

Temporal patterns of prairie dog populations in Badlands National Park,
South Dakota.

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INTRODUCTION

Understanding the historic patterns of habitats is one method for evaluating species distributions at a landscape level (Johnston and Naiman 1990, Jensen et al. 1992, Kienast 1993). How populations colonize an area, where those populations choose to colonize, and which environmental constraints control population size, are all important questions on the temporal aspects of species distributions (Cale and Hobbs 1994). In the past, temporal relationships for ecological relationships were modeled in simple equations with little spatial detail and a series of assumptions (Hunsaker et al. 1993, Johnston 1993). However, geographic information systems (GIS) and historical aerial photography can now accurately model species who modify their environment and change remotely-sensed environmental parameters (Dunn et al. 1991).

Temporal models describe patterns of population distribution by changes in location and population size over time (Dutilleul 1993). There are three aspects to changes in the temporal distribution of populations: (1) change in size--does the population grow over time; (2) change in shape--does the shape of the population become more convoluted with increased edge (Buechner 1987); and (3) change in location--does the population's position shift on the landscape over time (Jensen et al. 1992).

The Great Plains of North America is an expansive grassland patterned with large habitat patches (Cid et al. 1991). The distribution of these patches in time and space is a critical aspect of the mixed- and short-grass prairie dominating the western edge of the Great Plains (Cincotta et al. 1987, Bennett and Bock 1987, Agnew et al. 1986, MacCracken et al. 1990). With the introduction of ranching, some patch-forming organisms were removed as they interfered with landuse practices. Potentially, the continued removal of these organisms would reduce the overall diversity of habitat patches and associated species (Uresk 1980, Sharps and Uresk 1990, Sharps 1994).

In this study, I examine the temporal distribution of a patch-forming rodent inhabiting the Great Plains of North America. The black-tailed prairie dog (*Cynomys ludovicianus*) is a colonial fossorial rodent originally found from Saskatchewan, Canada to northern Mexico (Cebellos et al. 1993). Black-tailed prairie dogs create unique habitat patches by actively removing certain species of grasses and forbes, aerating the soils, and abandoning burrows and tunnels within a patch (Clark et al. 1989). The burrows, along with the vegetation changes promoted by the prairie dogs, have distinct signatures, visible in aerial photography and remotely-sensed images (Schenbeck and Myre 1986). These scars can be used as measures of temporal changes in animal distribution and can also elucidate environmental parameters influencing colony placement and movement (directed or random in space).

Specific objectives of this study are to: (1) describe changes in five prairie dog populations over time; (2) estimate patterns of growth of those populations (random or nonrandom) based on population centers (centroids); and (3) evaluate associations with preferred (based on population placements over time) habitat parameters and population growth or movement.

MATERIALS AND METHODS

Study site and species--This study was conducted in Badlands National Park, located on the eastern edge of the Black Hills of South Dakota. Badlands National Park (BADL) was first established as a National Monument in 1939, setting aside the unique erode clay cliffs of the White River dubbed "*Mauvais terra traverser*" (bad lands to cross) by eighteenth century French fur-trappers. Upgraded to a National Park in 1972, some of the management policies changed including the control policies on black-tailed prairie dog (*Cynomys ludovicianus*) colonies long considered by ranchers as livestock pests and competitors (Cincotta et al. 1987, Uresk and Paulson 1988). These historic control programs, including the designation of prairie dogs as predators to allow open-season hunting in the state of South Dakota (Peterson 1987) had fractured the once large prairie dog (pdog) colonies into small isolated populations. Other species dependent on those colonies also started to decline including the black-footed ferret (*Mustela nigripes*), swift fox (*Vulpes velox*), burrowing owls (*Athene cunicularia*), and ferruginous hawks (*Buteo*

regalis--Sharps 1994). The 1972 creation of the Sage Creek Wilderness Area as part of Badlands National Park, set aside over 1000 acres for the protection of both the pdogs as a keystone species, and all associated species.

Pdog colonies are arranged in social tiers which enhances their contribution to the patchy appearance of the grassland vegetation (King 1955). Pdogs are colonial, fossorial, harem-polygynous rodents and one of the largest members of the Scurid family--weighing 700-1500 grams (Hoogland 1982, 1985). The colonial habit concentrates pdogs into aggregations (colonies) consisting of several clusters (towns) composed of family groups (coteries). They preferentially graze some of the taller grass species such as buffalograss (*Buchloe dactyloides*), scarlet globemarrow (*Sphaeralcea coccinea*), threadleaf sedge (*Carex filifolia*), blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*--Collins et al. 1984, Apa et al. 1990). This preferential grazing alters the vegetation composition within their colonies by increasing forb species diversity, removing graminoids (Cincotta et al. 1989, Uresk 1984, 1985), and increasing visibility around the colonies (Garret and Franklin 1988).

Five prairie dog towns from three colonies within BADL were used for this study (Figure 1). Towns were chosen based on their clarity in all aerial photographs, colony longevity (at least 40 years old), and accessory information (towns where density surveys had been conducted). The Burns Basin colony (BB) is located in the eastern side of the park. There are three distinct lobes within the Burns Basin colony; however, as of 1990, the

three towns had grown together and were considered a single town (Bowser 1996).

Tyree Basin (Ty) is located in the south-central area of the park on the edge of the Sage Creek Wilderness. This colony is located on a high table that has several small towns scattered across its top; of these towns, the largest and most stable was used in this study. Kocher Flats (Ko) is on the western edge of the park and borders private land. Located completely in the Sage Creek Wilderness area, Ko is one of the largest colonies in the park, consisting of four towns, each in excess of 100 hectares. The central town, over 250 hectares, was used for this study.

