

Response of plant and rodent communities to removal of prairie dogs (*Cynomys gunnisoni*) in Arizona

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Received 1 April 2004; received in revised form 7 April 2006; accepted 24 May 2006

Available online 8 September 2006

Abstract

We conducted a natural removal experiment, utilizing a local outbreak of sylvatic plague (*Yersinia pestis*) as the removal agent, to test the effects of removal of Gunnison's prairie dogs (*Cynomys gunnisoni*) on plant and nocturnal rodent assemblages in three grassland habitats (ponderosa, pinyon-juniper, and desert grasslands) in northern Arizona. We measured plant cover, rodent abundance, plant and rodent species richness, and plant and rodent composition at three treatment locations: active prairie dog colonies ($n = 15$), inactive colonies ($n = 15$), and control locations ($n = 15$). Only the amount of plant cover differed significantly among treatments. As landscape level heterogeneity among habitat types increased, rodent abundance and species diversity increased, suggesting that intrinsic habitat characteristics are stronger drivers of plant and rodent assemblages than presence or removal of Gunnison's prairie dogs. We conclude that Gunnison's prairie dogs are not functioning as a keystone species in grasslands of northern Arizona.

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Keywords: Keystone species; Removal experiment; Arizona; Plague

1. Introduction

Over the past three decades, the ecological roles of prairie dogs (*Cynomys* spp.) in grassland ecosystems have been debated (Power et al., 1996; Stapp, 1998; Kotliar et al., 1999). They have alternately been described as pests that degrade rangeland (Bailey, 1931;

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Findley et al., 1975; Hoffmeister, 1986) and as a keystone species without which the function of prairie ecosystems may be inexorably changed (Slobodchikoff et al., 1988; Whicker and Detling, 1988; Miller et al., 1994; Bangert and Slobodchikoff, 2000). Recently, it has been argued that prairie dog impacts on grassland communities are more complex than previously determined (Whicker and Detling, 1988; Miller et al., 1994; Kotliar et al., 1999; Bangert and Slobodchikoff, 2000). Prairie dog grazing activity and burrow excavation increase habitat heterogeneity on patch- and landscape-level scales (King, 1955; Bangert and Slobodchikoff, 2000). Prairie dog grazing may also lead to a switch from grass- to forb-dominated vegetation communities (Coppock et al., 1983; Archer et al., 1987; Fahnestock and Detling, 2002), as well as to increased nitrogen levels in above-ground vegetation (Coppock et al., 1983; Whicker and Detling, 1988). There may be increased densities of ground nesting birds with reduced (Desmond et al., 2000; Manning and White, 2001) and increased (Baker et al., 1999, 2000) predation of bird nests on active prairie dog colonies.

It has been argued that diversity of plant, mammal, and bird species is higher where prairie dogs are present, and thus, prairie dogs are a keystone species (Clark et al., 1982; Miller et al., 1994; Ceballos et al., 1999; Bangert and Slobodchikoff, 2000). Paine's (1969) original definition of a keystone organism was applied to starfish and stated that a keystone would affect the integrity and persistence of a community. In 1996, Power et al. redefined a keystone species as an organism whose effects on a community are disproportionately large relative to its abundance, and added a quantitative measurement of the keystone's community importance.

Conclusions that prairie dogs act as keystone species have been countered by evidence of non-significant differences in species diversity on active colonies compared to control sites without prairie dogs (Weltzin et al., 1997; Davidson et al., 1999; Kretzer and Cully, 2001; Barko et al., 2001). In addition, Stapp (1998), Kotliar et al. (1999), and Kotliar (2000) have written essays that question the application of the keystone concept to prairie dogs and point out weaknesses in previous studies. Kotliar (2000) modified the keystone definition to include a lack of redundancy in functional role so that if the keystone was removed, no other organism could duplicate its ecological role in the community.

Past research on the ecological role of prairie dogs often failed to include all of the measurements recommended by Kotliar (2000). Conclusions about the roles of black-tailed prairie dogs in mixed grass habitats are often generalized to all *Cynomys* species throughout their geographic ranges. Furthermore, many studies sample only a few colonies with minimal replication of treatments. In response to these and other experimental design issues, Stapp (1998) suggested that future research involve comparative studies with "appropriate controls and adequate replication across a range of grasslands." Ideally, such studies would occur before and after prairie dog removal efforts, with the goal of assessing changes following the loss of this important community member.

Our research focused on Gunnison's prairie dogs (*Cynomys gunnisoni*) across all three grassland habitat types where they occur in Arizona. The occurrence of a sylvatic plague (*Yersinia pestis*) epizootic in *C. gunnisoni* populations throughout northern Arizona (Girard et al., 2004; Wagner and Drickamer, 2004; Wagner et al., 2006) allowed us to use an experimental design that mimicked a removal experiment. The "natural" removal of Gunnison's prairie dogs by plague allowed us to compare abundance (number of unique individuals captured), species richness, and composition of plants and nocturnal rodents

across three treatment types. These treatments were (1) active Gunnison's colonies, (2) inactive (≥ 2 years) colonies, and (3) control locations. Plants and rodents were chosen as indices of prairie dog impact because both constitute forage and prey resources for many organisms and thereby reflect a first-order community response to prairie dog presence or removal. Impacts of plague on rodent populations were assumed to be minimal in keeping with research, suggesting their general resistance to mortality from the plague bacillus and potential as reservoir hosts (Thomas et al., 1988; Anderson and Williams, 1997). We hypothesized that species diversity would differ across our three treatments, and predicted that rodent abundance, and plant and rodent species richness and composition would be greater on active colonies.

