton, SSW, 18.
	1947																		
Dawson	May 15 [2]							50						6					Lamesa, WSW, 13.
	Oct. 2–3	1	58			82										14			Lamesa, W, 8.
	1949																		
	Apr. 1		41			85										7			Lamesa, W, 11.
	Apr. 1								1							[3] 1			Do.
	Apr. 8					143										18			Lamesa, W, 13.
	Apr. 22										[4] 1					1			Lamesa, W, 8.
	1948																		
Gaines	Apr. 6–7		126			137										38			White City, SSE, 3.
	Apr. 13					22										12			White City, SSE, 3½.
	Apr. 14–15					86										22			White City, SSE, 4.
	May 1					43										3			Do.
	June 28								1					[5] 1					White City, S, 3.
	Aug. 18										[6] 1					1			Seminole, NE, 11
	1949																		
	Mar. 4				35		1							[7] 1					White City, S, 3.
	Mar. 8–9			5													3		White City, SSE, 3½.
	Mar. 10					64										5			White City, SSE, 4.
	Mar. 11			8													7		Do.
	Mar. 18	9				62										[5] 1			White City, SSE, 8.
	May 20										[8] 1					1			Seminole, NW, 10.
	May 24–27					163										24			Do.
	1948																		
Yoakum	Jan. 25–27					243										[9] 13			Plains, NE, 14.
	Do.	198														[9] 13			Do.
	Do.									1						[2,5] 1			Do.
	1949																		
	Jan. 28	1	1			36										2			Do.

[1] All collections by plague-typhus control unit except where otherwise shown for 1946 and 1947.
[2] Collected and tested by Plague Suppressive Measures Laboratory, San Francisco.
[3] From the preceding entry above.
[4] Complement fixation positive 1:10. This is suggestive only and not definitely indicative of plague.
[5] Found dead.
[6] Low titer agglutination confirmed by a complement fixation test.
[7] Fleas obtained by swabbing prairie dog burrows.
[8] Complement fixation test positive 1:40, but agglutination test negative.
[9] Nests of pack rats.

It was less prevalent in the spring and early summer when plague findings were most often recorded. Plague possibly involving *E. gallinacea* was proved in only mixed pools of fleas from pack rats. The other species in the pools was *O. sexdentatus.*

The oriental rat flea, *Xenopsylla cheopis,* was found exclusively on the domestic rat, *R. norvegicus;* a total of only 149 *X. cheopis* was taken from 1,240 domestic rats trapped mainly by county employees.

Fleas were found on only 2 percent of all the domestic rats examined; the 149 *X. cheopis* fleas were found on 27 of 60 rats trapped at only 13 premises in 7 of the 9 counties. Of 469 rat bloods successfully given the complement fixation test for murine typhus fever, 12 percent (56) were positive, indicating that fleas are occasionally numerous enough to maintain this disease and could possibly support plague for a short time.

At Midland and Odessa, in Midland and Ector Counties, respectively, scarcely 40 miles south of the proved plague foci, a similar spotty incidence of *X. cheopis* also was suggested. In the spring of 1949 at Odessa, 3 *X. cheopis* were taken from 2 of 26 *R. norvegicus* (8 percent), while at Midland 20 *X. cheopis* were taken from 3 of 125 rats (2 percent). Twelve cases of typhus occurred in these counties in 1948.

These findings indicate that, while the *X. cheopis* population generally was low in the nine-county study area, occasional premises were very heavily infested.

Ecological Considerations

Campestral plague was first revealed in the Cedar Lake area of northeast Gaines and northwest Dawson Counties (figs. 2 and 6) on April 6, 1948. Cedar Lake usually is dry and is in an area of predominantly uncultivated land. Inasmuch as most of the habitat types and animal species common to the South Plains were well represented, a thorough study of the area surrounding Cedar Lake was made during 1948 and the spring and summer of 1949. The areas trapped are divided into zones (fig. 6) which roughly indicate habitats of mesquite-shinnery oak or mesquite favorable for pack rats and most of the other rodents. The prairie dog colonies are in short grass habitat, and most of the remaining blank areas on the map are covered by shinnery oak.

Residents living at White City near Cedar Lake reported that nearby prairie dog colony 4 had an apparently normal population throughout 1946, and the population appeared normal in the fall of 1947 when the locality was first visited. In October 1947, nearby colony 1 also had a high population. In March 1948 it was evident that the population of both colonies 1 and 4 had declined, but colony 4 declined to a greater extent than colony 1. It seemed very likely that prairie dogs had died of disease, as neither the ranch owner nor the district agent of the U. S. Fish and Wildlife Service knew of any poisoning or other control activities in that location; the latter had planned to use it as a plentiful source of prairie dogs from which to prepare coyote bait in the spring of 1948. Prairie dogs were occasionally seen in colony 1, but became progressively less evident through June, and became nearly extinct by July 1948, remaining so until late spring of 1949, when 3 prairie dogs and 10 active burrows were noted near the south border. Colony 4 declined more rapidly and was almost extinct by late spring of 1948 although a small group of four or five prairie dogs survived through the summer. In November 1948, colony 4 appeared to be extinct, and it remained so until July 1949.

Zone III, lying between colonies 1 and 4, was first visited and trapped on April 15, 1948, when a high percentage of recently abandoned pack rat dens was apparent, suggesting a considerable die-off in pack rats earlier in the spring. Four days' trapping in May and July produced 3 pack rats, as compared to an average daily catch of 8 or 10 per day in comparable areas with normal populations.

The first plague finding in the vicinity of Cedar Lake on April 6, 1948, concerned pack rat fleas in zone V near colony 1, about a month after the population of colonies 1 and 4 began to decline visibly. During the next 3 weeks three additional findings of plague bacilli in fleas from pack rats were made in zone V within a mile of the first finding. Repeated catches in all zones until late summer of 1948 were negative, but on June 28 a plague-infected prairie dog was found dead near the middle of colony 3, a mile west of colony 1. No further plague was found in 54 prairie dogs taken from colony 3 between June 30 and September 3, 1948. Records for July and November 1948 showed the burrows to be 45-percent inhabited at the north end, grading to 10 percent at the south end, with an average of 30 percent. On March 7, 1949, this colony was found to have declined to an average population of 10-percent active burrows. Fleas swabbed from burrows near the north end on March 4, 1949, were plague-infected. In July 1949, colony 3 appeared to have increased its population to an over-all 20-percent active burrows. Inhabited areas showed a spotty distribution, and most of the prairie dogs observed were young animals. Cottontail rabbits had increased considerably in numbers and were occupying former prairie dog burrows.

Zone IV is a mesquite-covered ridge about one-eighth of a mile wide and 2 miles long, paralleling the east shore of the lake. The ridge separates colony 3 from colony 2, but it is not a barrier of any consequence since in many places the two colonies are separated by only 200 or 300 yards of scattered mesquite. Repeated trappings throughout this zone from the latter part of April to early September 1948 resulted in better than average catches of pack

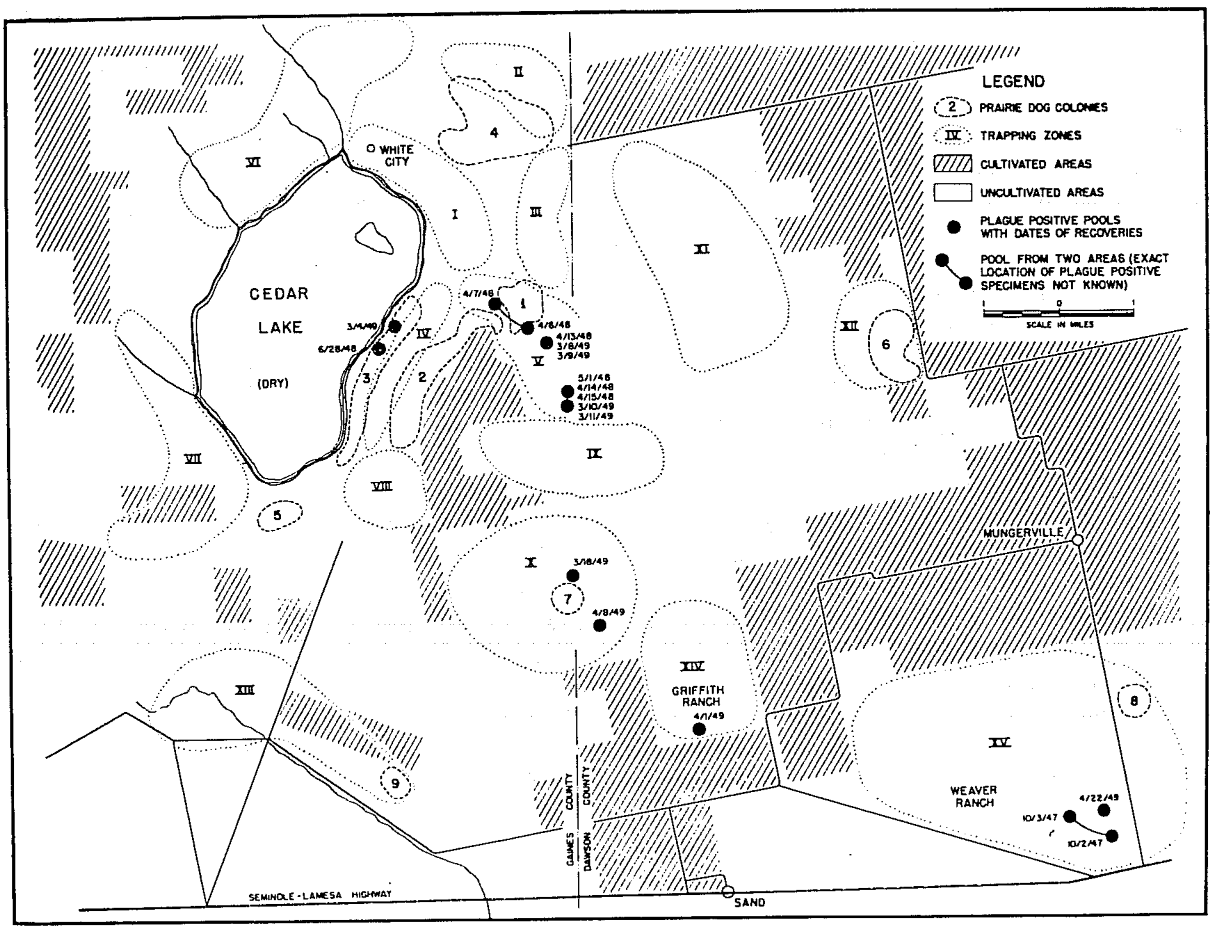

FIGURE 6. Cedar Lake area.

rats and other rodents, indicating apparently high populations. On March 15 and 16, 1949, no pack rats could be obtained and only a few other rodents were taken; most of the dens appeared to have been recently abandoned, probably during the winter or early spring.

Prairie dog colony 2, which borders zone IV and is separated from colony 1 by a strip of grassland only 200 yards wide, maintained a good population throughout the observations. Zone I also maintained normal rodent populations, as evidenced by good catches of pack rats and other rodents in April, May, and June 1948, and on May 17 and 18, 1949. This suggests that if colony 3 was infected by rodents from colony 1 or zone V in the spring of 1948, it was done without greatly involving colony 2 or zone I.

Retrapping in zone V, March 8 to 11, 1949, resulted in the finding of plague bacilli in a pool of fleas from pack rats and in two pools from grasshopper mice in essentially the same areas as in April 1948. The greatest die-off in pack rats was in this area just south of colony 1. Here again the heavy reduction in the pack rat population was not attributable to the relatively few specimens previously removed by trapping. Numerous pack rat dens had been abandoned. While large numbers of kangaroo rats were taken, the catch of pack rats in relation to the number of traps set was less than half that of the previous year.

On March 18, 1949, infected fleas from a pack rat found dead revealed a plague focus in zone X about 2 miles south of a previous focus near Cedar Lake. Another pool of infected fleas from pack rats was recovered in zone X on April 8, 1949, a mile south and east of the first finding. On April 1, 1949, infected fleas from pack rats were found in zone XIV on the Griffith ranch, 2 miles south and east of the point in zone X where fleas had been recovered on March 18. These later discoveries strongly suggested a connection between the Cedar Lake plague foci and the Weaver ranch plague focus discovered October 2, 1947 and located approximately 4 miles south and east of the Griffith ranch where infected fleas were recovered on April 1.

A plague-positive blood serum taken from a pack rat on the Weaver ranch April 22, 1949, suggested that the disease had persisted in that area from October 1947. However, repeated examinations of samples of fleas taken on the Weaver ranch between February 15, 1948, and June 24, 1949, resulted in no further plague findings. Other principal wild-type areas in the vicinity of the Weaver ranch were also thoroughly sampled in a futile effort to recover plague in rodents or fleas.

Discussion

Plague was rarely recovered from areas with apparently normal healthy rodent populations where large numbers of specimens could easily be secured. The majority of the specimens tested were taken from such areas, but plague was indicated to be present on only two occasions, one being a doubtful blood serum. Most of the plague findings, on the other hand, were from areas with visual evidence of epizootics where the available numbers of specimens often were much reduced by die-off of the rodents. Where plague was recovered with a minimum of sampling, the specimens were taken in areas with evident rapid die-off at the time of sampling. Even after epizootics had considerably decimated the rodent populations, the smaller numbers of available specimens were more productive of plague recoveries than were large numbers of samples from apparently normal rodent populations. Plague detection during an epizootic is largely dependent upon recovery of infected fleas from active, healthy rodents, and the difficulty of securing satisfactory numbers of specimens increases with progress of the rodent die-off. Because of the very limited period during which plague may be readily detected, it is evident that surveys of a few days' duration in the absence of epizootics are of little value in determining the presence of plague. Considering the relatively few plague foci discovered by the extensive sampling, it appears that plague detection is largely dependent upon chance coincidence of surveys and incipient epizootics in a given area.

The results of the continuous surveys for a period of more than 2 years over the nine-county area give no conclusive evidence of the spread of plague within the area. The data strongly indicate that plague is widespread throughout the region, is repetitious in its activity within small areas of habitat favorable for susceptible rodent species, and is usually recurrent within a few years. The infection appears to remain dormant locally during periods between epizootics as noted by Evans, Wheeler, and Douglas (*4*). The epizootics may, however, completely exterminate local colonies of susceptible rodents as shown by the finding of several extinct prairie dog towns in the nine-county area (figs. 2 and 6). Because of the large size and diurnal activity of prairie dogs, their colonial habit, and their high susceptibility to plague, the fluctuation in numbers of these rodents is a good indicator of presence or absence of plague in an area. All prairie dog towns which were extinct or showed definite signs of die-off during the 2-year period of observation were in large uncultivated areas which included other susceptible rodent species. On the other hand, the prairie dog colonies in small, natural areas enclosed by extensive cultivated fields showed no evidence of plague. Most of these areas were from a few acres to a square mile in size; some were 50 or more square miles of predominantly pasture land surrounded by cultivated land. This indicates probably that neither small rodents nor predatory birds or animals in this area were important in spreading the infection to small natural areas; otherwise some of the isolated colonies would have shown evidence of decimation by plague. It also indicates that cultivated areas serve as good protective zones.

Numbers of plague-bacilli recoveries from pack rats and grasshopper mice indicate that these rodents are a connecting link for spread of plague within uncultivated areas.

Several instances were noted in which pack rats were living in close association with domestic rats in or near farm buildings. Since no *X. cheopis* were found on sylvan rodents, the transfer of fleas between domestic and sylvan rodents appeared to be uncommon, but the presence of 12 *O. sexdentatus,* the common flea of pack rats, on *R. norvegicus* shows that some transfer does occur. The fact that 12 percent of the bloods of domestic rats tested for murine typhus were positive and the occurrence of human typhus in the region indicate that populations of *X. cheopis* in at least some premises are sufficiently high to maintain murine typhus in rats and occasionally to spread the infection to humans. Since this flea is as good a vector of plague as of murine typhus under similar conditions, a chance introduction of plague into a domestic rat population heavily infested with *X. cheopis* would probably cause a sharp, highly localized epizootic which might result in one or more human infections. Because of spotty distribution of *X. cheopis,* the epizootic probably would be restricted to premises in which the infection was introduced and eventually would die out by killing the rats concerned.

Summary

Nine west Texas counties were surveyed continuously for 2 years to determine the extent of campestral, or sylvatic, plague and to ascertain the nature of its spread and the danger of its being transmitted to the human population. Ectoparasites, principally fleas, from 15,954 wild rodents and rabbits and from 1,426 domestic rats were tested for plague by animal inoculations. Fleas secured from prairie dog burrows by swabbing and from pack rat nest material were also tested. Plague bacilli were recovered in 4 of the 9 counties from 22 lots of fleas and rodent tissue. Pack rats, *Neotoma micropus,* and their fleas, principally *Orchopeas sexdentatus,* were the source of 18 of the total plague findings.

Plague was readily recovered during epizootics but was difficult to detect in places where no die-off of rodents was evident. Because of the limited epizootic period during which plague can readily be detected, the nature of its spread could not be satisfactorily determined. The data indicate that the infection is widespread over the area studied and that plague activity is repetitious within small areas. Prairie dogs were affected in large uncultivated areas but not in small natural areas protected by extensive cultivated land. It was thus indicated that predatory birds and mammals were not important here in the spread of plague to areas surrounded by cultivation, and that the smaller rodents which have a limited home range were the principal means of plague spread within uncultivated areas. No plague bacilli were recovered from domestic rats or their fleas. The oriental rat flea, *Xenopsylla cheopis,* was rare in the area surveyed although domestic rats in occasional premises were heavily infested with this flea.

The introduction of plague into domestic rats from sylvatic rodents is probably uncommon although it can occur. Such an introduction into a domestic rat population heavily infested with *X. cheopis* would result in a sharp, highly localized epizootic which would tend to be self-limiting, but which might cause human cases before dying out.

Addendum

Late in March 1950, Dr. Robert Tinnley, Denver City, Tex., attended a white male, aged 9, son of an oil field worker residing near Denver City. The child was seriously ill. The right epitrochlear gland was quite swollen and inflamed, and there was enlargement of the right axillary gland. Both left epitrochlear and axillary glands also were palpable. The fever subsided rather promptly following treatment with chloromycetin. Subsequent attempts to obtain blood specimens for serologic study were unsuccessful. There was no history of contact with sick or dead animals. Dr. Tinnley believes this probably was a case of plague.

