

Implications of Black-tailed Prairie Dog Spatial Dynamics to Black- footed Ferrets

David S. Jachowski
Joshua J. Millsaugh¹

Department of Fisheries and
Wildlife Sciences
University of Missouri
302 Natural Resources Building
Columbia, MO 65211 USA

Dean E. Biggins

U.S. Geological Survey
Fort Collins Science Center
2150 Center Ave., Bldg. C
Fort Collins, CO 80526, USA

Travis M. Livieri

Prairie Wildlife Research
P.O. Box 308
Wellington, CO 80549, USA

Marc R. Matchett

U.S. Fish and Wildlife Service
Charles M. Russell National
Wildlife Refuge
P.O. Box 110
Lewistown, MT 59457, USA

¹ Corresponding author:
MillsaughJ@missouri.edu

ABSTRACT: The spatial dynamics of black-tailed prairie dog (*Cynomys ludovicianus*) colonies affect the utility of these environments for other wildlife, including the endangered black-footed ferret (*Mustela nigripes*). We used location data of active and inactive black-tailed prairie dog burrows to investigate colony structure, spatial distribution, and patch dynamics of two colonies at ferret recovery sites. We used kernel-based utilization distributions (UDs) of active and inactive burrows from two time periods (six and 11 years apart) as the basis for our analysis. Overall, the total extent of our prairie dog colonies changed little over time. However, within colonies, areas with high densities of active and inactive prairie dog burrows formed patches and the distribution of these patches changed in size, shape, and connectivity over time. At the Conata Basin site, high-density active burrow patches increased in total area covered while decreasing in connectivity as they shifted towards the perimeter of the colony over time. At the UL Bend site, we observed a similar but less pronounced shift over a longer period of time. At both sites, while at a large scale it appeared that prairie dogs were simply shifting areas of activity towards the perimeter of colonies and abandoning the center of colonies, we observed a dynamic interaction between areas of active and inactive burrows within colonies over time. Areas that previously contained inactive burrows tended to become active, and vice versa, leading us to hypothesize that there are shifts of activity areas within colonies over time as dictated by forage availability. The spatial dynamics we observed have important implications for techniques to estimate the suitability of ferret habitat and for the management of prairie dog colonies. First, fine-scale techniques for measuring prairie dog colonies that account for their patchy spatial distribution are needed to better assess ferret habitat suitability. Second, the shift of high-density areas of active prairie dog burrows, likely associated with changes in vegetation, suggests that through the management of vegetation we might be able to indirectly improve habitat for ferrets. Finally, we found that prairie dog distributions within a colony are a naturally dynamic process and that management strategies should consider the long-term value of both active and inactive areas within colonies.

Index terms: black-footed ferrets, Conata Basin, prairie dogs, spatial distribution, UL Bend

INTRODUCTION

Black-tailed prairie dogs (*Cynomys ludovicianus*) (hereafter referred to as prairie dogs) are diurnal, herbivorous, colonial rodents that live as distinct family groups or coterries in well-defined burrow systems (Hoogland 1995). Prairie dog colonies are composed of clusters of one or more coterries with adjacent, but rarely connecting, burrow systems. Colonies vary greatly in size and density but typically have well defined boundaries that can be identified by the extent of burrow entrances above ground. Because prairie dog colonies distinctively alter their environment through burrow systems, soil turnover, and vegetation modification, they are host to a variety of uniquely adapted species (Miller et al. 1994; Kotliar et al. 1999), including the critically endangered black-footed ferret (*Mustela nigripes*).

Colony dynamics and spatial distribution of prairie dogs are important determinants of habitat conditions for dependent species (Biggins et al. 2006a), and understanding these parameters is essential for establishing management goals. Current manage-

ment goals primarily focus on the area occupied by prairie dogs rather than their abundance and spatial distribution within the colony (U.S. Fish and Wildlife Service 2004). While measurements of average prairie dog density have been used to characterize colonies (Biggins et al. 1993), prairie dogs are unevenly distributed within a colony (Cincotta et al. 1989). Variations in the spatial distribution of prairie dogs within occupied areas could have large impacts on the assessment of habitat for dependent species such as the ferret, which has been shown to select for areas with high prairie dog burrow density (Biggins et al. 2006a).

We collected and used comprehensive data on active and inactive burrow locations to assess the colony structure, spatial distribution, and patch dynamics of prairie dogs over time in two prairie dog colonies that are ferret recovery sites. By applying spatial analysis techniques to geographic information system data, we looked for patterns in these attributes that could advance our understanding of prairie dog ecology and management and aid in the recovery of ferrets.

METHODS

Study Areas

UL Bend National Wildlife Refuge, Montana

The U.S. Fish and Wildlife Service, as part of the Charles M. Russell National Wildlife Refuge in north-central Montana, manages the UL Bend National Wildlife Refuge. The UL Bend contains one of the largest (1182 ha) prairie dog complexes in Montana. The UL Bend area has been a recovery site for ferrets since 1994 and has received 208 captive-born kits and produced over 191 wild-born kits, yet the spring 2005 population count revealed only 12 individuals. Our core study area at the UL Bend site was the Locke sub-complex with an area of 445 ha, which comprised 38% of the entire complex (Figure 1).

Conata Basin, South Dakota

The Conata Basin in southwestern South Dakota is a portion of the Buffalo Gap National Grassland administered by the U.S. Forest Service. The Conata Basin contains more than 8907 hectares occupied by prairie dogs. In contrast to the UL Bend, ferret reintroduction at the Conata Basin was a rapid success. Reintroductions began in 1996 and continued through 1999 with the release of approximately 146 captive-born animals over three years. In 2000, due to the large number of ferrets present and the belief that all available habitat was occupied, no more captive-born animals were released. In 2001 and 2002, 64 and 60 litters of wild-born kits were documented, respectively. Each year from 2003 to 2005, the total fall population count was estimated to be around 200 individuals (Livieri 2006). Our core study area was the North Enclosure of Sage Creek sub-complex with an area of 202 ha, which comprised about 2% of the entire area occupied by prairie dogs (Figure 1).

Sampling Methods

Large-scale, indirect techniques often are used to estimate prairie dog distribution

over large geographic areas based on the extent of burrows (Sidle et al. 2001; White et al. 2005). Such techniques lack accuracy compared to visual estimation and mark-recapture techniques (Severson and Plumb 1998; Biggins et al. 2006b), but frequently are more feasible given that prairie dogs spend a majority of the time below ground and that, in some cases, their colonies are distributed over large areas. The correlation between active burrows and the occurrence of prairie dogs is widely used in examining patterns of spatial distribution (Uresk et al. 1982; Biggins et al. 1993; Johnson and Collinge 2004; Biggins et al. 2006b). In addition, burrows provide habitat structure and escape cover for ferrets.

