

# A comparison of herpetofauna and small mammal diversity on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and non-colonized grasslands in Colorado

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## Abstract

Research suggests that prairie dogs play a keystone role in grassland ecosystems. We examined the relationship between black-tailed prairie dogs (*Cynomys ludovicianus*) and herptiles and small mammals in eastern Colorado. Using pitfall traps, funnel traps, and ground captures, we captured a total of 152 herptiles representing 10 species. Captures of herptiles and small mammals varied with annual precipitation. As predicted, we captured some species more frequently on colonies and others more commonly off colonies. Bullsnares (*Pituophis catenifer*) and prairie rattlesnakes (*Crotalus v. viridis*) comprised 49% of herptiles captured, with significantly more rattlesnakes captured on colonies, but more bullsnares (not significant) off colonies. We found similar herptile species richness and both Shannon–Wiener and evenness diversity indices on colonies and off-colony sites, but slightly higher diversity when calculated across the two habitat types. We inadvertently caught 134 mammals in traps; 59% on colonies and 41% on off-colony sites. Deer mice (*Peromyscus maniculatus*) represented the most frequent mammal caught. Captures of desert cottontail rabbits (*Sylvilagus audubonii*) were significantly higher on colonies. Higher species richness and diversity of small mammals was associated with colonies. These results support our hypothesis that the presence of prairie dogs increases diversity between habitats or ecosystems (i.e. beta diversity) on grasslands they inhabit.

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## 1. Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) act as ecosystem engineers (Jones et al., 1997) that change prairie landscapes through their burrowing, grazing, and other activities, altering floral (Whicker and Detling, 1988; Weltzin et al., 1997), vertebrate (Clark et al., 1982; Sharps and Uresk, 1990; Lomolino and Smith, 2003b; Shaughnessy and Cifelli, 2004), and invertebrate diversity (Kretzer and Cully, 2001b; Russell and Detling, 2003). An increasing body of literature suggests that black-tailed prairie dogs function as a keystone species, significantly affecting ecosystem function, composition, and structure in a manner that is disproportionate to their population size (Power et al., 1996; Kotliar et al., 1997, 1999, 2005; Smith and Lomolino, 2004). Kotliar et al. (1999) reviewed the literature on species associated with prairie dogs and suggested that at least 9 species are dependent on prairie dogs, 20 species appear to benefit from the presence of prairie dogs and their activities, and 117 species possess life history traits suggesting that they also benefit, but remain insufficiently studied. Since that time, additional research has found evidence that several more species appear to benefit from their association with prairie dogs (e.g. Ceballos et al., 1999; Manzano-Fischer et al., 1999; Desmond et al., 2000; Bak et al., 2001; Kretzer and Cully, 2001a, b; Lomolino and Smith, 2003b; Smith and Lomolino, 2004).

Black-tailed prairie dog populations (*C. ludovicianus*) throughout North America have declined by over 98% since the turn of the century (Marsh, 1984). It is estimated that colonies of the five species of prairie dogs originally covered between 40 and 100 million hectares of native mixed-and short-grass prairies (Marsh, 1984; Anderson et al., 1986). Traditionally considered a range and agricultural pest (Clark, 1989), prairie dogs have been subjected to systematic eradication efforts through poisoning and habitat destruction (Bell, 1921; Day and Nelson, 1929; Hansen, 1988; Sharps, 1988), in addition to severe losses due to sylvatic plague (Cully, 1993). Declines of prairie dogs continue despite research suggesting that prairie dogs' competition with livestock is much less than previously believed (Hansen and Gold, 1977; O'Meilia et al., 1982; Uresk and Paulson, 1988, but see also Vermeire et al., 2004). Eradication of prairie dog colonies has had a negative effect on some specialized animals dependent on these colonies.

Few studies have examined the relationship between prairie dogs and herptiles (Kretzer and Cully, 2001a; Lomolino and Smith, 2003b) or small mammals (Agnew et al., 1986; Tyler and Shackford, 2002; Shaughnessy and Cifelli, 2004). In this study, we compared the diversity of herptiles and small mammals on black-tailed prairie dog colonies to adjacent, uncolonized grasslands in central Colorado. We predicted that the diversity of both herptiles and small mammals would be similar on prairie dog colonies and non-colonized areas, but that species assemblages would differ, leading to higher diversity across these two types of habitats (i.e. beta diversity). We believed that this would occur because some species benefit from the changes wrought by prairie dogs, while others are negatively affected.

## 2. Materials and methods

### 2.1. Study area

This study was conducted on the Plains Conservation Center (PCC) in Arapahoe County, Colorado (39°39'N, 104°44'W) during May–September from 2001 to 2003. PCC is

located 6.4 km east of Cherry Creek State Park on E. Hampden Ave. and was originally used by the military in the 1940s and 1950s as a bombing (sand bombs only) and machine gun range before being deeded to the West Arapahoe Conservation District.