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signing captive programs or reintroduction techniques. A well-designed and well-monitored program increases efficiency and allows biologists to determine why a given process did or did not work. The latter is essential if techniques are to be improved (either increasing efficiency or "fixing" unanticipated problems), and if the program is to provide useful insights to other programs.

There are various measures for defining success of biological techniques for reintroduction, and the definition should be carefully chosen. Financial expense is a favorite of accountants, but it is much easier to count costs than benefits. A cheaper technique that establishes significantly fewer animals may not be thrifty over time. It is difficult to assess financial costs until survival rates are established.

Ultimately, the number of animals surviving to reproduce is the best comparative measure of techniques. But mortality is usually elevated in early reintroduction attempts, and survival comparisons are subject to high variability, making large sample sizes necessary. Postrelease evaluation of behavioral traits may therefore provide important information about release strategies that can be applied to increase survival in future attempts. Selection of behavioral attributes to be analyzed is primarily determined by two considerations: what attributes can be reliably recorded in free-ranging animals, and what traits seem most important to the animal's overall success (Biggins, Miller, and Hanebury 1992). We recommend using as many survivorship and behavioral indexes as possible. To evaluate the first black-footed ferret reintroduction, we analyzed causes of mortality, daily survival rate, fidelity to release site, litter effects, diet, and movements (Biggins, Miller, and Hanebury 1992).

Gaining knowledge for purposes of designing an optimum release technique may be the most important technical goal during initial releases. High mortality is not a failure unless biologists fail to learn enough to increase survival in future reintroductions. The comparative process associated with a rigorous and well-designed release offers the best opportunity to improve reintroduction and proceed rapidly toward recovery.

10

IDENTIFYING AND EVALUATING BLACK-FOOTED FERRET HABITAT

IDENTIFYING HABITAT FOR REINTRODUCTION

When it became clear in 1988 that the captive population would soon reach 200 breeding adults, previously established as the minimum necessary to begin reintroduction of surplus ferrets into their natural habitat (Wyoming Game and Fish Department 1987; U.S. Fish and Wildlife Service 1988), Region 6 formed the Black-Footed Ferret Interstate Working Group to coordinate states' efforts and help identify potential reintroduction sites. Ron Crete of Region 6 took on the herculean task of coaxing the various participating agencies to move in the same direction. The first reintroduction was slated to take place in Wyoming, a political decision that acknowledged the state as the original source of the captive ferrets. It was agreed that all other potential sites would be ranked by biological merit, using a comparative model devised by Biggins, Miller, et al. (1993).

Reintroduction requires finding and protecting healthy habitats, which for many endangered species is not an easy task. We are currently witnessing a worldwide decline of biotic diversity unmatched since the Cretaceous period, and the rate of biological depreciation is accelerating (Myers 1979; Wilson 1988). Destruction of habitat is one of the major reasons for this loss, and reintroduction attempts must carefully assess the remaining fragments of habitat. Biological evaluation should consider the animal's requirements, the presence and density of predators and competitors, the presence or absence of threatening diseases, spatial characteristics, and management considerations, among other assorted variables. Habitat evaluation must be standardized, and potential sites should be quantitatively assessed and compared before reintroduction is attempted.

Not surprisingly, Griffith et al. (1989) found that the success of reintroduction and translocation increases with increasing habitat quality. In some projects, reintroduction has been a component of a broader program to restore habitat (Holloway and Junigus 1973; J. L. Anderson 1986; Kleiman 1989; Stanley Price 1989; David 1990). Interestingly Griffith and his colleagues found that such programs were no more successful than those that did not improve habitat. It is possible, of course, that in the latter programs the habitat was already of sufficient quality, and enhancement was not necessary.

The decisiveness of several general habitat features is obvious. Is the original cause of the species' decline still present? If so, reintroduction or translocation may be a waste of time and money. Some variables (such as food, water, refugia, nesting or denning sites, and presence of endemic diseases) may be relatively easy to assess. Others, such as the degree of conflict with potential predators, are more difficult to analyze but very important. If natural predators are present at high densities, or if exotic predators are present, short-term predator-control programs may be warranted until the reintroduced animals adjust to their new environment (Kleiman 1989). Studies of captive-raised Siberian ferrets released to the wild indicated that survival was greater when predator numbers were lower (Biggins, Hanebury, et al. 1991). Such habitat variables as ecosystem resilience and stability are less intuitively important, but worthy of attention in systems characterized by frequent natural disturbances such as fires, volcanoes, and droughts (Kleiman 1989; Stanley Price 1989). The impact of reintroduction on other rare, sensitive, or endangered species must also be examined when assessing and comparing sites.

It is important to reintroduce animals into their former range. Griffith et al. (1989) found that translocations to the center of a species' former range were more likely to be successful than those occurring on the edge of or outside the former range. But the species' former range is not always suitable, especially when it is plagued by the presence of exotics (Witteman et al. 1990; J. W. Wiley et al. 1992).

ANALYZING THE MONTANA REINTRODUCTION SITE

Preliminary Evaluation of the Site

Site selection for the 1991 reintroduction was predicated on returning ferrets to their original location near Meeteetse, Wyoming. But plague, which had been active since 1984, continued to undermine the potential of the area to support ferrets. By 1989 the site had an estimated capacity of only 14 ferret families, and by summer 1990 this number had declined to fewer than 6 families. In September 1990, therefore, Wyoming substituted the backup site in Shirley Basin, which had the potential to support an estimated 142 ferret families (56 Fed. Reg. 41473–41490, 1991), as the location for the first reintroduction. The prairie dog colonies at Shirley Basin had been mapped and analyzed by the University of Wyoming Cooperative Research Unit for a potential ferret reintroduction (C. Conway 1989), and searches for other populations of ferrets had been performed sporadically in the area for nearly 10 years.

The black-tailed prairie dog complex in north-central Montana was another of the earliest sites identified and developed for reintroduction. A *prairie dog complex* is defined as a group of distinct prairie dog colonies, none more than 7 kilometers from its nearest neighbor (Biggins, Miller, et al. 1993). Seven kilometers—the longest move made in a single night by a black-footed ferret at Meeteetse—represents a wild-born ferret's ability to move between patches of habitat. Beginning in 1988, biological studies gathered data on the prairie dog ecosystem, searched for ferrets, censused potential predators, and monitored diseases in the area (Reading, Grensten, et al. 1989; Reading 1991, 1993).

Prairie Dog Colony Dynamics and Species Associations

Both the dynamics of black-tailed prairie dog colonies and the vertebrate species associated with them had been monitored and analyzed on the Montana reintroduction site between 1981 and 1988, but after the site was selected for potential ferret release the research and monitoring became more intensive. The prairie dog colonies were mapped using aerial photographs and 7.5-minute topographic maps, and colony area was determined from these maps with an electronic planimeter. This information made it possible to calculate annual expansion (or contraction) rates of prairie dog colonies. We also calculated burrow density and compiled lists of vertebrate species associated with prairie dogs. In 1988 there were some 170 prairie dog colonies, totaling 19,223 hectares, in the complex (58 Fed. Reg. 19221–19231, 1993).

Average size of the black-tailed prairie dog colonies in the reintroduction area increased between 1981 and 1988, but the rate of expansion decreased (Reading, Grensten, et al. 1989; Reading 1993). This reinforced the findings of Knowles (1982) and Garret, Franklin, and Hoogland (1982) that prairie dog populations exhibit logistic growth. Initial rates of increase were rapid, but eventually increased competition, reduced resources, less favorable habitat at the colony's edge, and physical barriers (such as steep slopes and dense vegetation) slowed growth.

The Montana prairie dog complex was compared to others across North America as a reintroduction site for black-footed ferrets. The 170 colonies averaged 103.8 ($\pm$SE of 3.3) burrows per hectare, but density was not significantly related to colony size (Reading 1993). Because density of burrows per se is not a reliable indicator of prairie dog population size (Menkens, Miller, and Anderson 1988), density of *active* burrows (Biggins, Miller, et al. 1993) was used to estimate the potential for 561 ferret families on the Montana prairie dog complex in 1988 (58 Fed. Reg. 19221–19231, 1993). Over 14,000 hours of surveys failed to produce evidence of a single living black-footed ferret (Reading 1991).

We compiled a list of 171 vertebrate species sighted on black-tailed prairie dog colonies, and found that larger colonies contained more species of birds (Reading 1993). Because prairie dog colonies resemble islands, the application of island biogeography theory has important implications for the preservation of species. The theory posits that patches of habitat maintain larger numbers of species when their area is larger and when sources of immigration (other islands) are closer (MacArthur and Wilson 1967). In other words, complexes of prairie dog colonies that are relatively large and linked like stepping-stones for dispersing prairie dogs and associated species can support more species than small distantly spaced colonies.

Other variables of the prairie dog complex were analyzed using a Geographic Information System (GIS), a computerized mapping system that represents a powerful tool for habitat analysis and management. The variables we examined included vegetation, soils, slope, aspect, land ownership, patch size, patch shape, and intercolony distance; actual colonies were compared with randomly distributed control areas.

Prairie dog colonies at the Montana reintroduction site are more prevalent on slopes of less than 4% and on elloam soil associations, suggesting that prairie dogs actively select these conditions (Reading 1993). On relatively level areas, it is easier to detect predators. Elloam soils, consisting of well-drained sandy loam to silty clay, provide the necessary depth and structural support for burrow systems and are unlikely to flood. Land ownership of prairie dog colonies is predominantly federal, which is unsurprising given the antagonistic attitudes of private ranchers toward prairie dogs. Such information can be used to develop a cartographic model of preferred habitat, which may facilitate prairie dog management, identification of potential habitat, and assessment of areas of possible expansion.

Predator and Disease Monitoring

Predator studies were undertaken in Montana to identify potential sources of predation, the primary source of known mortality in the 1991 and 1992 Wyoming black-footed ferret reintroductions. Between 1989 and 1991 predators were assessed by means of roadside raptor counts to identify diurnal avian predators (see Craighead and Craighead 1956) and scent-station surveys to identify mammalian predators (see Conner et al. 1983). Spotlight searching along transect

routes also produced an index of predator densities. In general, predator densities were lower on the Montana reintroduction site than in other parts of the ferret range (Reading 1993). A relatively low density of coyotes at the Montana site may be partially explained by the intensity of coyote-control programs in the area.

Plague and canine distemper are of supreme concern to biologists. Plague devastates the prairie dog prey base, and distemper attacks ferrets directly and fatally (E. S. Williams et al. 1988). The most effective methods of detecting both diseases are analyzing carnivore blood serum taken from coyotes and examining whole carcasses (Barnes 1993). Carnivore blood serum (derived from a 5- to 15-milliliter blood sample from the animal) can detect titers to both plague and distemper, but because many coyotes survive canine distemper a few animals should be sacrificed to examine for brain lesions. These lesions can indicate past infections of distemper even if blood titers show no immediate threat. Fresh feces, collected from the trap site or rectum of the coyote (by workers using latex gloves), can provide additional data on distemper (E. S. Williams 1990). Plague may be detected by collecting fleas from prairie dog burrows, but attempts to do so were not very successful in Montana (Knowles 1993). Montana has therefore tracked plague throughout the prairie dog complex by sampling coyotes. Successfully collecting flea samples would also identify the local flea species, which might provide important information about the movement and ecology of plague through the prairie dog complex.

Although canids, mustelids, and procyonids (raccoons) can all carry canine distemper, coyotes are probably the most important reservoir of the virus for black-footed ferrets (E. S. Williams 1990). Ten coyote carcasses from a given population should be sufficient to reveal presence of canine distemper about 97% of the time, and seropositivity can be detected from 20 blood samples about 95% of the time (E. S. Williams 1990). It is more difficult to predict the number of blood samples needed for plague detection; if plague is present at low densities, it may take as many as 250 (E. S. Williams 1990).

Wyoming has done a thorough job of disease survey at the Shirley Basin reintroduction site, with testing carried out at the Wyoming state veterinary laboratory in Laramie. In January 1983, 85 coyote carcasses were shipped from the Montana reintroduction site to the Wyoming laboratory for evaluation. Forty-six of those carcasses tested positive for plague antibodies (*Phillips County News* [Montana], 17 February 1993).

This was bad news. The Montana reintroduction site had experienced a 52% reduction in prairie dog hectares between 1988 and 1992. In other words, the site's potential had decreased from an estimated 561 ferret families to about 290 ferret families. Although most of this drop was due to plague, there was also evidence of illegal prairie dog poisoning (Reading 1993).

Because black-tailed prairie dog populations often decline by 95–98% in the presence of plague (Barnes 1993; Culley 1993; J. P. Fitzgerald 1993), the Centers for Disease Control recommended application of the pesticide permethrin to counter the spread of the disease (Barnes 1993). Plague is passed through a flea vector, and the pesticide works against the fleas. Evidence from black-tailed prairie dog colonies on the Rocky Mountain Arsenal in Colorado suggested that permethrin slows the spread of plague. During summer 1993, field workers applied the chemical to several colonies at the Montana reintroduction site. That effort significantly reduced the number of fleas (Knowles 1993), and dusted colonies showed no further declines by late 1993. Permethrin was not used by Wyoming at either Meeteetse or Shirley Basin, and plague was documented at both places. The prairie dogs near Meeteetse crashed, whereas those in Shirley Basin have remained stable.

In summary, for any release site investigators should evaluate ecological features, quantify habitat, census potential predators and competitors, analyze disease potential, map land-ownership patterns, and search for wild populations of the reintroduced species. Thorough knowledge of all these phenomena makes management of the species, and the natural system on which it depends, considerably easier. But finding a site suitable for reintroduction, though difficult, is only the first step. The second step is protecting the area from further degradation.

TAKING INTO ACCOUNT THE SIZE AND SHAPE OF PROTECTED AREAS

As we have seen, prairie dog colonies resemble islands. Although the prairie between colonies may not present a formidable barrier to dispersal for some vertebrates associated with prairie dogs, it may for others. If there are many habitat patches in proximity to each other, it is easier for immigrants to repopulate vacated patches.

Several discrete release sites could constitute metapopulations (separate subpopulations), with artificial migration or colonization forming a single large population (Gilpin 1991; Hanski 1991). Gilpin found the effective population size of metapopulations to be at least 10 times smaller than the number of individuals in the actual population (a typical N_e:N ratio is 1:3—see Chapter 8). To improve the ratio, Gilpin suggested maximizing persistence times of local populations, increasing the number of populations in existence, and augmenting gene flow between sites.

Although debate about metapopulation principles persists, most people agree that, for any given individual patch, larger is better (MacArthur and Wilson 1967; Diamond 1975; Gilpin and Diamond 1980; Hanski 1991). More specifically, the biology, genetic history, and ecology of the animal often suggest an appropriate reserve design. For example, there is little disagreement over the metapopulation approach for black-footed ferrets, whose susceptibility to canine distemper calls for natural barriers against transmission of the disease between distinct prairie dog complexes. Species with low genetic diversity may benefit from population subdivision if patches provide different selective pressures (Gilpin 1987). Factors such as high rates of predation along habitat edges may also influence shape requirements.

Buffer zones and corridors may benefit black-footed ferrets. Large colonies connected by corridors mean that ferrets spend less time traveling through the no-man's-land of burrowless prairie when moving among the colonies of a complex (although this benefit must be balanced against disease risk, even within a complex). Buffers necessarily imply some level of protection for the prairie dogs near a protected area. Even if the prairie dog densities in the buffer zone are not equal to those of the core refugia, they can still provide restless young ferrets with peripheral areas in which to operate, heightening their probability of persistence until a better territory opens up.

It is generally accepted that a protected area should provide for interactions of ecosystems across a landscape. Buffer zones can assure that corridors wide enough to encourage the movement of species link habitats. The use of buffer zones and corridors can help conserve the biotic integrity of a region—that is, the presence of the species native to an area, as opposed to generalists that invade fragmented habitats (Ratcliffe 1986). When generalists invade, the total species count may actually increase while the number of native species declines; thus simple species richness does not measure the quality of an area (Sampson and Knopf 1982; Van Horne 1983). The maintenance of native species usually requires large areas of relatively undisturbed original vegetation, whereas many generalists seem to survive almost anywhere (Kitchener et al. 1980; Humphreys and Kitchener 1982; Noss 1983).

But there is more to habitat protection than theories of metapopulations, island biogeography, and landscape ecology. When conservationists are faced with the prospect of trying to save what little habitat remains from overexploitation, debates about size and shape are moot; you have to take what you can get. In most cases, protecting habitat has remained a contentious and politically charged issue. As a result, only 16% of listed endangered species have critical habitat designated under the Endangered Species Act (U.S. General Accounting Office 1992). The black-footed ferret, for example, has an extremely simple and well-understood dependence on prairie dogs. Yet the federal government has not designated critical habitat for ferrets, and prairie dog poisoning programs continue to receive federal financial support. In the next section, we will examine how Mexico is handling prairie dog management.

PROTECTING A PRAIRIE DOG COMPLEX IN CHIHUAHUA, MEXICO

Potential Value to Conservation

The Centro de Ecología of the Universidad Nacional Autónoma de México is initiating a high-plains protected area in northern Chihuahua, Mexico, about 70 kilometers south of the New Mexico bootheel. The project holds tremendous promise for protecting the largest remaining black-tailed prairie dog complex in North America and for reintroducing the black-footed ferret.

The Chihuahuan Desert, which sprawls across the Mexico–U.S. border extending from New Mexico and Trans-Pecos Texas south to San Luis Potosi, is critical to the maintenance of regional and hemispheric biodiversity. The area is evolutionarily unique, biotically diverse, sensitive, threatened, and one of the least-studied parts of North America (Wauer and Riskind 1977; Tanner 1985). As evidence of Chihuahua's remoteness, the endemic Bolson tortoise *(Gopherus flavomarginatus),* North America's largest land tortoise, was discovered there only 30 years ago (Morafka and McCoy 1988), and a small herd of wild bison *(Bison bison)* still roams the area.

Grasslands in and around the proposed protected area support the largest black-tailed prairie dog complex in North America, some 55,000 hectares containing as many as 1.6 million prairie dogs (Ceballos et al. 1993). One single colony of the complex measures 34,000 hectares, and approximately 60% of the land area in the complex is covered by prairie dog colonies (typically, only about 20% of the area in a complex is covered by prairie dogs).