In 1994, we mapped all active and inactive burrows on the study area at UL Bend ($n = 12,244$ burrows). In 1999, we mapped all active and inactive burrows on the study area at Conata Basin ($n = 21,798$ burrows) (Biggins et al. 2006a). In 2005, we resurveyed both sites (UL Bend $n = 13,996$ and Conata $n = 27,890$ burrows) using the same equipment and methodology as in the previous surveys. The northern boundary of the Conata Basin study area is adjacent to Badlands National Park. We did no mapping of prairie dog burrows within the park in 1999. Teams of 2-4 persons collected data at each site with Trimble CMT MC-V GPS receivers (Trimble Navigation Limited, Sunnyvale, CA) with data loggers mounted on all-terrain vehicles. Stopping at each burrow entrance, the observer classified the burrow, recorded GPS coordinates, and marked the burrow with flour to prevent re-mapping. Based on the presence of a prairie dog, prairie dog fecal material, or fresh digging, burrows were classified as: (1) active, (2) inactive, or (3) plugged (Dullum 2001). To minimize the potential for observer error in classifying burrows, we provided training to all personnel involved in collecting data. We conducted all mapping between May and September in 2005 to match previous sampling seasons and to sample during summer when prairie dog populations are at their maximum size and exhibit the highest activity levels.

Statistical Analyses

The locations of active and inactive burrows at each study site formed the basis for our spatial analyses. We evaluated whether the cumulative distribution of active burrows across each site was distributed randomly or showed a positive or negative tendency to cluster using a Ripley's K function (Ripley 1977, 1981):

$$K(t) = N^{-2} A \sum_i \sum_{j \neq i} I_t(u_{ij})$$

in program R (Dalggaard 2002) where t is the radius of a circle centered on a burrow i , N is the total number of burrows, A is the area of the prairie dog colony, and I_t is a counter-variable that is set to 1 if the distance between burrows i and j is $\leq t$, otherwise $I_t = 0$.

We created utilization distributions (UDs) from the active and inactive burrow spatial data (van Winkle 1975) using a fixed kernel approach (Kernohan et al. 2001) to estimate the distribution of active and inactive burrows across each study area.

The UD value $[\hat{f}_{UD}(x, y)]$ at location (x, y) represents the relative number of burrows at that location (or cell) relative to other locations on the site and results in a probability density function. We calculated UD values in Matlab (The Mathworks Incorporated, Natick, MA) as the 100% extent of prairie dog burrows using the 'Kde folder' (Beardah and Baxter 1995) and "plug-in" methods for bandwidth selection (Wand and Jones 1995; Gitzen et al. 2006).

We used a volume of intersection (VI) index (Seidel 1992; Millsbaugh et al. 2004) analysis to quantify how the overall spatial distribution of active and inactive prairie dog burrows changed over time at UL Bend and Conata Basin. We defined the VI index as

$$VI = \iint \hat{f}_1(x, y), \hat{f}_2(x, y) dx dy$$

where \hat{f}_1 is the estimated UD for one burrow data set (e.g., 1994 UL Bend ac-

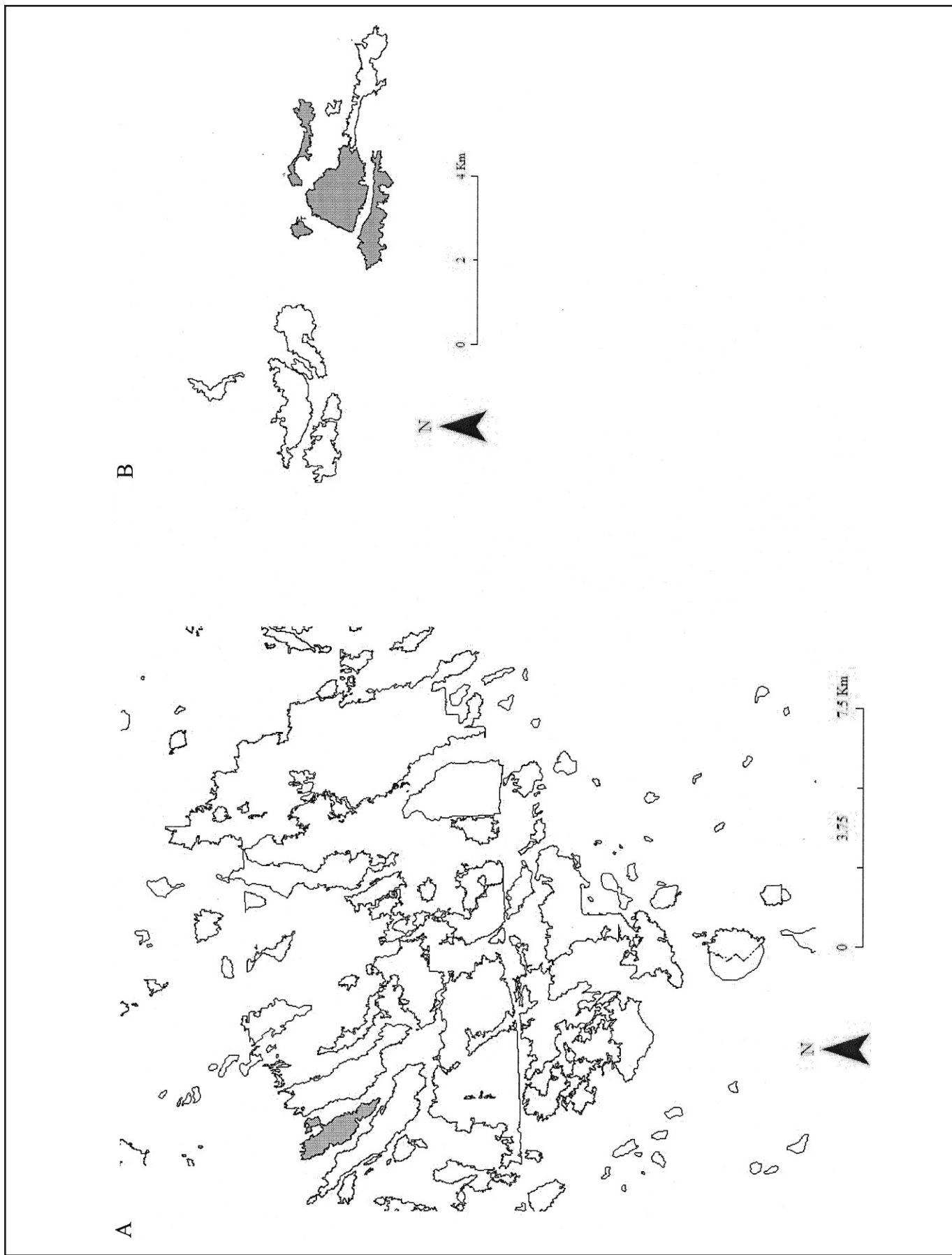


Figure 1. Perimeter map of black-tailed prairie dog colonies in the Conata Basin, South Dakota (A) and UL Bend National Wildlife Refuge, Montana (B), with study areas depicted in solid shading.