2. Methods

2.1. Study site

All Gunnison's prairie dog colonies, we examined were located within 200 km of Flagstaff, Arizona, Coconino County, where annual precipitation averages 54.15 cm, with average maximum and minimum temperatures of 16.2 and 0.8°C, respectively (Flagstaff Airport Weather Service Office, Arizona). Our study spanned 1 year of severe drought (2002) and 1 year of higher than average seasonal rainfall (2003) (NOAA, NCDC 2003). Thus, community responses to *C. gunnisoni* were recorded at two precipitation levels. Study site elevations ranged from approximately 1200–2700 m. This gradient was marked by changes in life zones from montane conifer forests at 1700–2700 m, to Great Basin conifer woodland at 1500–2300 m, and Great Basin desert scrub from 1200 to 2200 m (Brown, 1994). We sampled plant and nocturnal rodent assemblages in grasslands at all life zones where Gunnison's prairie dogs occur in Arizona. Grassland habitat types are hereafter referred to by the name of the dominant tree species in each life zone, i.e. ponderosa, pinyon-juniper (PJ), and desert (no trees present).

2.2. Experimental design

Plant and nocturnal rodent species diversity was measured from May through August of 2002 and 2003, at 15 sites randomly selected from previously located Gunnison's prairie dog colonies. Seven sites were sampled from May through August in 2002 (three ponderosa, two PJ, and two desert), and eight new sites were sampled from May through August in 2003 (two ponderosa, three PJ, and three desert). Each site included three treatments:

- (1) an active prairie dog colony, where prairie dogs, fresh scat, and fresh digging at burrows were present;
- (2) a colony that had been inactive for ≥ 2 years, where no prairie dogs, fresh scat, or fresh digging were present;
- (3) and a control location where no visible evidence of past or current prairie dog activity was present.

Colonies were defined as inactive if previous surveys (Wagner and Drickamer, 2004; Wagner et al., 2006) had recorded no sign of prairie dogs present, and the same conditions

held at the time of our visit. All active colonies were selected randomly from a list of known colony locations (Wagner and Drickamer, 2004). When activity at a colony was verified, the nearest inactive colony and control location were sampled simultaneously with this active colony. In order to ensure that control sites were similar to active and inactive colonies, we chose sites similar in size to colonies within a minimum of 500 m and a maximum of 10 km from any signs of prairie dog activity. Plants and nocturnal rodents were sampled in each treatment within a 64 m × 64 m grid located at the approximate center of the colony being sampled (Fig. 1).

2.3. Colony size and burrow density

Colony size and burrow density were used as indices of prairie dog abundance. Colony size was obtained by walking two transects (north-south and east-west) that intersected the middle of the grid and extended to colony edges. Transect lengths were measured with a Trimble Geoexplorer III GPS unit. Colony size (hectares) was estimated by calculating area from the length of the north-south transect by width of east-west transect. Burrow density was calculated by counting the number of prairie dog burrows with open entrances in 64 m × 64 m grids at active and inactive treatment locations. Burrows were counted by

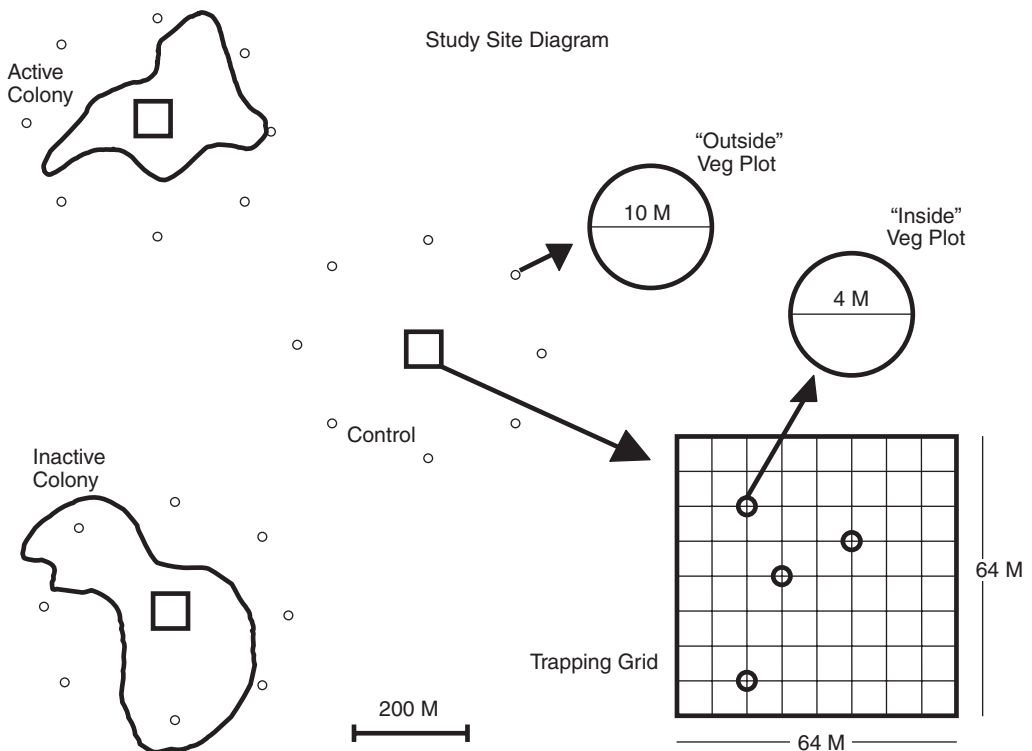


Fig. 1. Experimental design: each site included three treatments (active, inactive and control). Each treatment included an 8 m × 8 m trapping grid. Sixty-four Sherman live traps were placed at every 8 m. Four 4-m diameter vegetation sampling plots were located randomly within the trapping grid. Eight 10-m diameter vegetation sampling plots were located in eight cardinal directions 200 m outside the center of each trapping grid.

walking through grids and hand-mapping open burrow locations on graphic representations of the grids.

2.4. *Vegetation sampling*

Four circular vegetation plots were sampled in each grid (Fig. 1) at all treatment locations. Vegetation plots were 4 m in diameter and were placed at randomly selected grid intersections. All plants within a plot were identified to species except grasses, which were identified to genus. Percent plant cover was estimated by visual evaluation of stem and leaf area in each plot quarter. Quarter plot cover values were averaged for a single plot cover value. Plot cover values in a treatment grid were averaged for total grid cover estimation. Plant abundances were measured by visual estimation of percent cover of each species present. Total plant percent cover and species richness measurements for each of the four vegetation plots were averaged to obtain one measure of each per grid.