The Chihuahuan prairie dog complex houses the full diversity of life supported by the keystone species. A keystone species is an organism that is essential to the structure and process of a community or ecosystem—in other words, a species that in some way supports other forms of life. Ecologically, the prairie dog ecosystem is an oasis of species diversity on the arid plains. In the United States, due to poisoning programs, several species dependent on the prairie dog ecosystem are either listed or proposed for listing under the Endangered Species Act, including ferruginous hawks, mountain plovers *(Charadrius montanus),* swift foxes *(Vulpes velox),* and black-footed ferrets. Burrowing owls *(Athene cunnicularia)* have also declined and are designated as species of concern in several states. Ferruginous hawks, burrowing owls, mountain plovers, and kit foxes (considered a subspecies of *V. velox* by Hall 1981) are all found on the prairie dog colonies of the Chihuahuan prairie dog complex.

The protection of Chihuahuan habitats is important to large and small mammals, to the biological diversity of the prairie dog ecosystem, to herpetological fauna, to insects, and to resident and migratory birds. Indeed, Raitt and Pimm (1977) emphasized that the northern Chihuahuan grasslands are the principal winter habitats for many North American grassland birds. As a group, endemic populations of grassland birds have declined more rapidly, more consistently, and over a wider geographic area in the last 25 years than any other group of birds (Knopf 1993). For example, three western grassland birds, the lark bunting *(Calamospiza melanocorys),* the mountain plover, and the Cassin's sparrow *(Aimophila cassinii)* have declined more than 60% since 1968 (Knopf 1993).

Approximately 500 plant species with economically valuable genetic resources also exist along the Mexico–U.S. border, and 60–75 of those plants are threatened by inappropriate land uses (Nabhan 1990). Nabhan suggests that protected areas would enhance the economic potential of these resources. He specifically mentions the Chihuahuan Desert's unique richness and encourages management practices that would enhance long-term persistence.

Threats to Biodiversity in Chihuahua

The recent population shift toward the Mexico–U.S. border has imposed sudden and heavy demands on surrounding ecosystems. Migrants from other parts of Mexico, who come to speculate on a border economy, do not understand or appreciate the arid environment (Ezcurra and Halffter 1990). Economic and technological development following this population increase has not integrated ecological considerations. Proximity to an international border, with striking income differences on the two sides, aggravates the problem. The resulting environmental degradation has depleted biodiversity and economically valuable natural resources. Desertification in Mexico is rapidly becoming a reality, with erosion and greater pressure on semiarid areas (Sonnenfeld 1992). The unique prairie and montane habitats of northern Chihuahua are declining, and biodiversity in Mexico and the United States is at risk (Dittmer 1951; J. Brown 1971; Wauer and Riskind 1977; Ezcurra and Halffter 1990). The protected area thus offers a tremendous opportunity for international action toward conservation, and the black-footed ferret represents an excellent bridge to that cooperation. The species, the supporting ecosystem, and hemispheric biodiversity would all benefit.

Potential for Black-Footed Ferret Reintroduction

Application of the model developed by Biggins, Miller, et al. (1993) indicated that the Chihuahua prairie dog complex could accommodate 1,280 adult female black-footed ferrets with families (Ceballos et al. 1993). With the inclusion of adult males and offspring, the total summer black-footed ferret population could exceed 6,000 individuals, by far the largest existing or proposed reintroduction site. Although there is yet no evidence about the history of plague, large numbers of prairie dogs have been present on this complex for at least 100 years without major population crashes. Because of its enormous size and density, the Chihuahua prairie dog complex represents the best opportunity for the long-term recovery of the black-footed ferret, and of many other species that depend on prairie dogs. As an appealing symbol of the declining prairie grasslands, the black-footed ferret will give as good as it gets by focusing international attention on the protected area.

The reintroduction could also provide employment opportunities for the local population around the proposed protected area, stimulate further research on managing complex biological interactions, enhance career development of conservation biologists in Mexico, and augment environmental education. The cooperative bonds forged by this venture could benefit the conservation of many other sensitive species presently managed in both Mexico and the United States and enhance conservation strategies that span the international political border.

The reintroduction in Mexico also presents opportunities to address many of the obstacles to recovery that have been discussed at recent Black-Footed Ferret Interstate Working Group meetings. For example, Region 6 funding to help states manage endangered species (called Section 6 funding) was recently reduced from $1 million to $442,000 (1992 Black-Footed Ferret Interstate Working Group meeting minutes).

As a result of the cuts, several Region 6 representatives to the 1992 Interstate Working Group meeting recommended that the ferret program pursue partnerships with private entities and creative funding to replace the shrinking Section 6 funds. They predicted very little Section 6 money for reintroduction after 1994 (1992 Black-Footed Ferret Interstate Working Group meeting minutes). The cuts occurred when the program was expanding to develop more reintroduction sites than the single one in Wyoming.

The site in Mexico offers an opportunity to utilize sources of international money unavailable for recovery efforts in the United States. For example, both the U.S. Agency for International Development and the Mexican government have made generous contributions to this project. The benefits of these contributions would extend north of the Mexico–U.S. border as well, in that the development of a viable wild population in northern Mexico could reduce the expenses of captive-breeding centers in the United States and Canada. With the potential production of ferret offspring in Mexico, the translocation of wild-caught juveniles from Chihuahua to other sites across the former range would be less expensive, and would probably enjoy a higher success rate, than use of captive-born stock. If successfully repopulated with ferrets, the reintroduction site in northern Mexico could eliminate total dependence on captive breeding, and could serve as a wild ferret farm to supply other United States and Canadian reintroduction sites.

Because there are no recognized subspecies of black-footed ferrets (E. Anderson et al. 1986), it is unlikely that problems would arise from moving animals across their former range. The climate in Chihuahua is typical of high-plains grasslands, with snow from December to February. Temperatures vary from −10° to +45°C. Plains vegetation in Chihuahua consists of short grasses (grama grasses, *Bouteloua* spp.; muhley grasses, *Muhlenbergia* spp.; three awns, *Aristida* spp.) and prostrate herbs, similar to that of the high-plains grasslands that extend north into Canada (Warnock 1977).

The lack of subspecies makes biological sense. The black-footed ferret hunts the same prey across its range, and prairie dog burrows offer a relatively constant environment regardless of the surface temperature (F. R. Henderson et al. 1974). The evolutionary forces that selectively shaped morphology, genetics, and behavior were therefore uniform across the animal's entire range.

The U.S. Fish and Wildlife Service (1988) recovery plan specified that 10 or more self-sustaining black-footed ferret populations are necessary for downlisting (reclassification to a less threatened status in accordance with the Endangered Species Act). In 1994 black-footed ferrets were reintroduced in Wyoming, Montana, and South Dakota. The cutback in Section 6 funding may hinder the development of new sites if the potential financial burden combines with opposition from the local agricultural community to delay or eliminate reintroductions.

The Chihuahua site could come close to producing a viable population of black-footed ferrets all by itself. It could therefore be critical to the long-term recovery requirements of the animal. The 1990 Interstate Working Group meeting recognized the importance of complex size to survival potential, and passed a resolution that all reintroduction sites should be ranked in terms of their biological potential to the ferret. Many reintroduction sites are vulnerable to poisoning or severe fluctuations in the prairie dog population. In 1992 potential reintroduction areas in Wyoming and Colorado suffered prairie dog population crashes (1992 Black-Footed Ferret Interstate Working Group meeting minutes). In 1990 a similar prairie dog crash had occurred on the proposed Utah reintroduction site (1990 Black-Footed Ferret Interstate Working Group meeting minutes). Prairie dog populations on the Montana reintroduction site have declined by 50% or more since 1988. South Dakota poisoned 185,600 hectares of black-tailed prairie dogs between 1980 and 1984 (Hanson 1988) and another 90,000 hectares in 1986 and 1987 (Tschetter 1988). The Bureau of Indian Affairs proposed poisoning on approximately 24,000 hectares of black-tailed prairie dogs on two South Dakota reservations, and several Montana reservations want to poison their prairie dogs (1992 Black-Footed Ferret Interstate Working Group meeting minutes).

The consistently high numbers of prairie dogs in northern Chihuahua for the last 100 years, the comparative rarity of poisoning in Mexico, and the proposed protected area offer some insurance against population crashes and threats of poisoning that occur in other parts of the historical range. Indeed, the local government in Chihuahua recently chose the plan for a protected area over a proposal to poison the prairie dogs. This attitude is not apparent at any other existing or potential reintroduction site.

At present, the published range of the black-footed ferret extends into the Chihuahuan Desert of southern New Mexico but not into Mexico (Hall 1981). The nearest modern museum specimen was located 70 kilometers north of the border. Nevertheless, black-footed ferrets were probably coterminous with prairie dogs. The U.S. Fish and Wildlife Service (1988) recovery plan and agreements with Wyoming, Montana, and South Dakota all characterize black-footed ferrets as probably endemic to northern Mexico (1993 U.S. Fish and Wildlife Service draft rules for South Dakota and Montana; also, 56 Fed. Reg. 41473–41490, 1991).

Fossil ferret specimens from the northern (A. H. Harris 1977) and southern (Messing 1986) portions of the Chihuahuan Desert were both found with prairie dog remains. The lack of modern museum records south of the border is probably due to lack of investigation. According to S. Anderson (1972), the first scientific collections in the state of Chihuahua occurred in 1907, when 190 specimens were analyzed; very few specimens were collected from 1911 to 1930 because of the Mexican Revolution. Only about 6,300 museum specimens had been collected from all parts of the state of Chihuahua (one-twelfth of the entire area of Mexico) as of 1970, about 4,800 of them obtained between 1930 and 1970 (S. Anderson 1972). By 1930, northern Mexico had already suffered some of the effects of fragmentation and islandlike extinction patterns (Dittmer 1951; J. Brown 1971). It is unsurprising that scanty investigations over an area this large failed to produce a modern specimen of a nocturnal, semifossorial species as secretive as a ferret.

Findley and Caire (1977) argued that describing the fauna of a region solely by referring to recorded specimens can be inaccurate; the completeness of the published record can be dictated by chance and by the relative vigor of search efforts. They proposed an alternative way to define the fauna of a region by investigating the assemblage of mammalian species co-occurring over a geographic area with the same overriding biological factors as the region in question. By statistically analyzing quadrants, they presented evidence in support of the technique. Coincidentally, their statistical sample included the Chihuahuan grassland of northern Mexico, and the mammals of the sampled areas coincided with similarly adapted fauna of the Great Plains in Kansas (Findley and Caire 1977). By applying this technique, one can conclude that black-footed ferrets probably lived with black-tailed prairie dogs on the grasslands south of the Mexico–U.S. border, just as they did throughout the rest of the Great Plains.

The Mexico reintroduction site was first proposed to the Interstate Working Group in 1989 by Gerardo Ceballos of the Centro de Ecología, Universidad Nacional Autónoma de México. Since then searches for ferrets have continued, and several graduate students are now working full-time in the region. It was proposed as a black-footed ferret site again at the 1992 and 1993 Interstate Working Group meetings, but as of mid-1994 there had been no decision about including the Chihuahua prairie dog complex in the ranking process for future black-footed ferret reintroductions. If Region 6 decides to rank the Chihuahua prairie dog complex with the other potential locations, the area will be prepared along the lines described earlier in this chapter.

11
CONSERVING THE PRAIRIE DOG ECOSYSTEM

> Man is always marveling at what he has blown apart, never at what the universe has put together, and this is his limitation. He is at heart a fragmenting creature.
>
> Loren Eiseley

FRAGMENTATION OF THE PRAIRIE DOG ECOSYSTEM

The prairie dog ecosystem provides biological niches to dozens of vertebrate species that rely on prairie dog activity, at least in part, for survival (Reading 1993). Ecologically, this ecosystem is an oasis of species diversity on the arid grasslands. It sustains higher numbers of small mammals and arthropods, nearly six times the number of terrestrial predators, higher numbers of avian predators, and greater avian species diversity and density than does the surrounding prairie (Hansen and Gold 1977; Clark, Campbell, et al. 1982; O'Meilia et al. 1982; Agnew et al. 1986; Kreuger 1986). The presence of prairie dogs favors plant diversity and promotes growth of perennial grasses and forbs grazed by livestock and large native ungulates (hoofed animals) (Bonham and Lerwick 1976). Before the onset of poisoning campaigns, prairie dogs extended across the Great Plains and created an ideal habitat for hundreds of millions of bison, elk *(Cervus elaphus)*, and pronghorn antelope *(Antilocapra americana)*, as well as prairie birds such as mountain plovers and burrowing owls. Their burrows provided refugia for myriad small mammals, reptiles, and amphibians, and their biomass supplied the nutritional needs of innumerable carnivores and raptors. In sum, prairie dogs are ecosystem regulators that enrich primary productivity, species densities, species

diversity, soil structure, and soil chemistry by their burrowing and grazing activities (Detling and Whicker 1988; Sieg 1988; Reading, Grensten, et al. 1989).

Several of the other species that rely on prairie dogs may soon join the black-footed ferret on the federal endangered-species list. The black-footed ferret is charismatic enough to serve as a flagship species, whose protection could enhance the other components of the prairie dog ecosystem by educating people about the folly of destroying the prairie. However, the black-footed ferret recovery program has not yet adequately addressed attitudes toward prairie dog eradication.

As we saw in Chapter 2, the program to exterminate prairie dogs began because ranchers wanted potential competitors with livestock eliminated. Livestock eat grass, and prairie dogs eat grass. So prairie dogs must go. The historical rationale was that simple. Since the turn of the century, prairie dog ranges have been reduced from a historical level of 40 million hectares, by conservative estimate, to about 600,000 hectares by 1960 (Marsh 1984). These figures represent at least a 98% decline in the original geographic distribution of the five species of prairie dogs (other estimates of historical prairie dog distribution go up to 100 million hectares). The few remaining prairie dog colonies are both fragmented and isolated, and thus more susceptible to extirpation by a number of factors, most prominently sylvatic plague.

A decline of this magnitude would be sufficient to qualify most species for some level of protected status, but the prairie dog suffers from a century of misinformation and bad publicity. Prairie dogs, particularly the black-tailed species, are maligned by strong western agricultural interests, and protection by the U.S. Fish and Wildlife Service would be a politically controversial act. Indeed, prairie dog colonies are not even listed as critical habitat for the endangered black-footed ferret.

Some proponents of the status quo argue that the prairie dog population is not seriously threatened because prairie dogs can still be found across their historical ranges. But to conclude that prairie dog populations are safe because remnant colonies are still scattered throughout a geographical region between Canada and Mexico masks the severity of habitat fragmentation. Fragmentation threatens species that depend on a particular habitat in three ways: demographic units are eliminated or reduced in size, and the remaining small isolated colonies are more susceptible to extinction by means of disease, genetic problems, demographic events, or natural catastrophes; sources of immigration are destroyed; and habitat alteration between colonies precludes recolonization and genetic exchange (Wilcox and Murphy 1985). As a result, the risk of extinction from habitat disruption may rise disproportionately to the extent of habitat reduction (Wilcox and Murphy 1985; Wilcove et al. 1986). In some cases, reductions in the numbers of one species can cause a wave of secondary extinctions that affects species diversity (Wilcox and Murphy 1985; Wilcove et al. 1986). This is undoubtedly true of the prairie dog.

Although prairie dogs may meet the biological criteria for legal protection under the Endangered Species Act, political antipathy runs deep. Several state governments have legally declared the prairie dog a pest and mandated its extermination on private, state, and even federal lands. The South Dakota Department of Agriculture even went so far as to "order and require" the U.S. Bureau of Reclamation to eradicate 24 hectares of prairie dogs deemed "a menace to neighboring lands" (South Dakota Department of Agriculture memo, 12 December 1992). In Montana, similarly, state regulations require that lessees of state lands poison the prairie dogs on those lands or risk losing their leases (Reading 1993).

"Pest status" has legitimately been granted to introduced exotics, but the prairie dog is an endemic species of the Great Plains. In fact, prairie dogs were a critical element in developing and maintaining the integrity of the short-grass and midgrass prairies. To label such an important keystone species a pest is unsound conservation policy with a high price tag in lost biodiversity.

PRAIRIE DOGS AND LIVESTOCK: FINANCIAL ASPECTS OF POISONING

Prairie dog control policies remain largely unaffected by the results of scientific studies. Policy is usually strongly influenced by past policies, internal resources, and preferences of key decision makers. Thus it is not surprising that ecological findings have not brought about change in prairie dog poisoning programs. Even the theory of incompatibility between livestock and prairie dogs has not been supported by rigorously collected data.

Some livestock studies have reported no significant difference in market weight between steers that coexist with prairie dogs and those that do not (Hansen and Gold 1977; O'Meilia et al. 1982). Because grass is shorter on prairie dog towns, range managers in earlier eras concluded that there was less food for cattle. But in reality both the nutrient content and the digestibility of forage are enhanced when prairie dogs are present. Thus the reduction in standing crop is apparently compensated for by increased quality, digestibility, and productivity of grasses and forbs (O'Meilia et al. 1982; Coppock et al. 1983; Krueger 1986).

In fact, domestic cattle and bison prefer to graze on prairie dog towns because the grass is more succulent (Coppock et al. 1983; Wydeven and Dahlgren 1985; Krueger 1986; Detling and Whicker 1988). Uresk (1987) reported that early successional range conditions were best for cattle management, and that prairie dogs

promoted such a situation. Indeed, later successional stages were not found on prairie dog colonies. In light of these studies, and the fact that 300 prairie dogs eat only about as much as 1 cow-calf unit (Uresk and Paulson 1989), poisoning campaigns do not seem to be worth the financial expenditure.

In fact, a cost-benefit analysis revealed that poisoning programs operate at a net financial loss (Collins et al. 1984). The poison simply costs more than any grazing benefits to cattle after prairie dogs are poisoned. Because the federal government subsidizes the costs, there is little incentive for ranchers to worry about cost-effective actions. In one area of southeastern Colorado, the poisoning costs would have exceeded the market value of the land.