PCC consists of 445 ha of gently rolling clayey and loamy plains within the short-grass steppe biome and extends over an elevation range of 1728–1783 m. The terrain is primarily 1–9% slope, rarely 30%. An intermittent stream runs south to north through the property. Major soils types are Buick loam, Fondis silt loam, Fondis–Colby silt loam, Renohill–Buick loam, and Renohill–Litle–Thedalund complex. Dominant native grasses include blue grama (*Chondrosium gracile*), western wheatgrass (*Pascopyrum smithii*), and green needle grass (*Stipa viridula*), followed by needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and buffalo grass (*Buchloe dactyoides*). Predominate native forbs include broom snakeweed (*Gutierrezia sarothrae*), western wallflower (*Erysimum asperum*), sand dropseed (*Sporobolus cryptandrus*), and gumweed (*Grindelia squarrosa*). Four species of cactus (*Opuntia compressa*, *O. polyacantha*, *Coryphantha vivipara*, *C. missouriensis*) are abundantly distributed as are rabbitbrush (*Chrysothamnus parryi*) and fourwing saltbush (*Atriplex canescens*). Invasive, exotic plants include cheatgrass (*Bromus tectorum*), common mullein (*Verbascum thapsus*), Canada thistle (*Cirsium arvense*), and Russian thistle (*Salsola australis*).

In 1982, a prairie dog colony was established on PCC by prairie dogs relocated from habitat impacted by housing development. A plague outbreak in 1989–1990 claimed nearly all prairie dogs. Subsequent additions of relocated prairie dogs over time resulted in three separate colonies, covering approximately 2.5 ha each.

## 2.2. Methods

We used each of the three colonies on PCC in this study. Two non-colonized areas of comparable size were selected to serve as controls in 2001. A third off-colony (control) site was added in 2002–2003, but a portion of one of the off-colony sites was colonized by prairie dogs in 2002 and so excluded from further analyses. Off-colony areas were established at distances of 582–878 m from colonies and selected based on their topographic similarity to their respective study colonies.

Within the study colony and off-colony areas, six drift fence arrays (2/site) were distributed randomly. Drift fence arrays were composed of three arms of 0.58 m tall galvanized sheet metal, 7.6 m long, set 9.6 cm into the ground, and radiating out from a center point at 120°. The sheet metal was held upright by a series of stakes. At the end of each arm and center of each array we buried a 22.7 l bucket, serving as a pitfall trap ( $n = 4$  pitfall traps/array). Each pitfall trap had a 43 × 43 cm piece of plywood with short legs attached covering the opening of the trap to provide shade and rain cover. At the bottom of each pitfall trap, a piece of plywood supported on 7.2 cm legs provided animals with a hiding area and escape from sudden flooding of the traps. In addition, every arm of each array had at its center a funnel trap (Fitch, 1987) made from wire mesh ( $n = 3$  funnel traps/array in 2001,  $n = 6$  funnel traps/array in 2002–2003). Each funnel trap had a plywood cover providing shade. In total, 40 pitfall traps (24 on colony and 16 on off-colony sites) and 30 funnel traps (18 on colony and 12 on off-colony sites) were used in 2001. Forty-eight pitfall traps (24 on both colonies and off-colony sites) and 72 funnel traps (36 on both colonies and off-colony sites) were used in 2002–2003. Free-roaming herptiles captured on study sites were also included in the study. Although we targeted herptiles, a large number

of small mammals were also captured in the pitfall and funnel traps. We analysed these data separately.

Beginning mid-May of each year, traps were opened 7–10 days for each trapping session. Trapping sessions ran twice a month until mid-September. Traps were checked daily during each trapping session. All vertebrate animals caught were released at least 8.6 m away from the trapping array. Herptiles were marked prior to release. All snakes were tagged with a Passive Integrated Transponder (PIT) chip. Lizards, toads, and frogs were toe-clipped using a simplified numbering system (Alford et al., 1994). Tiger salamander (*Ambystoma tigrinum*) identities were recorded using drawings of dorsal spot patterns. We recorded the following data for all individuals of herptiles trapped: Date captured, sex (determined visually or by sexing probes in the case of snakes), snout-vent length, total length, colony or control area name, array number, and marking code. Data on small mammals trapped included only identification to at least genus level, date, colony or off-colony area name, and array number. Environmental data were recorded, such as 24 h max./min. temperatures and precipitation.

We calculated relative abundance (number of individuals captured each year), species richness, Shannon–Wiener diversity index, and an evenness index for each study site, as well as for all colonies combined, all off-colony sites combined, and across the study area (colonies and off-colony sites combined). We computed the Shannon–Wiener index as

$$H' = - \sum p_i (\ln p_i),$$

where  $p_i$  is the decimal percentage of individuals of the total sample belonging to the  $i$ th species. We computed the evenness index as

$$e = H' / \ln S,$$

where  $H'$  is the Shannon–Wiener index as above and  $S$  is the number of species in the sample.