2.5. *Small mammal trapping*

We sampled nocturnal rodent species using 64 Sherman live traps (23 × 8 × 9 cm) placed at 8-m intervals in a grid pattern. Traps were baited with a peanut butter-oat mix, set in the early evening, and checked early the following morning over a five-night trapping session. Trapping sessions occurred throughout the lunar cycle, except for the night before, after, and during the full moon. Rodents were identified to species, sexed, aged, marked with unique hair-clip patterns, and released at the point of capture. Traps in which rodents were captured were washed with a diluted chlorine solution (Yunger and Randa, 1999) before being reused in the trapping grid.

2.6. *Surrounding vegetation community*

To investigate the possibility that rodent species assemblages were responding to heterogeneity in vegetation types outside trapping grids, we compared heterogeneity measurements inside and outside trapping grids. Heterogeneity was measured as total percent cover and variance (squared deviations from mean) in vegetation types (tree, shrub, grass, and forb). Reduction in the number of parameters measured in plots outside our trapping grids enabled us to increase the size of our sample plots to 10 m in diameter. Cover measurements were collected from one plot in each of eight compass directions (north, northeast, east, southeast, etc.) at a distance of 200 m from the center of each trapping grid. Due to variation in colony size, plots sometimes fell on the edge or outside colony boundaries.

2.7. *Statistical analyses*

Data were tested for normality (Shapiro-Wilk, 1965) and homogeneous variances Levene's test (Zar, 1996). All data had homogeneous variances, and all data were non-normally distributed except % plant cover ($W = 0.96$, $p = 0.16$). Non-normal data were analysed with non-parametric tests (PCOrd and Manly's randomization). Randomization analyses produced results similar to ANOVA and linear regression to two decimal places, thus results are reported as F values. To test for differences in plant and rodent data among

treatments we used treatment, habitat, and a treatment X habitat interaction term as independent factors, with plant and rodent species richness, total percent cover, and abundance as dependent variables. A blocked ANOVA design was used to test treatment effects while excluding effects of site and habitat variables.

Independent variables were tested for differences across years using a two-sample *t*-test (Zar, 1996), assuming equal variances. Plant species richness data differed across years ($t = 4.77$, $p < 0.0001$), so plant richness was analysed separately in 2002 and 2003. Otherwise, data were pooled across years. Relationships between prairie dog burrow density, colony size, and rodent abundance and species richness were analysed with linear and quadratic regression.

Differences in plant and rodent species composition among treatments were tested with multi-response permutation procedures (MRPP) analyses in the PCOrd statistical program (McCure and Mefford, 1999). MRPP was used to compare plant and rodent composition (abundance of species within a group) among treatment types. MRPP output is presented as an *A* statistic that is calculated from a comparison of observed and expected average within-group dissimilarity and represents within-group homogeneity compared to that generated by randomly assigning samples to different groups. PCOrd summary function was used to calculate measures of plant and rodent diversity (Shannon and Weaver, 1949) and evenness, $E = H'/\ln(\text{richness})$ (Pielou, 1969). Diversity and evenness values were calculated for species within treatments, and then tested for differences between treatments with ANOVA.

Two-way ANOVA (Zar, 1996) and linear and quadratic regression analyses were conducted using the JMP IN statistical software package (SAS Institute Inc., 2001). Randomization tests were conducted using RT-2 (Manly, 1997). Habitat heterogeneity comparisons were made using two-way ANOVA, testing for differences in plant cover and variance of plant cover of four vegetation types (tree, shrub, grass, and forb), with plot position (inside or outside trapping grids), treatment type (active colony, inactive colony, and control location), and a plot position X treatment type interaction as independent variables. Separate comparisons were made for each habitat type (ponderosa, PJ and desert).

3. Results

3.1. Colony size and burrow density

Colony size ranged from 4.2 to 196.6 ha. There were no significant linear or hyperbolic relationships between colony size and rodent abundance, plant richness, or rodent richness in active or inactive colonies. However, there was a significant negative relationship between colony size and percent plant cover ($F = 11.47$, $p = 0.002$), with plant cover inside our trapping grids decreasing as colony size increased. Open burrow density averaged 45.27 and 11.93 m⁻² on active and inactive treatments respectively. Although the number of open burrows was significantly greater ($F = 21.84$, $p < 0.000$) in trapping grids on active colonies, no significant relationships existed between the number of open burrows and rodent abundance, plant richness, or rodent richness.

3.2. Plant response to removal of prairie dogs

In 2002, 78 plant species were identified, with 35 additional species identified in 2003. Species accumulation analyses suggest that although four plots/grid showed minimal

increase in species accumulation by the fourth plot in PJ and desert habitats, vegetation measurements in ponderosa habitat may have included more species with the addition of more plots. Plant species richness was greater in 2003 than in 2002. As expected, there were significant differences in plant richness and cover among the three habitat types. However, we found that plant species richness did not differ significantly among active, inactive, and control treatments during 2002 ($F = 0.3$, $p = 0.75$) or 2003 ($F = 1.57$, $p = 0.24$) (Table 1). These results do not support our prediction that species richness would be greater on active colonies than on inactive colonies and control locations. Percent plant cover was significantly different among active and control treatments ($F = 6.10$, $p < 0.01$), with higher plant cover in control than in active treatments (Tukey HSD $q = 2.4$, $p < 0.05$). However, there was no relationship between plant cover and rodent abundance or species richness ($F = 0.013$, $p = 0.91$ and $F = 0.0009$, $p = 0.98$, respectively). In an effort to remove variation in plant richness and cover associated with site and habitat type, we used a blocked design with site and habitat as blocked variables. However, blocking did not result in a significant relationship in plant richness or cover among treatments. Interactions between treatment and habitat did not contribute significantly to variation in plant richness or cover (Table 1).