The economic analysis of Collins et al. was conservative and did not consider the long-term costs of a degraded ecosystem, costs that are later transferred to society as a whole. For example, the eradication of prairie dogs may have eliminated a natural control of mesquite in the Southwest (J. A. Miller 1991). Prairie dogs eat mesquite seeds and contribute significantly to seedling mortality by stripping bark. Coincidental with recent prairie dog decline, mesquite has proliferated and now interferes with the livestock industry, preempting grass for livestock and making roundups difficult (J. A. Miller 1991). Additionally, 32% of the winter diet of prairie dogs is prickly pear cactus (*Opuntia polycantha*), a plant that cattle do not eat and that proliferates when livestock overgraze an area (Summers and Linder 1978). Furthermore, the Collins et al. (1984) economic analysis did not consider the intangible value of biological diversity as a public benefit or recognize depletion of biotic resources as a loss of potential or actual wealth (McNeely 1988).

Federally owned land is also poisoned, though by definition it is protected in the interests of the entire nation, because a handful of grazing lessees influence management policy. For example, permittees on South Dakota's Buffalo Gap National Grassland, managed by the U.S. Forest Service, make up only 2% of the state's livestock industry (Sharps 1988) yet influence poisoning policy. And less than 5% of the beef weight produced in the United States is on public land in the West (Ferguson and Ferguson 1983; U.S. General Accounting Office 1988a). Many ranchers perceive financial losses when they share rangeland with prairie dogs, and this deep-seated view is not easily countered with facts.

As a result, local livestock interests continue to pressure agencies to poison these federally owned lands. There is a total of 357,059 hectares on Buffalo Gap National Grassland in South Dakota and Nebraska, and it is prime prairie dog habitat. As recently as 1980, 17,520 hectares of prairie dogs had persisted through earlier poisoning campaigns. In 1988, the U.S. Forest Service proposed restricting prairie dogs to only 1,248 hectares; alternative proposals ranged up to 3,520 hectares (unpublished U.S. Forest Service biological assessment, 17 August 1988). Similar examples of prairie dog poisoning occur on other national grasslands, on public lands managed by the U.S. Bureau of Land Management, and even in a few national parks.

The sway of local agricultural interests is well illustrated by a memo from the state government of South Dakota about black-footed ferret reintroduction, which would require a certain population of prairie dogs:

> You are hereby advised that the Governor is totally opposed to the reintroduction of black-footed ferrets into South Dakota. Direct your staff to cease their work on evaluating black-footed ferret recovery potential and its effect in South Dakota. The reintroduction of black-footed ferrets meets with adamant opposition from the agricultural community and has no economic benefit to the state. (State of South Dakota, 8 November 1988)

The historical composition of prairie communities has all but disappeared because of this intolerance. Poisoning afflicts the wildlife community both by eliminating a critical link in the food chain and by inadvertently poisoning nontarget species. Specialized predators are the most vulnerable, and the black-footed ferret was a major casualty of the campaign against prairie dogs.

THE RESULT: AN ENDANGERED SPECIES

Black-footed ferrets evolved to utilize prairie dog colonies with extraordinary economy, but the cost of this specialization is vulnerability to habitat disruption. Eradication of habitat via prairie dog poisoning campaigns (a deterministic event) eliminated some black-footed ferret populations entirely and reduced overall numbers; the remaining habitat was fragmented. Thus black-footed ferrets lived in small isolated populations, which have a higher probability of extinction caused by diseases, disaster, demographic variance, and genetic problems (stochastic events): the smaller the population, the higher the probability of collapse. Black-footed ferrets at Meeteetse each used about 50 hectares of white-tailed prairie dogs (Forrest, Clark, et al. 1985a). Under those circumstances, a 1,000-hectare prairie dog colony could hold several thousand prairie dogs, but would only support about 20 ferrets. Thus it is easy to see how the forces of small-population biology can eliminate a ferret population even though the prairie dog colony survives.

When a given black-footed ferret population winked out, fragmented habitat made recolonization difficult, a difficulty compounded with each lost colony. These losses in turn reduced gene flow and genetic diversity via genetic drift. The small litter size of black-footed ferrets, particularly when compared to the con-

specific Siberian ferret, may be a result of inbreeding in isolated populations (an ecological explanation was also discussed in Chapter 6). In short, the black-footed ferret followed a general pattern of extinction set off by a deterministic event (poisoning) and knocked out by stochastic events.

The black-footed ferret recovery plan requires protection of at least 75,000–100,000 hectares of prairie dog complexes strategically placed within the former range to minimize vulnerability to catastrophe (U.S. Fish and Wildlife Service 1988). Because ferrets can be compatible with livestock grazing, that amount of land—a mere 0.1% of the total western rangeland—can easily be sheltered from poisoning without financial loss to ranchers (Turnell 1985; U.S. Fish and Wildlife Service 1988). Indeed, 0.1% is very modest considering that prairie dogs historically covered about 20% of the natural short-grass and midgrass prairies (Summers and Linder 1978). But poisoning policy has developed a great deal of momentum, and the philosophy has been ingrained by a century of misinformation. Livestock producers cling to traditional beliefs, and agency decision makers remain unconvinced by ecological evidence—or unwilling to face the wrath of the agricultural community. Significant policy changes are therefore unlikely to occur without greater receptivity to scientific information on the part of decision makers and a change in the attitude of the ranching community. As long as the federal government continues to subsidize poisoning, there is little incentive for either change to occur.

AN INTEGRATED SOLUTION

Legal Intervention via the Endangered Species Act

Protecting individual species has been an important step in slowing the decline of many species toward extinction (Bean 1992). During the early years of environmental action, a number of species were already in desperate straits, and action was necessary to prevent further loss. However, conservation is much more complex than biologically analyzing the status of each species separately and then applying legal protection to those that have reached a state of crisis. Acting only when crisis is full-blown narrows opportunities for success, increases financial costs, and escalates conflict between conservation and local interests (Wemmer and Derrickson 1987). Handling species individually is also slow and laborious. In the United States about 650 species are listed as threatened and endangered, and another 600 candidate species await possible inclusion (U.S. General Accounting Office 1992). Yet the U.S. Fish and Wildlife Service has added an average of only 44 species a year to the endangered-species list, so it could take years to address these candidates (U.S. General Accounting Office 1992).[1] Between

3,000 and 5,000 other species in the United States may be threatened with extinction, based on available data, but are not yet included as candidates (U.S. General Accounting Office 1992). In the 1980s, 34 species went extinct while awaiting federal listing (Cohn 1993). Only 16 species placed on the endangered-species list have been officially removed (delisted): 4 because the original data were in error, 5 that recovered, and 7 that went extinct (U.S. General Accounting Office 1992).

As a result of such statistics, legal experts and biologists have begun advocating a shift of focus from managing individual species toward managing entire ecosystems (E. M. Smith 1984; J. M. Scott, Csuti, et al. 1987; Rohlf 1991). Ecosystem management would address plants and animals in groups, and could potentially speed the process of protection considerably. But agreement is lacking about what ecosystem management entails. The concept is widely cited as a panacea, and the U.S. Department of Interior has invoked a need to manage systems instead of species. But what is to be managed, how, and by whom are seldom defined. The concept is therefore palatable to all political persuasions. It can be cited to generate research support for conservation biologists, but also to gut the protection provided by the Endangered Species Act before an alternative exists to replace it. And there is another reason to move carefully toward ecosystem management: given our poor record with single species, why should we assume that working at a more complex level will be easier or more successful?

But the prairie dog, as a keystone species, provides an excellent opportunity to forge a gradual transition from traditional single-species management to management of a system. It is preferable, of course, to manage species proactively, before legal intervention is necessary, but prairie dogs have already declined too severely to avoid some kind of legal recognition, particularly with poisoning programs still active. The Endangered Species Act can play an enormous role in the preservation of biodiversity by offering protection to a keystone species and therefore to all species dependent on it (Rohlf 1991).

Protecting a threatened keystone species would have fiscal and educational benefits as well. Protection of keystone species gives managers an avenue to educate the public about the value of ecosystem conservation and the links between animals and their habitat. The transition from species to system would be straightforward because the keystone species helps maintain the system. Fiscally, the federal government would be spared the burden of maintaining an expensive support system for other species that would become imperiled as the keystone species continued to decline. No matter how polemical the situation, protecting a keystone species is far more cost-effective than trying to protect each individual species dependent upon it. This is particularly true for the prairie dog. Each year, the federal government and several state governments subsidize both

prairie dog poisoning and preservation of species that depend on the prairie dog. In 1991 the federal government spent more than $1.5 million on recovery of the black-footed ferret (U.S. Fish and Wildlife Service 1992); the same year, it probably spent several million dollars poisoning prairie dogs. As a direct result of poisoning expenditures, ferret-recovery expenses will continue to rise and more species will need to be placed on the federal dole. By the time this book reaches print, for example, it is likely that the mountain plover—a bird that selectively nests on prairie dog colonies throughout much of its range—will have been added to the threatened- or endangered-species list.

In 1994 Region 6 rejected an internal proposal to list the black-tailed prairie dog as a candidate species. Candidate status would have focused attention and money on the problem, and because of the prairie dog's reproductive potential, it could have reversed the downward trend without the restrictions of full endangered status. Assigning candidate status to the prairie dog would have been an excellent step toward the systems management that the Department of Interior says it favors. It appears, however, that Region 6 has chosen instead to list individual species that depend on prairie dogs and not to list the root cause of lost diversity.

Habitat Protection and Conservation Issues

Conservation of most species depends on more than legal protection. Many species are protected by law, but enforcement in the field can be difficult, and legal maneuvers can both circumvent the intentions of endangered-species legislation and create unproductive conflict.

Initiating sustainably usable protected areas on the grasslands of Canada, the United States, and Mexico (see Chapter 10) would allow for integration of conservation and economic potential, and a system of incentives or rebates could assure ecologically sound use. Federally owned lands in the United States offer excellent opportunities to use this strategy, although in many cases federal lessees wield tremendous power over government agencies and use the lands at a level above their ecologically sound carrying capacity.

Overgrazing—forage consumption that exceeds the regenerative capacity of natural vegetation—is a serious and continuing threat to the health of many federal lands (Vale 1975; U.S. General Accounting Office 1988a). According to F. R. Henderson (1980), "Over-abundance of prairie dogs, in many cases, is a sign of poor range management. We perpetuate poor rangeland management by advocating killing prairie dogs only." Total production is higher on pastures supporting only prairie dogs (and even on those supporting both prairie dogs and cattle) than on pastures supporting only cattle; thus cattle reduce total production more than prairie dogs do (Uresk and Bjugstad 1983). Furthermore, the presence of prairie dogs may just amplify problems caused by excessive livestock densities; poisoning prairie dogs when livestock are the major offenders will only increase the economic and ecological burden on the land. Yet grazing-reform proposals are routinely defeated by powerful western Congressmen representing the livestock industry (or timber and mining). This is despite the fact that the West is heterogenous and there are many other groups with a direct stake in the wise stewardship of federal lands.

Local socioeconomic issues and conservation of natural resources cannot be separated. Large corporations may have the capacity to exploit an area for a quick profit and then move to another region after its resource wealth has been drained. The average working family, however, is considerably more limited in its options. When the trees have all been cut, the ground is barren, or the environment is otherwise degraded, the local human population eventually suffers. Local residents are left with fewer economic opportunities and the environmental costs that exploiters have left behind. A watershed fouled by deforestation, food productivity lost because of eroded soil fertility, desertification, pollution, and decline of clean water supplies are examples of economic costs to society directly related to a degraded environment (Lovejoy 1986). In short, areas that fail to maintain environmental quality are also least successful at providing a decent standard of living (Mishra et al. 1987; Durning 1989; Homer-Dixon et al. 1993).

The majority of the human population depends on basic resources for immediate survival, and if those resources are not managed well, people's fundamental needs cannot be met (Frazier 1990). Environmental protection does not necessarily mean conflict, and human land uses can be part of ecosystem management if development uses the potential as it exists rather than imposing exotic agricultural uses (Cloudsley-Thompson 1988). With an integrated plan, the economic needs of the local population and preservation of biodiversity can be balanced.

Western (1989) asserts that wildlife has a better chance of survival when linked with humanity than when isolated from it, and various biomes of our planet provide value to both humans and wildlife. For example, La Tigre National Park in the cloud forest of Honduras produces high-quality water throughout the year, accounting for 40% of the water supply in the capital city of Tegucigalpa (McNeely 1988). McNeely's *Economics and Biological Diversity* (1988) presents a compelling argument that the fundamental constraint on conservation is the ability to exploit short-term profits without paying the full social and economic costs. These costs are usually undervalued or ignored in the present, then transferred to society as a whole when payment comes due. Accurate assessment of future costs, combined with present-day economic incentives to use resources wisely, is necessary to change attitudes and move from overexploitation to sustainable use.

We offer a philosophical caveat about the term *sustainable development*. Like

ecosystem management, this term is frequently undefined, and as a result is used by many people in many different ways (often in self-interest). Genuine sustainable development is not a mechanism to further concentrate or maintain wealth and power in the hands of a few. Poverty and environmental problems feed on each other in a vortex of despair, and overconsumption in one region combined with poverty in another will prevent us from living within the carrying capacity of the planet. The ramifications of unequal distribution of wealth, exploding birth rates, and limited resources could be catastrophic, and they should not be glossed over by a buzzword.

In conclusion, because people are part of the ecosystem, separating ecological concerns from socioeconomic ones simply does not work very well. Many people depend heavily on local natural resources for sustenance, and setting aside a large chunk of land for the exclusive use of vacationers (or scientific researchers) can create bitter feelings. In many cases, positive economic incentives can balance the slate.

An Economic Incentive to Conserve Prairie Dogs

Establishing protected areas, reserves, and conservation areas will do a great deal to benefit the prairie dog ecosystem. But constraints on the size of protected areas, combined with habitat fragmentation, will limit the safety net for large or specialized species. The federal government needs to find a way to restore biological integrity on private lands as well, without adversely affecting the dominant consumptive uses of the range.

The Endangered Species Act addresses the need for incentives:

> Encouraging the states and other interested parties, through Federal financial assistance and a system of incentives, to develop and maintain conservation programs which meet national and international standards is a key to meeting the Nation's international commitments and to better safeguarding, for the benefit of all citizens, the Nation's heritage in fish, wildlife, and plants. (Endangered Species Act, Section 2[a][5])

Instead of spending money to poison prairie dogs, the federal government could offer financial compensation to ranchers whose land-management practices are compatible with the prairie dog ecosystem (Miller, Wemmer, et al. 1990). Tax breaks, product-marketing help, and free publicity might also be appropriate incentives for ranchers who manage their lands both for livestock and for black-footed ferrets and prairie dogs (e.g., "This beef produced on a privately owned and managed black-footed ferret reserve"). Because attitudes are entrenched in the western agricultural community on the issue of prairie dog management, it may take such positive incentives for any public-education program to work. In

Montana, Reading (1993) showed that increased knowledge alone did not change negative perceptions of black-footed ferrets and prairie dogs (see Chapter 12). Similar results were obtained from other wildlife studies (Arthur et al. 1977; Kellert 1990).

Because of these entrenched attitudes, it will not be possible for education programs to address misconceptions about the prairie dog ecosystem while federal and state agencies continue to subsidize prairie dog poisoning. Words may say one thing, but actions quickly override them. To continue the poisoning subsidy will reinforce misconceptions and undermine all other efforts to conserve biological diversity on the western grasslands.

A positive incentive can be accomplished by reallocating money and personnel now used for prairie dog poisoning to monitoring activities for prairie dog conservation (establishing the policy of paying the incentive, allocating the money, etc.). Because such an incentive is outside the traditional prairie dog management paradigm, it would require a comprehensive education program (see Dietz and Nagagata 1986) and an economic model demonstrating the financial feasibility of environmentally sound livestock practices. For long-term effectiveness, this plan would probably require legislative action as well.

Public land should simply not be poisoned. The environmental and fiscal costs of prairie dog poisoning are too great, and the percentage of U.S. beef weight produced on western public land is too small. On leased public land, ranchers are charged a federal grazing fee based on the amount of forage they use. Forage is measured in *animal unit months* (AUMs), and one AUM sustains a cow-calf unit, a horse, or five sheep for one month (U.S. General Accounting Office 1988a). Lessees using public land could receive compensation for the policy change in the form of grazing-fee credits (free AUMs). There is also a move afoot to increase grazing fees on public lands. But simply raising grazing fees without addressing the factors that are degrading the prairie benefits no one. A portion of that increase could be rebated to ranchers who graze their cattle on land that includes prairie dogs.

Conservation incentives, whether on private or public land, will work only when stocking rates are within the carrying capacity of the land. A balance between grazing impact and forage capacity is an elusive but essential goal, and even today livestock overgrazing persists on public lands (Vale 1975; U.S. General Accounting Office 1988a). Carrying capacity depends on the quality of forage as well as its quantity, so livestock numbers are related to that tradeoff. In proper balance, cattle and prairie dogs can coexist (Krueger 1988).

One part of a Region 6 strategy to make ferret reintroduction more palatable to ranchers is "prairie dog block clearance," whereby ferret reintroduction sites are not poisoned but poisoning is made easier elsewhere (U.S. Fish and Wildlife Service 1990). Region 6 is considering changing the term "block clearance" to the more innocuous "ferret-free areas." Whatever the strategy is called, it still means poisoning, and it has five serious problems. First, block clearance does not address antiquated but prevailing misconceptions about the prairie dog ecosystem. By sanctioning the use of poison, Region 6 is reinforcing the view that prairie dogs have little value in the prairie ecosystem.

Second, even if block clearance is only part of an overall Region 6 strategy, it will probably remain the central tool simply because poisoning is familiar. It always seems easier to walk a known path, but the urgency of the prairie dog situation indicates that we should be examining other ideas. We cannot find adequate solutions by confining our thought within the paradigm that caused the problem.

Third, block clearance potentially rewards regions that have pursued vigilant poisoning campaigns. If formerly excellent prairie dog habitat was poisoned, leaving just a few small colonies, that area could be a candidate for block clearance to obliterate the remaining fragments of the prairie dog community.

Fourth, poisoning is not cost-effective. The federal budget is already overburdened and growing, and scientific evidence does not support the idea that prairie dogs are range pests.

Fifth, block clearance is a political maneuver subject to the pressures of local political whims. To quote Lynn Greenwalt (1988), former director of the U.S. Fish and Wildlife Service:

> In spite of its strength, the [Endangered Species] Act is vulnerable; its armor is not seamless. The Act is vulnerable to political intervention and to decisions based on political expediency rather than what is best for the species. It is not easy to resist the pressure to make special arrangements which provide for the advance of projects or programs or political proposals.

