

# Spatial Analysis of Effects of Mowing and Burning on Colony Expansion in Reintroduced Black-Tailed Prairie Dog (*Cynomys ludovicianus*)

Jason Northcott,<sup>1</sup> Mark C. Andersen,<sup>2,3</sup> Gary W. Roemer,<sup>3</sup> Ed L. Fredrickson,<sup>4</sup> Michael DeMers,<sup>5</sup> Joe Truett,<sup>6</sup> and Paulette L. Ford<sup>7</sup>

## Abstract

Factors governing the rate and direction of prairie dog (*Cynomys* spp.) colony expansion remain poorly understood. However, increased knowledge and ability to control these factors may lead to more effective reintroductions of prairie dogs and restoration of grassland habitats. We present density and directional analyses of the establishment of new burrows on three reintroduced colonies of Black-tailed prairie dog (*Cynomys ludovicianus*) in southern New Mexico; the study colonies had been subjected to mow and burn treatments in the second year of the study. Our hypotheses were that prairie dogs will preferentially dig new burrows in the treatment plots versus control plots and that the colonies will expand in the

direction of the treatment plots. The results support these hypotheses; analysis of burrow counts by site and treatment shows that prairie dogs preferentially colonized both mow and burn treatments compared to untreated areas at the periphery of the colonies. Directional analysis showed a significant posttreatment orientation of new burrows toward the treatment plots for all colonies. Our results show that the direction of expansion of prairie dog colonies can be manipulated. Effective control of the expansion of prairie dog colonies may lead to more successful reintroductions.

**Key words:** Black-tailed prairie dogs, *Cynomys ludovicianus*, directional analysis, fire, grasslands, reintroductions.

## Introduction

Given suitable habitat and exclusion of factors such as recreational hunting, poisoning, habitat loss, and *Yersinia pestis* (the bacterium causing the plague), reintroduced prairie dog (*Cynomys*) colonies will typically expand from year to year (Halpin 1987; Garrett & Franklin 1988; Hoogland 1995). In this study, we define colony size as the area occupied by a prairie dog colony and expansion as colonization of new habitat outside the existing colony boundaries. Colony expansion occurs mainly during the spring with emergence of juveniles; the direction of colony expansion depends on the availability of vegetation with suitable height and cover type and on low-slope areas with soil suitable for burrowing (King 1955; Koford 1958; Cincotta et al. 1988; Hoogland 1995). Nevertheless, factors

and processes that could be manipulated to control colony expansion remain poorly understood.

Historically, the public did not view prairie dogs favorably. Eradication programs were encouraged by government agencies due to the fear of disease transmission and competition with livestock for forage (Merriam 1902; Hoogland 1995). Today, attitudes toward prairie dogs are improved (Zinn & Andelt 1999) due to better science, introduction of financial compensation and incentive programs (Coon 2002; Lybecker et al. 2002), the importance of prairie dogs to the recovery of the critically endangered Black-footed ferret (*Mustela nigripes*; Forrest et al. 1988; Biggins et al. 1993), and popular opinion favoring restoration of ecosystems to "pristine" conditions (Cole 2000a, 2000b; Landres et al. 2001). These factors provide a favorable social and political context for prairie dog reintroduction and restoration programs.

The Black-tailed prairie dog (*Cynomys ludovicianus*) is a member of the squirrel family Sciuridae (Murie & Michener 1984). These fossorial rodents occupy open flat grasslands with little or no woody vegetation (King 1955; Koford 1958; Butler 1995). In North America, there are four other species of prairie dog: Gunnison's (*C. gunnisoni*), Utah (*C. parvidens*), Mexican (*C. mexicanus*), and White-tailed (*C. leucurus*). Populations of all five prairie dog species have declined dramatically in the past 100 years. The Utah prairie dog is classified as threatened, and the Mexican prairie dog is classified as endangered

<sup>1</sup> The Nature Trust of British Columbia, 260-1000 Roosevelt Crescent, North Vancouver, British Columbia, Canada V7P 3R4

<sup>2</sup> Address correspondence to M. Andersen, email manderse@nmsu.edu

<sup>3</sup> Department of Fishery and Wildlife Sciences, New Mexico State University, Las Cruces, NM 88003-0003, U.S.A.

<sup>4</sup> USDA, Agricultural Research Service, Jornada Experimental Range, Las Cruces, NM 88003-0003, U.S.A.

<sup>5</sup> Department of Geography, New Mexico State University, Las Cruces, NM 88003-0003, U.S.A.

<sup>6</sup> Turner Endangered Species Fund, Glenwood, NM 88039, U.S.A.

<sup>7</sup> USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM 87102-3497, U.S.A.

(Hoogland 1995). Of all these species, the Black-tailed prairie dog is the most abundant and widespread (Graves 2001).