MRPP comparisons of plant species composition showed no significant grouping of species composition among treatments ($A = -0.02$, $p = 0.86$) (Fig. 2). When plant species composition was grouped by treatment separately in each habitat type, no significant grouping was present across treatments within ponderosa, PJ or desert grasslands ($A = 0.006$, $p = 0.34$; $A = -0.015$, $p = 0.65$; $A = -0.036$, $p = 0.93$ respectively). Tests for differences in plant species diversity (H) and evenness (E) between treatment types produced no significant results. Similar tests for differences in plant diversity and evenness

Table 1

Mean (± 1 S.E.) rodent richness, rodent abundance, plant cover, and plant richness among treatments (active, inactive, and control), and results of a two-way ANOVA ($n = 45$) are reported, with habitat, treatment, and habitat X treatment interaction as independent factors and rodent richness (a), rodent abundance (b), plant cover (c), and plant richness in 2002 (d) and 2003 (e) as dependent factors

Parameter	Active	Inactive	Control		
Rodent species richness ^a	2.1 \pm 0.3	2.5 \pm 0.3	2.1 \pm 0.4		
Rodent abundance ^b	11.7 \pm 4.0	10.6 \pm 2.8	12.6 \pm 4.1		
Plant cover ^c	52.9 \pm 3.9	62.8 \pm 3.8	69.3 \pm 2.9		
Plant species richness 2002 ^d	3.8 \pm 0.4	4.3 \pm 0.4	4.6 \pm 0.9		
Plant species richness 2003 ^e	6.8 \pm 1.2	8.2 \pm 1.2	7.7 \pm 0.7		
Parameter	<i>n</i>	df	Treatment <i>F</i> , <i>p</i>	Habitat <i>F</i> , <i>p</i>	Interaction <i>F</i> , <i>p</i>
a	45	44	0.5, 0.61	3.6, 0.04	0.16, 0.96
b	45	44	0.11, 0.89	14.97, <0.0001	0.38, 0.82
c	45	44	6.10, <0.01	4.07, 0.03	0.92, 0.46
d	21	20	0.3, 0.75	0.6, 0.56	0.39, 0.81
e	24	23	1.57, 0.24	24.91, <0.0001	2.18, 0.12

^aNumber of rodent species collected in 216,000 trap nights.

^bNumber of individual rodents captured per grid.

^cPercent cover by plot ($n = 4$) averaged for total grid cover.

^dNumber of plant species collected per grid in 2002.

^eNumber of plant species collected per grid in 2003.

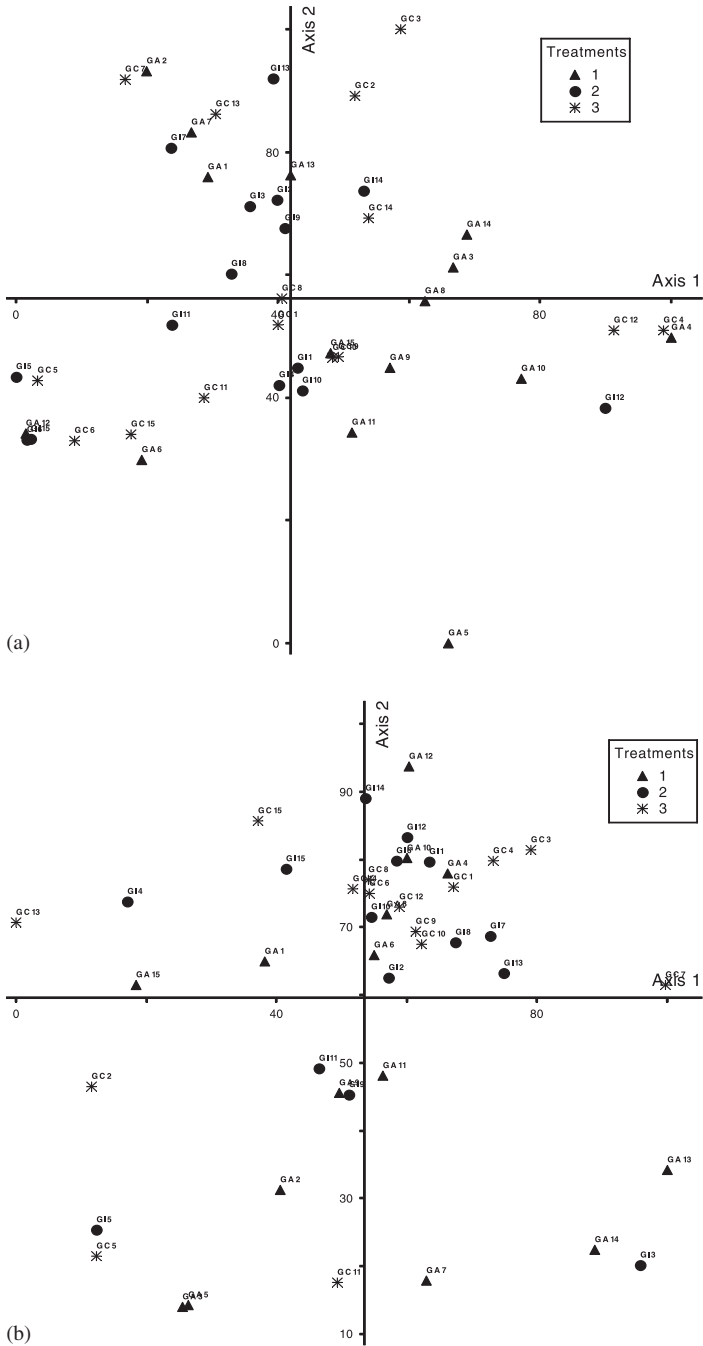


Fig. 2. Ordination and multi-response permutation procedure (MRPP) found no significant grouping of (a) rodents and (b) plants across treatments. Treatment 1 shows grouping of rodent composition on active colonies, treatment 2 on inactive, and treatment 3 on controls.