An example is a memo from the South Dakota Department of Agriculture (R. Scheide, 17 December 1992) about the risk of poisoning an area inhabited by ferrets in the course of block clearance:

> In reference to your letter, I must reiterate that it is our position that surveys are not required for use of zinc phosphide as the label states "Do not apply in areas known to be inhabited by black-footed ferrets." There are presently no such areas in South Dakota. If you have any questions, please contact me.

Simple as that—no muss, no fuss.

During negotiations with local ranchers about prairie dog block clearance, there will be heavy pressure from livestock interests to limit colony size at the black-footed ferret reintroduction site. It is easy to envision a scenario in which well-intentioned biologists must settle for less than they believe adequate because of such political pressure. Ferguson and Ferguson (1983), Montgomery (1990), and Boyle (1993) have discussed the unfortunate fate of several federal biologists who raised environmental concerns in the face of exploitative forces.

During negotiations about prairie dogs and ferrets, one of the first questions posed is always "What is the minimum necessary?" If a minimum area or population size is offered, it tends to become the absolute best that can then be achieved. Minimum population sizes are purely speculative even with the best of intentions, and their management would be unlikely to provide for long-term stability in the carrying capacity of the environment. The resulting minimum area would be eligible for black-footed ferret reintroduction, but it would probably be a small population vulnerable to random events and lacking opportunity to expand. In this situation, maintenance of a wild population would require intensive management. R. B. Harris et al. (1989) have estimated that population sizes below 120 will periodically go extinct within 100 years (the smaller the population, the more likely it will be lost). Thus the ferret colony would probably require periodic restocking from captive or other wild populations. Some ferrets would be out of captivity, but the federal government would be bankrolling a long-term and expensive project. And, while the federal government continues to pay for prairie dog poisoning, the U.S. Fish and Wildlife Service will eventually need to add other species to the list of endangered and threatened organisms.

Black-footed ferret recovery must be based on conservation of the ecosystem on which it depends. The black-footed ferret has the charisma necessary to be a flagship species, shedding light on the decline of the prairie dog ecosystem. But if we fail to recognize the endangered black-footed ferret as a symptom of an imperiled ecosystem, the drain on species diversity and the federal budget will only increase. Continuing to destroy the prairie dog ecosystem, and the diversity that it supports, while reintroducing black-footed ferrets into a few isolated sites is nothing more than an expensive and cosmetic attempt to cover our inability to preserve prairie biodiversity. Yet this is what is happening. The integrated management program that we have discussed in this chapter is an alternative to the conflicting directives of poisoning policy and endangered-species management (Miller, Wemmer, et al. 1990; Miller, Ceballos, and Reading 1994). An ecologically and fiscally sensible program that educates the public, restores the integrity of the western grasslands, and rewards environmentally sensitive members of the livestock industry would be far more responsible than continued mass poisoning.

12
PUBLIC ATTITUDES ABOUT BLACK-FOOTED FERRETS AND PRAIRIE DOGS

> They're not concerned about the small picture; they're concerned with the overall picture.
>
> Wyoming Farm Bureau executive, denouncing conservationists' efforts on behalf of grizzly bears, September 1993

On a sunny day in north-central Montana, a muddy and well-used pickup truck tops a small butte. The two biologists inside scan the expanse of short-grass prairie, which extends to the horizon. Almost without noticing what they are doing, they abruptly stop talking and switch off the truck's radio. Something is amiss. Although prairie dog mounds dot the landscape, the only visible animals are a few sheep, the only sound an occasional bleat muffled by a stiff, dry wind.

Domestic oats growing from the mouths of the burrows betray the reason for the prairie's emptiness. The prairie dog colony was poisoned, thoroughly and illegally. Not a single prairie dog remains alive. The colony is on public land administered by the U.S. Bureau of Land Management, and it is part of a large complex slated for a future black-footed ferret reintroduction. But many ranchers do not like prairie dogs, and they do not like black-footed ferrets because they believe the Endangered Species Act gives animals and plants priority over people.

Favorable public attitudes are obviously crucial to successful conservation efforts. By assessing public views and knowledge of wildlife, conservationists can design effective education programs and public-relations campaigns. But it is not just the attitudes of the general public that matter; so do the attitudes of recovery-program participants. Because the decisions and actions of key players are influ-

Head to Head

Overestimation bias in estimate of black-tailed prairie dog abundance in Colorado

By Sterling D. Miller, Richard P. Reading, Bill Haskins, and David Stern

Abstract White et al. (2005) estimated the area occupied by "active" colonies of black-tailed prairie dog (*Cynomys ludovicianus*) in Colorado as 255,398 ha (95% CI of±9.5%) based on data collected with aerial transect surveys during 2001–2002 by staff of the Colorado Division of Wildlife (CDOW). During 2004 we conducted on-the-ground examinations of a sample of the colony intercept data used by White et al. (2005) and found evidence of misclassifications that would yield significant overestimation bias. We found that 25.4% of the total length of the colony intercepts we examined was incorrectly classified as being a prairie dog colony (these segments had no prairie dog burrows of any age). We also found that 50.3% of the length of examined intercepts fell on currently inactive colonies or portions of colonies (vacant burrows but no living prairie dogs) and only 24.3% fell on active prairie dog colonies with signs of living prairie dogs at our examinations 2 years after the survey reported by White et al. (2005). Further, in Bent and Kiowa counties, where plague (*Yertsina pestus*) and poisoning were active, we examined 36.9 km of reported active prairie dog intercepts and subjectively classified only 1.6% as active at normal-appearing prairie dog densities. Our fieldwork demonstrated that the estimate by White et al. (2005) was based on data with substantial errors as well as overestimation biases that will be repeated if protocols are not modified for future surveys.

Key words aerial surveys, bias, black-tailed prairie dogs, Colorado, *Cynomys ludovicianus*, population estimation

In 2001–2002 the Colorado Division of Wildlife (CDOW) conducted aerial surveys to estimate the area of active black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Colorado (Colorado Division of Wildlife [CDOW] 2003, White et al. 2005). Following techniques originally described by Sidle et al. (2001), CDOW recorded intercepts of burrow aggregations (hereafter colonies) along parallel transects in Colorado (CDOW 2003, White et al. 2005). This data collection technique estimates area occupied by prairie dogs across large areas (Miller and Cully 2001, Sidle et al. 2001). Accuracy of data collected, however, depends on the protocol used, observer rigor in following the protocol, and observer ability to correctly identify and classify prairie dog colonies. In areas where sylvatic plague (*Yertsina pestus*) or poisoning of prairie dogs occurs, areas with unoccupied prairie dog burrows usually persist for many years on all or a portion of a formerly larger active area. Plague or poisoning also may greatly reduce density of prairie dogs. Both plague and poisoning are common in Colorado (Cully and Williams 2001).

The survey protocol used in Colorado called for classifying entire colonies as active even if prairie dogs no longer lived on portions of the colony (White et al. 2005). This protocol may overestimate the area occupied by living prairie dogs. Errors also may occur if observers incorrectly classify areas as prairie dog colonies from the air or incorrectly classify portions of colonies as being active based on diggings by other species. Ground inspections to assess the extent of such errors can help identify these sources of bias.

We conducted ground inspections in southeastern Colorado during 2004, 2 years after the data used by White et al. (2005) was collected in our study areas to determine whether such problems existed in the data used to estimate prairie dog abundance in Colorado (CDOW 2003, White 2005). Our studies represent a preliminary step toward estimating the magnitude of the problems in the estimate by White et al. (2005). We are aware of no other ground survey work conducted to document such problems in aerial transect surveys for prairie dogs.

Methods and study area

White et al. (2005) describe the procedures followed in the CDOW aerial survey flights. Biologists flew low-elevation parallel transects in fixed-wing aircraft and recorded coordinates where transects entered and exited active prairie dog colonies. The CDOW used a Global Positioning System (GPS) separate from the GPS used for aircraft navigation to record colony intercepts. Colonies were classified as active if a single prairie dog or active prairie dog digging was observed. The protocol required that biologists observe burrows on both sides of the aircraft for an intercept to be recorded. White et al. (2005) estimated area occupied by prairie dogs in Colorado based on the proportion of transect lines that intercepted colonies classified as active.

We conducted ground examinations of a sample of the White et al. (2005) reported intercepts. The CDOW provided the database with entry and exit coordinates for all intercepts used by White et al. (2005). In an effort to work cooperatively to refine the methodology, we invited CDOW and G. White to participate in all of our field surveys. We walked the entire length of 18 of the 1,596 intercepts of active prairie dog colonies reported in the CDOW aerial survey database during June 27–July 2, 2004. These 18 intercepts totaled 41.1 km or 3.9% of the 1,059.8 km total used by White et al. (2005) to derive their estimate. We defined intercepts >395 m as "long," and our sample included 4.7% of the total length of 947 "long" intercepts reported by CDOW. Our sample included 16 intercepts in northern Bent County and 1 in adjacent Kiowa County in southeastern Colorado. We concentrated on this area because CDOW identified it as having a "high density" of colonies based on the CDOW aerial survey database (CDOW 2003). In Bent County our sample included 20.5% of the 157.2 km of long intercepts reported to occur. Our sample also included 1 long intercept in Boulder County in west-central Colorado. We selected intercepts to examine because 1) they were long (defined as >395 m); 2) we had access permission from landowners (on private land) or grazing leaseholders (on state-owned land); and 3), they were concentrated in the same geographic area (to minimize commuting time and reduce the number of landowners we had to contact). We focused our efforts on long intercepts because White et al. (2005) concluded that the statewide estimate was robust to data errors for small intercepts.

We used Garmin *e*trex® (Garmin International Inc., Olathe, Kans.) GPS units to locate and navigate along intercepts. To avoid coordinate entry errors, we directly uploaded coordinates from the CDOW database to our GPS units. Three people navigated the entire length of each intercept and, to be conservative, we explored both sides of the intercept to about 40 m. We classified a segment as active if, within this band of approximately 80 meters, any observer found evidence of current prairie dog activity (animals, recent diggings, or fresh scat). When we found colonies that had expanded beyond the endpoints of reported intercepts, we included this additional length. We classified segments of intercepts into 3 categories based on activity type:

Active prairie dogs, based on observations of living prairie dogs, some active digging by prairie dogs, or fresh scat (similar to the CDOW protocol but more inclusive because we also used the presence of fresh scat to identify activity);

Inactive prairie dog burrows (typically with plugged openings, heavy webbing by spiders across entrances, and no other signs of current activity, such as fresh digging or scats);

No evidence of prairie dog burrows of any age.

Probably as a consequence of plague or poisoning, many colonies with some prairie dog activity had a large proportion of inactive burrows. We made distinctions between active and inactive portions of colonies; the CDOW protocol, in contrast, classified as completely active all colonies wherein any level of prairie dog activity was observed (White et al. 2005). We also report subjective distinctions between areas that appeared to be active at normal densities and those that appeared to support very low densities of prairie dogs.

We incorporated and analyzed all data into a Geographic Information System (GIS) using Arc/INFO 7.2 and ArcView 3.2 (Environmental Systems Research Institute, Redlands, Calif.). We employed the same horizontal datum that CDOW used to record intercept coordinates: WGS 84 (F. Pusateri, CDOW, personal communication). This datum also was recorded on the CDOW intercept database for each county. When plotted, both reported intercepts and waypoints we recorded while walking the intercepts fell on the same line. The CDOW protocol specified that the first transect in each county occurred on its north border. Since our plotted intercepts also fell on the north border of counties plotted using the WGS 84 datum, we were confident both we and CDOW used the same datum.

In Bent, Kiowa, and Boulder counties, the CDOW surveys occurred during 2002 (White et al. 2005). The CDOW surveys occurred 2 years prior to our 2004 ground survey work in these same counties.

Results

We found no evidence of current prairie dog activity on 75.7% of the total length of intercepts we examined (Table 1). We classified 24.3% of the length of intercepts we examined as having some level of prairie dog activity (Table 1).

Intercept segments that showed no evidence of

Table 1. Results of ground examinations conducted during 2004 of intercepts of "active" prairie dog colonies reported by Colorado Division of Wildlife based on aerial surveys conducted during 2002 and used to estimate area occupied by active prairie dog colonies by White et al. (2005).

			Ground truthing results Total length of segments by activity type (m)			
CDOW intercept identifier (County)	CDOW reported intercept length (m)	Size rank[a]	Active[b]	Currently only inactive burrows	Without any burrows (old or new)	Total length of intercept examined
B005 (Bent) [d]	5,788	1	1,722	4,137	0	5,859
B077 (Bent)	5,485	2	0	0	5,490	5,490
KC 95 (Kiowa)	4,587	4	229	3,734	809	4,772
B060 (Boulder)	4,238	6	3,639	268	329	4,236
B029 (Bent)	2,523	30	1,068	843	660	2,571
B026 (Bent)	2,347	40	815	1,534	0	2,349
B028 (Bent)	2,313	42	169	1,624	528	2,321
B040 (Bent)	2,216	46	466	965	803	2,234
B043 (Bent)	2,197	47	0	1,700	499	2,199
B020 (Bent)	2,093	53	0	1,818	274	2,092
B017 (Bent)	1,831	92	582	854	241	1,677
B038 (Bent)	1,387	140	0	1,373	49	1,422
B022 (Bent)	1,348	146	899	399	142	1,440
B016 (Bent)	664	542	0	532	152	684
B042 (Bent)	599	624	0	389	213	602
B017 (Bent)	518	729	194	128	183	505
B037 (Bent)	514	736	387	285	185	857
B023 (Bent)	504	749	0	458	55	513
Totals	41,152		10,170	21,041	10,612	41,823
Percent			24.3	50.3	25.4	100

[a] Rank of intercept relative to all intercepts reported by CDOW in Colorado.

[b] Active using CDOW definition; most of this length had very low densities of prairie dogs (see text).

[c] Period these were inactive could not be objectively determined; many appeared to have become inactive subsequent to the CDOW surveys 2–3 years earlier.

[d] Intercept B005 had almost no burrows north of the intercept line (on the Kiowa County side) but frequent, mostly inactive, burrows south of the line. The south value is included in the tabulation but 4,927 m of B005 (and 1,010 m on other transects) were classified in the field as protocol violations because burrows did not occur on both sides of the transect.

[e] Apparent westward expansion in this colony since earlier CDOW survey. Prairie dogs recently dead from sylvatic plague found on this colony.

Figure 1. Portion of a 2-km-long segment of intercept KC 95 that was recorded by Colorado Division of Wildlife as intercepting 4.6 km of active prairie dog colony (Kiowa County, southeastern Colorado). This segment had no evidence of prairie dog burrows, and the landowner informed us that because of a high water table, prairie dogs never occurred in this segment. There were active prairie dog colonies of both ends of this reported intercept. Photo by S. D. Miller.

prairie dog burrows (neither active, inactive, old or new) constituted 25.4% (10.6 km) of the length of examined intercepts (Table 1). The second-longest intercept reported in the CDOW database (B077, 5.5 km long) contained no evidence of prairie dog burrows on or within sight of its entire length (Figure 1). This single intercept constituted 51.7% of the total length of intercept segments with no evidence of burrows in our sample (Table 1).

We found inactive burrows on 50.3% of the length of examined intercepts (Table 1). We could not determine when these burrows became inactive. Conversations with landowners about recent poisoning activity, direct observations of poisoning during spring 2004, the appearance of the burrows, and evidence of sylvatic plague indicated that some currently inactive segments probably were active, at some level, 2–3 years earlier when CDOW conducted their surveys. Eleven of the 18 intercepts we examined included both active and inactive segments (Table 1). Of the 28,223 m that CDOW reported for these 11 intercepts, we found that 14,771 m (52.3%) intercepted inactive burrows in 2004 (Table 1).

We subjectively classified many segments of intercepts as active only at very low densities (58.5% of the length of segments with some activity). Only portions of the intercept in Boulder County and one short segment (579 m of intercept B022) of 17 intercepts we examined in Kiowa and Bent counties apparently fell on healthy-appearing prairie dog colonies. The rest would have been classified as human-modified following the protocol used in Wyoming (<50% active burrows; M. Grenier, Wyoming Game and Fish Department, personal. communication). Overall, we classified 10.2% (41,152 m) of our sample of intercepts as active at normal densities. In Kiowa and Bent counties, we classified 1.6% of the length of examined intercepts as having normal densities of prairie dogs.

Discussion

Accurate estimates of abundance require unbiased data. Our on-the-ground examination of aerial survey intercepts used by White et al. (2005) to estimate prairie dog abundance in Colorado found errors that would overestimate prairie dog abundance. The most clear-cut evidence of misclassification error resulted when intercepts or intercept segments were classified as active, but we found no evidence of burrows, active or inactive, on or near (>40 m) the reported intercept (25.4% of the total length of the 18 intercepts we examined).

Incorrect inclusion of segments most frequently resulted when the intercept included some segments with no burrows and other segments with burrows. An example occurred on intercept KC 95. This intercept incorrectly included 809 m (17% of the reported intercept length) in an area with a high water table and no prairie dog burrows (Figure 2). The landowner confirmed that prairie dogs never inhabited this area because of the high water table. Prairie dog colonies did occur on higher ground both east and west of the segment in the wet area; we observed no burrows north or south of the wet area segment.

On the second-longest intercept reported in the CDOW database (B077 at 5.5 km), we found no evi-

Figure 2. Reported prairie dog colony intercept B077 in Bent County, southeastern Colorado. On this dry rangeland site, we found no evidence of prairie dog burrows anywhere along or near this reported 5.5-km intercept of an active prairie dog colony. B077 was the second longest reported intercept in the data used by White et al. (2004) to estimate abundance of black-tailed prairie dogs in eastern Colorado. Photo by S.D. Miller.

dence of current or former prairie dog activity anywhere along or within sight of the entire intercept (Table 1). This intercept occurred on dry rolling rangeland with no evidence of cultivation or other activities that could obscure current or former prairie dog burrows (Figure 1). On other nearby transects in similar habitat that were poisoned and "bladed" (mechanically treated to discourage recolonizaton) 2–3 years previously, the former burrows remained obvious. In an area with more annual rainfall (39.7 cm) in comparison to our area (31.2 cm), it took several years for revegetation of poisoned prairie dog burrows to be observed (Uresk and Schenbeck 1987). We are confident that there were no prairie dogs burrows on this very long intercept 2 years earlier when the CDOW surveys were conducted and that this intercept was erroneously recorded.