Prairie dogs are social animals that live in colonies or towns (Costello 1970). Black-tailed prairie dogs are the most colonial prairie dog species (Graves 2001). Benefits of coloniality are well documented and include increased predator detection, mate selection, and location of food sources through communication (Patterson 1965; Munro & Bedard 1977; Bertram 1978; Hoogland 1981; Wittenberger & Hunt 1985; Hoogland 1995). Physical barriers such as arroyos, streams, or roads within a colony may further divide the colony into subcolonies or wards (King 1955). Thus, there is at least one ward per colony. In addition, there are family units called coterie consisting of a single breeding adult male, three or four females, and juveniles (Hoogland 1995). Within the coterie's territory, all members have unlimited access to about 60–70 burrow entrances connected through branching underground tunnels; underground connections between coterie have not been documented (Hoogland 1995).

At times, historic colonies were immense landscape features spanning thousands of square kilometers and containing millions of individuals, such as the famous prairie dog town near Lubbock, Texas, that covered approximately 6,475,000 ha (Bailey 1905; Agnew et al. 1986). The largest present-day colony is near Janos, Mexico, occupying approximately 15,000 ha (Van Pelt 1999; Marce-Santa 2001). Today, most existing colonies are fragmented over the landscape owing to habitat loss due to agriculture and urban development (Hoogland 1995).

Burrowing rodents have been shown to have profound effects on vegetation and soils in a variety of systems (Zhang et al. 2003; Arias et al. 2005; Eldridge et al. 2006). These effects are often in conflict with human land use patterns. Thus, there is a need to manage habitat use by such species, particularly when they form large colonies as prairie dogs do. Although studies have assessed the use of nonlethal methods such as visual barriers to constrain prairie dog colony expansion (Hygnstrom 1996; Van Pelt 1999; Hendrie 2004), very little work has been done on how habitat manipulations such as mow and burn treatments can affect the direction of prairie dog colony expansion. A recent study conducted in North Dakota (the northern extent of the Black-tailed prairie dog range) by Milne-Laux and Sweitzer (2006) has shown that prairie dogs venture more readily and dig burrows into experimental plots treated by burning and mechanical brush removal. It is reasonable to expect colony expansion to be related to vegetation structure because Black-tailed prairie dogs have difficulty colonizing areas with tall and/or dense plant cover (Garrett & Franklin 1988; Wolff 1999). Thus, manipulation of vegetation structure through mow and burn treatments can promote colony expansion. In this study, we analyze changes in the spatial pattern of burrows in three study colonies pre- and posttreat-

ment to determine whether the treatments influence colony expansion.

We hypothesize that prairie dogs will preferentially dig new burrows in or near plots treated by mowing or burning, thus influencing the rate and direction of colony expansion. We analyze this cause-and-effect relationship in two parts. First, we use analyses of burrow density to examine whether new burrows are preferentially located in the treatment plots. Then, we use directional analysis to examine whether the colonies are expanding in the direction of the treatment plots.

## Methods

### Study Area

The Armendaris Ranch in southern New Mexico contains some of the last natural remnants of Chihuahuan Desert grassland and occupies 145,750 ha in the Jornada del Muerto Basin. Chihuahuan Desert landscapes are composed primarily of semidesert grassland and Chihuahuan Desertscrub. Dominant grasses in the study area are perennial bunchgrasses including Alkali sacaton (*Sporobolus airoides*), Tobosa (*Pleuraphis mutica*), and Burrograss (*Scleropogon brevifolius*; Brown 1994; Hartsough 2002). These species form clumps varying in height from 10 to 60 cm. Desertscrub is dominated by Vine mesquite (*Panicum obtusum*) and Creosote bush and is typically not a suitable habitat for prairie dogs because the height and spatial arrangement of the grasses and shrubs make visual predator detection difficult. Black-tailed prairie dogs were reintroduced to the Armendaris Ranch into areas from which native colonies had been extirpated as late as 1965 (Oakes 2000). Currently, there are 14 introduced prairie dog colonies on the Armendaris Ranch; these colonies were established using the methods of Truett and Savage (1998) and Truett et al. (2001). The three colonies we studied were Red Lake (12 ha), established in 1998, and S-Curve (8 ha) and Deep Well (5 ha), both established in 1999; all three are located in desert grassland portions of the ranch.

### Data Collection

Characteristics of prairie dog burrows were recorded during four survey periods from 2000 to 2004. These periods were pre-treatment: summer 2000; posttreatment: summer 2001 and fall 2001; and 2 years posttreatment: fall 2003 for Deep Well and S-Curve and summer 2004 for Red Lake. For each survey, all new burrows were marked with a steel peg and numbered tag; their locations (in Universal Transverse Mercator coordinates) were recorded using the Trimble Geo-Explorer III (Trimble Navigation Limited, Sunnyvale, CA, U.S.A.). The point data were differentially corrected and then imported into ArcMap as shapefiles to create digital spatial maps for each colony.

Several characteristics of prairie dog burrows were recorded including the activity status of burrows. Status was determined by the presence of fresh digging, tracks, scat, and/or visual observation. Inactive burrows were not used in the analyses reported here; only active burrows were used because this characteristic more accurately reflects population density (Cincotta et al. 1988; Biggins et al. 1993; Hoogland 1995).