Aerial Photography--Black and white, and color infrared aerial photography were collected in approximately ten-year intervals to represent five decades--1954 to 1991 (Table 1). Photography came from three sources: United States Geologic Survey (USGS), National Aerial Photography Program (NAPP), and Natural Resource Conservation Service (NRCS, formerly Soil Conservation Service-SCS). Each photograph was scanned using a Tangent Composite Color Drum Scanner (Tangent Engineering 1991) set at 500 bits per inch, using green (for black and white) or Red-Green-Blue (RGB--for color infrared) filters. A small high-contrast section of each photograph was scanned first to create a color histogram table using greyscale setting with green filters. This lookup table was then used to scan the rest of the photograph using a log 8 scale with either RGB or green filters. This method helps to clarify grain and improve the clarity of the resultant digital image (Dr. R. Root, Technology Transfer Division, National Biological Service).

Scanned images were rectified (a mapping transformation from one coordinate system to another) using Geographic Resource Analysis Support System (GRASS) modules, a geographic information systems (GIS) software for UNIX workstations. Scanned photographs have an x,y coordinate system can be rectified to Universe Transverse mercator (UTM) cylinder projection system in GRASS by calculating a least squares regression between the two coordinate systems using a set of known positions or control points that can be identified on both scanned images and target database (US Army CERL, GRASS4.1 User Manual, 1993). Color infrared photographs (1:50,000 [inches to feet]; 1981) were rectified directly to a USGS 7.5 minute (1:24,000) topographic (topo) map. The larger coverage of the 1981 (1:50,000) photography helped increase the number of useable control points thereby reducing distortion (between photograph and base image--either topo map or 1981 photographs) as measured by the residual mean square error (RMSE). All other smaller-coverage photographs were rectified to the 1981 image.

Environmental surfaces--Digital databases (Digital Line Graphs [DLG], Digital Elevation Model [DEM], soils [DLG format], and vegetation [raster map based on soils and vegetation surveys] Butler 1993) were obtained from the USGS, NRCS, and National Park Service (NPS). Data were imported into a GRASS coverage and corrected for projection and reference surfaces. Because BADL lies between UTM zones 13 and 14,

digital surfaces had to be corrected along the UTM zone boundaries. There was some distortion associated with the edges of UTM zones and the fit may be imperfect.

Data analysis--All spatial data analyses were performed using GRASS, a raster-based GIS. Vector databases (DLG) were first translated into raster format before analyses in GRASS4.1. The soils database (vector format) was brought from ARC/INFO into GRASS (raster format). The boundaries of identified pdog towns were digitized in GRASS from the scanned aerial photography. Area, perimeter, and centroid locations were determined from these digitized polygons using GRASS modules and UNIX shell scripts. Polygons were overlaid on environmental databases and used as a mask to determine the composition of each town based on the environmental database.

Surface Roughness--Environmental variation was expressed as surface roughness using nearest neighborhood analysis on slope, aspect, soils, and vegetation data layers. Each layer was redefined by using a roving window that assigned a diversity value to each cell on a surface based on the values of its neighbors (Berry 1995). Neighborhoods were created in GRASS using either 3X3 neighborhoods, or 7X7 cell neighborhoods for the coarser database. Each surface was redrawn as a roughness-layer where cells had either high- or no- roughness values.

Prairie dog surveys--Pd dog density surveys were conducted in 1989 and 1991 for all towns in BADL. These transect surveys provided estimates of pdog density based on a count of

active burrows following protocols established for the reintroduction of the black-footed ferret *Mustela nigripes* (Bessken and Vaughen 1990). These transects were not adjusted for different activity patterns within a town, nor do they account for heavier activity along the perimeter of large towns (B. Bessken, Natural Resource Management Specialist, Badlands National Park, South Dakota).

Figure 2 highlights the elements incorporated from each database to address the following three hypotheses: (1) pdog populations have increased within Badlands National Park since the establishment of the monument in 1939; (2) the shape of populations as perimeter to area ratio is higher for rapidly growing towns since pdog activity tends to be concentrated along the edges (Garrett and Franklin 1988, Devenport 1989); and (3) pdog populations expand randomly--population centroids do not shift significantly over time.

Statistical Significance--Statistical analyses were performed with SPLUS on a UNIX system, SYSTAT on a DOS system, and The R Package for multivariate statistics on a Macintosh PC. Changes in area were estimated using Pearson's Chi Square analysis among years for all towns. Changes in town shape over-time were estimated by calculating the perimeter to area ratio (p/a) for each town and plotting those ratios against time for a visual inspection for patterns. Changes in centroid locations were examined by plotting each set of coordinates (UTM northing and easting) and triangulating neighborhoods of influence around each starting centroid location. These polygons were based on the Thiessen polygon model where coordinates of points are used to examine

spatial patterns and associations in space. Polygons of equal shape would indicate a spatial distribution of centroids that was random with no pattern, or clumping because of high regions of geographic association (Upton and Fingleton 1989, Legendre and Vaudor 1991).

RESULTS

All five pdog populations expanded from 1954 to 1991; however the rate of increase was different among towns (Figure 3). Three towns, Kocher Flats (Ko), and Burns Basin 1 and 2 (BB1, BB2) all demonstrated rapid growth between 1981 and 1991. Town areas significantly changed over time (Pearson's Chi Square=12,975,047; $df=16$; $p=0.00$), however, in contrast, prairie dog density for those same towns was thought to have declined from 1989 to 1991 from an average density of 56.9 to 51.0 for all three Burns Basin towns (Bessken and Vaughen 1990).

Centroid positions for the five prairie dog towns showed weak patterns of non-random movement indicating some directionality (Figure 4). North and east centroid shifts were conservative for most towns with the exception of BB1 and Ko: both demonstrated jumps in centroid locations during periods of rapid growth. Plotting geographic regions of attraction (Figure 5) also showed no strong spatial patterns; Thiessen triangles were irregular with some localized clumps (Burns Basin towns).

Perimeter/area (p/a) ratios for the five towns did not reveal strong patterns, nor were there any trends within a town to increase p/a ratios over time with the exception of BB2 (Figure 6). Visual overlays of town perimeters on aerial photography highlight the conservation of shape among towns, with the exception of Ko which had a highly convoluted edge (Figure 7).