In contrast to the areas with no burrows, the intercept segments we examined that had inactive burrows (50.3% of the length of examined intercepts) or very low densities of prairie dogs (58.5% of the length of segments with some level of activity) may or may not represent errors in the CDOW data. These intercept segments may have become fully or largely inactive in the 2 years since CDOW collected the aerial transect data. However, if the activity status we found in 2004 also existed during 2002 or during future surveys, these inactive areas would be misleadingly classified as active. This demonstrated problems with the protocols used by CDOW. The CDOW classified a whole colony as active if any portion of it included living prairie dogs. We suspected, and our data support, that in areas where plague and poisoning are common, only portions of colonies include burrows occupied by living prairie dogs while other portions encompass only vacant burrows. On the intercepts we examined in 2004, the CDOW protocol would have misleadingly classified as "active" 57.5% of the length of 9 intercepts (25% of the total length we examined) because other portions of the colony were active (Table 1).

The CDOW also classified areas as active if they observed any evidence of prairie dogs, regardless of how sparse the evidence was. We found that many areas that included some level of activity supported only very low densities of living prairie dogs, probably as a consequence of plague or poisoning. We observed evidence of both plague and poisoning during our fieldwork, and landowners told us of ongoing poisoning efforts. Improving the definition of "active" may be especially important on the long intercepts that White et al. (2005) concluded were most important to the accuracy of their estimate because small colonies may be more likely to be either completely eliminated or unaffected by plague or poisoning. We suggest that aerial surveys using line intercept techniques to estimate prairie dog abundance in areas where plague or poisoning occurs should differentiate between active and inactive segments within a colony.

Further, we recommend a more ecologically meaningful definition of what constitutes an active colony. A colony sparsely inhabited by prairie dogs likely does not fulfill its ecological function (Kotliar 2000, Miller and Reading 2005). We do not believe meaningful estimates of prairie dog abundance are possible if intercepts many kilometers long include large areas with only inactive burrows. The Wyoming Game and Fish Department currently classifies colonies as "healthy" only if ≥50% of the colony shows signs of living prairie dogs and as "human-modified" if <50% shows such signs (M. Grenier, Wyoming Game and Fish Department, personal communication). All colonies in our study and most colonies in Wyoming clearly were either much more or much less than this 50% threshold, so this classification was not difficult to make (M. Grenier, Wyoming Game and Fish Department, unpublished data). We recommend such an approach for future surveys using aerial transect techniques for prairie dogs.

Because we did not examine a random sample of the CDOW-reported intercepts, we can not derive a corrected estimate for prairie dog abundance in Colorado. Based on qualitative surveys of additional intercepts in the CDOW database we conducted elsewhere in Colorado, however, we suspect the problems we report here were widespread. At places where reported intercepts crossed roads, we examined portions of an additional 7 long intercepts reported in Bent, Otero, and Crowley Counties. We found approximately 5% of the portions of these intercepts we could observe currently were active during spring 2004. We made these observations from roads because we lacked permission from landowners to walk along the reported intercepts.

In addition to classification errors (Table 1), we found instances where CDOW included portions of intercepts that violated CDOW protocol requiring the presence of burrows on both sides of the transect line (White et al. 2005). The most clear-cut example occurred on intercept B005 (at 5.8 km, the longest intercept in the CDOW database). This intercept ran along a conspicuous fence on Bent County's north border, rendering it impossible to for observers in aircraft to mistake the correct location of the transect line. We found no prairie dog burrows (active or inactive) along 84% of the north side of this intercept.

The CDOW criticized our work because we only examined intercepts reported in the CDOW database used by White et al. (2005) and did not survey areas where new colonies might have formed during the 2–3 year period between the CDOW surveys and our studies (T. Remington, CDOW, personal communication). Since we examined only long intercepts and make no effort to provide a corrected statewide estimate, we believe this criticism has no merit. New, large colonies cannot appear quickly on the landscape because prairie dogs reproduce relatively slowly (Hoogland 2001) and White et al. (2005) acknowledged that most of the power of their estimate derives from the long intercepts. Where we found prairie dogs had expanded beyond the endpoints of reported intercepts, we included this additional intercept length (Table 1). During a 2-year period, we believe expansion of existing large colonies is more likely than establishment of new large colonies.

White et al. (2005) suggested that the similarity between their estimate of prairie dog occupancy in Colorado (1.9%) and that reported for Wyoming supports the accuracy of their analysis. We find no basis for assuming that different states should contain similar proportions of habitat occupied by prairie dogs. Estimates of percent occupancy in both Colorado and Wyoming, for example, were dissimilar to Montana (<0.2%, Luce 2003). In South Dakota, a state without plague, prairie dogs occupy 0.7% of available habitat on nontribal lands (South Dakota Department of Game, Fish and Parks, unpublished prairie dog management plan).

White et al. (2005) claimed to find a visual pattern that supported their claim that the large colonies they reported were largely active: "Almost all of the large intersections (the 1 exception being a 4.2 km intersection in Boulder County) occurred in parallel lines." However, we did not find this pattern in an objective analysis of the adjacent intercepts (adjacent defined as intercepts within 4 km). We found no intercepts of comparable length to the north or south of the longest CDOW intercepts ($n=9$ intercepts >4.0 km with a cumulative length =42.2 km). The mean length of adjacent intercepts ($n=18$) was 1.4 km (total length=25.6 km). No adjacent intercept was longer than 3.4 km. Our subjective examination of plotted long intercepts also failed to confirm the pattern claimed by White et al. (2005). The longest intercept in the CDOW database (B005 in Bent County, Table 1), for example, was conspicuous by its isolation from other long intercepts.

White et al. (2005) also asserted that observer fatigue would result in missed colonies or activity, leading to an underestimation bias. We agree that fatigue might cause observers to miss small colonies, but White et al. (2005) acknowledged that their estimate was robust to errors in the number and size of small colonies. We doubt that even tired CDOW biologists and pilots would miss large colonies. Observer fatigue, however, may explain some of errors we found where areas with no burrows were mistakenly reported as active intercepts.

We appreciate that CDOW provided us with their database so we could conduct our studies. Our work could have been completed within a year of the original surveys if these data were provided when first requested. We continue to hope that CDOW will work cooperatively to assess the accuracy of future surveys. In response to correspondence documenting our findings and concerns, CDOW said, "…none of these potential problems, even if they occurred, [would] alter the final estimate significantly" (T. Remington, CDOW, personal communication). This response indicates that CDOW rejected our concerns and findings even though they reported no effort to evaluate the accuracy of their data. Since our data indicate data collection problems occurred that would alter the final estimate significantly, we believe it was necessary to report our findings.

We believe credible estimates of prairie dog abundance in Colorado cannot be made using the aerial survey technique reported by White et al. (2005) until the issues we identified are addressed. During future surveys some of the problems and errors we found could be avoided or quantified by conducting replicate surveys in selected counties or using ground examinations of reported intercepts. The misclassification errors and protocol violations we found likely would have been detected if CDOW had conducted independent, replicate surveys using different observers. Knowledge that such re-surveys would be conducted also might encourage observers to be more rigorous in applying established protocols. Problems associated with not differentiating between inactive and portions of colonies and with classifying low-density activity as equivalent to normal activity, however, will not be resolved until survey protocols are modified.

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Ref

The Keystone-Species Concept in Ecology and Conservation

Management and policy must explicitly consider the complexity of interactions in natural systems

L. Scott Mills, Michael E. Soulé, and Daniel F. Doak

Will the extinction of a single species in a community cause the loss of many others? Can we identify a set of species that are so important in determining the ecological functioning of a community that they warrant special conservation efforts? The answer to these questions hinges on the existence of a limited number of species whose loss would precipitate many further extinctions; these species have often been labeled keystone species.

The term *keystone species* has enjoyed an enduring popularity in the ecological literature since its introduction by Robert T. Paine in 1969: Paine (1969) was cited in more than 92 publications from 1970 to 1989; an earlier paper (Paine 1966), which introduced the phenomenon of keystone species in intertidal systems but did not use the term, was cited more than 850 times during the same period.

As used by Paine and other ecologists, there are two hallmarks of keystone species. First, their presence is crucial in maintaining the organization and diversity of their ecological communities. Second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance.

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The term *keystone species* is poorly defined and broadly applied

Given the assumed importance of keystone species, it is not surprising that biologists have advocated that key or keystone species be special targets in the efforts to maximize biodiversity protection (e.g., Burkey 1989, Frankel and Soulé 1981, Soulé and Simberloff 1986, Terborgh 1986) and as species in need of priority protection (e.g., Cox et al. 1991). Management to protect keystone species has been suggested to resolve general policy and land-use dilemmas. For example, it has been proposed that management for individual keystone species should be a focus for the management of whole communities (Rohlf 1991, Woodruff 1989). Further, Carroll (1992) argues that managed keystone species could be used to support populations of other species in reserves that would otherwise be too small to contain viable populations. Conway (1989) suggested that, for restoration, keystone species are necessary to help reestablish and sustain ecosystem structure and stability.

Such policy recommendations imply that a clear operational definition exists for *keystone species*. In contrast, we argue that the term is broadly applied, poorly defined, and nonspecific in meaning. Furthermore, the type of community structure implied by the keystone-species concept is largely undemonstrated in nature, although it has fundamental implications for conservation and food-web theory. These ambiguities and uncertainties motivate this discussion of the implications of the keystone-species concept for ecology and conservation, as well as the dangers inherent in shaping conservation strategies around keystone species.

The varied meanings of the term *keystone species*

The term *keystone species* was originally applied to a predator in the rocky intertidal zone:

> [T]he species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time...are determined by their activities and abundances (Paine 1969).

Subsequently, the term has been applied to many species at many trophic levels. For heuristic purposes, we have collapsed the usages of *keystone species* into five types (Table 1). This categorization is not meant to imply mutually exclusive groups or an exhaustive review of the term's application, but rather to show the diversity of keystone effects referred to in the literature.

Keystone predator. Paine (1966, 1969) noted that experimental removal of some rocky intertidal carnivores (such as the starfish *Pisaster*) led to nearly complete dominance of the substrate by one or two sessile species (mussels), resulting in greatly decreased species diversity. In this and other cases, the importance of the keystone predator derived from two requisites (Paine 1969, Pimm 1980): the predator preferentially ate and controlled the density of a primary consumer, and the consumer was capable of excluding (through competition or predation) other species from the community. Essentially, then, the early connotation was that keystone predators are important because they control the densities of important competitor or predator species.

Predators have also been labeled *keystone* when they control the densities of other types of ecologically significant prey species. For example, sea otters (*Enhydra lutris*) have often been referred to as keystone predators (e.g., Duggins 1980, Estes and Palmisano 1974) because they limit density of sea urchins (*Strongylocentrotus* spp.), which in turn eat kelp and other fleshy macroalgae that form the basis of a different community than is present in their absence (VanBlaricom and Estes 1988). Thus, otter removal has community-level influences, by releasing from predation a primary consumer that eats a plant that harbors other organisms.

Other authors have ignored the original requisites for the keystone-predator label and merely require that the species in question has a major effect on community composition. Risch and Carroll (1982) described fire ants (*Solenopsis geminata*) as keystone predators because their absence increases the number of individuals and species of arthropods potentially harmful to agriculture. The ants are generalist species preying on herbivores, which in turn are not highly competitive; hence, neither of the original requisites for keystone predators apply.

Table 1. Categories of presumed keystones and the effects of their effective removal from a system.

Keystone category	Effect of removal
Predator	Increase in one or several predators/consumers/competitors, which subsequently extirpates several prey/competitor species
Prey	Other species more sensitive to predation may become extinct; predator populations may crash
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers
Link	Failure of reproduction and recruitment in certain plants, with potential subsequent losses
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources

Keystone prey. In a theoretical analysis that assumed no competitive interactions between prey species, Holt (1977, 1984) demonstrated that a preferred-prey species that is able to maintain its abundance in the face of predation (via a high reproductive rate) can affect community structure by sustaining the density of a predator, thus reducing the density of other prey. Holt (1977) called such a predator-tolerant prey a *keystone species* "inasmuch as its properties control the density of the predator and restrict the range of parameters open to other prey." As an anecdotal example, Holt describes the contraction of habitat use of arctic hares after the introduction of snowshoe hares on Newfoundland, indicating that the snowshoe hare may have increased lynx populations, which then heavily preyed on the more vulnerable arctic hare. As the term *keystone prey species* was used by Holt, removing the keystone prey species would increase, not decrease, overall species diversity in the community.

However, Noy-Meir (1981) suggested that Holt's model involving a predation-tolerant keystone prey could be modified so that the removal of keystone prey would decrease species diversity. If the predator switches to the keystone prey when numbers of other prey species are low, then sensitive prey that otherwise would have been driven to extinction may coexist in the presence of the predator-tolerant keystone prey. Thus, we again see that the label *keystone* has been applied to species whose removal would either increase or decrease species diversity in their communities.

Keystone mutualists. Some species have been considered to be keystone because they are critical to mutualistic relationships. Gilbert (1980) introduced the term *mobile links* to describe "animals that are significant factors in the persistence of several plant species which, in turn, support otherwise separate food webs." The implication was that mobile links are a kind of keystone species, and mobile links have since been frequently cited as examples of keystone species. In addition to the mobile-link pollinators and seed dispersers described by Gilbert (1980), other examples of this type of keystone species include hummingbird pollinators and mammalian dispersers of mycorrhizal fungi (Wilcox and Murphy 1985).

Keystone hosts. If mobile links, or keystone mutualists, depend critically on ecologically important host plants, then it follows that these hosts also receive the label *keystone*. Included in this group are those plants that support generalist pollinators and those fruit dispersers that are considered critical mobile links (Gilbert 1980). Terborgh (1986) considered palm nuts, figs, and nectar to be keystone resources because they are critical to tropical forest nectar or fruit eaters, including primates, squirrels, rodents, and many birds. Together, these vertebrates account for as much as three-quarters of forest bird and mammal biomass.

Keystone modifiers. The activities of many species greatly affect habitat features without necessarily having direct trophic effects on other species. If the modified habitat affects the survival of many other species, the modifying species has been considered a keystone species. The North American beaver (*Castor canadensis*) was described as a keystone species because its dams alter hydrology, biogeochemistry, and productivity on a wide scale (Naiman et al. 1986). Likewise, the Brazilian termite (*Cornitermes cumulans*) has been called a keystone species because loss of its large, abundant, and uniquely structured mounds would likely precipitate loss of obligate and possibly opportunistic users of the mounds (Redford 1984).

Many species have been called keystone herbivores because their foraging causes drastic habitat modification. Based on the observation that large herbivores (more than 1000 kg) can readily convert closed thicket or forest into open grassy savanna, Owen-Smith (1987) posited a keystone-herbivore hypothesis to explain the late Pleistocene extinction of approximately half of the mammalian genera with body masses of 5–1000 kg. This theory posits that the elimination of large herbivores initiated vegetational changes that were deleterious to the fauna.

A keystone-herbivore hypothesis was also advanced to describe red-naped sapsuckers (*Sphyrapicus nuchalis*), which create sap wells in tree bark, thereby providing resources for other herbivores (Ehrlich and Daily 1988). Sea urchins have been called keystone because their grazing prevents the change from a system dominated by encrusting algae to a system dominated by large, fleshy algae (Fletcher 1987, see also VanBlaricom and Estes 1988). Similarly, pocket gophers (*Thomomys bottae*) were described as keystone because they maintain mountain meadow communities by slowing down aspen invasion of the meadows (Cantor and Whitham 1989). After the removal of what they called a "keystone guild" of kangaroo rats (*Dipodomys* spp.), Brown and Heske (1990) documented drastic changes in vegetation type and accompanying changes in the rodent community. Clearly, the distinction between keystone predation and keystone modification becomes fuzzy for those species that modify habitat through predation on plants.

Useful contributions of the keystone-species concept

We have seen that the label *keystone* has been applied to a plethora of species with very different effects—both qualitative and quantitative—on their communities. Given the diversity of the usages of the term *keystone species* in the ecological literature, what are the contributions and liabilities of this concept for ecological and conservation research?

One fundamentally important contribution is the attention these studies have drawn to differing interaction strengths in community food webs.

Table 2. Predicted or observed effect of removing presumed keystones, based on articles in which authors called a species *keystone* and predicted a community composition change upon removal.

Author	Presumed keystone (community type)	Effect of removal
Paine (1966, 1969)	Starfish (rocky intertidal)	Observed reduction of system from 15 to 8 species
Fletcher (1980)	Sea urchins (subtidal)	Observed takeover of large fleshy algae, resulting in loss of approximately one-half of grazers
Terborgh (1986)	Palm nuts, figs, and nectar (tropics)	Predicted loss of one-half to three-quarters of total bird and mammal biomass
Owen-Smith (1987)	Herbivores more than 1000 kg (Pleistocene)	Hypothetical mechanism for loss of approximately half of mammalian genera during late Pleistocene

Robert Macarthur (1972) first advocated close scrutiny of interaction strengths, defining a strong interactor simply as a species whose "removal would produce a dramatic effect." Studies of presumed keystone species have certainly demonstrated the presence of strong interactors in many systems.

To gain some quantitative feel for the extent to which the removal of presumed keystone species may decrease overall species diversity, we reviewed all published studies we could find that refer to a species as a keystone and that predict or describe specific community composition changes occurring on removal of the presumed keystone. Despite the fact that investigators encountered enormous methodological problems and employ different trophic and taxonomic criteria to circumscribe the relevant assemblage, an interesting consistency is revealed (Table 2). Ecologists identify as keystone those species whose removal is expected to result in the disappearance of at least half of the assemblage considered. For reasons we will detail below, however, we hasten to warn against the use of a 50% loss rule as an operational criterion for identifying a species as keystone.

The second important contribution of the keystone paradigm is its implication that only a small minority of species have strong interactions that affect community composition. In other words, reference to a particular species as keystone implies that it is unusual, standing out from the majority of the other species in its effects on community structure or function. If we define the community importance of a given species as the percentage of other species lost from the community after its removal, we can illustrate this assumption by plotting, for a hypothetical community, the relative community importance of each species (Figure 1). The keystone concept assumes that frequencies of community-importance values are strongly skewed, with only a few species having large effects on the composition or structure of the community (Figure 1a).