tive burrow UD) and \hat{f}_2 is the UD for a second burrow data set (e.g., 2005 UL Bend active burrow UD). A VI index score of 1 implies that the 3-D surfaces of the two UDs are identical.

We used the active burrow UDs to assess fine-scale shifts in prairie dog burrow distribution and patch dynamics. We estimated the relative change in prairie dog burrow distribution by subtracting UD values at time $t+1$ from UDs at time t for both sites. This produced values for the relative change in prairie dog burrow distribution over time throughout each colony. We also evaluated the change in patch characteristics over time. To assess patch dynamics, we classified use-intensities of the active burrow UDs into a five-level, ordered factor based on the quantiles of the UD (i.e., Type 1 contained the lowest density patches and Type 5 contained the highest density patches). We used program FragStats (McGarigal et al. 2002) to estimate patch spatial attributes related to the size and distribution of all patches. While multiple metrics can be derived from the spatial distribution of patches, we focused on the number, size, connectivity, and percentage of the study area covered by each patch type at both sites during both time periods. We measured patch connectivity using a connectance index,

$$Connectivity = \left[\frac{\sum_{j=k}^n c_{ijk}}{n_i(n_i - 1)} \right] \frac{2}{2}$$

where c_{ijk} is the joining between patch j and k ($0 =$ unjoined, $1 =$ joined) of the corresponding patch type (i), within 200 m of each other, and n_i is the number of patches in the landscape of the corresponding patch type (class). We combined patches of Types 4 and 5 to represent high-density patches due to the potential value of these areas to ferrets (Biggins et al. 2006a). By estimating mean active burrow density within each patch type, we examined how burrow density varied between sites and between years.

RESULTS

The spatial distribution of active burrows was highly variable at both sites and showed a tendency to cluster into high-density areas (Figures 2 and 3). The Ripley's K function values (Figure 4) for both study sites and both sampling periods indicated a strong tendency for active burrows to be clustered at all distance scales. Visual inspection of UDs (Figures 2 and 3) supported the Ripley's K result and showed the variability in active burrow density across each site, as well as the tendency for clustering of burrows in high-density areas.

While the maximum spatial extent of active prairie dog burrows changed very little over time at either site (Figures 2 and 3), we found that the relative distribution of burrows changed at both sites over time. The total area of colonies at the UL Bend site changed from 906.84 to 965.07 ha over an eleven-year period and colonies at the Conata Basin site changed from 618.48 to 643.02 ha over a six-year period. UL Bend had a relatively high VI score for active burrows of 0.93 between 1994 and 2005, while Conata Basin had a lower score of 0.82 between 1999 and 2005, suggesting a greater degree of change in the spatial distribution of active prairie dog burrows at Conata Basin. This was further supported by an increase in the ratio of active to inactive burrows over time at Conata Basin (Table 1), while the ratio remained relatively constant at UL Bend.

Finer-scale analyses of active prairie dog burrow distributions demonstrated a tendency for high-density burrow patches to shift over time. At UL Bend, the cumulative area of high-density patches increased

slightly, but the number of such patches decreased (Table 2). The connectance index at UL Bend was relatively low among patches at both time periods (Table 2). Despite these modest changes, there was a trend towards an increased number of high-density patches on the perimeter of the colony (Figure 3). Similarly, at Conata Basin, the cumulative area of high-density patches increased. Although Conata Basin had a higher degree of connectivity than UL Bend (Table 2), the connectance index decreased from 1999 to 2005 (Table 2). The decrease in the connectance index was the result of high-density patches shifting toward the periphery of the colony (Figure 2), which also resulted in lower relative densities in the interior (Figures 2). High-density patches made up a slightly higher percentage of the colony area at Conata Basin than at UL Bend (Table 2).

We observed a dynamic relationship between active and inactive burrows over time. At both study sites, we observed a shift from active to inactive, and vice versa, over time (Figures 5 and 6). For example, the highest relative density of active burrows at UL Bend in 1995 became the highest relative density of inactive burrows in 2005 (Figure 6).

DISCUSSION

We found that prairie dogs formed distinct high-density patches of occurrence within their colonies and that the size, shape, and connectivity of these patches changed over relatively short time scales. Despite these internal dynamics, colonies changed little in total extent at either site. While others have reported rapid expansion of colonies (Knowles 1986, 1987), we attribute

Table 1. Ratio of active:total, inactive:total, and inactive:active burrows at each study site during both time periods.

Site	Year	Active:Total	Inactive:Total	Inactive:Active
Conata Basin	1999	1:1.1	1:9.4	1:8.3
	2005	1:1.2	1:5.7	1:4.6
UL Bend	1994	1:1.1	1:10.7	1:9.7
	2005	1:1.2	1:10.1	1:8.6