Environmental associations for towns across five decades were weak. Although several habitat types appeared consistently within town boundaries, even the finest resolution of 30 meters for the environmental databases was insufficient to detect changes among years. *Agropyron Smithii* with *Buchloe dactyloides* on dense clay or *A. smithii* on silty soils were the dominant vegetation and soils classes for all Burns Basin towns and Kocher Flats respectively (dominant was considered greater than 50% of the town polygon composition). In contrast, Tyree Basin was dominated by *Festuca octoflora* on a thin upland soil. This soil type was common for tables in the badlands regions (as an older more erosive layer from the Oligocene inter-tidal seas), and represented 90% of the soil found under Tyree towns. There was some visual evidence for towns to stay within some physical boundaries (streams for Burns Basin towns, an elevated table for Tyree Basin and badland walls for Kocher Flats).

There was insufficient resolution within the environmental layers to test environmental associations directly. When barriers were combined into regions of environmental

roughness, the percentage of roughness within each town was quite low (Figure 8). Combinations of roughness surfaces into a "preferred" surface using GRASS to add layers and category values indicated associations with areas of preferred types may be strong (Figure 9). The resolution of the preferred surface was insufficient to detect changes over time.

DISCUSSION

Pdog towns in Badlands National Park grew rapidly over the last 40 years with accelerated growth after the creation of the Sage Creek Wilderness Area in 1972. Pdog populations within BADL expanded from 1954 to 1991 with little evidence of non-random expansion. All towns within this study expanded with little shifting of the centroid location that would be suggestive of directed population growth. Visual inspection of aerial photography does indicate the environmental barriers influence prairie dog population growth; towns in Burns Basin expanded to fill an area bordered by several streams and did not cross those barriers. However, as smaller new colonies separated from the parent colonies in the Burns area, they may not be as distinguishable on aerial photography as larger stable towns. Despite the rapid growth, towns stayed centered within a given area without strong patterns that would suggest towns moving toward the park boundary (assuming vacant towns from controlled areas would be an attraction), nor did towns readily cross physical barriers such as streams or badlands. This is not to say

that individual animals do not disperse across these areas, nor that small satellite towns may not become established in these areas.

Town shape changed for those towns rapidly expanding (Ko). Koc her Flats was situated on a table with a variety of soil types, surrounded by gullies and badland walls (Figure 10). The edges of this town were convoluted and difficult to map as the color band signature for the pdog colonies was weak. The town edges were indistinct on the higher scale (1:50,000) 1981 photography making digitizing the perimeter impossible. As pdog activity is higher at town perimeters than the centers, areas with high edge activity are likely to also have a faster growth rate. This is suggestive of town shape being a more accurate predictor of population growth potential than environmental boundaries. In addition, assuming the immediate edges of towns are likely to have the greatest concentration of pdogs, the p/a ratio corrected for a buffer zone may provide a more accurate count of pdog density than line transects across the town.

Town locations showed some signs of non-random movement over time. While towns themselves appeared to stay centered within a location, expanding equally in all directions, the centroids showed some patterns of shifting in a particular direction. This weak movement is validated by poor geographic influence (Thiessen triangles) among centroid points; although, as the centroid shifts appear to be correlated with rapid growth, this result may be misleading. Pdog control was eased for many towns in 1972 with the creation of the Sage Creek Wilderness area. All towns with the exception of Tyree Basin,

rapidly grew between 1977 and 1991. As these towns grew, they may be reinvading preferred habitat types and the shapes distort as they grow. Towns that were more stable, such as Tyree Basin, show lower p/a ratios and more random centroid movement.

Aerial photography combined with GIS provided several insights on the historic distribution of pdogs in Badlands National Park and provide some insights for future model efforts. Schenbeck and Myre (1986) demonstrated rapid pdog town expansion on the controlled areas of the Buffalo Gap National Grassland areas adjacent to BADL, but there was little discussion on direction of movement or potential environmental barriers. Future studies should compare control and uncontrolled towns for patterns of movement to provide important insight on population dynamics of a patch-forming rodent such as the prairie dog. In addition, high resolution photography combined with detailed environmental layers would provide a more accurate model of town movement over time. Such a model could be used to predict pdog town growth--along with the direction of growth--as an important service for land managers with large pdog populations.

Figure 1. Three-dimension elevation map of black-tailed prairie dog (*Cynomys ludovicianus*) populations in Badlands National Park, South Dakota. Five large, persistent towns (in yellow) were used in this study. From the top: Burns Basin, Tyree Basin, Kocher Flats.