In contrast to this assumption, food-web theorists have generally assumed either that species-by-species interaction strengths are drawn from symmetrical distributions (e.g., Figure 1b, normal distributions; Cohen and Newman 1988) or else are uniform (Figure 1c, an implicit assumption of static food webs; see Pimm and Kitching 1988). Although species-by-species interaction strengths are unlikely to directly correspond to community-importance values as defined here, there is likely to be considerable correlation between the two. In particular, it is difficult to imagine a species having a large effect on species diversity (community importance) without having strong interactions with other species. Thus, the keystone concept's implicit assumption about interaction strengths appears to be in conflict with the more explicit, but not necessarily more realistic, food-web models (Lawton 1992).

This apparent dichotomy between food-web theory and the keystone-species concept is certainly worth exploring. The two conceptualizations imply different patterns of community structure and hence require different conservation strategies. If many or most species are of similar importance (Figure 1b,c), any efforts to save

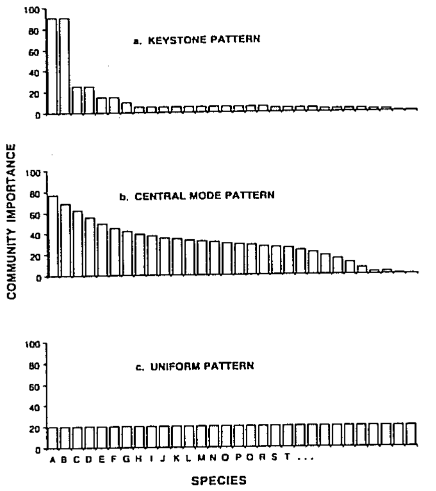

Figure 1. Expected distributions of community importance values (percent of species lost from a community upon removal of a given species) for a hypothetical community based on the keystone-species model (a) and based on food-web theory (b and c). Axes are arbitrarily scaled to demonstrate the general shape of the distributions.

only a few keystones will inevitably fail to protect the rest. Conversely, if only a few species have strong interactions/community effects, then detailed understanding and protection of the few important taxa would be critical to the well-being of the overall community.

What do the data say about this conflict? To date, only one study has addressed the distributions of interaction strengths in part or all of an ecological community. Paine (1992) developed an index of per capita interaction strength and found that only two of seven species of intertidal grazers strongly affect brown algae, which are their major food and also a profound modifier of the local environment. These results indicate "a few strong interactions embedded in a majority of negligible effects" (Paine 1992), supporting an assumption of highly skewed interaction strengths (Figure 1a). Although suggestive, it is premature to generalize this result: Paine looked at only one type of interaction for each species (herbivory of brown algal sporlings) and he looked at only a subset of the grazers within a single community. Indeed, his finding that 29% of the species were strong interactors could be interpreted as indicating that a large fraction of species have strong effects. Clearly, more studies of this type are needed in many more communities.

Keystones and conservation

What role should the keystone-species concept play in conservation efforts? Currently, implementation of the Endangered Species Act often amounts to emergency-room conservation (Scott et al. 1987), whereby the bulk of conservation resources are spent on single species that are on the brink of extinction. In the absence of comprehensive biodiversity legislation and/or increased funding and support for the Endangered Species Act, it has been suggested that "The Act could serve as an extremely useful tool for preserving keystone species, thus indirectly benefiting the many other life forms in some way dependent upon those species" (Rohlf 1991; see also Burkey 1989, Westman 1990).

We see both technical and philosophical liabilities associated with reliance on keystone species in a conservation context. (See Landres et al. 1988 for a parallel critique regarding labeling certain species "indicator species.") The overriding technical difficulty is one of definition. Before keystone species become the centerpiece for biodiversity protection or habitat restoration, we must be able to say what is and is not a keystone species.

Lacking any a priori definition, the best way to identify keystone species would be perturbation experiments whereby the candidate keystone species are removed and the responses of a predefined assemblage of species are monitored. Such tests would require adequate experimental replication and careful attention to defining the relevant assemblage (MacMahon et al. 1978 give a useful organism-centered definition of community), as well as consideration of time scales over which responses should be measured.

Bender et al. (1984) evaluated mathematical approaches for evaluating the consequences of the inevitable omission of certain species in perturbation experiments and the impact of lumping together the interactions of related groups of organisms (e.g., combining data for related ant species to measure the effect of removing a granivorous rodent). Extraordinary difficulties await researchers attempting such experiments (see Bender et al. 1984, Carpenter et al. 1985). The problem of objectively defining which species are keystone makes it likely that subjectively chosen subsets of species will be so labeled, whereas other species of similar importance will be ignored.

Even if keystone species could readily and reliably be identified for a given location at a given time, several philosophical dangers arise. First, the term is burdened with historical connotations that, as shown earlier, mean different things to different people. The lack of a clear operational definition hinders any political or legal implementation. Second, the term *keystone species* is misleading because it indicates the existence of a species-specific property of an organism, when in actuality the keystone role is particular to a defined environmental setting, the current species associations, and the responses of other species (Gautier-Hion and Michaloud 1989, Jackson and Kaufmann 1987, Levey 1988, Palumbi and Freed 1988). Thus, it is exceptionally difficult to confidently define a priori which local populations (not to mention species) are keystone (Elner and Vadas 1990, Foster and Schiel 1988). Another problem is that removal of combinations of nonkeystone species could have effects as large as removal of a keystone.

Finally, a conservation criterion that favors the maintenance of keystone species—and with them the majority of species in a community—may fail to protect other species of interest to conservationists or the public at large. For example, spotted owls, wolverines, grizzly bears, and California condors may have little role in the maintenance of species richness in their respective habitats, yet the protection of these charismatic species has been advanced because their fates are thought to indicate the integrity or health of their habitats, or because the viability of many such species requires large areas; these areas may ensure, in turn, sufficient habitat heterogeneity and space for large numbers of other species, some of which may have specialized requirements.

In sum, both the complexity of ecological interactions and ignorance of them militates aganst the application of the keystone-species concept for practical management recommendations. Despite its heuristic value, we see more harm then good in the formalization of the term in laws and policy guidelines that have rigid practical implications.

Conclusions

The lack of data addressing both the range of interaction strengths within communities and the generality of trends across communities leads us to suggest that neither the science of ecology nor the protection of biodiversity is advanced by continuing to label certain species as keystone. Instead, we advocate the study of interaction strengths and subsequent application of the results into management plans and policy decisions. Emphasizing strengths of interactions instead of a keystone/nonkeystone dualism is more than a semantic improvement; it recognizes the complexity, as well as the temporal and spatial variability, of interactions.

Although Paine's 1992 study is compelling in its demonstration of the existence of just a few strong interactors for the rocky intertidal zone, no data address whether other systems have similarly distributed interaction strengths. Paine's tantalizing results should inspire theoreticians to explore the implications of assemblages structured with many weakly interacting species and only a few strong interactors. At the same time, further empirical studies could assess, at the level of both short- and long-term effects (Carpenter and Kitchell 1988), the generality of skewed interaction strengths and trophic cascades (e.g., Carpenter et al. 1985, Paine 1980, Power 1990) or mesopredator release in the absence of a larger predator (Soulé et al. 1988).

If they abandon the keystone-species concept and the rigid structure it imposes on species interactions, investigators are less likely to assume that interactions or their strengths and distributions are constant in space and time. The concept has been useful in demonstrating that under certain conditions some species have particularly strong interactions, and we recognize that in recommending the abandonment of a popular and evocative concept there is a danger of making it more difficult for biologists to communicate with policy makers, managers, and the public. We think, however, that the inconvenience caused by the dropping of the label *keystone species* will, in the long run, be compensated by the development of management and policy guidelines that more explicitly accounts for the complexity of interactions in natural systems.

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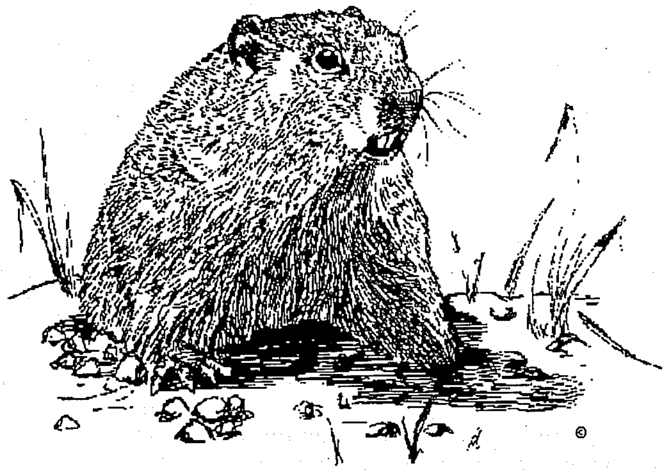

Black-Tailed Prairie Dog Status and Future Conservation Planning

Daniel W. Mulhern[1] and Craig J. Knowles[2]

Abstract.-The black-tailed prairie dog is one of five prairie dog species estimated to have once occupied up to 100 million ha or more in North America. The area occupied by black-tailed prairie dogs has declined to approximately 2% of its former range. Conversion of habitat to other land uses and widespread prairie dog eradication efforts combined with sylvatic plague, Yersinia pestis, have caused significant reductions. Although, the species itself is not in imminent jeopardy of extinction, its unique ecosystem is jeopardized by continuing fragmentation and isolation.

INTRODUCTION

The black-tailed prairie dog, Cynomys *ludovicianus* Ord, is the most widespread and abundant of five species of prairie dog in North America. Two species, the Utah prairie dog, C. *parvidens* J.A. Allen and the Mexican prairie dog, C. *mexicanus,* are currently listed as threatened and endangered, respectively, under the Endangered Species Act of 1973. The two other widespread species are the white-tailed prairie dog, C. *leucurus* Merriam and the Gunnison's prairie dog, C. *gunnisoni* Baird.

The black-tailed prairie dog is native to the short and midgrass prairies of North America. Its historic range stretches from southern Canada to northern Mexico and includes portions of Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming (Hall and Kelson 1959). The eastern boundary of prairie dog range is approximately the western edge of the zone of tallgrass prairie, from which prairie dogs are ecologically excluded. The western boundary of this species is roughly the Rocky Mountains. Its range is contiguous with, but generally does not overlap, ranges of other prairie dog species.

With the exception of Arizona, from which it has been extirpated, the species still occurs in all the states (including Canada and Mexico) within its historic range. Yet, widespread reductions have occurred in population numbers and occupied areas throughout this broad range. Historic evidence suggests that the total area occupied by all species of prairie dogs may have declined by as much as 98% during the first half of this century (Miller et al. 1994).

METHODS

We sent letters of inquiry to state and federal conservation and land management agencies and consulted published reports. This information was augmented by telephone interviews with individuals knowledgeable about prairie dog management. The area surveyed included all states within the original range of the black-tailed prairie dog. Although responses were received from all states and agencies queried, the quality of survey information varied. Therefore, this report is a picture of prairie dogs in the mid-1980s rather than an accurate assessment of 1995 populations.

Prairie dog abundance and distribution is probably better documented at present than at any previous time due to improved mapping techniques and greater interest in prairie dogs by land management agencies. Yet, prairie dog occupied acreage can still only be grossly estimated. A primary factor contributing to this uncertainty is that much of the mapping effort is temporally distributed over a decade or more and there is no method available to assess prairie dog abundance over a broad area within a short span of time. Typically, prairie dog populations change substantially within a few years due to the threats discussed below and to climatic factors and prairie dog reproductive ecology. Another factor contributing to errors in determining prairie dog abundance is a lack of information from private and state lands.

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THREATS TO THE PRAIRIE DOG

A number of causes have been identified or proposed to account for the reductions in the acreage occupied by black-tailed and other prairie dog species. We believe that four areas of threat warrant further discussion: 1) loss of habitat due to conversion of prairie to other land uses; 2) intentional poisoning or other eradication or control efforts, primarily prompted by the livestock industry; 3) shooting for recreation or as a control effort; and 4) sylvatic plague, *Yersinia pestis.*

LOSS OF PRAIRIE

Prairie dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, and buffalograss, *Buchloe dactylides* (Nutt.) Engelm., possibly due to its relatively flat topography, is among the first grassland converted to.agriculture (Dinsmore 1983). As a result, Graul (1980) noted that as much as 45% of this prairie type has been lost to other land uses. Reductions in all shortgrass and midgrass prairies is expected to be similar or possibly greater in some midgrass regions where precipitation may be more suitable for agriculture. Although National Grassland acreage in the northcentral region of the Forest Service represents only about 5% of that agency's land base, it also represents the majority of the native prairie remaining in this region of North and South Dakota (Knowles and Knowles 1994).

Currently, with the exception of some areas of the northwestern portion of the black-tailed prairie dog's range, conversion of prairie to agricultural has lessened. This is because much of the arable land is already in cultivation or has been converted to nonnative grasses for forage. Municipal and industrial development probably account for most of the present losses to native prairies in the United States. While these losses are minor compared with those that occurred during settlement of this country, they continue to reduce habitat availability for prairie dogs and other species.

ERADICATION OR CONTROL EFFORTS

Eradication efforts have been carried out against prairie dogs on a very large scale, affecting several million ha of land (Anderson et al. 1986; Bell 1921). Clark (1979) reported that in some years prairie dogs were intentionally poisoned on more than 8 million ha in the United States. During the early 1980s, 185,600 ha of prairie dogs were eradicated on the Pine Ridge Indian Reservation in South Dakota (Hanson 1988; Sharps 1988). In 1986 and 1987, a South Dakota black-tailed prairie dog complex of 110,000 ha was destroyed, eliminating the largest remaining complex in the United States (Tschetter 1988).

Virtually every federal land management agency has been involved in this effort. The U.S. Fish and Wildlife Service used compound 1080 until its ban in 1972. In 1976, this agency approved the use of zinc phosphide as a prairie dog control agent, hoping to avoid secondary poisoning of nontarget species while maintaining its prairie dog poisoning program. It is estimated that permitting activities by both the Environmental Protection Agency and the Animal and Plant Health Inspection Service account for the annual poisoning of 80,000 ha of prairie dogs in the United States (Captive Breeding Specialist Group 1992). Much of this effort occurs on federally-owned and managed land, despite the fact that less than 5% of the United States beef weight is produced on these lands (United States General Accounting Office 1988). Most poisoning on federal land is due to private land concerns, not necessarily federal forage concerns.

The legal designation indicating the regulatory status of the black-tailed prairie dog varies among the 10 states in which it still occurs. In four states the species is designated a legal agricultural pest, with some level of either state or local mandatory controls in effect. This includes statewide legislation mandating control of prairie dogs in Wyoming. In Colorado, Kansas, and South Dakota, state legislation allows counties or townships to mandate controls on landowners. In 1995, Nebraska repealed their long-standing legislation that mandated statewide control, thereby joining the states of Montana, New Mexico, North Dakota, Oklahoma, and Texas, where control is not mandatory but assistance may be provided to landowners who believe they have a prairie dog population problem that requires control.

PRAIRIE DOG SHOOTING

Shooting of prairie dogs, either for recreation or to reduce or control their numbers, is widespread across the range of all species in the United States.

The impact this activity has on overall populations remains unclear, but preliminary monitoring results by the Bureau of Land Management (BLM) in Montana indicate that some level of shooting might impact the growth and expansion of prairie dog colonies (Reading et al. 1989). Fox and Knowles (1995) suggested that persistent unregulated shooting over a broad area of the Fort Belknap Indian Reservation in Montana might have significantly influenced prairie dog populations. However, they further concluded that it would require approximately one recreational day of shooting for every 6 ha of prairie dogs to result in such an impact. This level of shooting pressure is unlikely over the hundreds of thousands of ha of currently occupied range.

SYLVATIC PLAGUE

Prairie dogs have coexisted with a variety of predators for many centuries on the plains and have adapted means of persisting in spite of this predation. However, a more recent threat has arrived to which the prairie dog has no adaptive protection. A flea-borne bacterium, the sylvatic plague, was introduced into North America just before the turn of the century. First discovered in black-tailed prairie dogs in Texas in the 1940s (Cully 1989), small rodents such as prairie dogs apparently have no natural immunity to the plague, which now occurs virtually throughout the range of the black-tailed prairie dog.

The impacts of plague are more adverse than just the killing of many individuals. The plague persists in a colony resulting in a longer population recovery time than is common in colonies that have been poisoned (figure 1). Four years following impact, plague-killed colonies on the Rocky Mountain Arsenal National Wildlife Refuge had recovered to only 40%, while poisoned colonies had recovered to over 90% (Knowles 1986). Knowles and Knowles (1994) suggested that prairie dogs have survived the introduction of this disease simply due to their large, highly dispersed populations. Further reductions in these populations could make prairie dogs much more susceptible to local or regional extirpations due to the plague.

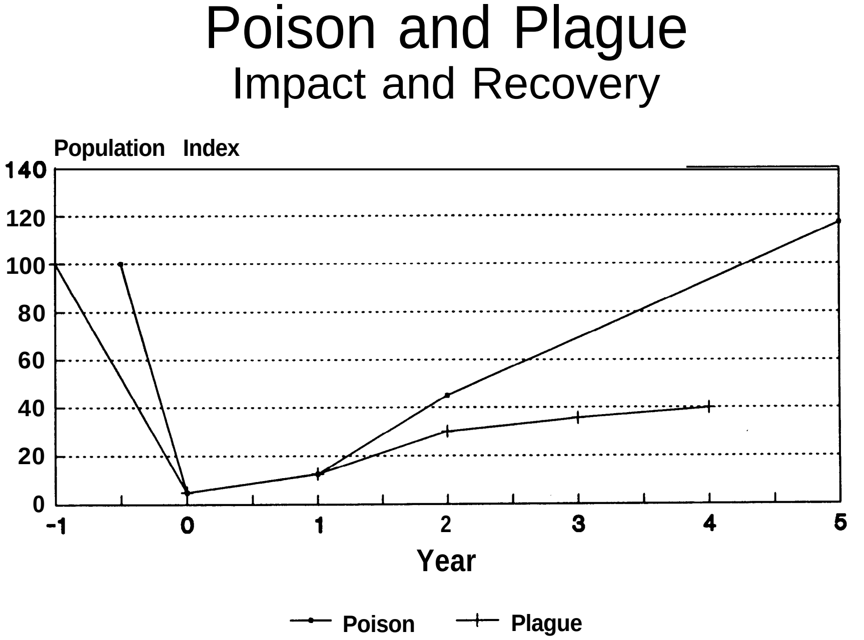

Figure 1. Comparison of prairie dog population recovery at the Rocky Mountain Arsenal National Wildlife Refuge following plague and at two colonies following control with zinc phosphlde (Knowles 1986).