### Study Design

Multiple 50 × 50-m plots were established on the periphery of the three study colonies. There were a total of 11 plots at Deep Well, 14 at S-Curve, and 23 at Red Lake. Six of these plots were randomly chosen to receive mow ( $n = 3$ ) or burn ( $n = 3$ ) treatments at Deep Well and S-Curve colonies, and eight of the plots were randomly chosen to receive mow ( $n = 4$ ) and burn ( $n = 4$ ) treatments at Red Lake colony. Treatment type (mow vs. burn) was then randomly assigned to each plot that had been selected to receive either the mow or the burn treatment. Plots not selected for treatment were control plots.

### Data Analysis

Burrow densities were calculated for all plots at all three sites for the pre-treatment (summer 2001) and first post-treatment (fall 2001) periods. We calculated the difference in burrow counts (pre-treatment vs. posttreatment) and the percent change in burrow counts from the pre-treatment period to the posttreatment period. Finally, we used analysis of variance (ANOVA) to assess differences between burrow counts due to site and treatment effects.

Directional analyses examined the orientation of colony expansion to test whether new burrows were oriented toward the treated plots relative to their nearest neighbor from the previous year, regardless of whether those new burrows were located in the treated plots or not. Directional data have two components: a magnitude and an angle (Burt & Barber 1996). In this case, the magnitudes represent distances from a new active burrow to the nearest active burrow from the preceding field survey. Angles were measured between these nearest neighbors from successive field seasons. The directional statistics we present here used only the angle data.

These measurements resulted in three directional datasets derived over four survey periods: pre-treatment, post-treatment, and 2 years posttreatment (2.5 years in the case of Red Lake). The magnitude and direction of these vectors were plotted graphically using rose diagrams or circular histograms (Davis 1986; Burt & Barber 1996). Mean direction,  $X_0$  (Mardia 1972), mean resultant length,  $R$ , and circular variance,  $S_0^2$  (Davis 1986; Burt & Barber 1996), were calculated for vector data using the following equations:

$$X_0 = 360^\circ - (\arctan(\sum \sin\theta / \sum \cos\theta)) \quad (1)$$

$$R = \left( \left( \sum \sin\theta \right)^2 + \left( \sum \cos\theta \right)^2 \right)^{1/2} \quad (2)$$

$$S_0^2 = 1 - (R/n), \quad (3)$$

where  $\theta$  is the observed angle and  $n$  is the total number of observations. The mean resultant length is a measure of dispersion of a sample of directional measurements (Burt & Barber 1996). Circular variance complements  $R$  and is a measure of variability (Davis 1986; Burt & Barber 1996). The mean resultant  $R$  and  $S_0^2$  both range from 0 to 1. These ranges are opposite; for  $R$ , 1.0 means a strong mean vector with little dispersion, whereas for  $S_0^2$ , the maximum variability or dispersion equals 1.0 (Davis 1986; Burt & Barber 1996). There are no units associated with  $R$  or  $S_0^2$ . Statistical hypothesis tests based on the von Mises distribution (the circular equivalent of the normal distribution) were performed to assess directional randomness ( $H_0: \kappa = 0$ ,  $H_1: \kappa > 0$ ) in the data (Mardia 1972; Davis 1986). The concentration parameter,  $\kappa$ , is a function of  $R$ . If  $\kappa = 0$ , then the data can be assumed to follow a circular uniform distribution (Davis 1986); if this hypothesis is rejected, then a preferred direction exists. The mean direction ( $X_0$ ) can only be calculated in the presence of such a trend. This  $X_0$  was calculated and superimposed on the rose diagrams (Mardia 1972).

Directional statistics have been used in studies of animal behavior (Christman & Lewis 2005), especially animal orientation (Marchetti & Scapini 2003; Zimmerman et al. 2003), and in studies of plant growth (e.g., Macek & Leps 2003). However, this study is the first, to our knowledge, to use directional statistics to examine expansion of occupied habitat, which is typically studied using methods based on diffusion (Okubo & Levin 2001) or random walk models (Turchin 1998). The statistical techniques used in this study can have broad application in analyzing wildlife movements and habitat expansions.

### Results

Results support the hypothesis that both mow and burn treatments created conditions conducive to colony expansion by *Cynomys ludovicianus*. ANOVA showed that burrow densities increased from pre-treatment to post-treatment on treatment plots versus control plots for all colonies (Table 1); the two treatments did not differ ( $p < 0.0001$ ). The differences between the burrow counts pre- and posttreatment are always greater for treatment plots versus control plots, indicating that prairie dogs moved preferentially to the treatment plots.

From these results, it can be expected that because prairie dogs preferentially colonized treatment plots versus control plots, the overall direction of colony expansion

**Table 1.** Difference in burrow densities between treatment and control plots for all colonies from summer 2001 (pre-treatment) survey to fall 2001 (first posttreatment) survey; overall test of treatment effect significant at  $p < 0.001$  in an ANOVA with colony as a random effect and treatment as a fixed effect (Pinheiro & Bates 2004).