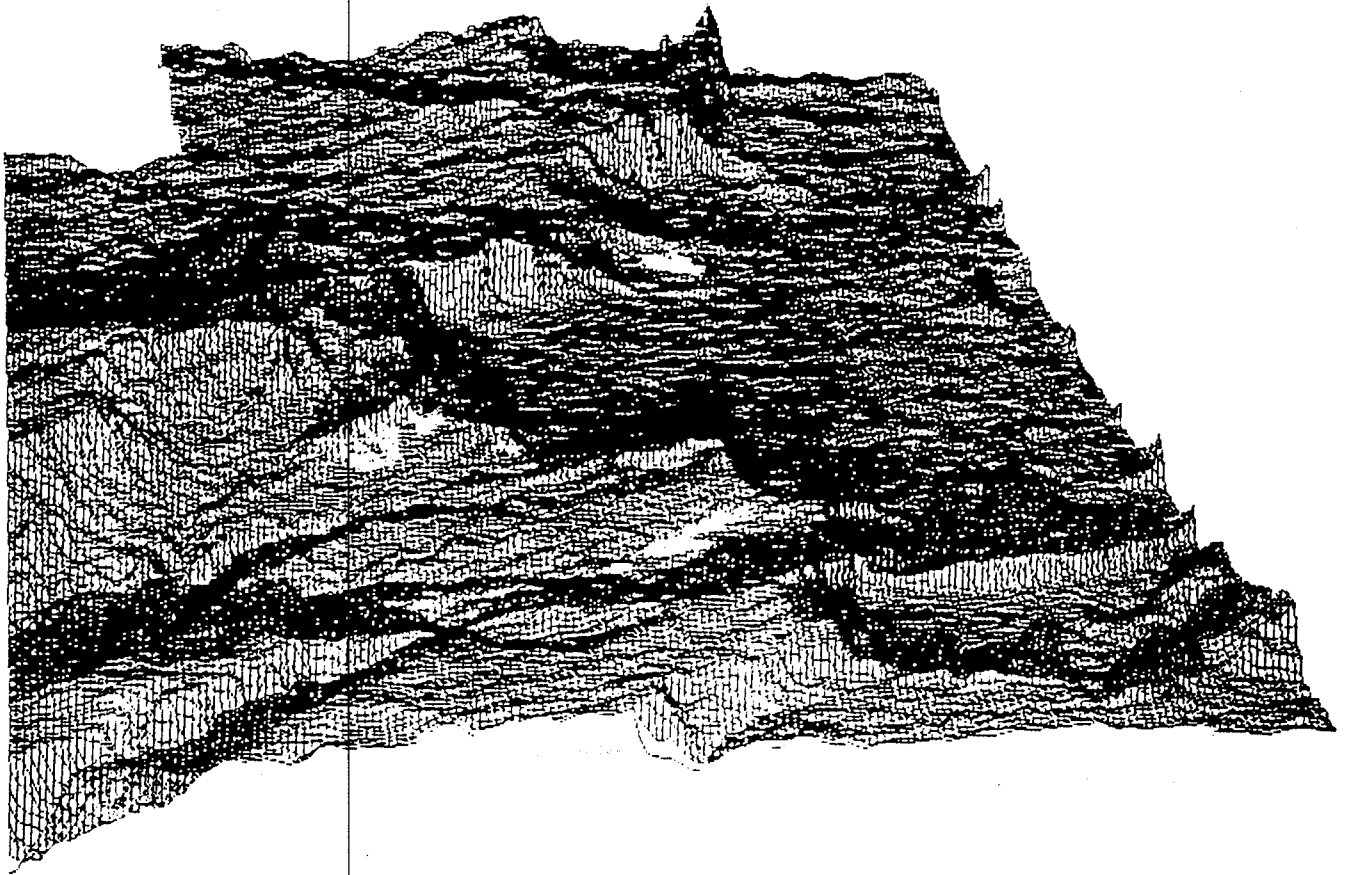


Figure 2. Cartoon of data flow for historic reconstruction of prairie dog (pdog) towns in Badlands National Park, South Dakota. Main hypotheses addressed by this study are indicated as three products: (1) how does the population size of pdog towns change over time; (2) is there a change in population shape over time; and (3) does the location of the population change over time.

Data Bases

Hypotheses

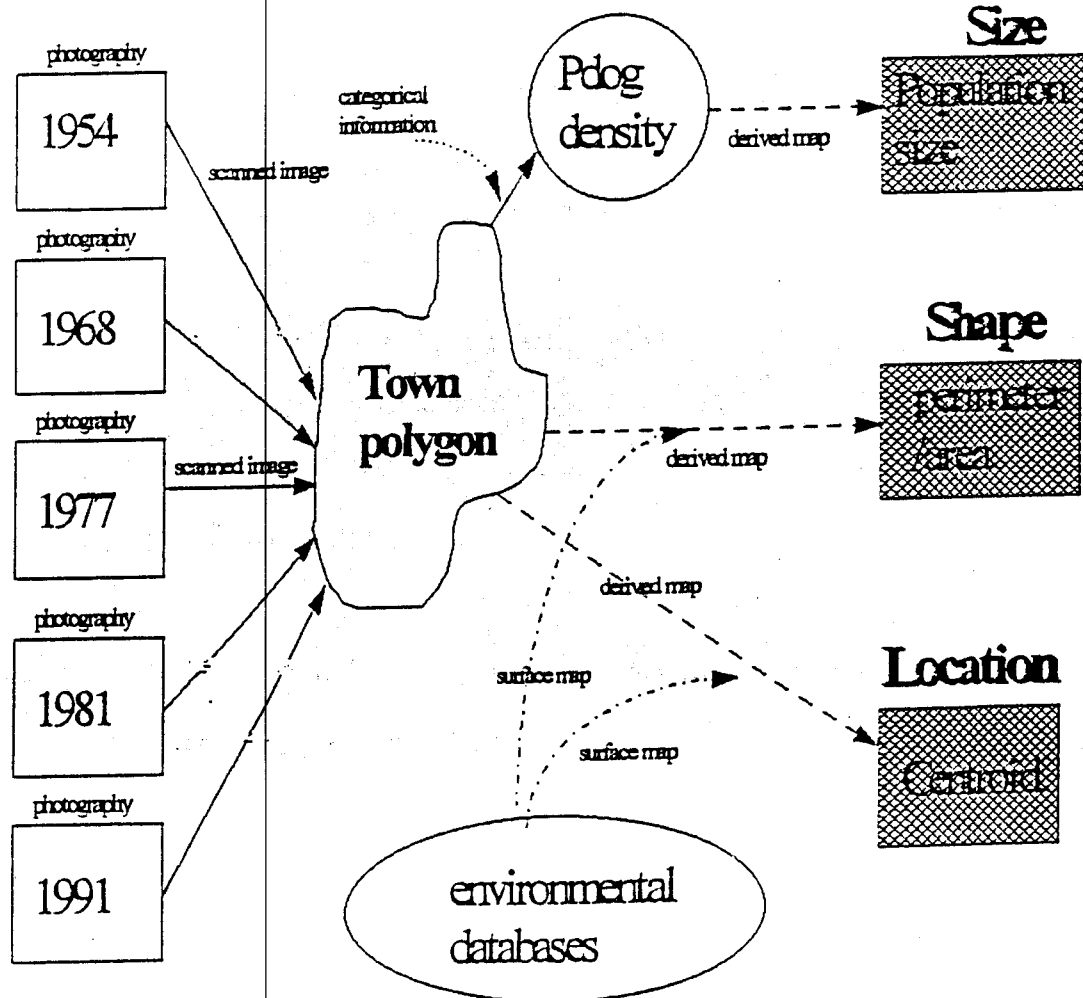


Table 1. Digital databases and aerial photography available for prairie dogs (*Cynomys ludovicianus*) in Badlands National Park, South Dakota. Both digital databases and aerial photography are summarized here. All databases were imported into GRASS4.1 mapset as raster files.