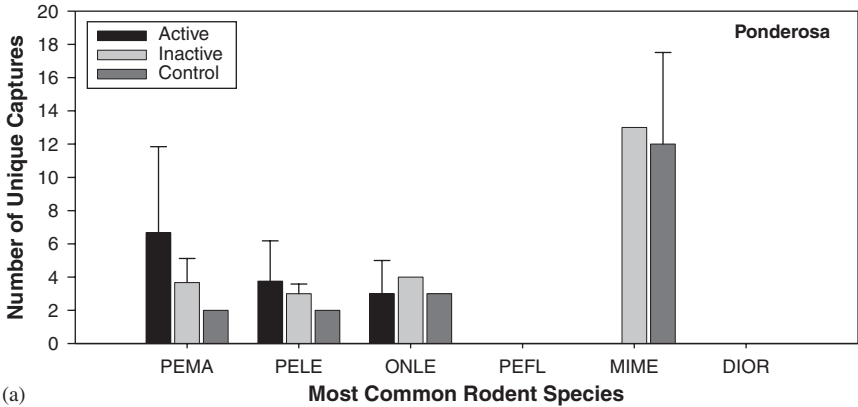
between habitat types were also insignificant, with a trend of slightly lower diversity and less evenly distributed species assemblages in ponderosa habitat.

3.3. Rodent response to prairie dog removal

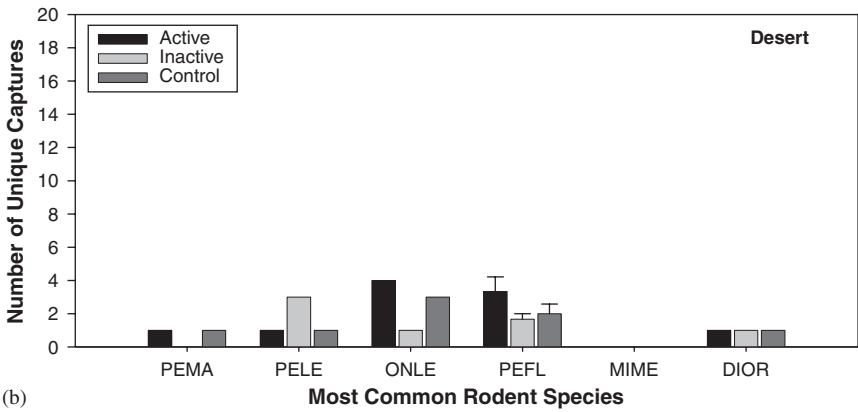
Ten nocturnal rodent species were captured in 2002, with three additional species captured in 2003 (Appendix A). Common rodent species captured in each treatment type in ponderosa, PJ, and desert habitats are shown in Fig. 3. Although active treatments consistently had lower species richness than either inactive or control, analyses of prairie dog impacts on nocturnal rodent communities indicated that neither rodent abundance nor species richness differed significantly among treatment types (Table 1, Fig. 3). These findings did not support our prediction that abundance and richness of rodents would decrease with the removal of Gunnison's prairie dogs. In an effort to remove variation in rodent richness and abundance associated with site and habitat type, we used a blocked design with site and habitat as blocked variables. However, blocking did not result in a significant relationship between rodent richness or abundance among treatments. Interactions between treatment and habitat did not contribute significantly to variation in rodent abundance or richness (Table 1). Tests of rodent response to plant cover among treatments yielded no significant relationship between rodent abundance or richness and availability of cover on active, inactive or control locations.

MRPP analysis of rodent species composition among active and inactive colonies and control locations showed no significant grouping of species composition across treatments ($A = 0.002$, $p = 0.62$) (Fig. 2). Additionally, when rodent species composition was grouped by treatment separately in each habitat type, no significant grouping was present across treatments within ponderosa, PJ, or desert grasslands ($A = -0.04$, $p = 0.73$; $A = 0.005$, $p = 0.43$; $A = -0.1$, $p = 0.99$ respectively). Tests for differences in rodent species diversity (H) and evenness (E) between treatment types produced no significant results, with a trend of slightly lower diversity and less evenly distributed species assemblages in controls. Similar tests for differences in rodent diversity and evenness between habitat types showed significant differences in rodent evenness, with species assemblages in desert habitats less evenly distributed than either ponderosa or PJ ($F = 4.25$, $p = 0.02$). There were also insignificant trends of lower diversity and less evenly distributed species assemblages in ponderosa habitat.

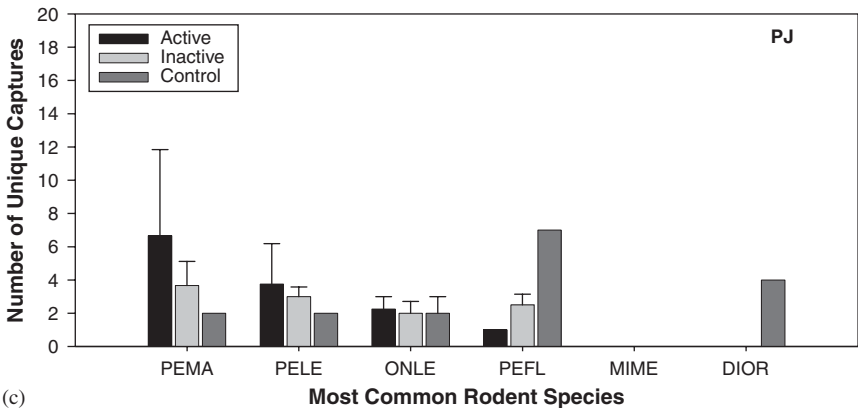
We found significant differences in rodent abundance and richness among the three habitat types, with fewer species in desert grasslands, and higher abundance in ponderosa grasslands. Several species were found only in specific treatment types. A western harvest mouse (*Reithrodontomys megalotis*) was captured in an active colony in PJ habitat. This species occurs in early stage dry weedy or grassy areas (MacMahon, 1985), which is consistent with disturbance caused by prairie dog burrowing and grazing activity. We captured a plains pocket mouse (*Perognathus flavescens*) in a desert control. This species is typically found in sandy soil near shrubs. As active prairie dog colonies are generally denuded of woody vegetation, it is unsurprising that this pocket mouse was found in a desert control location where shrubs are more common. Conversely, open understories found in active colonies are preferred by *Peromyscus* species (Birch, 1977). This was supported by higher numbers (non-significant) of deer mice (*Peromyscus maniculatus*) and white-footed mice (*Peromyscus leucopus*) on our active treatments than on our inactive or



(a)



(b)



(c)

Fig. 3. Mean (+1 S.E.) rodent species captured at 15 sites (2002 and 2003). Number of individuals captured in each treatment (active, inactive, and control), is shown by habitat type: ponderosa (a), desert (b), and PJ (c). Only most common (captured \geq five times during two seasons) rodent species are shown: *Peromyscus maniculatus* (PEMA), *Peromyscus leucopus* (PELE), *Onychomys leucogaster* (ONLE), *Perognathus flavus* (PEFL), *Microtus mexicanus* (MIME), and *Dipodomys ordii* (DIOR).

control locations. Although rodent species richness was highest on inactive treatments and controls this trend was not significant.