Colony	Treatment	Average Difference	% Density Increase
Deep Well	Burn	14.0	309
	Mow	7.33	240
	Control	2.20	62.5
S-Curve	Burn	4.33	291
	Mow	5.67	290
	Control	1.75	143
Red Lake	Burn	4.25	480
	Mow	3.0	400
	Control	-1.3	51

"Average difference": (fall 2001 burrow count) - (summer 2001 burrow count); "% Density increase": (average difference/summer 2001 burrow count) × 100%.

will be oriented toward the treatments (Fig. 1). Directional statistical analyses showed no detectable preferred direction for the pre-treatment datasets (Table 2). However, posttreatment and 2 years posttreatment (2.5 years posttreatment for Red Lake) significant directions were detected. Posttreatment mean directions ( $X_0$ ) were oriented toward the treatment plots on the colony periphery (Figs. 2-4). The mean direction for new burrows 2 years posttreatment (2.5 years posttreatment at Red Lake) deviated slightly from the 1 year posttreatment direction at Deep Well (287°) and S-Curve (334°) but deviated substantially for Red Lake colony (162°). Our hypothesis is supported; mow and burn treatments influence the location of new burrows at both the plot and the whole-colony scales.

Based on the above results, it is reasonable to ask if the treatments also had an effect on the rate of colony expansion. To assess this, we performed an ANOVA with the same treatment structure as the analysis reported in Table 1; however, in this analysis, the experimental units

**Table 2.** Rayleigh's test for the presence of a directional trend in orientation of new burrows for the three colonies for the three time periods.

Colony	Time Period	Calculated Value for Mean Resultant Length, $R$	$X_0$	$S$
Deep Well	Pre-treatment	0.125	—	—
	Posttreatment	0.354*	278°	0.997
	2 years later	0.205*	287°	0.998
S-Curve	Pre-treatment	0.089	—	—
	Posttreatment	0.297*	315°	0.998
	2 years later	0.320*	344°	0.995
Red Lake	Pre-treatment	0.218	—	—
	Posttreatment	0.313*	357°	0.994
	2 years later	0.359*	162°	0.993

A preferred direction exists only for the two posttreatment periods.  
 \*Mean direction significant in a test of directional randomness ( $H_0: \kappa = 0, p \leq 0.05$ ).

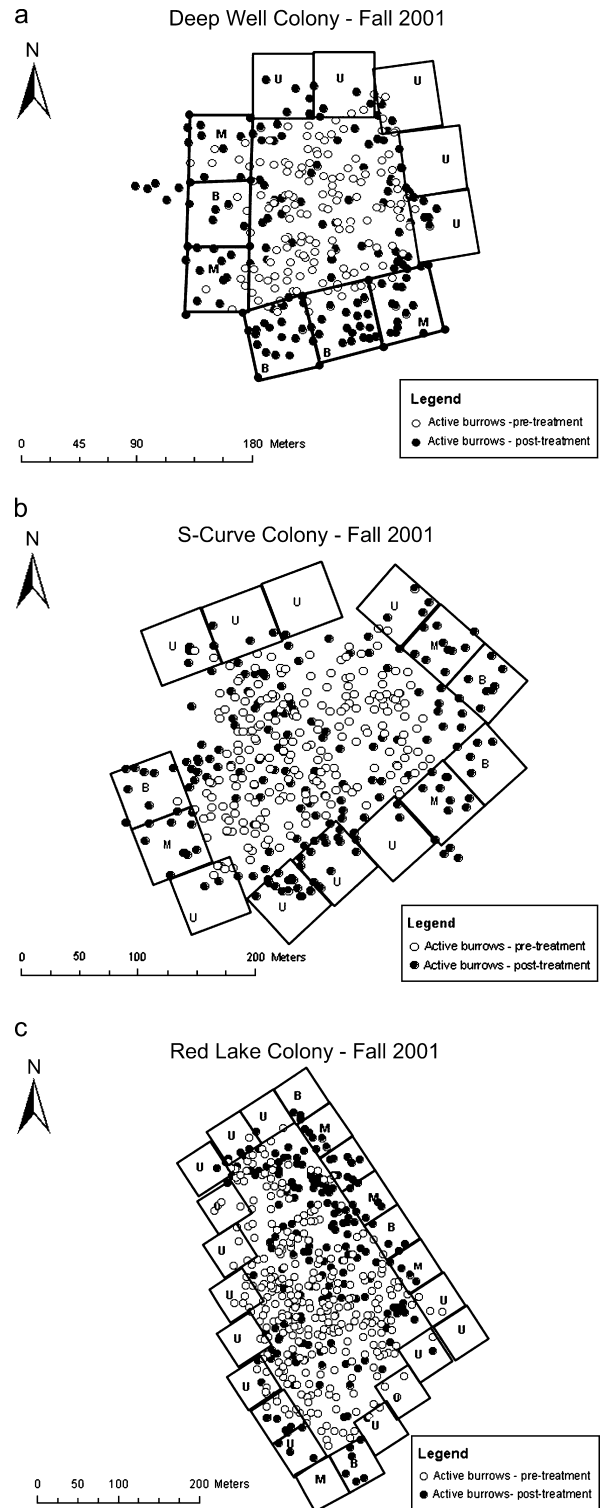


Figure 1. (a) Overview of Deep Well colony displaying location of treatment plots' active burrows from pre-treatment: summer 2001 to posttreatment: fall 2001. (b) Overview of S-Curve colony displaying location of treatment plots' active burrows from pre-treatment: summer 2001 to posttreatment: fall 2001. (c) Overview of Red Lake colony displaying location of treatment plots' active burrows from pre-treatment: summer 2001 to posttreatment: fall 2001. B, burned plots; M, mowed plots; U, untreated (control) plots.