Year	Source	Scale ^a	Resolution ^b	RMSE ^c	Format ^d
PHOTOGRAPHY					
1954	ASCS ^e	1:20,000	1 meter	3.98	raster
1967	ASCS	1:20,000	1 meter	6.68	raster
1977	ASCS	1:40,000	1 meter	8.27	raster
1981 ^f	USGS	1:58,000	1 meter	5.74 ^g	raster
1991	USGS/NPS	1:24,000	1 meter	10.56	raster
DIGITAL DATABASES					
DLG	USGS	1:250,000	1 meter	----	vector
DEM	USGS	1:24,000	30 meters	----	raster
Vegetation ^h	NPS	1:12,000	30 meters	----	raster
Landuse ⁱ	NPS	1:24,000	1 meter	----	vector
Soils	USGS	1:250,000	1 meter	----	vector

a= Scale is inch on map to feet on the ground; b= Resolution is based on the size of a pixel in the GIS database. This is independent of the scale of the map, or the precision (based on map to ground relationships). c= RMSE is the residual mean square error of correcting a point on one surface to the same point on another. High RMSE indicates distortion on the surface. USGS map standards for topo maps accept an RMSE of 4 to 11 meters. d= Format of the original surface--all surfaces were transformed to a raster database for analyses in GRASS. e= ASCS (American Soil Conservation Service) is now NRCS. f= This photography was used as a base layer--all other photographs were rectified directly to this photography. g= RMSE is to USGS 7.5 minute topographical map. h= Butler 1992. i= M.Gudorf, National Park Service GIS laboratory, Denver, Colorado 1995. j= edges of UTM zones tend to be distorted but is not measured as RMSE (Berry 1995).

Figure 3. Area for five prairie dog (pdog) towns in Badlands National Park, South Dakota. Area is in meters squared calculated from digitized polygons from scanned aerial photography. Town abbreviations are: BB= Burns Basin complex, Ty= Tyree Basin, Ko= Kocher Flats.