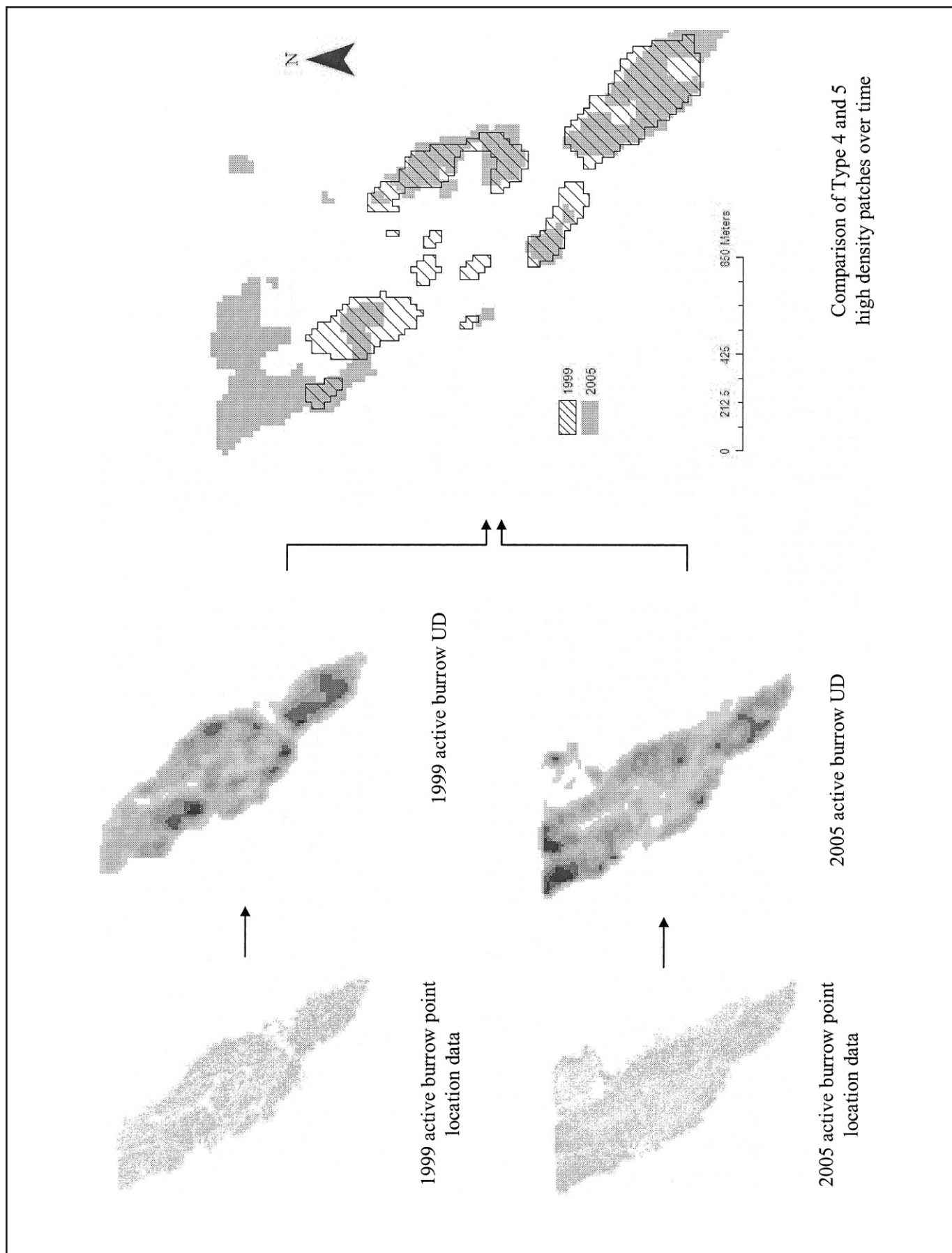


Figure 2. From left to right, active burrow locations, kernel utilization distribution grids created from burrow locations where dark shading represents high-density areas, and the area covered by Type 4 and 5 patches in 1999 and 2005 at the Conata Basin site in South Dakota.

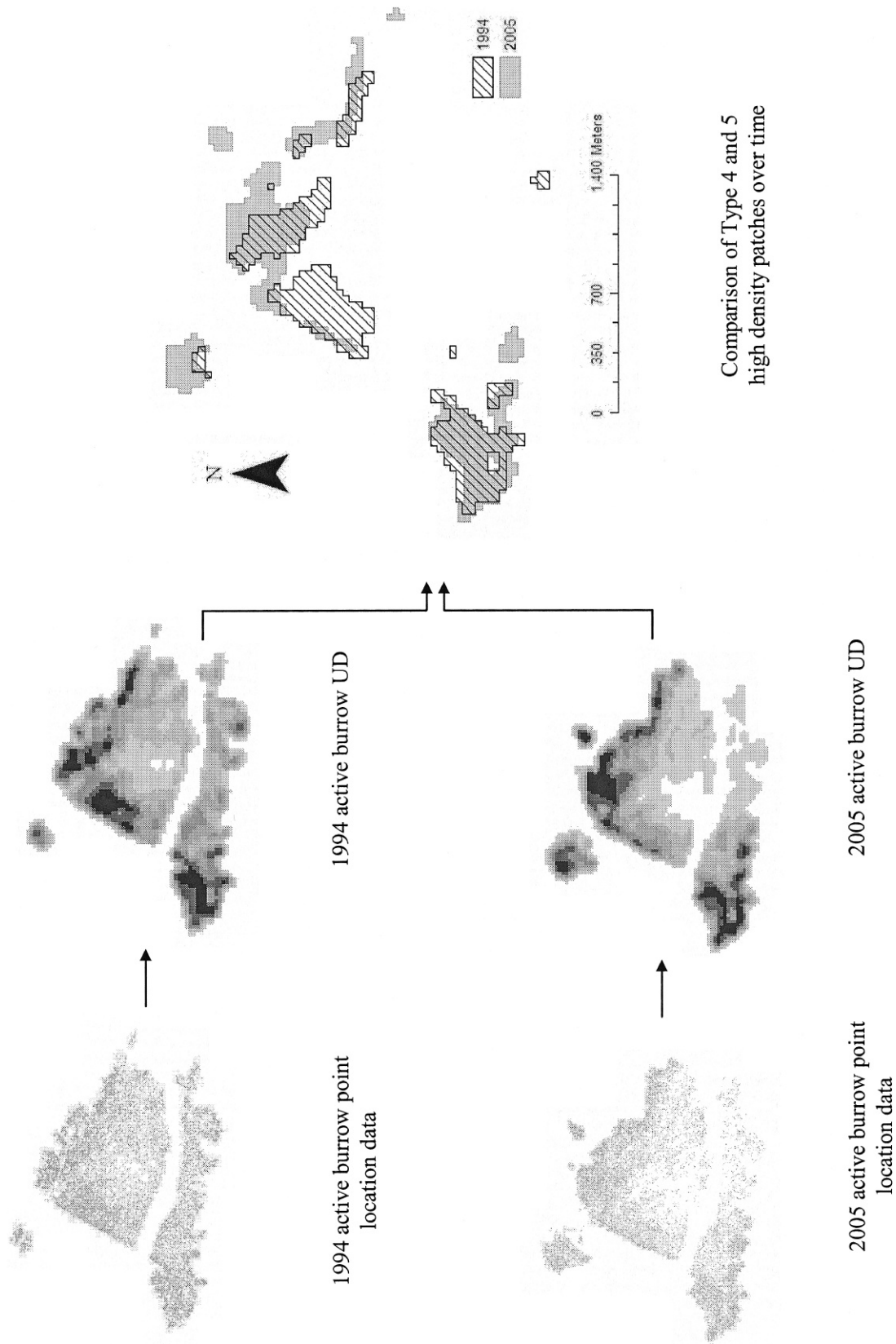


Figure 3. From left to right, active burrow locations, kernel utilization distribution grids created from burrow locations where dark shading represents high-density areas, and the area covered by Type 4 and 5 patches in 1994 and 2005 at the UL Bend site in Montana.