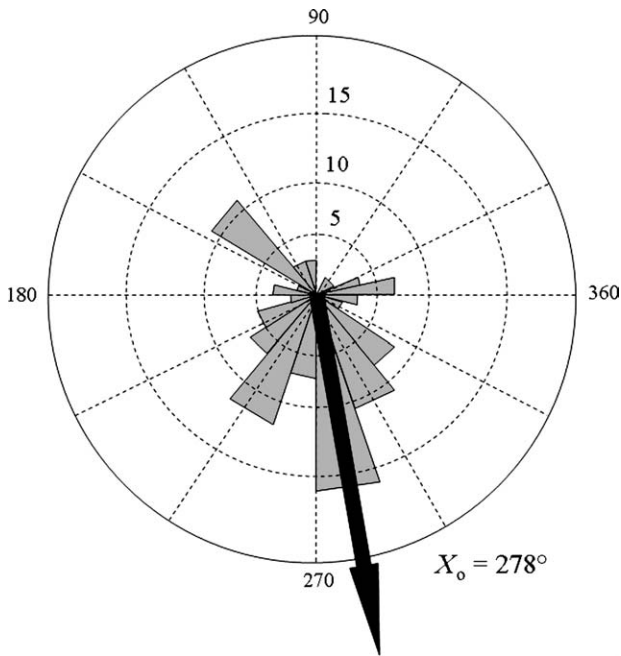


Figure 2. Rose diagram for Deep Well colony showing distributions of vectors from each active burrow at the pre-treatment period to the nearest new burrow at the posttreatment period. Mean direction  $X_0 = 278^\circ$ , significant in a test of directional randomness ( $H_0: \kappa = 0, p \leq 0.05$ ).

were the individual new burrows and the response variable was the distance from each new burrow to the nearest active burrow from the previous burrow census. These distances were significantly greater posttreatment than pre-treatment, indicating that the treatments increased the rate of colony expansion in addition to influencing its direction (Table 3).

### Discussion

Preferential colonization of the treatment plots did indeed cause the colonies to expand in a preferred direction. In the absence of the treatments, one would expect equal-sized plots at the colony periphery to contain roughly equal numbers of new burrows (i.e., those not present in the preceding census). Instead, densities of new burrows were consistently higher in the treatment plots than in the control plots. In the absence of the treatments, one would also expect that the colonies would expand more or less uniformly around their entire periphery, subject to the constraints of available habitat into which to expand. We found that new burrows tended to be concentrated in the direction of the treatment plots, whether those new burrows were located in the treatment plots or not. The treatments also led to an increase in the mean distance from existing burrows to new burrows. These treatments therefore can be used to manipulate the rate and direction of Black-tailed prairie dog colony expansion. Similar results have been found in similar studies (Milne-Laux & Sweitzer 2006).

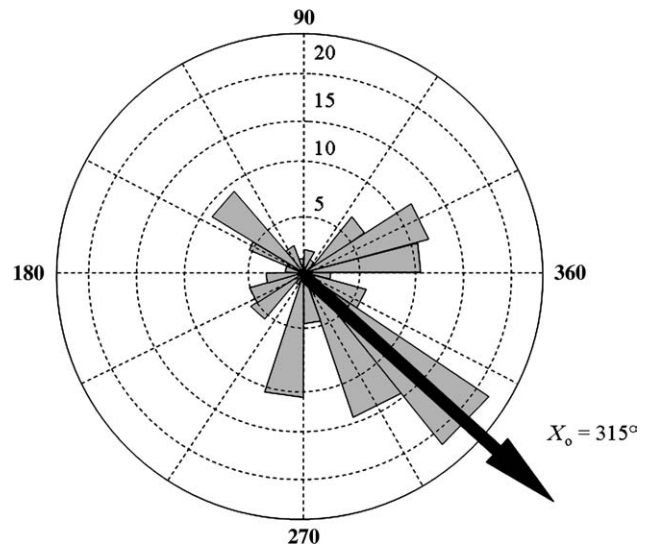


Figure 3. Rose diagram for S-Curve colony showing distributions of vectors from each active burrow at the pre-treatment period to the nearest new burrow at the posttreatment period. Mean direction  $X_0 = 315^\circ$ , significant in a test of directional randomness ( $H_0: \kappa = 0, p \leq 0.05$ ).