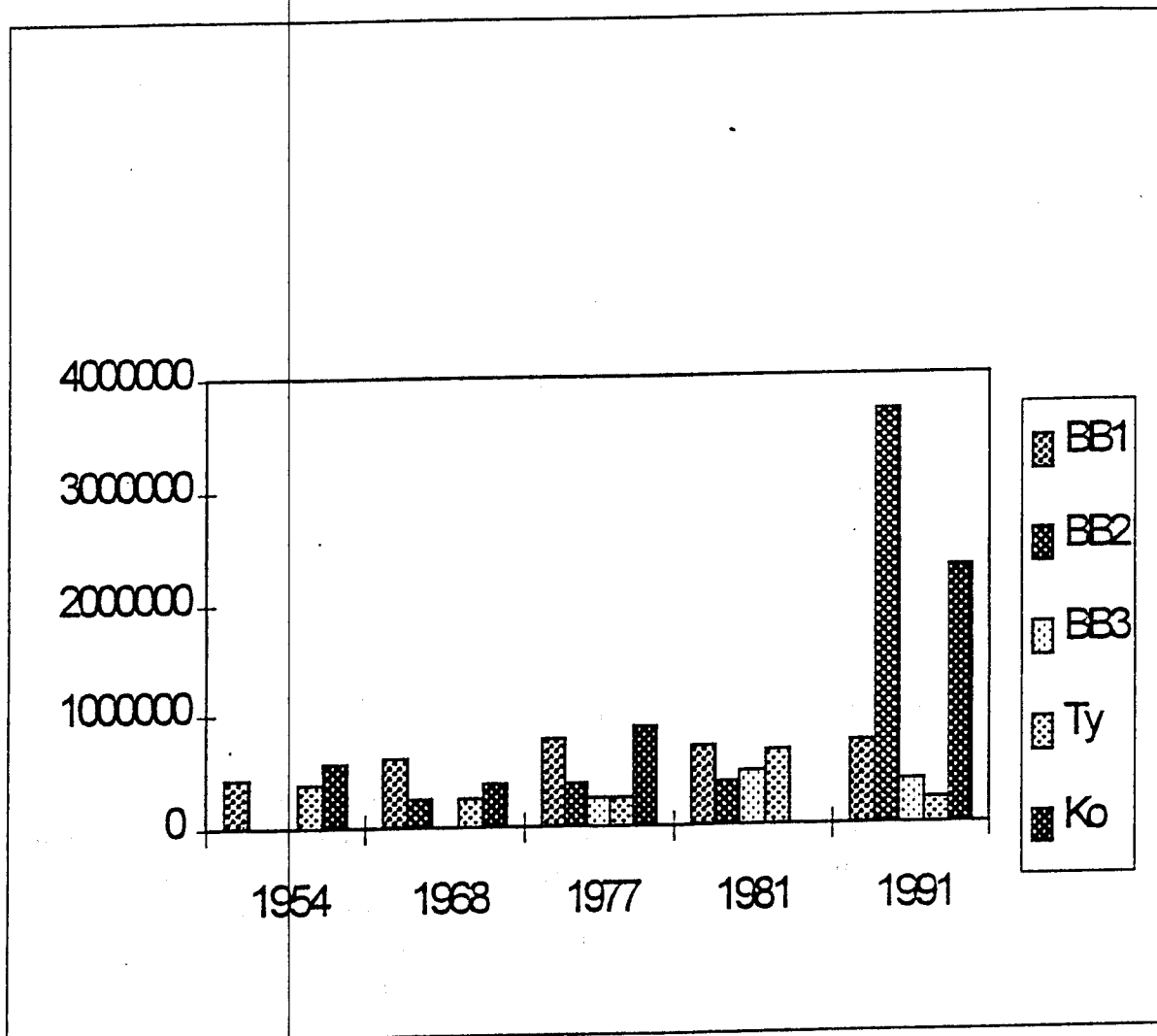


Figure 4. Centroid locations for five prairie dog (pdog) towns: 1954-1991. Centroids are expressed in adjusted Universe Trans Mercator (UTM) northings and eastings in zone 13 and 14. The coordinates were adjusted to reflect the small scale. All eastings are in grid 732000; northings are 4850000.

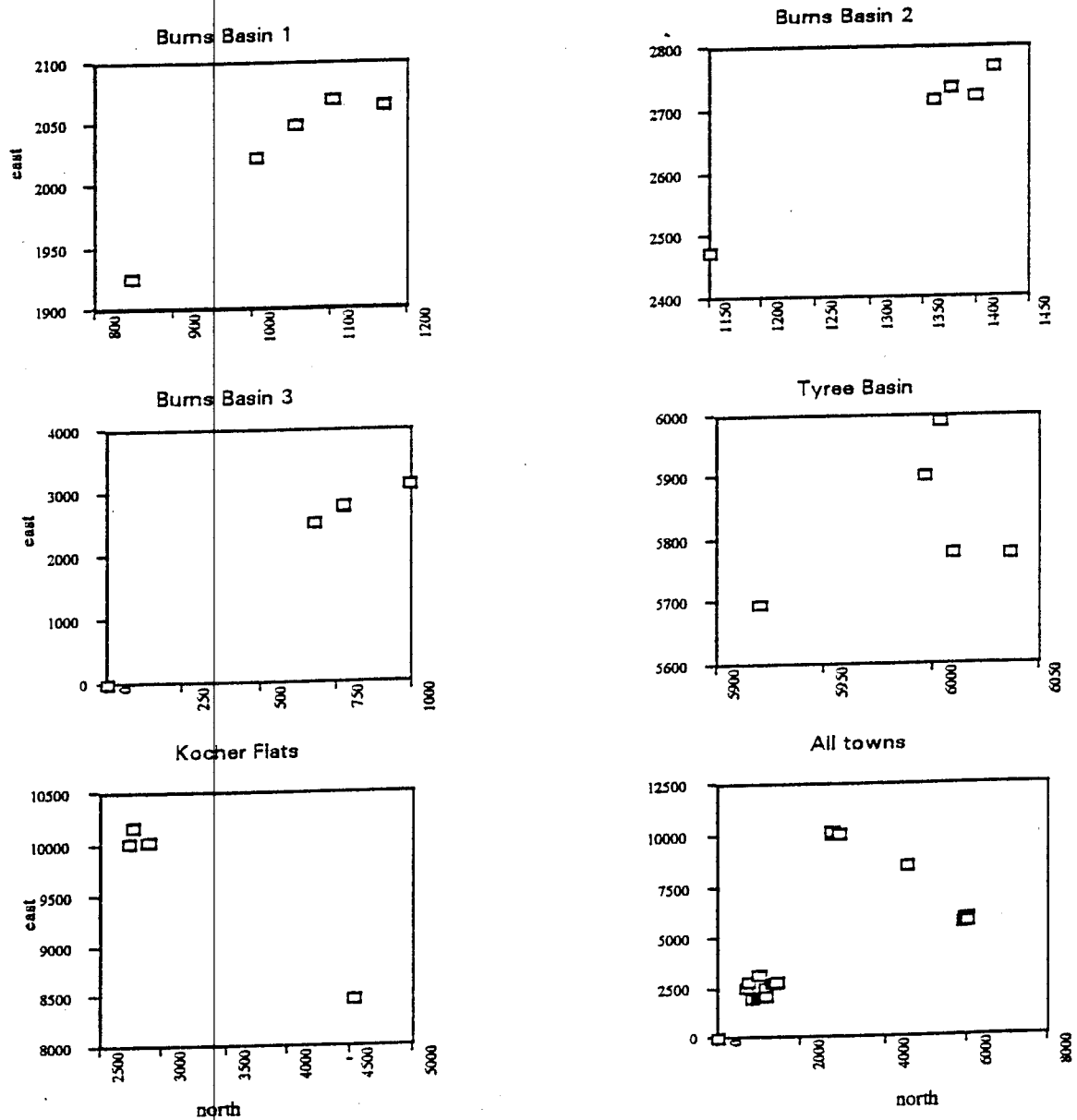


Table 2. Prairie dog (*Cynomys ludovicianus*) population area and sizes for five populations in Badlands National Park, South Dakota. Area is in meters squared based on digitized polygons from historical aerial photography. The Kocher Flats (Ko) town area was not calculated for 1981 because of poor boundary resolution.

TOWN AREA						
Populations	1954	1968	1977	1981	1991	density 1992
BB1	459908.9	600352.6	771339	722956	742362	51.0
BB2	13477.6	249395.3	393098.3	383098.3	3672000	51.0
BB3	0	7418.2	271098.3	499840.7	4095000	51.0
Ty	382500	248406	257400	645973	220500	46.5
Ko	580500	408600	881100		2264400	44.8

Figure 5. Thiessen tessellation of centroid locations for five towns over five years in Badlands National Park using Delauney Triangulation. Polygons indicate the zone of geographic influence around each points for an unconstrained triangulation, gray lines indicate lines drawn by Delauney triangulation to show relationships among points, while black lines indicate tiles as zone of geometric influence (Thiessen polygons) around each point (Upton and Fingelton 1989, Legendre and Vaudor 1991). Numbers represent towns (in consecutive years 1954-1991): 1-5=BB1, 6-10=BB2, 11-15=BB3, 16-20=Ty, 20-24=Ko.