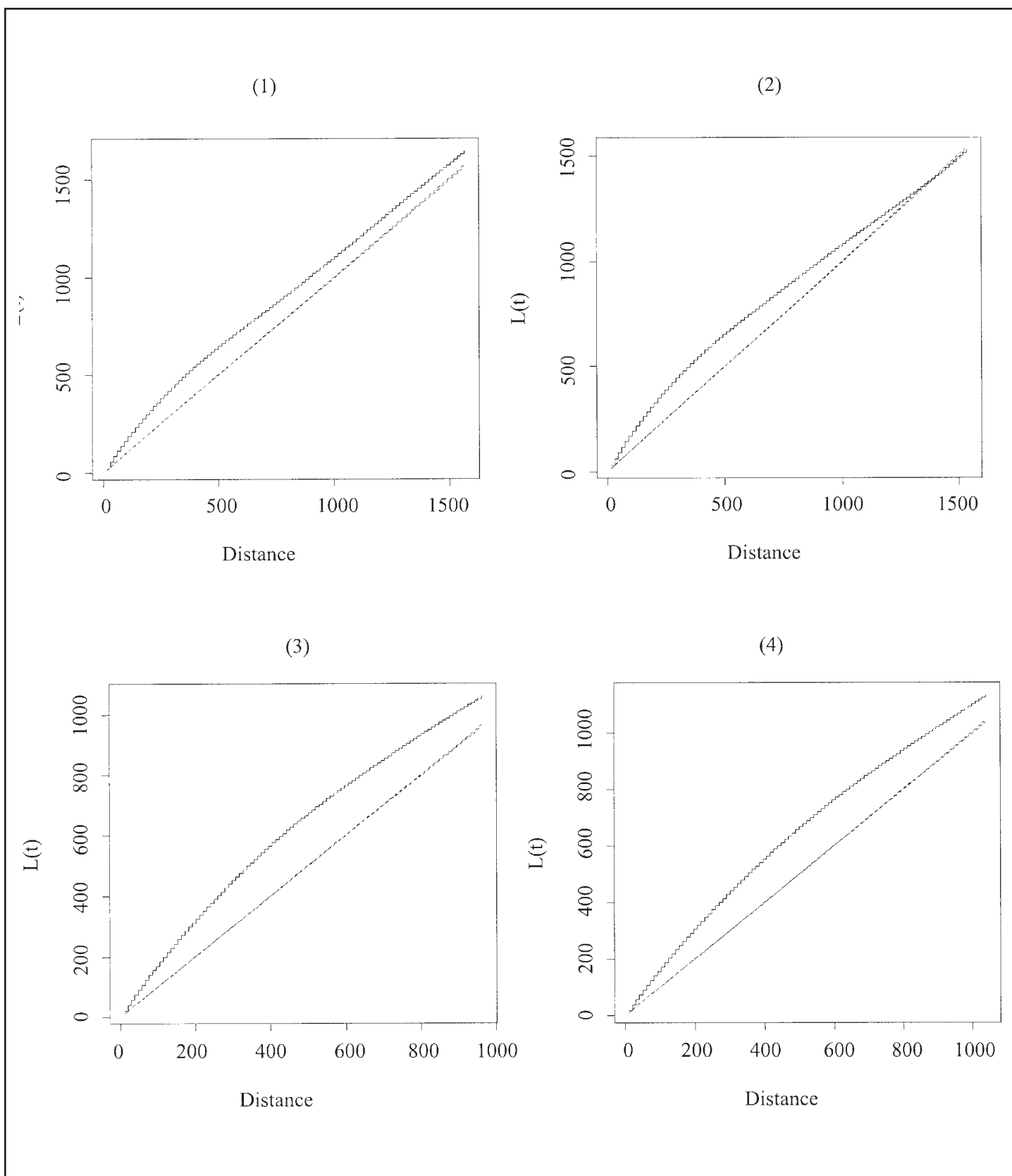


Figure 4. Output for Ripley's K analysis showing that the spatial distribution of active burrows across each area tends to be clustered for (1) UL Bend 1994 ($n = 11,317$, $k = 100$), (2) UL Bend 2005 ($n = 11,921$, $k = 100$), (3) Conata Basin 1999 ($n = 19,105$, $k = 100$), and (4) Conata Basin 2005 ($n = 22,671$, $k = 100$). Dashed lines represent 95% confidence envelopes that delineate significant departures from randomness. Solid lines above the envelopes represent the tendency of points to form a clumped rather than regular (below envelope) or random (within envelope) distribution.

Table 2. Patch attributes by patch type for UL Bend, Montana and Conata Basin, South Dakota at each time interval.

Location	1994 UL Bend					2005 UL Bend					1999 Conata Basin					2005 Conata Basin				
Patch Type	1	2	3	4 and 5		1	2	3	4 and 5		1	2	3	4 and 5		1	2	3	4 and 5	
Cumulative Area (ha) ¹	555.14	187.69	104.87	59.14	560.08	260.32	80.36	64.31	426.61	64.44	82.01	45.42	400.90	104.11	81.58	56.43				
Percentage of landscape ²	61.22	20.70	11.56	6.52	58.04	26.97	8.33	6.66	68.98	10.42	13.26	7.34	62.35	16.19	12.69	8.78				
Number of patches	1	4	18	10	3	2	12	8	1	6	1	10	2	2	6	9				
Connectance Index ³	0.00	33.33	11.76	8.89	100.00	100.00	19.70	10.71	0.00	46.67	0.00	33.33	0.00	100.00	33.33	11.11				
Mean active burrow density ⁴	0.00	10.84	41.27	83.72	0.00	9.85	45.13	89.02	0.00	15.44	104.39	210.17	0.00	27.18	106.78	197.15				

¹ Total area covered by patch type (Patch type 1 includes area of UD surrounding actual extent of prairie dog burrows)

² Percentage of measured area covered by patch type

³ The number of functional joinings between all patches of the corresponding patch type within 200m of each other, divided by the total number of possible joinings between all patches of the corresponding patch type, multiplied by 100 to convert to a percentage.