We compared capture rates between colony and off-colony sites using the Pearson  $\chi^2$ -test with a Yate's correction and Fisher's exact test, but report only the  $\chi^2$  with Yate's correction here, as it was more conservative and results were similar. For herptiles, tests were conducted with all captures and with captures of new individuals only; however, since the results were similar (varying only in degree, but not in significance or direction of difference), we only report on analyses of new individuals here. We used pooled or separate variance  $t$ -tests on log transformed data to compare capture rates for individual species on and off of colonies or Mann–Whitney  $U$  test for data we could not normalize. Species richness and evenness were compared using Kruskal–Wallis and Mann–Whitney  $U$  tests. We tested for differences in species composition between sites with and without prairie dogs and controlling for year using a two-way analysis of similarity (ANOSIM), which is a distribution-free analogue of analyses of variance (Clarke, 1993). To test for differences in the Shannon–Wiener index we computed a  $t$  statistic following Magurran (1988) as

$$t = \frac{H'_1 - H'_2}{(\text{var } H'_1 + \text{var } H'_2)^{1/2}},$$

where  $H'_n$  is the the Shannon–Wiener index for sample  $n$ , and  $\text{var } H'_n$  is the variance for the Shannon–Wiener index in sample  $n$ . We computed  $\text{var } H'_n$  as

$$\text{var } H'_n = \frac{\sum p_i (\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} + \frac{S - 1}{2N^2},$$

where  $N$  is the total number of individuals caught,  $S$  the number of species caught, and  $p_i$  the proportion of individuals in the  $i$ th species. We computed the degrees of freedom as

$$df = \frac{(\text{var } H'_1 + \text{var } H'_2)^2}{(\text{var } H'_1)^2/N_1 + (\text{var } H'_2)^2/N_2}.$$

We used logistic regression to examine the effects of location (colony or off colony) and year on diversity indices. Significance was  $p < 0.05$ . Means are reported  $\pm 1$  standard error (SE).

### 3. Results

#### 3.1. Herptiles

We captured a total of 152 herptiles representing 10 species during the 2001–2003 study. In 2001 we captured 60 herptiles representing 10 species (Table 1). We captured more animals in funnel traps (42%,  $n = 25$ ), followed closely by ground captures (40%,  $n = 24$ ), and pitfall traps (18%,  $n = 11$ ). In 2002, a severe drought struck and PCC introduced cattle for weed control. A complete lack of water-filled ponds precluded amphibian breeding that year. Thus, only 20 herptiles were captured, comprising 6 species (Table 1).

Table 1  
Herptiles captured using different trapping methods on and off of black-tailed prairie dog colonies in Colorado, 2001–2003

Common name	All sites combined				On colonies				Off colonies			
	2001	2002	2003	All	2001	2002	2003	All	2001	2002	2003	All
Plains garter snake	3	1	7	10	0	0	5	5	3	0	2	5
W. terr. garter snake	1	1 (2)	4	6 (2)	1	0	2	3	0	1 (2)	2	3 (2)
Rattlesnake	13	9 (2)	19	41 (2)	10	6	12	28	3	3 (2)	7	13 (2)
Bullsnake	16	6 (1)	11	33 (1)	7	2	4	13	9	4 (1)	7	20 (1)
Lined snake	1	0	1	2	0	0	0	0	1	0	1	2
Short-horned lizard	11	2	0	13	11	2	0	13	0	0	0	0
Many-lined skink	3	1 (1)	3	7 (1)	0	1	2	3	3	0 (1)	1	4 (1)
Tiger salamander	6	0	13	19	4	0	1	5	2	0	12	14
Spadefoot toad	4	1	11	16	2	0	3	5	2	1	8	11
Chorus frog	2	0	3	5	2	0	1	3	0	0	2	2
Totals	60	20 (6)	72	152 (6)	37	11	30	78	23	9 (6)	42	74 (6)

Numbers in ( ) = animals caught in a grid that was colonized by prairie dogs during the 2002 trapping season; these individuals were not used in data analyses. Table includes all captures, but only unmarked (i.e., previously uncaptured individuals) were included in the study.

Most captures were in funnel traps (75%,  $n = 15$ ), followed by pitfall traps (15%,  $n = 3$ ), and ground captures (10%,  $n = 2$ ). In 2003, we caught 72 herptiles, representing 9 species. Again, we captured more animals in funnel traps (56%,  $n = 40$ ), followed by pitfall traps (29%,  $n = 21$ ), and ground captures (15%,  $n = 11$ ).