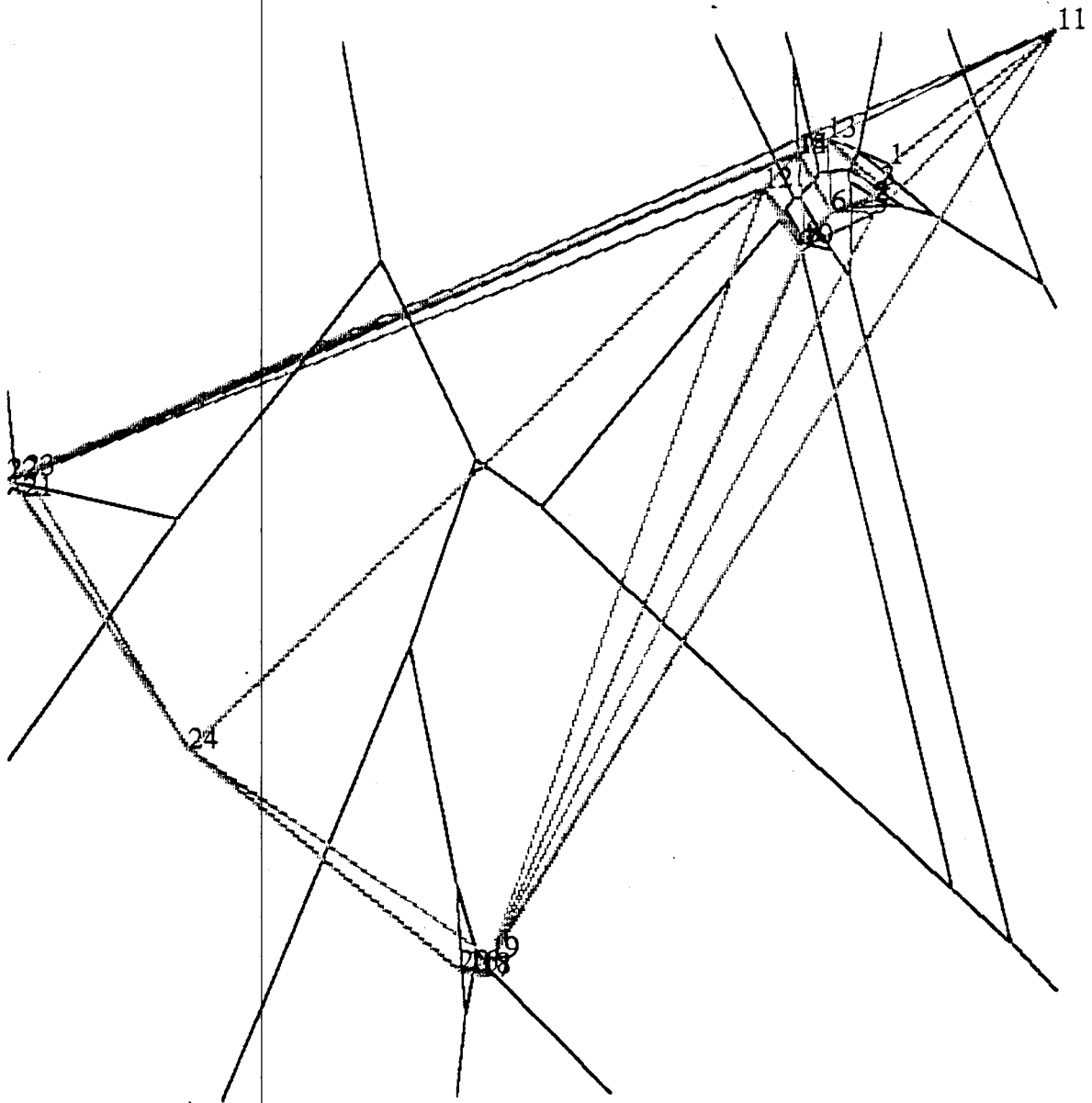


Figure 6. Perimeter/area (p/a) ratios for five prairie dog towns over five decades in Badlands National Park, South Dakota. Perimeters were determined by digitizing town boundaries off of scanned aerial photography using GRASS GIS. The p/a ratio is one method to represent polygon shape (Buechner 1987).