⁴ Mean burrow density of each patch type calculated as active burrows per ha

their relative stability at our study sites to several factors, including topographic and vegetative barriers (Hoogland 1995, 2006). The observed shifting of patches with relatively high densities of active burrows has important implications for how we currently assess ferret habitat, the management of prairie dog colonies, and overall ferret recovery.

Estimating prairie dog abundance and distribution is a critical factor in establishing management goals and assessing habitat for dependent species, such as the black-footed ferret. Current management plans frequently set prairie dog management goals based on the commonly used measurements of total acreage covered by prairie dog colonies as defined by the maximum extent of burrows (Knowles 1999; Cooper and Gabriel 2005) and average burrow density (Biggins et al. 1993). These methods, while valuable in measuring habitat at a large scale, fail to account for the patchy distribution of prairie dogs within colonies that might be crucial to ferret resource selection and survival. Assuming that female ferrets select for areas with high prairie dog burrow density within a colony (Biggins et al. 2006a), we hypothesize that the ability of a site to maintain a self-sustaining ferret population is partly influenced by the size, availability, and density of high-density patches of prairie dogs. This supposition is supported by the greater connectivity of high-density patches and percent of area in mid to high-density patches at the Conata Basin where ferret reintroduction has resulted in a self-sustaining population.

How areas of high active burrow density shift over time is not solely limited to colony expansion, but likely occurs at smaller scales within colonies as dictated by forage availability and soil type. Prairie dog occupancy has been shown to drive plant community structure over time (Cincotta et al. 1989), and prairie dog distribution likely responds to changes in vegetation species composition and productivity. The vegetation zones on prairie dog colonies have been noted to form concentric rings (Garrett et al. 1982). Changes in vegetative cover and species composition over time have been attributed to prolonged

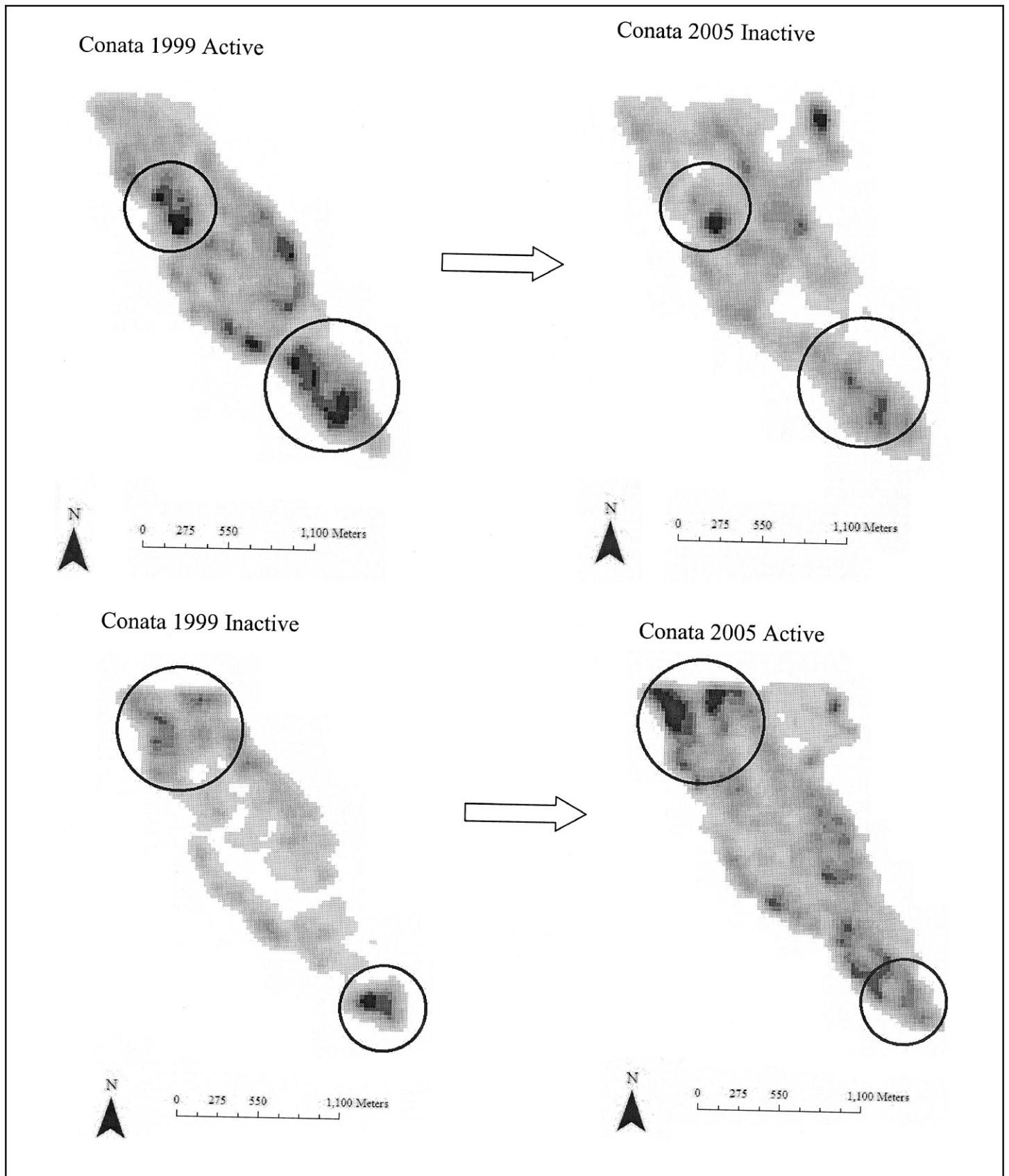


Figure 5. Utilization distributions of active and inactive burrows across the Conata Basin study sites during both mapping occasions depicting the shift in prairie dog activity areas over time. Areas within circles show areas within colonies that previously had high densities of active burrows and have since become inactive, or areas within colonies that previously had high densities of inactive burrows and have since become active over time.