3.4. Surrounding vegetation community

Habitat heterogeneity comparisons produced significant differences between plant cover inside and outside grids in ponderosa habitat. In ponderosa habitat, tree cover was greater outside trapping grids than inside ($F = 6.17$, $p = 0.02$). Likewise, variance in tree and shrub cover was greater outside grids in ponderosa habitat ($F = 5.48$, $p = 0.03$, $F = 4.60$, $p = 0.04$ respectively), while other vegetation types did not differ significantly inside and outside grids in the three habitats. Except for variance in shrub cover in PJ habitat, habitat heterogeneity did not differ significantly among treatment types. In PJ grasslands, shrub cover variance was greater in active colonies than in inactive colonies ($F = 4.63$, $p = 0.02$, Tukey HSD $q = 2.48$, $p < 0.05$), but did not differ from control locations.

Analyses of relationships between rodent abundance or species richness and habitat heterogeneity outside grids indicated significant influence of specific vegetation types on rodents in ponderosa and PJ, but not desert habitats. In ponderosa habitat, rodent species richness decreased with increases in tree cover ($F = 11.81$, $p = 0.006$) and forb cover variance ($F = 6.16$, $p = 0.03$). In PJ habitat, abundance of rodents increased with increased shrub cover variance ($F = 7.38$, $p = 0.002$), and with increases in forb cover variance ($F = 7.39$, $p = 0.02$).

4. Discussion

Our data and analyses suggest that Gunnison's prairie dogs may not act as keystone species during variable climatic conditions in grassland habitats of northern Arizona. Neither plant richness nor composition was significantly different among treatment types, in agreement with earlier reports (Agnew et al., 1986; Archer et al., 1987; Slobodchikoff et al., 1988). We found no significant differences in rodent abundance, richness or composition among treatment types. Although there were no significant relationships between treatment type and rodent diversity or evenness, we did find trends of lower diversity and less even species assemblages at control locations. This may be related to a lack of prairie dog burrows. If burrows are evenly distributed, and if related resources (refugia, vegetation) are spaced evenly around burrows, then a lack of burrows may decrease even distribution of resources and thereby rodents at control sites.

Although reports of decreased plant cover on active prairie dog colonies are generally consistent throughout the literature, conclusions vary regarding relationships between prairie dog activity and plant and rodent richness and composition. Previous research on ecological role(s) of prairie dog species has focused on black-tailed prairie dog colonies in a single grassland habitat type (O'Meilia et al., 1982; Coppock et al., 1983; Agnew et al., 1986; Archer et al., 1987; Whicker and Detling, 1988; Barko et al., 2001). In addition, studies of prairie dog impacts were conducted with minimal replication of treatment types (Coppock et al., 1983; Agnew et al., 1986; Archer et al., 1987; Whicker and Detling, 1988; Slobodchikoff et al., 1988; Davidson et al., 1999; Ceballos et al., 1999). It is difficult to determine whether conclusions from such research reflect prairie dog impacts on plants and vertebrates, or represent anomalous small-scale variation in isolated communities. Our research design included adequate replication of treatment types in all three grassland

types where Gunnison's prairie dogs occur in Arizona. We feel confident that the results of our analyses reflect relationships between Gunnison's prairie dogs and associated plant and rodent communities.

Several studies of prairie dog impacts on plant and rodent communities involved replication of treatment types (O'Meilia et al., 1982; Barko et al., 2001). Lomolino and Smith (2003) compared vertebrate species diversity on 36 active prairie dog colonies to 36 paired sites without signs of prairie dog activity. They found similar mammal species diversity at active colonies and paired sites across 3 years during summer seasons, as in our analyses. In contrast to our findings, they noted significant differences in species composition between active colonies and paired sites. However, they surveyed both diurnal and nocturnal mammals, including large ungulates and mesocarnivores, as well as rodents. Of the nocturnal rodents captured, grasshopper mice (*Onychomys leucogaster*) were the only species associated with active prairie dog colonies. Grasshopper mice were found in highest abundance on our active colonies, though this trend was not significant. Although rodent species composition varied significantly with habitat type, we found no significant associations of individual rodent species with treatment types.

Long- and short-term climatic variation may have significant impacts on plant communities (Allen and Breshears, 1998; Kotliar et al., 1999). Barko et al. (2001) found no difference in plant composition between active black-tailed prairie dog colonies and control locations ($n = 8$) but noted that drought conditions during the year of data collection lead to dormancy in many plant species. Similarly, variation in plant species richness at our sites between 2002 and 2003 can be explained by extreme drought conditions in 2002. Reduced diversity and abundance of plants likely corresponded to decreased forage and cover availability for rodents.

Direct and indirect effects of the 2002 drought on rodents may have resulted in decreased populations during the drought and into the second year of our study. The mean number of rodents captured in ponderosa habitat was similar in both 2002 and 2003. However, in PJ habitat, the mean number of rodents captured in 2002 was twice the mean number captured in 2003 (35 vs. 15). In the desert habitat type, this trend in means was reversed with twice as rodents in 2003 as in 2002 (5.5 vs. 10). These data suggest that plant and rodent communities may respond to drought conditions differently or with some lag time effect. Plant and rodent communities may experience scale-dependent impacts of prairie dogs as grassland habitats change across a landscape. Kotliar et al. (1999) suggest that measurability of prairie dog impacts may change with the scale of a study area. Without the advantage of a larger scale, long-term data set it is difficult to accurately determine if Gunnison's prairie dogs impact plant communities or vice versa.