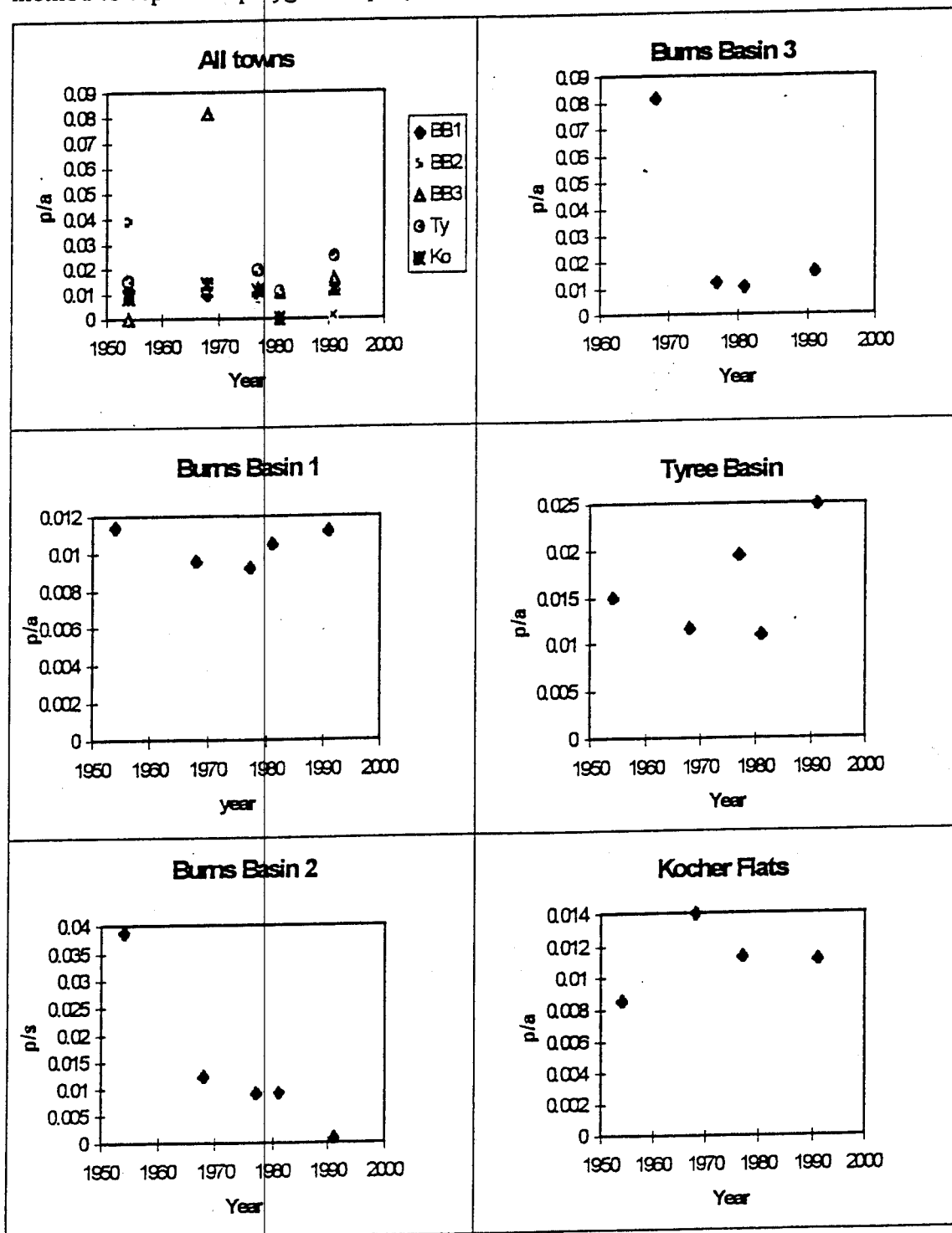


Figure 7. Visual overlay of town perimeter (Kocher Flats) on aerial photography. Each year is indicated by a different color to highlight changes in town shape and patterns of town growth. Background photography is black and white 1991 1:24,000. Centroid locations are indicated by white X's.



Figure 8. Surface roughness (as a function of neighborhood boundaries (green) and town perimeters (black). The roughness polygons is a function of the resolution of the meter pixels). Town perimeters are plotted at the highest resolution and thus have a smoother appearance than the roughness polygons. Basin; B= Kocher Flats.

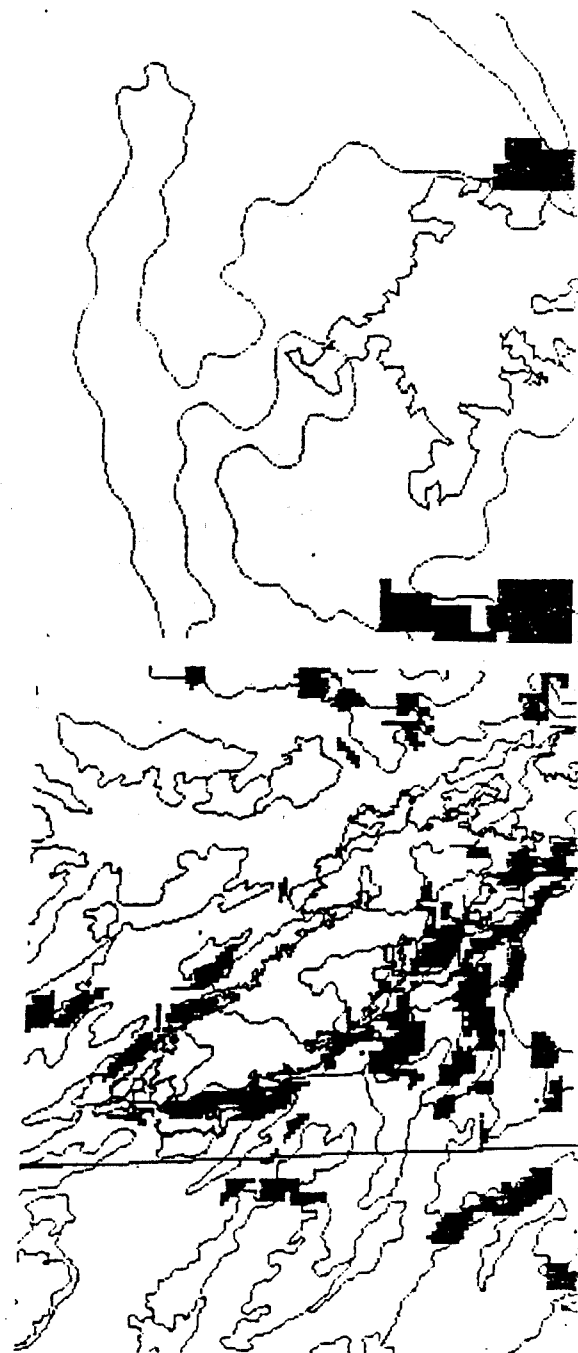


Figure 9. Preferred surfaces for pdog populations parkwide. Preference was determined by the environmental composition of towns over time. Elements that appeared consistently within town boundaries and represented greater than 50% of the town composition were classified as preferred. All of these surfaces were combined and all unpreferred habitat types were assigned to zero category value. The resulting surface is obtained by redrawing the combined preferred surfaces using their category values: the green represents high category values, all other areas (white) are zero category values. Town perimeters are indicated in black.



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