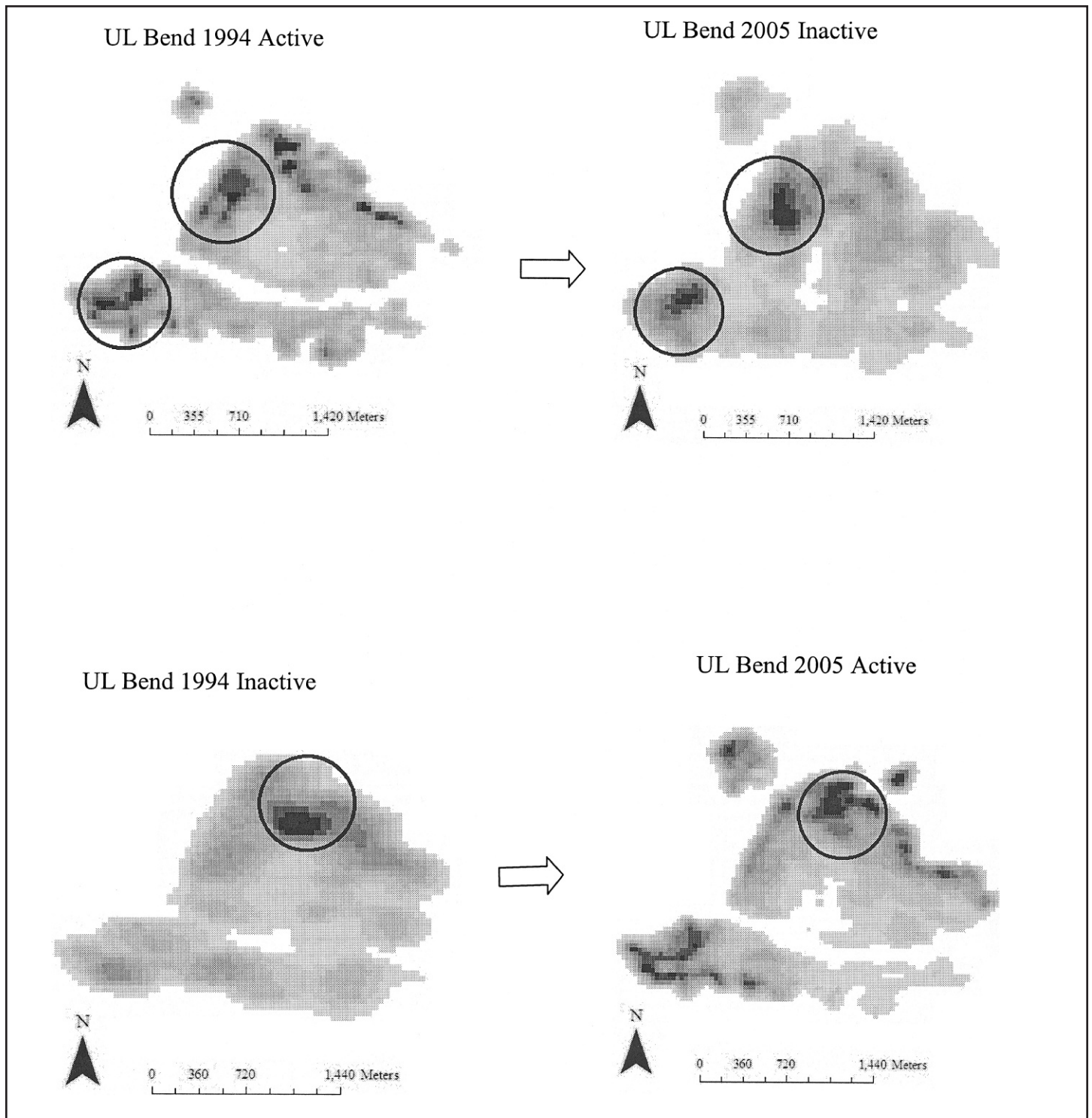


Figure 6. Utilization distributions of active and inactive burrows across the UL Bend study site during both mapping occasions depicting the shift in prairie dog activity areas over time. Areas within circles show areas within colonies that previously had high densities of active burrows and have since become inactive, or areas within colonies that previously had high densities of inactive burrows and have since become active over time.

intensive grazing pressure, with palatable perennial grass species shifting to the perimeter of colonies, and being replaced in more central areas by weedy annual species (Coppock et al. 1983; Archer et

al. 1987; Detling and Whicker 1987). At a large scale, our results support these previous findings and show that prairie dogs moved towards the perimeter of colonies over time. However, looking more closely

at prairie dog distribution within colonies, we found that previously occupied areas within colonies become inactive and vice versa (Figures 5 and 6). Multiple factors could explain these cyclical shifts from

activity to inactivity over time ranging from the potential effect of sustained ferret occupancy and predation to the potential effects of non-epizootic or enzootic sylvatic plague (Matchett et al., in prep). However, the most likely factor to induce these observed shifts are changes in vegetative cover. We hypothesize that the relationship between vegetative cover and prairie dog occupancy is likely a dynamic process, where activity areas of prairie dogs shift spatially within colonies over time, thereby enabling long-term occupancy of a defined area or burrow system. Thus, the inactive portion of prairie dog colonies should not be viewed as low in habitat value over the long term because these sites might again become populated.

Our findings also suggest that where climate and soil conditions allow, management of vegetation structure might serve as a tool to create and sustain patches of high prairie dog density and patch connectivity, thus improving habitat for dependent species. Given that ferrets select and likely compete for areas of high prairie dog density (Biggins et al. 2006a), the spatial dynamics we observed have important implications for techniques to estimate the suitability of ferret habitat and for the management of prairie dog colonies. The shifting of high-density areas of active prairie dog burrows within colonies over time, likely associated with changes in vegetation, suggests that through the management of vegetation we might be able to improve habitat for ferrets by creating large high-density areas.

ACKNOWLEDGMENTS

This work was supported by funds from the U.S. Fish and Wildlife Service, University of Missouri, the National Fish and Wildlife Foundation, and the South Dakota Department of Game, Fish, and Parks Wildlife Diversity Small Grants Program. We are extremely grateful to the field support provided by R. Jachowski, J. McRoberts, N. Eisenbraun, J. Eisenbraun, M. Lockhart, P. Gober, S. Larsen, and D. Sargent. We thank R. Jachowski, B. Gitzen, and two anonymous reviewers for valuable comments on the manuscript.

David S. Jachowski is a M.S. student in the Department of Fisheries and Wildlife Sciences at the University of Missouri.

Joshua J. Millspaugh is an Associate Professor of Wildlife Conservation and an Adjunct Assistant Professor of Statistics at the University of Missouri.