The most common species captured on both colonies and off-colony sites for all years combined was the prairie rattlesnake, representing 27% of total herptile captures, followed by bullsnakes (*Pituophis catenifer*), representing 22%. We captured significantly more prairie rattlesnakes (*Crotalus v. viridis*) on colonies than off colonies ( $t_{12.6} = 2.26, p = 0.04$ ). We found no other significant differences ( $p > 0.10$ ) in capture rates on colony and off-colony sites for any other species. We looked at species composition, richness, and diversity indices for each year and all years pooled, using data for each array independently and all the data pooled (Fig. 1). Differences in herptile species composition between colony and off-colony sites were not significant ( $R < 0.01, p = 0.53$ ) when we controlled for year effects. Alternatively, year effects were more important ( $R = 0.28, p = 0.057$ ) for all three years, with significant differences between 2001 and 2002 ( $R = 0.45, p < 0.01$ ) and 2002 and 2003 ( $R = 0.66, p = 0.03$ ), but not between 2001 and 2003 ( $R = -0.16, p = 0.76$ ). Within each year, species richness and diversity indices were very similar on colonies and off-colony sites (Fig. 1). All measures of diversity were much lower in 2002 than in 2001 for both off-colony sites and colonies.

We analysed diversity using means of sites and data pooled for all sites by year and for all three years of the study combined (Fig. 1). We found similar species richness for data pooled across sites (4–9 species/year), capturing 9 species of herptiles both on colonies and off colonies over the three years of the study (Table 3 and Fig. 1). Although mean species

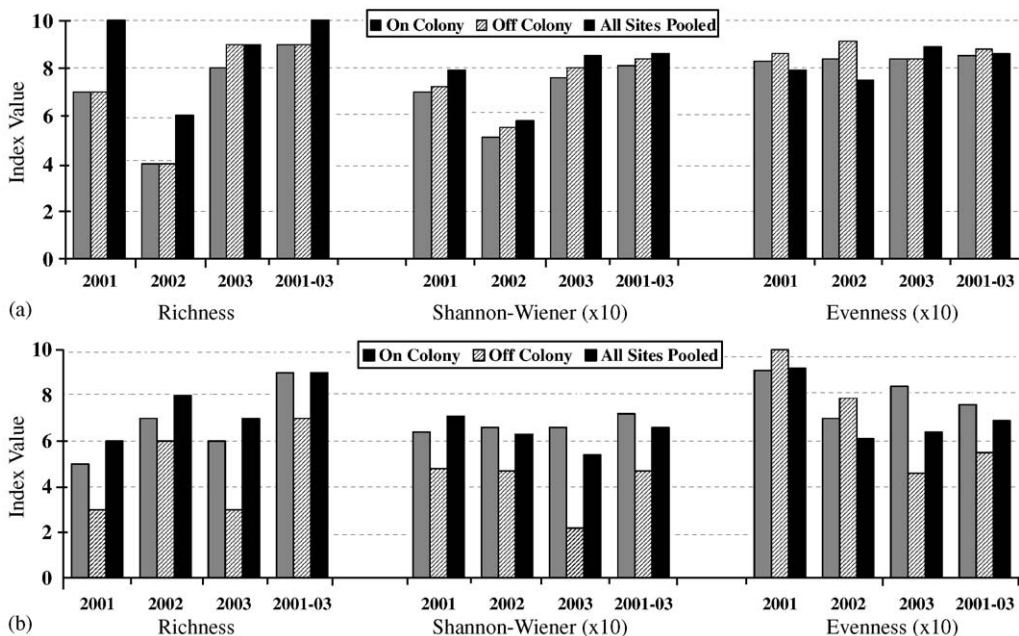


Fig. 1. Diversity indices of herptiles (a) and small mammals (b) captured on and off of black-tailed prairie dog colonies in Colorado, 2001–2003. Note: The Shannon–Wiener and evenness indices are  $\times 10$ .

richness was consistently higher on off-colony sites ( $3.00 \pm 1.00$ – $6.50 \pm 0.50$  species) compared with colony sites ( $2.33 \pm 0.33$ – $5.00 \pm 0.76$  species), this difference was not significant ( $U = 35.00, p = 0.34$ ). We found significantly lower species richness of herptiles on both colonies and off colonies in 2002, compared with 2001 and 2003 (Table 2).