As mentioned above, untreated colonies would be expected to expand uniformly around their periphery subject to constraints of available habitat, including variation in habitat quality, vegetation height, soil properties, roads, etc. In addition, colony shape might be expected to influence the direction of colony expansion, so that, all other things being equal, a growing colony with unlimited available habitat would tend to become circular in shape (note, however, that the details of prairie dog foraging might favor more perimeter relative to area than allowed by a circular colony). Thus, there are a number of potential complications in our directional analysis. However, the analysis of burrow counts can only provide information about burrows located within the treatment and control plots. The directional analysis on the other hand provides information about the overall direction of colony expansion. Thus, the two analyses that were presented in Tables 1 and 2 are complementary rather than redundant.

Black-tailed prairie dog alarm calls provide communal defense against predators (Hoogland 1981, 1995). Increased visibility may increase the effectiveness of predator detection and cooperative defense because Black-tailed prairie dogs visually locate predators and utter alarm calls to alert conspecifics that predators have been detected (Hoogland 1981, 1995). Black-tailed prairie dogs clip tall vegetation to improve predator detection, unlike *C. leucurus* which use tall vegetation for cover from predators (Hoogland 1995). Thus, the mow and burn treatments likely increased both visibility and available habitat for the prairie dogs.

There is some evidence of long-term influences of treatments. Our final survey for Deep Well and S-Curve was carried out at 2 years posttreatment; at that time, the vegetation on the treated plots remained similar to that on the

**Table 3.** Distances from each new burrow on the three study colonies to the nearest extant burrow from the preceding burrow census.

Colony	Time Period	Mean Distance (m)	n	SE
Deep Well	Pre-treatment	7.426	39	0.512
	Posttreatment	9.129	38	1.065
	2 years later	11.659	29	1.382
S-Curve	Pre-treatment	8.477	39	0.736
	Posttreatment	12.270	40	1.156
	2 years later	9.855	31	1.418
Red Lake	Pre-treatment	9.055	42	0.564
	Posttreatment	11.988	26	1.807
	2 years later	15.661	36	2.104

Factorial ANOVA shows that the three sites differ significantly ( $p = 0.018$ ,  $F = 4.073$ ,  $df = 2,311$ ), as do the three time periods ( $p < 0.001$ ,  $F = 8.926$ ,  $df = 2,311$ ).

rest of the colony, with considerably shorter overall vegetation height and more bare ground than off-colony areas. At the final survey, colony expansion continued toward the treatment plots. Although the influence of the treatments decays over time because the colony expands beyond the treatment plots, colony expansion appears to have some “momentum” because the colony continues to expand in the same direction as for both posttreatment surveys.

However, this effect was not observed at the Red Lake colony; the mean direction of colony expansion was oriented away from the treatment areas at the final survey 2.5 years posttreatment. One plausible reason why this effect was not observed at Red Lake might have to do with population fluctuations on the colonies during the study. Partly due to the drought conditions prevailing during the study, Red Lake, the largest of the study colonies, was the only one of the three colonies that had

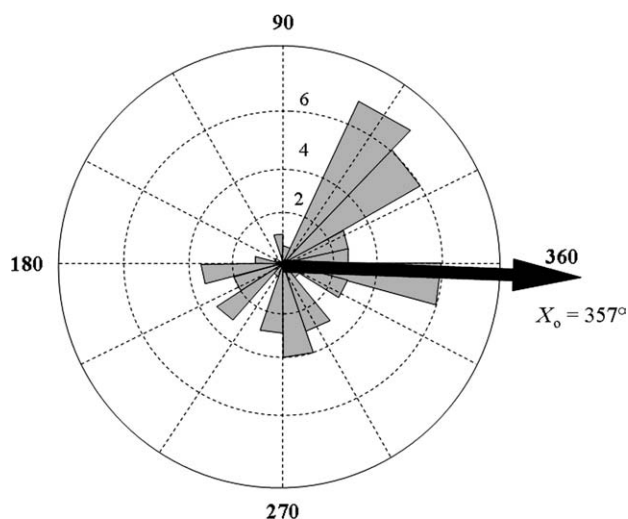


Figure 4. Rose diagram for Red Lake colony showing distributions of vectors from each active burrow at the pre-treatment period to the nearest new burrow at the posttreatment period. Mean direction  $X_0 = 357^\circ$ , significant in a test of directional randomness ( $H_0: \kappa = 0$ ,  $p \leq 0.05$ ).

a declining population between the first and the second posttreatment surveys (A. Facka 2004, NMSU researcher personal communication). The low population numbers at Deep Well and S-Curve resulted in fewer new active burrows at those colonies. Deep Well and S-Curve experienced a decline in burrow establishment from posttreatment to 2 years posttreatment. At posttreatment, there were 110 new burrows tagged on Deep Well colony, but only 84 tagged at 2 years posttreatment, a 24% decline; S-Curve experienced a 52% decline. The number of new burrows at Red Lake colony remained relatively stable throughout the course of the study. This decline in population and thus new burrows may explain why mean directions deviated only slightly from one another during posttreatment and 2 years posttreatment at Deep Well and S-Curve.