Many researchers report increased habitat heterogeneity across spatial scales correlated with increased diversity in a variety of invertebrate, vertebrate, and plant species (Chamberlain et al., 1999; Kotliar et al., 1999; Wagner et al., 2000; Weibull et al., 2000; Bestelmeyer and Wiens, 2001). Heterogeneity outside our trapping grids was related to variation in rodent richness and abundance in two out of three habitat types. Increased variation in tree cover and reduction in rodent richness at ponderosa sites may have been related to perch availability for raptors and thus increased predation threat in this habitat. Increases in variance of shrub cover at PJ sites could provide increased edge habitat or refugia from predation for rodents, explaining increased rodent abundance in this habitat. Similarly, increases in variance in forb cover and rodent abundance could be interpreted as increasing forbs leading to increased populations of seed-eating rodents.

Our analyses of habitat heterogeneity showed that, in PJ grasslands, increased plant cover variance outside our trapping grids corresponded with increases in abundance of rodents inside our grids. In an area approximately 64 m in diameter, rodent abundance and species richness was not related to measures of heterogeneity, whereas in an area approximately 464 m in diameter, rodent abundance and richness increased with increasing habitat heterogeneity. This suggests that rodent response to habitat heterogeneity occurred on larger spatial scales but not at microhabitat scales.

Kotliar (2000) suggested that keystone status might occur along a continuum of abundance. She proposed that fluctuations in abundance of a keystone species could alter the importance of the role of that organism in a community. Whicker and Detling (1988) found that plant species richness on active colonies was highest at intermediate disturbance levels, supporting Connell's Intermediate Disturbance Hypothesis (1978). If greater prairie dog densities (greater abundances) lead to greater disturbance, then this indicates that prairie dogs will positively impact community species diversity only at abundance levels associated with intermediate disturbance. Although we did not measure Gunnison's prairie dog abundance per se, we used colony size and burrow density as indices of prairie dog abundance. Our tests for linear and hyperbolic relationships between colony size and rodent abundance and plant/rodent species richness were not significant. Nor did we find significant linear or hyperbolic relationships between burrow density and rodent abundance and plant/rodent species richness. These findings indicate that even at varying abundances, Gunnison's prairie dogs have little impact on plant or nocturnal rodent species diversity in grasslands of northern Arizona.

Kotliar (2000) suggests that a species may act as a keystone at certain spatial scales or abundances but not others. We accepted this definition of keystone species and tested it according to Stapp (1998) for one species of prairie dog in three grassland habitat types in northern Arizona. Our findings indicate that factors such as climate and habitat variation explain variation in plant and rodent assemblages better than presence or absence of Gunnison's prairie dogs. There is strong evidence that prairie grassland ecosystems are declining markedly from historic ranges in North America, and with them a host of related organisms (Samson and Knopf, 1994; Noss et al., 1995). Although *Cynomys* species roles may differ among grassland communities, existing associations between prairie dogs and plant or vertebrate species of conservation concern indicate that their place in grassland ecosystems is an important one (Slobodchikoff et al., 1988; Desmond et al., 2000; Lomolino and Smith, 2003). Findings like those we report here will contribute to understanding the role(s) of prairie dogs in grassland communities. That knowledge, in turn, will aid conservation efforts.

Acknowledgments

This report is based on the M.S. degree thesis of Ms. Bartz at Northern Arizona University. We thank the following individuals for their assistance with field work: Michael Alright, Russell Benford, Kristin Covert, Ron Deckert, Kristina Ecton, Kaey Gilliland, Eileen Henniger, Carri LeRoy, Alberta Peralta, Glenn RInk, and Andrew Miller. The National Fish and Wildlife Foundation, Kaibab National Forest, and Northern Arizona University provided funding to support this research. We also thank the Coconino National Forest, Navajo Nation, and many property owners in northern Arizona for permission to work on their lands.

Appendix A. Supplementary materials

Plant families found in each habitat, in 2002 and 2003. Species in each family are expressed as Total, Mean, and RA (Relative Abundance: number of individual species in a family divided by total number of species in all families in that habitat and year).

Rodent species found in each habitat, in 2002 and 2003. Species are expressed as Total, Mean, and RA (Relative Abundance; number of individual species divided by total number of species in that habitat and year).

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2006.05.018.

References

- Agnew, W., Uresk, D.W., Hansen, R.M., 1986. Flora and fauna associated with the prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* 39, 135–139.
- Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Ecology* 95, 14839–14842.
- Anderson, S.H., Williams, E.S., 1997. Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming. *Journal of Wildlife Diseases* 33, 720–732.
- Archer, S., Garrett, M.G., Detling, J.K., 1987. Rates of vegetation change associated with prairie dogs (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72, 159–166.
- Bailey, V., 1931. Mammals of New Mexico. North American Fauna 53. US Department of Agriculture, WA, DC.
- Baker, B.W., Stanley, T.R., Sedgwick, J.A., 1999. Predation of artificial ground nests on white-tailed prairie dog colonies. *Journal of Wildlife Management* 63, 270–277.
- Baker, B.W., Stanley, T.R., Plumb, G.E., 2000. Nest predation on black-tailed prairie dog colonies. *Journal of Wildlife Management* 64, 776–784.
- Bangert, R.K., Slobodchikoff, C.N., 2000. The Gunnison's prairie dog structures a high desert grassland landscape a keystone engineer. *Journal of Arid Environments* 46, 357–369.
- Barko, V.A., Palmer, M.W., Stewart, J.G., Engle, D.M., 2001. Vascular plant communities associated with black-tailed prairie dogs in southern shortgrass prairie. *Proceedings of the Oklahoma Academy of Science* 81, 11–19.
- Bestelmeyer, B.T., Wiens, J.A., 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing versus natural heterogeneity. *Ecological Applications* 11, 1123–1140.
- Birch, W.L., 1977. Ecological Separation of *Peromyscus maniculatus* Bairdii and *P. leucopus* Novelbaralensis (Rodentia) in Southcentral Ohio. Ohio State University, Columbus, OH.
- Brown, D.E., 1994. Biotic Communities of the Southwest. University of Utah Press, Salt Lake City.
- Ceballos, G., Pacheco, J., List, R., 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* 41, 161–172.
- Chamberlain, D.E., Wilson, A.M., Browne, S.J., Vickery, J.A., 1999. Effects of habitat type and management on abundance of skylarks in the breeding season. *Journal of Applied Ecology* 36, 856–870.
- Clark, T.W., Campell, T.M., Socha, D.G., Casey, D.E., 1982. Prairie dog colony attributes and associated vertebrate species. *Great Basin Naturalist* 42, 572–582.
- Cornell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Coppock, D.L., Detling, J.K., Ellis, J.E., Dyer, M.I., 1983. Plant–herbivore interactions in a North American mixed-grass prairie. *Oecologia* (Berlin) 56, 1–9.
- Davidson, A.D., Parmenter, R.R., Gosz, J.R., 1999. Responses of small mammals and vegetation to a reintroduction of Gunnison's prairie dogs. *Journal of Mammalogy* 80, 1311–1324.
- Desmond, M.J., Savidge, J.A., Eskridge, K.M., 2000. Correlations between burrowing owl and black-tailed prairie dog declines: a 7-years analysis. *Journal of Wildlife Management* 64, 1067–1075.
- Fahnestock, J.T., Detling, J.K., 2002. Bison–prairie dog–plant interactions in a North American mixed-grass prairie. *Oecologia* 132, 86–95.
- Findley, J.S., Harris, A.H., Wilson, D.E., Jones, C., 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, New Mexico.