The Shannon–Wiener diversity index was similar between colony and off-colony sites, but the index was higher off colonies for data both pooled across sites and means of all sites for all years (Fig. 1). Means of sites by year varied from  $0.33 \pm 0.09$  to  $0.62 \pm 0.02$  for colonies and  $0.49 \pm 0.15$ – $0.72 \pm 0.03$  off colonies, while pooled data varied from 0.51 to 0.76 for colonies and from 0.55 to 0.80 off colonies. Similarly, pooling data across years for all colony and off-colony sites yielded similar Shannon–Wiener values of 0.81 and 0.84, respectively. The Shannon–Wiener diversity indices were not significantly different ( $p \geq 0.05$ ) between colonies and off-colony sites within years or among years; this was true if we used indices for individual colony and off-colony sites or pooled sites. Logistic regression of unpooled data by site also found an insignificant effect of colony

Table 2

Effect of black-tailed prairie dogs (on vs. off colony site) and year on diversity of herptiles and small mammals in the shortgrass prairie of Colorado, 2001–2003

Vertebrate group Index Variable	Parameter			
	Estimate	SE	<i>t</i> -score	<i>p</i>
<b>Herptiles</b>				
Richness ( $F_{3,11} = 7.69, P = 0.01, R^2 = 0.59$ )				
Colony (relative to off-colony)	−0.83	0.57	−1.47	0.17
2001 (relative to 2002)	2.20	0.68	3.24	0.01
2003 (relative to 2002)	3.00	0.68	4.42	0.001
Shannon–Weiner ( $F_{3,11} = 5.76, P = 0.01, R^2 = 0.51$ )				
Colony (relative to off-colony)	−0.08	0.06	−1.36	0.20
2001 (relative to 2002)	0.22	0.07	2.93	0.01
2003 (relative to 2002)	0.28	0.07	3.74	0.003
Evenness ( $F_{3,11} = 1.00, P = 0.43, R^2 = 0.00$ )				
Colony (relative to off-colony)	−0.02	0.03	−0.72	0.49
2001 (relative to 2002)	−0.05	0.04	−1.35	0.20
2003 (relative to 2002)	−0.05	0.04	−1.38	0.20
<b>Mammals</b>				
Richness ( $F_{3,12} = 3.85, P = 0.04, R^2 = 0.36$ )				
Colony (relative to off-colony)	1.28	0.77	1.66	0.12
2001 (relative to 2002)	−2.20	0.97	−2.28	0.04
2003 (relative to 2002)	−2.47	0.93	−2.66	0.02
Shannon–Weiner ( $F_{3,11} = 4.54, P = 0.03, R^2 = 0.43$ )				
Colony (relative to off-colony)	0.22	0.10	2.09	0.06
2001 (relative to 2002)	−0.26	0.12	−2.09	0.06
2003 (relative to 2002)	−0.37	0.12	−2.96	0.01
Evenness ( $F_{3,11} = 3.65, P < 0.05, R^2 = 0.36$ )				
Colony (relative to off-colony)	0.32	0.17	1.82	0.10
2001 (relative to 2002)	−0.11	0.21	−0.53	0.61
2003 (relative to 2002)	−0.54	0.21	−6.05	0.02

vs. off-colony (Table 2). Yet, logistic regression found a relatively large and significant effect of year, with both 2001 and 2003 having significantly higher Shannon–Wiener scores than 2002 (Table 2).

Evenness indices were also similar for colonies and off-colony sites, especially for 2001 and 2003 (Fig. 1). Pooled evenness indices were consistently higher off colonies (0.84–0.91) than on colonies (0.83–0.84). Similarly, mean evenness was higher in 2002 off colonies ( $1.00 \pm 0.00$ ) than on colonies ( $0.91 \pm 0.04$ ); however, mean evenness indices for 2001 and 2003 were slightly higher on colonies ( $0.90 \pm 0.02$  and  $0.90 \pm 0.04$ , respectively) than off colonies ( $0.89 \pm 0.05$  and  $0.88 \pm 0.00$ , respectively). As with the Shannon–Wiener diversity index, evenness was not significantly different ( $p > 0.05$ ), using the Mann–Whitney  $U$  test between colonies and off-colony sites within years or among years using individual or pooled sites. The logistic regression of unpooled data by site also found no significant difference in evenness scores for colonies and off-colony sites, or with respect to year (Table 2).

We pooled colony and off-colony sites to produce overall diversity indices (Fig. 1). For each year and all years pooled, the Shannon–Wiener index was higher than it was for either colony or off-colony sites pooled. However, these differences were not significant ( $p \geq 0.05$ ). The overall evenness index was lower in 2001 and 2002, but higher in 2003 than were the evenness indices for both colony and off-colony sites pooled. These differences were not significant ( $K-W = 1.89, p = 0.39$ ).

### 3.2. Small mammals

One hundred thirty-four mammals were inadvertently caught in both pitfall and funnel traps (Table 3). Of the total mammals caught, 59% ( $n = 79$ ) were captured on colonies, while 41% ( $n = 56$ ) were captured on off-colony sites. Three orders were represented: Rodentia, with 4 families (Sciuridae, Geomyidae, Heteromyidae, and Muridae) and 7 genera; Insectivora, with 1 family (Soricidae) and 1 genus; and Lagomorpha, with 1 family (Leporidae) and 1 genus (Table 3). Small mammal catches totaled 17 in 2001, increased to 87 in 2002 (coinciding with drought) and then declined to 30 in 2003.