Dean E. Biggins is a Research Wildlife Biologist with U.S. Geological Survey, Fort Collins Science Center.

Travis M. Livieri is the Executive Director of Prairie Wildlife Research.

Marc R. Matchett is the Senior Wildlife Biologist for the Charles M. Russell National Wildlife Refuge.

LITERATURE CITED

- Archer, S., M.G. Garrett, and J.K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Plant Ecology* 72:159-166.
- Beardah, C.C., and M.J. Baxter (eds.). 1995. MATLAB routines for kernel density estimation and the graphical representation of archaeological data. Leiden University, Rapenburg, The Netherlands.
- Biggins, D.E., J.L. Godbey, M.R. Matchett, and T.M. Livieri. 2006a. Habitat preferences and intraspecific competition in black-footed ferrets. Pp. 129-142 in J.E. Rolle, B.J. Miller, J.L. Godbey, and D.E. Biggins, eds., *Recovery of the black-footed ferret – progress and continuing challenges*. Scientific Investigations Report 2005-5293, U.S. Geological Survey, Reston, Va.
- Biggins, D.E., B. Miller, L. Hanebury, R. Oakleaf, A. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. Pp. 73-78 in J. Oldemeyer, B. Miller, and R. Crete, eds., *Management of prairie dog complexes for reintroduction of the black-footed ferret*. Biological Report 13, U.S. Fish and Wildlife Service, Washington, D.C.
- Biggins, D.E., J.G. Sidle, D.B. Seery, and A.E. Ernst. 2006b. Estimating the abundance of prairie dogs. Pp. 94-107 in J.L. Hoogland, ed., *Conservation of the Black-tailed Prairie Dog*. Island Press, Wash.
- Cincotta, R.P., D.W. Uresk, and R.M. Hansen. 1989. Plant compositional change in a colony of black-tailed prairie dogs in South Dakota. Pp. 171-179 in A.J. Bjstad, D.W. Uresk, and R.H. Hamre, tech. coord., *Ninth Great Plains Wildlife Damage Control Workshop*, Ft. Collins, Colo.
- Cooper, J., and L. Gabriel. 2005. South Dakota black-tailed prairie dog conservation and management plan. South Dakota Department of Game, Fish and Parks, Pierre.
- Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1-9.
- Dalgaard, P. 2002. *Introductory Statistics with R*. Springer-Verlag, New York.
- Detling, J.K., and A.D. Whicker. 1987. Control of ecosystem processes by prairie dogs and other grassland herbivores. Pp. 23-29 in D.W. Uresk, G.L. Schenbeck, and R. Cefkin, tech. coord., *Great Plains Wildlife Damage Control Workshop Proceedings*. University of Nebraska, Lincoln.
- Dullum, J.L.D. 2001. Efficacy of translocations for restoring populations of black-tailed prairie dogs in north-central Montana. M.S. thesis, University of Montana, Missoula.
- Garrett, M.G., J.L. Hoogland, and W.L. Franklin. 1982. Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). *American Midland Naturalist* 108:51-59.
- Gitzen, R.A., J.J. Millspaugh, and B.J. Kernohan. 2006. Bandwidth selection for fixed kernel analysis of animal range use. *Journal of Wildlife Management* 70:1334-1344.
- Hoogland, J.L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press, Chicago, Ill.
- Hoogland, J.L. 2006. Demography and population dynamics of prairie dogs. Pp. 27-52 in J.L. Hoogland, ed., *Conservation of the Black-tailed Prairie Dog*. Island Press, Wash.
- Johnson, W.C., and S.K. Collinge. 2004. Landscape effects on black-tailed prairie dog colonies. *Biological Conservation* 115:487-497.
- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 126-166 in J.J. Millspaugh and J.M. Marzluff, eds., *Radio Tracking and Animal Populations*. Academic Press, San Diego, Calif.
- Knowles, C.J. 1986. Population recovery of black-tailed prairie dogs following control with zinc phosphide. *Journal of Range Management* 39:249-251.

-
- Knowles, C.J. 1987. Reproductive ecology of black-tailed prairie dogs in Montana. *Great Basin Naturalist* 47:202-206.
- Knowles, C.J. 1999. A species conservation plan for the black and white-tailed prairie dogs in Montana. FaunaWest Wildlife Consultants, Boulder, Mont.
- Kotliar, N.B., B.W. Baker, A.D. Whicker, and G.E. Plumb. 1999. A critical review of assumptions about prairie dogs as a key-stone species. *Environmental Management* 24:177-192.
- Livieri, T.M. 2006. Ten-year history of the Conata Basin black-footed ferret population: 1995-2005. Prairie Wildlife Research, Wall, S. Dak.
- McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps, Version 3.0. University of Massachusetts, Amherst.
- Miller, B., G. Ceballos, and R.P. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8:677-681.
- Millsbaugh, J.J., R.A. Gitzen, B.J. Kernohan, M.A. Larson, and C.L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32:148-157.
- Ripley, B.D. 1977. Modeling spatial patterns. *Journal of the Royal Statistical Society Series B* 39:172-212.
- Ripley, B.D. 1981. *Spatial Statistics*. J. Wiley, New York.
- Seidel, K.D. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. M.S. thesis, University of Washington, Seattle.
- Severson, K.E., and G.E. Plumb. 1998. Comparison of methods to estimate population densities of black-tailed prairie dogs. *Wildlife Society Bulletin* 26:859-866.
- Sidle, J.G., D.H. Johnson, and B.R. Euliss. 2001. Estimated aerial extent of colonies of black-tailed prairie dogs in the northern Great Plains. *Journal of Mammalogy* 82:928-936.
- U.S. Fish and Wildlife Service. 2004. Black-tailed prairie dog species assessment and listing priority assignment form. U.S. Department of the Interior, Washington D.C.
- Uresk, D.W., J.G. MacCracken, and A.J. Bjugstad. 1982. Prairie dog density and cattle grazing relationships. Pp. 199-201 in R.M. Timm and R.J. Johnson, eds., *Fifth Great Plains wildlife damage control workshop proceedings*. University of Nebraska, Lincoln.
- van Winkle, W. 1975. Comparison of several probabilistic home-range models. *Journal of Wildlife Management* 54:322-330.
- Wand, M.P., and M.C. Jones. 1995. *Kernel Smoothing*. Chapman and Hall, London.
- White, G.C., J.R. Dennis, and F.M. Pusateri. 2005. Area of black-tailed prairie dog colonies in eastern Colorado. *Wildlife Society Bulletin* 33:265-272.