### Implications for Practice

- Although much prairie dog habitat has been converted to agriculture and suburbs, conflict between prairie dog colonies and humans could be reduced through management interventions to control colony expansion.
- As ecosystem engineers (Jones et al. 1994), prairie dogs create suitable habitat for many other species (Miller et al. 1994; Stapp 1998; Ceballos et al. 1999; Kotliar et al. 1999; Bangert & Slobodchikoff 2000), which has been recognized by many public and private protected areas, parks, and as a result, these conservation lands have begun reintroducing prairie dog colonies.
- Expansion of prairie dog colonies can be manipulated. Where suitable vegetation cover exists on the colony periphery, mow and burn treatments can be used to influence the rate and direction of colony expansion.
- Further studies could combine the use of visual barriers with vegetation management to determine if this combination results in more effective control of colony expansion.
- Additional research and a history of successful reintroductions may eventually allow management of prairie dog colonies in urban settings with minimal human-wildlife conflict.

### LITERATURE CITED

- Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* **39**:135–139.
- Arias, S. M., R. D. Quintana, and M. Cagnoni. 2005. Vazcacha's influence on vegetation and soil in a wetland of Argentina. *Rangeland Ecology and Management* **58**:51–57.
- Bailey, V. 1905. Biological survey of Texas. United States Department of Agriculture Biological Survey, North American Fauna **25**:9–161.

- Bangert, R. K., and C. N. Slobodchikoff. 2000. The Gunnison's prairie dog structures a high desert grassland landscape as a keystone species. *Journal of Arid Environments* **46**:357–369.
- Bertram, B. C. R. 1978. Living in groups: predator and prey. Pages 64–96 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford, United Kingdom.
- Biggins, D. E., B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. Pages 73–88 in J. L. Odemeyer, D. E. Biggins, B. J. Miller, and R. Crete, editors. *Management of prairie dog complexes for the reintroduction of the black-footed ferret*. U.S. Fish and Wildlife Service Biological Report 13, Fort Collins, Colorado.
- Brown, D. E. 1994. Desert grasslands. Pages 123–131 in D. E. Brown, editor. *Biotic communities: southwestern United States and northwestern Mexico*. University of Utah Press, Salt Lake City.
- Burt, J. E., and G. M. Barber. 1996. *Elementary statistics for geographers*. 2<sup>nd</sup> edition. The Guilford Press, New York.
- Butler, D. R. 1995. *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, Cambridge, United Kingdom.
- Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* **41**:161–172.
- Christman, M. C., and D. Lewis. 2005. Spatial distribution of dominant animals within a group: comparison of four statistical tests of location. *Animal Behaviour* **70**:73–82.
- Cincotta, R. D., D. W. Uresk, and R. M. Hansen. 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. Pages 30–33 in D. W. Uresk, G. L. Schenbeck, and R. Cefkin, editors. *Eighth Great Plains wildlife damage control workshop proceedings*. General Technical Report 121, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, Colorado.
- Cole, D. N. 2000a. Natural, uncrowded or free: which of these should wilderness be? *International Journal of Wilderness* **6**:5–8.
- Cole, D. N. 2000b. Paradox of the primeval: ecological restoration in wilderness. *Ecological Restoration* **18**:77–86.
- Coon, C. 2002. Stakeholders establishing landowner incentive program. *New Mexico Farm and Ranch Magazine* January 20.
- Costello, D. F. 1970. *The world of the prairie dog*. J.B. Lippincott Co., New York.
- Davis, J. C. 1986. *Statistics and data analysis in geology*. 2<sup>nd</sup> edition. John Wiley and Sons, Inc., New York.
- Eldridge, D. J., C. Constantinides, and A. Vine. 2006. Short-term vegetation and soil responses to mechanical destruction of rabbit (*Oryctolagus cunicularis* L.) warrens in an Australian box woodland. *Restoration Ecology* **14**:50–59.
- Forrest, S. C., D. E. Biggins, L. Richardson, T. W. Clark, T. M. Campbell, K. A. Fagerstone, and E. T. Thorne. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985. *Journal of Mammalogy* **62**:261–273.
- Garrett, M. G., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy* **69**:236–250.
- Graves, R. 2001. *The prairie dog: sentinel of the plains*. Texas Tech University Press, Lubbock.
- Halpin, Z. T. 1987. Natal dispersal and the formation of new social groups in a newly established town of black-tailed prairie dogs (*Cynomys ludovicianus*). Pages 104–118 in B. D. Chepko-Sade and Z. T. Halpin, editors. *Mammalian dispersal patterns: the effects of social structure on population genetics*. University of Chicago Press, Chicago, Illinois.
- Hartsough, M. J. 2002. Foraging ecology, dietary preferences, and diet quality of black-tailed prairie dogs (*Cynomys ludovicianus*) in northern Chihuahuan Desert grasslands. M.Sc. thesis. New Mexico State University, Las Cruces.
- Hendrie, M. N. 2004. Experimental manipulation of expansion trajectory in translocated black-tailed prairie dog colonies in a Chihuahuan Desert grassland. M.Sc. thesis. New Mexico State University, Las Cruces.
- Hoogland, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* **62**:252–272.
- Hoogland, J. L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press, Chicago, Illinois.
- Hynstrom, S. E. 1996. Plastic visual barriers were ineffective at reducing recolonization rates of prairie dogs. Pages 74–76 in R. E. Masters and J. G. Huggins, editors. *Twelfth Great Basin wildlife damage control workshop proceedings*. Noble Foundation, Ardmore, Oklahoma.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contributions from the Laboratory of Vertebrate Biology* **67**:1–123.
- Koford, C. B. 1958. Prairie dogs, whitefaces, and blue gramma. *Wildlife Monographs* **3**:1–78.
- Kotliar, N. B., B. W. Baker, and A. D. Whicker. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* **24**:177–192.
- Landres, P., M. W. Brunson, and L. Merigliano. 2001. Naturalness and wildness: the dilemma and irony of ecological restoration in wilderness. *Wild Earth* **10**:77–82.
- Lybecker, D., B. L. Lamb, and P. D. Ponds. 2002. Public attitudes and knowledge of the black-tailed prairie dog: a common and controversial species. *BioScience* **52**:607–613.
- Macek, P., and J. Leps. 2003. The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L. *Plant Ecology* **168**:31–43.
- Marce-Santa, E. 2001. Distribucion actual y fragmentacion de las colonias de perros llaneros de cola negra (*Cynomys ludovicianus*) en el noroeste de Chihuahua, Mexico. B.Sc. thesis. Universidad Nacional Autonoma de Mexico, Distrito Federal, Mexico.
- Marchetti, G. M., and F. Scapini. 2003. Use of multiple regression models in the study of sandhopper orientation under natural conditions. *Estuarine, Coastal, and Shelf Science* **58S**:207–215.
- Mardia, K. V. 1972. *Statistics of directional data*. Academic Press, New York.
- Merriam, C. H. 1902. The prairie dog of the Great Plains. Pages 257–270 in *Yearbook of the U.S. Department of Agriculture 1901*. U.S. Government Printing Office, Washington, D.C.
- Miller, B., G. Ceballos, and R. P. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* **8**:677–681.
- Milne-Laux, S., and R. A. Sweitzer. 2006. Experimentally induced colony expansion by black-tailed prairie dogs (*Cynomys ludovicianus*) and implications for conservation. *Journal of Mammalogy* **87**:296–303.
- Munro, J., and J. Bedard. 1977. Gull predation and creching behaviour in the common eider. *Journal of Animal Ecology* **46**:799–810.
- Murie, J. O., and G. R. Michener. 1984. *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality*. University of Nebraska Press, Lincoln.
- Oakes, C. L. 2000. History and consequences of keystone mammal eradications in the desert grasslands: the Arizona black-tailed prairie dog (*Cynomys ludovicianus arizonensis*). Ph.D. thesis. University of Texas, Austin.
- Okubo, A., and S. A. Levin. 2001. *Diffusion and ecological problems*. Springer-Verlag, New York.
- Patterson, I. J. 1965. Timing and spacing of broods of black-headed gull (*Larus ridibundus*). *Ibis* **107**:433–459.