Table 3  
Small mammals captured on and off of black-tailed prairie dog colonies in Colorado, 2001–2003

Common name	All sites combined				On colonies				Off colonies			
	2001	2002	2003	All	2001	2002	2003	All	2001	2002	2003	All
Deer mouse	5	49	19	73	4	22	7	33	1	27	12	40
Harvest mouse	2	7	1	10	2	3	1	6	0	4	0	4
N. grasshopper mouse	0	10	3	13	0	8	3	11	0	2	0	2
Vole	2	5	2	9	1	2	1	4	1	3	1	5
Hispid pocket mouse	0	3	0	3	0	3	0	3	0	0	0	0
Pocket gopher	1	1	1	3	0	0	1	1	1	1	0	2
13-lined ground squirrel	0	3	1	4	0	1	1	2	0	2	0	2
Shrew	2	0	0	2	2	0	0	0	0	0	0	0
Desert cottontail	5	9	4	18	5	9	3	17	0	0	1	1
Totals	17	87	30	134	14	48	16	78	3	39	14	56

Deer mouse (*Peromyscus maniculatus*) captures displayed the greatest year-to-year fluctuation during the study and were the most frequently caught mammal, comprising 54% of all mammals. There were no significant differences ( $p > 0.05$ ) in capture rates of rodents on and off colonies, although grasshopper mice demonstrated a strong trend, being captured more often on colonies ( $n = 11, 85\%$ ;  $t_{12} = 1.79, p < 0.10$ ). We trapped several desert cottontail rabbits (*Sylvilagus audubonii*, 13% of total) as young of the year, primarily on colonies ( $n = 17, 94\%$ ), and exclusively in funnel traps. Capture rates were significantly higher on colonies than off ( $t_{9,7} = 2.58, p = 0.03$ ).

Mammal species composition did not differ significantly between colony and off-colony sites ( $R = 0.24, p = 0.135$ ) when we controlled for year effects. Overall, species composition differences between years were not significant ( $R = 0.07, p = 0.30$ ), nor were any year-to-year comparisons ( $p > 0.05$ ).

We analysed diversity for mammals species using means of sites and data pooled for all sites by year and for all three years of the study combined (Fig. 1). Species richness was higher on colonies than off colonies for all years combined and for each year (Fig. 1). This difference was insignificant whether we compared sites separately ( $U = 18.00, p = 0.15$ ) or pooled ( $U = 1.50, p = 0.18$ ). Shannon–Wiener diversity indices were consistently higher on colonies than off colonies regardless of how we calculated the index, with mean Shannon–Wiener diversity indices ranging from  $0.32 \pm 0.18$  to  $0.59 \pm 0.02$  on colonies and from  $0.12 \pm 0.12$  to  $0.51 \pm 0.11$  off colonies. Indices pooled across sites ranged from 0.64 to 0.66 for colonies and 0.22 to 0.48 for off-colony sites (Fig. 1). These differences were significant for pooled data in 2002 ( $t_{73,4} = 1.82, p < 0.05$ ), 2003 ( $t_{28,2} = 2.21, p < 0.05$ ), and all years combined ( $t_{101,9} = 2.86, p < 0.01$ ), but not in 2001 ( $t_{3,4} = 0.55, p > 0.05$ ). In contrast to the herpetological data, when we pooled data across all sites (on-colony and off-colony together), the Shannon–Wiener index was lower than the index for on-colony sites in all years except 2001, although these differences were not significant ( $p \gg 0.05$ ; Fig. 1). Logistic regression found no significant effect of treatment (although it was close,  $p = 0.06$ ), but a significantly lower index in 2003 relative to 2002 (Table 2).

Mean evenness values for colonies ( $0.53 \pm 0.28$ – $0.92 \pm 0.01$ ) were consistently higher than those for off-colony sites ( $0.24 \pm 0.24$ – $0.71 \pm 0.15$ ), while the pooled data demonstrated mixed results (Fig. 1); evenness index values were 0.64–0.91 for colonies and 0.79–1.00 for off-colony sites. None of the differences were significant ( $p > 0.05$ ) using Mann–Whitney  $U$  tests. Overall evenness values, calculated for colony and off-colony sites combined, were generally lower than or fell between values for on colonies and off-colony sites (Fig. 1). Logistic regression results for evenness found only a significantly lower value for 2003 compared to 2002 (Table 2).