- Girard, J.M., Wagner, D.M., Vogler, A.M., Keys, C., Allender, C.J., Drickamer, L.C., Keim, P., 2004. Differential plague transmission dynamics determine *Yersinia pestis* population genetic structure on local, regional, and global scales. *Proceedings of the National Academy of Sciences* 101, 8408–8413.
- Hoffmeister, D.F., 1986. *Mammals of Arizona*. University of Arizona Press and the Arizona Game and Fish Department, Tucson.
- 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, University of Michigan* 67, 1–123.
- Kotliar, N.B., 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? *Conservation Biology* 14, 1715–1721.
- Kotliar, N.B., Baker, B.W., Whicker, A.D., Plumb, G., 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24, 177–192.
- Kretzer, J.E., Cully Jr., J.F., 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. *Southwestern Naturalist* 46, 171–177.
- Lomolino, M.V., Smith, G.A., 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Biological Conservation* 115, 89–100.
- MacMahon, J.A., 1985. *The Audubon Society Nature Guides: Deserts*. Alfred A. Knopf, New York.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, second ed., *Texts in Statistical Science*. Chapman and Hall, London, UK.
- Manning, A.E.E., White, C.M., 2001. Nest selection by mountain plovers (*Caradrius montanus*) in shrub steppe habitat. *Western Naturalist* 61, 229–232.
- McCure, B., Mefford, M.J., 1999. *Multivariate Analysis of Ecological Data*. Version 4.20, MjM Software, Glenden Beach, OR.
- Miller, B., Ceballos, G., Reading, R., 1994. The prairie dog and biodiversity. *Conservation Biology* 8, 677–681.
- National Oceanic & Atmospheric Administration, National Environmental Satellite, Data, and Information Service, National Climatic Data Center (NOAA, NCDC), 2003. <http://www.ncdc.noaa.gov/oa/climate/research.html>.
- Noss, R., LaRoe, E.T., Scott, J.M., 1995. *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation*. United States National Biological Service, Washington, DC Report 0611-R-01.
- O’Meilia, M.E., Knopf, F.L., Lewis, J.C., 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35, 580–585.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *American Naturalist* 103, 91–93.
- Pielou, E.C., 1969. *An Introduction to Mathematical Ecology*. Wiley, New York.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Catilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *BioScience* 46, 609–620.
- Samson, F.B., Knopf, F.L., 1994. Prairie conservation in North America. *Bioscience* 44, 418–421.
- SAS Institute Inc., 2001. *JMPin*. Version: 4.0.4 Duxbury, Thomson Learning Academic Center. Pacific Grove, CA.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52, 591–611.
- Slobodchikoff, C.N., Robinson, A., Schaack, C., 1988. Habitat use by Gunnison’s prairie dogs. In: *Management of Amphibians, Reptiles, and small Mammals in North America*. General Technical Report RM-160. US Department of Agriculture, Forest Service, Washington, DC, pp. 403–408.
- Stapp, P., 1998. A reevaluation of the role of prairie dogs in great plains grasslands. *Conservation Biology* 12, 1253–1259.
- Thomas, R.E., Barnes, A.M., Quan, T.J., Beard, M.L., Carter, L.G., Hopla, C.E., 1988. Resistance and susceptibility to *Yersinia pestis* in two populations of northern grasshopper mice *Onychomys leucogaster*. *Journal of Wildlife Diseases* 24, 327–333.
- Wagner, H., Wildi, O., Ewald, K.L., 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* 15, 219–227.
- Wagner, D.M., Drickamer, L.C., 2004. Abiotic habitat correlates of Gunnison’s prairie dog in Arizona. *Journal of Wildlife Management* 68, 188–197.
- Wagner, D.M., Drickamer, L.C., Krpata, D.M., Allender, C.J., Van Pelt, W.E., Keim, P., 2006. Persistence of Gunnison’s prairie dog colonies in Arizona, USA. *Biological Conservation* 130, 331–339.

- Weibull, A.C., Bengtsson, J., Nohlgren, E., 2000. Diversity of butterflies in agricultural landscapes: the role of farming system and landscape heterogeneity. *Ecography* 23, 743–750.
- Weltzin, J.F., Dowhower, S.L., Heitersmidt, R.K., 1997. Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist* 42, 251–258.
- Whicker, A.D., Detling, J.K., 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38, 778–785.
- Yunger, J.A., Randa, L.A., 1999. Trap decontamination using hypochlorite: effects of trappability of small mammals. *Journal of Wildlife Management* 80, 1336–1340.
- Zar, J.H., 1996. *Biostatistical Analysis*, third ed. Prentice-Hall, Upper Saddle River, NJ.