- Pinheiro, J. C., and D. M. Bates. 2004. Mixed-effects models in S and S-Plus. Springer-Verlag, New York.
- Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. *Conservation Biology* **12**:1253–1259.
- Truett, J. C., J. L. D. Dullum, M. R. Matchett, E. Owens, and D. Seery. 2001. Translocating prairie dogs: a review. *Wildlife Society Bulletin* **47**:379–400.
- Truett, J. C., and T. Savage. 1998. Reintroducing prairie dogs into desert grasslands. *Restoration and Management Notes* **16**:189–195.
- Turchin, P. 1998. Quantitative analysis of animal movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts.
- Van Pelt, W. E. 1999. The black-tailed prairie dog conservation assessment and strategy fifth draft. Nongame and Endangered Wildlife Program, Arizona Game and Fish Department, Phoenix.
- Wittenberger, J. F., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Pages 1–78 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian biology*, vol. 7. Academic Press, New York.
- Wolff, J. O. 1999. Behavioral model systems. Pages 11–40 in G. W. Barrett and J. D. Peles, editors. *Landscape ecology of small mammals*. Springer-Verlag, New York.
- Zhang, Y. M., Z. B. Zhang, and J. K. Liu. 2003. Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanieri* in alpine meadow ecosystems on the Tibetan Plateau. *Mammal Review* **33**:284–294.
- Zimmerman, P. H., S. J. Pope, T. Guilford, and C. J. Nicol. 2003. Navigational ability in the domestic fowl (*Gallus gallus domesticus*). *Applied Animal Behaviour Science* **80**:327–336.
- Zinn, H., and W. Andelt. 1999. Attitudes of Fort Collins, Colorado residents toward prairie dogs. *Wildlife Society Bulletin* **27**:1098–1106.