## 4. Discussion and conclusions

### 4.1. Herptiles

Some herptiles appear to benefit from the changes engineered by black-tailed prairie dogs on the shortgrass steppe of Colorado, while other species appear to be negatively affected. Species that utilize prairie dog burrows as refugia to escape extreme weather and predators or as hibernacula would obviously benefit from the large number of burrows on a prairie dog colony, many of which are little used (Hoogland, 1995; Ceballos et al., 1999; Kotliar et al., 1999). Alternatively, species that require dense, tall vegetation would likely

be negatively affected. Our results support these predictions. In our study, of the eight species found both on and off-colonies, tiger salamanders, spadefoot toads, and bullsnakes were caught most often off colonies, while prairie rattlesnakes were more common on colonies. In contrast, the lined snake was captured only on off-colony sites, the short-horned lizard only on one colony. The remaining four species were caught with equal frequency or almost equal frequency on and off colonies.

The higher number of rattlesnakes captured on colonies compared to off-colony sites may reflect their ecology. In all of our study colonies, prairie rattlesnakes used numerous burrows for hibernation (see also Holycross, 1995; Cunningham et al., 1996). In the plains grasslands where few rock outcroppings exist to serve as hibernacula, rattlesnakes appear to rely more heavily on burrows dug by other species. During spring, rattlesnakes emerging from prairie dog burrows move away from colonies in which they hibernate and enter adjacent grassland. Rattlesnakes may be more easily caught on colonies in the autumn and spring, during movements to and from colonies that serve as hibernacula. They may also utilize burrows as overnight refugia. In addition, rattlesnakes hunt on colonies due to the higher number of small mammals present. Rattlesnakes may be more widely dispersed off-colony, comparatively. More research is necessary.

Use of prairie dog burrows by herptiles has been documented, but not well studied (Stromberg, 1978; Clark et al., 1982). Kolbe et al. (2002) found that tiger salamanders use prairie dog burrows, especially burrows near water sources. Similarly, in our study site, we observed tiger salamanders emerging from prairie dog burrows in March on two separate occasions. Yet, we caught most salamanders off colonies. This likely was due to the fact that one of our off-colony sites was much closer to a human-made pond (~10 m) than the nearest colony site (~670 m). A chorus frog was captured in a pitfall trap on a prairie dog colony, and we suspect that prairie dog burrows may provide alternative over-wintering sites as well as protection from extended drought periods. We observed many-lined skinks in and around prairie dog burrows, primarily as juveniles.

Herptile captures appeared to vary with annual precipitation. In 2001, a total of 42 cm of precipitation fell, and that year we caught a total of 60 herptiles. In 2002 the Denver area experienced a drought, with total precipitation of only 19 cm. The addition of cattle from early spring until early summer, introduced by PCC in an attempt to control weeds, enhanced the effect of the drought by further reducing plant cover and height. Cattle were removed permanently in mid-summer 2002 to prevent severe over-grazing. Total herptile captures declined to 20 that year. The following year, 2003, saw more abundant precipitation totaling 35 cm. Many low areas filled with water, which remained through the trapping season. Abundant vegetative growth also occurred, both on colonies and off-colony sites. Populations of two plant species, common sunflower (*Helianthus annuus*)—a native, and Russian thistle (*Salsola australis*)—a European invasive, suddenly irrupted on off-colony sites and, to a lesser extent, colonies. In addition, the native forb, woolly plantain (*Plantago patagonica*), expanded to cover all three prairie dog colonies in a thick blanket, greatly reducing areas of exposed soil. In that year, herptile captures rebounded to total 72. Observed vegetative changes may have caused declines in the populations of some herptile species. For example, the expansion of woolly plantain after the heavy rains of 2003 may have strongly and negatively affected the ecology of the short-horned lizard, which was not seen in 2003. Preferring open, bare soil, short-horned lizards hunt insects by sight and burrow to escape heat, predators, and low temperatures (Reynolds, 1979; Hammerson, 1999). Alternatively, the changes in herptiles captures may,

at least partially, reflect behavioral changes, rather than solely changes in populations. Herptile capture rates may decline when sampling in xeric conditions, because many species sequester themselves underground to avoid excessive heat and drying during such times (Fitch, 1992; Jenkins et al., 2003).

Like our study, studies in southeastern Kansas (Kretzer and Cully, 2001a) and Oklahoma (Lomolino and Smith, 2003a, b) also reported similar herptile richness on and off black-tailed prairie dog colonies. Kretzer and Cully (2001a) found similar Shannon-Wiener and evenness diversity indices for herptiles on colony and off-colony sites, but higher diversity when calculated across two habitat types. However, they found a higher increase in both richness (from  $2.60 \pm 0.51$ – $4.43 \pm 0.75$  species/site to 9.00 species overall) and diversity ( $H = 0.33 \pm 0.09$ – $0.48 \pm 0.10$  for individual sites to  $H = 0.72$ – $0.85$  overall) than we did going from individual sites to across habitat types. Since black-tailed prairie dogs usually exist in colonies forming a mosaic of colonized and uncolonized prairie (Hoogland, 1995; Kotliar et al., 1999), these results suggest that prairie dogs increase the beta diversity (e.g. diversity between habitats or ecosystems) of herptiles, while having little impact on alpha diversity (e.g. diversity in one location) or evenness.