HISTORIC AND CURRENT STATUS

Rangewide

Seton (1929) estimated that in the early part of this century, there may have been 5 billion prairie dogs in North America. Around that time, prairie dog colonies were estimated to occupy 40 million to 100 million ha of prairie in North America, but by 1960 this area was reduced to approximately 600,000 ha (Anderson et al. 1986; Marsh 1984). These estimates result in the often-cited figure of a 98% decline in population among the five species of prairie dog. So, while the black-tailed prairie dog still occurs in all but one of the states in its historic range, significant reductions in its total colony area have taken place rangewide.

Table 1. Historic 920) and recent (post-1980) estimates of total area (ha) occupied by black-tailed prairie dogs in the United States.

State	Historic	Recent	% Chancre
AZ	1	extirpated	-100
C O	2,833,000		
KS	810,000	18,845	-98
MT	595,000	35,545	-94
NE		24,415	1
NM2	4,838,460	201,220	-96
ND	85,000	8,500	-90
OK		3,850	1
SD	711,000	100,000	-86
TX	23,000,000	12,145	-99.9
WY		82,590	-75
United States	40,000,000 to 100.000.000	550,000	-98 to -99

1 *Reliable data unavailable for analysis.*
2 *Includes black-tailed and Gunnison's prairie dogs.*

PRAIRIE DOG STATUS IN EACH STATE

Current status information was solicited from state and federal agencies and from tribal authorities in all eleven states in the historic range of the black-tailed prairie dog (table 1). The following summary provides updated status and population data for those states.

Arizona

The Arizona Game and Fish Department (Duane L. Shroufe, Director, *in litt.* 1995) confirms that the black-tailed prairie dog, in the form of the Arizona subspecies C. *ludovicianus arizonensis*, is extirpated from the state. However, it still occurs nearby in Mexico and New Mexico. Arizona still supports populations of Gunnison's prairie dogs.

Colorado

On the Comanche and Pawnee National Grasslands, the Forest Service *(in litt.)* currently estimates a total of 2,455 ha of active prairie dogs, compared with 910 ha from 1978 to 1980 (Schenbeck 1982). This represents more than a doubling in area, but also represents only 0.5% of the area available on these public lands. Bent's Old Fort National Historic Site contains 325 ha of black-tailed prairie dogs (NPS, *in litt.).* Fort Carson and surrounding private lands contain approximately 1,620 ha, Pinyon Canyon less than 810 ha of prairie dogs (FWS, *in litt.).* The Rocky Mountain Arsenal NWR (FWS, *in litt.)* prairie dog population declined from 1,850 ha to 100 ha between 1988 and 1989, due to plague. Burnett (1918) estimated that three combined species of prairie dog occupied 5,665,720 ha in Colorado in the early 1900s. Based on geographic distribution of black-tailed, white-tailed, and Gunnison's prairie dogs in the state, it may be assumed that black-tailed prairie dogs accounted for approximately half this figure. There is no reliable estimate of the total area occupied by black-tailed prairie dogs statewide at this time.

Kansas

The National Park Service *(in litt.)* reports approximately 16 ha of prairie dogs at the Fort Larned National Historic Site. On the Cimarron National Grassland, the Forest Service *(in litt.)* currently estimates 440 ha of active prairie dog colonies compared with 20 ha estimated from 1978 to 1980 (Schenbeck 1982). This represents more than a twenty-fold increase on this 44,000-ha area, yet still only 1% of the total area of the Grassland. Both Lee and Henderson (1988) and Powell and Robe1 (1994) reported that selected counties had reductions of 84% since the beginning of the century (Lantz 1903, cited in Lee and Henderson 1988). A survey completed in 1992

(Vanderfoof et al. 1994) estimates 18,845 ha of prairie dogs in Kansas, just over 2% of the 810,000 ha estimated by Lantz (1903) some 90 years ago.

Montana

Flath and Clark (1986) estimated that black-tailed prairie dogs occupied 595,000 ha of land in Montana from 1908 to 1914. Estimated prairie dog occupied area by the early 1980s had declined to 50,600 ha (Flath and Clark 1986) and subsequent estimates show further declines in prairie dogs (40,500 ha, Campbell 1986; 35,545 ha, FaunaWest Wildlife Consultants 1995). This most recent estimate indicates a statewide reduction in occupied area of approximately 94% since the early 1900s.

Nebraska

On the Oglala National Grassland and Nebraska National Forest, the Forest Service *(in litt.)* currently estimates 105 ha of active prairie dog colonies, compared with 145 ha estimated from 1978 to 1980 (Schenbeck 1982). Current estimates represent 1.4% of land available. In 1973, prairie dog occupied area in Nebraska was estimated at 6,075 ha (Lock 1973). By 1982, this figure had increased to an estimated 32,400 ha (Frank Andelt, Nebraska Game and Parks Commission, cited in FaunaWest Wildlife Consultants 1995). By 1989, prairie dogs statewide occupied approximately 24,415 ha (Kevin Church, Nebraska Game and Parks Commission, *in litt.).* Plague and increased eradication efforts, resulting from state legislation mandating prairie dog control, have reduced this figure significantly since the 1980s, with less than 0.22% of the Nebraska landscape currently occupied by the species (FaunaWest Wildlife Consultants 1995). Historic estimates are unavailable.

New Mexico

The BLM *(in litt.)* reports that prairie dogs may be extirpated from several sites, with only 140 ha remaining on BLM land in the state. The White Sands Missile Range (Department of Army, *in litt.)* contains just over 300 ha of prairie dogs. Around 1919 the area in New Mexico occupied by prairie dogs, both Gunnison's and black-tailed (including C. *l. arizonensis),* was approximately 4,838,460 ha, but was estimated to have been reduced to 201,220 ha by 1980 (Hubbards and Schmitt 1984). This is a 96% reduction. Hubbards and Schmitt (1984) further estimated that the range of the black-tailed prairie dog in New Mexico has been reduced by one-fourth, primarily from the range of *arizonensis.*

North Dakota

Theodore Roosevelt National Park reportedly contains less than 360 ha of prairie dogs (NPS, *in litt.),* approximately 1% of the total Park land area. There are believed to be currently 2,690 ha of prairie dogs on the 660,435 ha of Custer National Forest in North and South Dakota (Forest Service, *in litt.).* This represents 0.4% prairie dog occupancy of these lands. The Forest management plan calls for an occupancy level at or around 2,225 ha. The North Dakota Game and Fish Department *(in litt.)* reports approximately 8,300 ha of prairie dogs statewide, which may be a reduction of 90% or more from historic levels. In 1992, only six complexes of over 400 ha were identified.

Oklahoma

The Department of the Army *(in litt.)* has no current estimate of prairie dog areas on Fort Sill, but report that they have declined markedly in the past 10 years. Shackford et al. (1990) reported a statewide estimate of 3,850 ha in 1967, increasing by 93% to 7,440 ha in 1989.

South Dakota

On the Buffalo Gap and Fort Pierre National Grasslands, the Forest Service *(in litt.)* estimates 3,025 ha of active prairie dog colonies and an additional 2,600 ha of colonies are subject to periodic rodenticide treatments. This compares to 17,600 ha estimated from 1978 to 1980 (Schenbeck1982). The 500,285 ha Black Hills National Forest and Custer and Elk Mountain Ranger Districts currently support 53 ha of prairie dogs. In the early 1920s there may have been 711,000 ha of prairie dogs statewide (FaunaWest Wildlife Consultants 1995). The South Dakota Animal Damage Control office currently estimates 80,000 to 100,000 ha of active prairie dog colonies in the state; the Bureau of Indian Affairs estimates 65,000 ha of these on tribal lands (Cheyenne River Sioux Tribe, *in litt.).* These estimates suggest at least an 86% decline in prairie dog occupied area across the state.

lands and Wind Cave National Parks currently contain 1,660 and 3,085 ha of prairie dogs, respectively (NPS, *in litt.).* These numbers represent 2 and 4% respectively, of the area available on these public lands.

Texas

There were an estimated 31,385 ha of prairie dogs in northwest Texas in 1973 (Cheatham 1973). In 1991, there were at least 12,145 ha of prairie dogs estimated in Texas (Peggy Horner, Texas Parks and Wildlife, *in litt.).* Comparing this with a statewide historic estimate of 23,000,000 ha (Merriam 1902) results in a decline of over 99% in this century.

Wyoming

On Thunder Basin National Grassland, the Forest Service *(in litt.)* currently estimates 1,500 ha of active prairie dog colonies, with an additional 4,900 ha subject to periodic rodenticide treatment. Colony area for the period 1978 to 1980 was reported to be 2,550 ha (Schenbeck 1982). These numbers represent 0.6% of this 231,500 ha public grassland area. Devil's Tower National Monument contains approximately 16 ha of black-tailed prairie dogs (NPS, *in litt.);* 3% of the area available. Black-tailed prairie dogs in Wyoming may have increased in abundance near the turn of the century as a result of sheep and cattle grazing, with an estimated 53,650 ha by 1971 (Clark 1973). However, Campbell and Clark (1981) estimated a 75% reduction in prairie dog occupied areas since 1915. Current estimates indicate between 53,000 and 82,590 ha statewide (Wyoming Game and Fish Department, cited in FaunaWest Wildlife Consultants 1995).

SUMMARY OF PRAIRIE DOG STATUS IN EACH STATE

FaunaWest Wildlife Consultants (1995) attempted to estimate the amount of land area within the range of the black-tailed prairie dog that is currently occupied by the species. They included seven Great Plains states in their analysis and concluded that the states have less than a 1% occupancy of land surface within the species' range. The states included in this assessment and the percent of prairie dog occupancy within available area are Colorado (0.35%), Kansas (0.14%), Montana (0.17%), Nebraska (0.22%), North Dakota (0.17%), South Dakota (0.80%), and Wyoming (0.60 to 0.88%).

While these individual state accounts do not represent an exhaustive rangewide status review, they unfortunately provide the best information available. Significant reductions in occupied area have and continue to occur throughout the species' range; losses in some places exceeded 95%. Although the species still occurs in all but one state in its historic range, the eastern boundary of this distribution may be receding to the west. Figures indicate that there may be more than 550,000 ha of occupied black-tailed prairie dog range remaining in the United States, which is consistent with the estimate of 600,000 ha (Marsh 1984) cited previously. Over half the known prairie dog acreage in the central and northern Great Plains occurs on private land, almost 30% is on Indian reservations, and about 6% each occurs on Forest Service and Bureau of Land Management property (figure 2, FaunaWest Wildlife Consultants 1995). Neither Park Service nor Fish and Wildlife Service lands support significant acreage of any prairie dog species.

There is a need to develop a standardized survey technique for assessing prairie dog status. Presently, two methods are commonly employed and both involve mapping of individual prairie dog colonies either by ground reconnaissance or from aerial photo interpretation. Both methods are time consuming and expensive, making it unreasonable to expect a survey of over 500,000 ha of prairie dog colonies on the Great Plains within a short time period. Prairie dog colonies represent clumped patches on a broad landscape and there already exist nonmapping techniques that might be capable of statistical sampling of this distribution (Marcum and Loftsgaarden 1980). A statistical approach to monitoring prairie dog colony acreage may be a more appropriate technique than trying to map all prairie dog colonies.

PRAIRIE DOGS AND LIVESTOCK

Efforts to eradicate the prairie dog by the livestock and agricultural industry have existed for most of this century. Merriam (1902) estimated that prairie dogs caused a 50 to 75% reduction in range productivity. Taylor and Loftfield (1924) concluded that the prairie dog is"one of the most injurious rodents of the

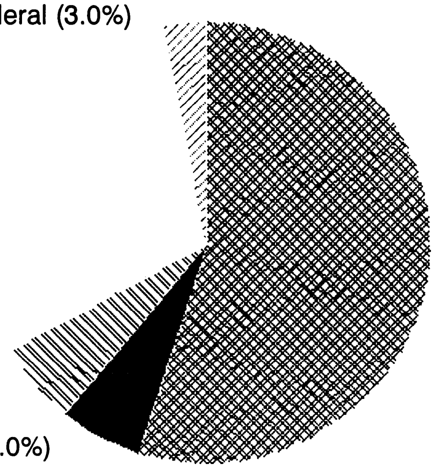

Figure 2. Distribution of black-tailed prairie dog colonies by land ownership in seven states in the northern and central Great Plains.

southwest and plains regions," and results in "the removal of vegetation in its entirety from the vicinity." Reports such as these were largely responsible for the escalating effort by range managers on the Great Plains to eradicate the prairie dog.

The conflict between the livestock industry and the prairie dog will likely not end easily or quickly, despite reports that prairie dog foraging does not significantly affect weight gain of cattle (O"Meilia et al. 1982; Hansen and Gold 1977). Others have reported the beneficial effects of prairie dogs on long-term range condition, including increased plant species diversity, richness, and overall plant production in prairie dog colonies (Archer et al. 1987; Uresk and Bjugstad 1983; Bonham and Lerwick 1976; Gold 1976). Uresk (1985) demonstrated that up to four years following prairie dog control, plant production was not increased whether the range was grazed or ungrazed by cattle.

Conversely, Hanson and Gold (1977) reported dietary overlap between cattle and prairie dogs, suggesting there may be some competition for the same species of forage plants. An estimation of true competition would be dependent on a variety of factors, including density of prairie dogs, stocking rate of cattle, ground cover, forage species present, and others (Uresk and Paulson 1988). Collins et al. (1984) reported that the annual cost of prairie dog poisoning was higher than the annual value of the forage gained by these measures. This issue requires more study, with input from both sides of the debate.

PRAIRIE DOGS AND BIODIVERSITY

The prairie dog, an integral component of the shortgrass prairie biotic community, is capable of transforming its own landscape and creating habitat alterations on a scale surpassed only by humans on the Great Plains. The ecosystem that is maintained by the prairie dog is valuable to many other species, with over 100 species of vertebrate wildlife reportedly using prairie dog colonies as habitat (Sharps and Uresk 1990; Clark et al. 1989; Reading et al. 1989). While few of these species are critically dependent on prairie dogs for all their life requisites, the increased biodiversity associated with prairie dog colonies indicates the importance of this habitat. Agnew et al. (1986) reported greater avian densities and species richness on prairie dog colonies. Also, numerous researchers have documented the preferential feeding of wild and domestic ungulates on prairie dog colonies (Coppock et al. 1983; Detling and
1987; Knowles 1986; Krueger 1986; Wydeven and Dahlgren 1985).

A number of rare and declining species are associated with prairie dogs and the habitat they provide. The black-footed ferret, *Mustela nigripes* Audubon and Bachman, 1851, is considered a true prairie dog obligate because it requires the prairie dog ecosystem for its survival. As one of the most endangered mammals in North America, this species has come to symbolize the decline in native grassland biodiversity. At least two species that are candidates for listing under the Endangered Species Act are also associated to a lesser degree with prairie dogs. The mountain plover, *Charadrius montanus* Townsend, 1837, and the swift fox, *Vulpes velox* Say, *1823,* are attracted to the vegetative changes and possibly increased food availability in prairie dog colonies. The association of other species that are either declining or vulnerable indicate the problems facing this habitat.

CONSERVATION EFFORTS

Prairie dogs are managed either directly or indirectly within the survey area by at least six federal agencies, 11 state wildlife departments, state agriculture departments, departments of state lands, and numerous weed and pest districts, counties and private landowners. Prairie dog management goals and objectives vary significantly among these entities. Even management within agencies but between areas varies significantly. This variation can range from total protection of prairie dogs to a legal mandate to exterminate. All states have simultaneously classified the prairie dog as a pest and as wildlife, often with opposing management goals. Federal policy regarding prairie dogs has been inconsistent over time and across geographic regions. The legal mechanisms responsible for the decline of prairie dogs during this century are still intact. Restoration of the prairie dog ecosystem may not be possible without major changes in management policy.

At least two federal agencies have taken the initiative to begin to address the problems associated with declining prairie dog occupied areas and to involve other interested parties. The Forest Service initiated a working group comprised of various federal land and resource agencies throughout the northern states in the Great Plains, involving the Bureau of Land Management, Park Service, Bureau of Indian Affairs, and Fish and Wildlife Service. The function of this group is to encourage development of conservation assessments and strategies for the species across broad landscapes.

In January 1995, the Fish and Wildlife Service convened a meeting of federal, state, and nongovernmental entities to discuss problems facing the shortgrass prairie ecosystem, including the prairie dog as a focal species. Consensus recommendations were: 1) Fish and Wildlife Service will develop conservation strategies to keep prairie species from becoming listed under the Endangered Species Act and to recover declining species before a listing occurs; and 2) work with the Western Governor's Association to investigate ways to coordinate and communicate with all involved parties on prairie issues. The Fish and Wildlife Service recognizes that prairie dog management remains within the jurisdiction of the various state and federal land management agencies. Therefore, this agency is particularly interested in participating in cooperative agreements with other agencies so that the prairie dog may be managed as a wildlife species rather than simply controlled as a pest.

CONCLUSION

The black-tailed prairie dog does not appear to be in danger of becoming extinct in the foreseeable future, given current management. However, the additional negative impacts resulting from habitat fragmentation (Wilcox and Murphy 1985) could seriously impact the ability of some prairie dog populations to persist or become re-established. Habitat fragmentation adversely quickly affects highly specialized species (Miller et al. 1994) and the myriad of species associated with prairie dog colonies recover from habitat or population losses at different rates. This could result in a significant disruption of the ecosystem overall functioning, further delaying its recovery. Such effects are already evident for the endangered black-footed ferret. The future recovery or extinction of this species is inextricably entwined with the decisions resource managers make today regarding the conservation of the prairie dog ecosystem.

Management of the black-tailed prairie dog must give greater consideration to developing an abundance and distribution of prairie dogs that will ensure long-term population persistence of associated species. As a minimum, we believe that broad areas of suitable grasslands should have from 1 to 3% of the area occupied by prairie dogs. Federally-owned lands should assume a greater share of this responsibility, with a goal of from 5 to 10% occupancy by prairie dogs. Maintaining this level of occupancy may allow resource managers to determine what actually constitutes a functioning prairie dog ecosystem, so attempts may be made to preserve this system into the future.

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