Our results indicate that there may be significant variables affecting herptile communities within prairie dog ecosystems. Seasonal changes in weather, especially precipitation, along with long-term climatic changes can influence species composition and richness (Lomolino and Smith, 2003a). During periods of increased precipitation, when vegetative growth increases, prairie dog colony habitat and adjacent matrix distinctiveness tends to be much more pronounced (Lomolino and Smith, 2003b). The loss or decline of herptile species positively associated with prairie dog colonies may indicate pronounced declines in prairie dog ecosystem extent and integrity over time (Tyler and Shackford, 2002). Moreover, slow recovery times for colonies devastated by plague or human control operations (e.g. poisoning) may result in long-term alterations to herptile assemblages. Further research is needed to examine changes in herptile populations associated with prairie dog colonies over extended time periods.

#### 4.2. Small mammals

Only a few rigorous studies of small mammals on and off of prairie dog colonies have been conducted (O'Meilia et al., 1982; Agnew et al., 1986, 1988; Ceballos et al., 1999; Davidson et al., 1999; Everett, 2002; Lomolino and Smith, 2003b). Most other assessments included small mammals as part of broader studies of associated species using techniques that miss the vast majority of small, nocturnal mammals (e.g. Reading et al., 1989; Ceballos et al., 1999; Tyler and Shackford, 2002; Smith and Lomolino, 2004). Our study differed from Agnew et al. (1986, 1988), Ceballos et al. (1999), Davidson et al. (1999), Everett (2002), and O'Meilia et al. (1982) in that we did not use bait or traps designed specifically to capture small mammals; we targeted herptiles with our trapping effort. Still, we believe it useful to compare captures on and off colonies because of the relatively large number of small mammals captured.

Davidson et al. (1999) differed from our study in that they focused on a reintroduced population of Gunnison's prairie dog (*C. gunnisoni*) only one year after reintroduction. They found no differences between control and experimental sites. As with our study, Agnew et al. (1986, 1988), Ceballos et al. (1999), Everett (2002), and O'Meilia et al. (1982) found a greater abundance of small mammals on colonies than off colonies, this difference

was significant for the latter two studies. In contrast, both Agnew et al. (1986, 1988) and O'Meilia et al. (1982) found lower species richness and diversity on colonies than off colonies, while we consistently found the opposite. Ceballos et al. (1999) found intermediate diversity on an off-colony site compared with two colony sites.

Some of the differences and similarities between the three main studies contrasted here may be explained by the type of grassland in which the research took place. O'Meilia et al.'s (1982) study and our work were conducted on shortgrass prairie in the southern plains, Ceballos et al. (1999) studied arid grasslands in northern Chihuahua, and Agnew et al.'s (1986, 1988) research was conducted in the mixed grass prairies of South Dakota. Yet, more research that captures a greater number of animals over a longer time period is probably required to better understand these differences and whether or not they are ecologically and statistically significant.

A variety of features that characterize prairie dog colonies probably attract or repel small mammals, including the presence of burrows (many of which go largely unused by the prairie dogs), differences in vegetative communities, and the amount of bare ground on colonies (Detling, 1998; Everett, 2002). Small mammals use empty burrows to escape predation and climatic extremes. They may also use them as hibernacula. The vegetation and bare ground differences between colonies and off-colony prairie probably affect small mammal distributions due to differences in foraging patterns and diets among the various species. In addition, the features of prairie dog colonies influence the abundance and species composition of invertebrates inhabiting colonies (O'Meilia et al., 1982; Agnew et al., 1986, 1988; Kretzer and Cully, 2001b; Russell and Detling, 2003; Bangert and Slobodchikoff, 2004; Guarisco et al., 2004). Since many small mammals, such as grasshopper mice, prey on invertebrates, these differences likely influence their distributions (O'Meilia et al., 1982; Agnew et al., 1988). In turn, the abundance and distribution of small mammals may influence carnivore distributions, but thus far the evidence for this remains poor (Ceballos et al., 1999; Shaughnessy and Cifelli, 2004) and likely requires more rigorous study.

Finally, although we captured far fewer herptiles during the extreme drought year (2002), we found just the opposite for small mammals—far greater captures in 2002 than in 2001 or 2003. We hypothesize that while herptiles were less likely to move, emerge from below ground, or reproduce during the drought, the severe conditions may have induced greater movement in small mammals who were forced to travel greater distances to forage. Furthermore, plant species composition and distribution altered by drought, in terms of species substitution (native or exotic), could have resulted in increases in primary food production, such as seeds, which attract rodents. Additional data on movement patterns during drought and non-drought years would help elucidate this issue.

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