



# Comparison of bird and mammal communities on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and uncolonized shortgrass prairie in New Mexico

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## ABSTRACT

Black-tailed prairie dogs (BTPD; *Cynomys ludovicianus*) have often been labeled as keystone species because of their ability to strongly influence grassland ecosystems. I used line-transect surveys and distance sampling to compare breeding bird and mammal communities on shortgrass prairie occupied by BTPD colonies versus similar uncolonized habitat in New Mexico, and to identify species that were either strongly associated with, or that avoided, BTPD colonies. Overall, I detected 32 bird and 8 mammal species during three years. Mountain plover (*Charadrius montanus*), ferruginous hawk (*Buteo regalis*), burrowing owl (*Athene cunicularia*), curve-billed thrasher (*Toxostoma curvirostre*), desert cottontail (*Sylvilagus audubonii*), and American badger (*Taxidea taxus*) were more abundant on, or at least strongly associated with, colonies, while long-billed curlew (*Numenius americanus*), horned lark (*Eremophila alpestris*), vesper sparrow (*Poecetes gramineus*), lark sparrow (*Chondestes grammacus*), Cassin's sparrow (*Aimophila cassinii*), and western meadowlark (*Sturnella neglecta*) were more abundant on, or strongly associated with, uncolonized prairie. Observed responses of several species differed from other studies suggesting that a species' response to BTPD activities may vary by location, grassland type, or season. Although BTPDs negatively impacted a suite of grassland bird species, biodiversity is maximized in this landscape by maintaining a mixture of colonized and uncolonized habitats.

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## 1. Introduction

Historically, large and small grazing animals, along with fire and other abiotic disturbances, played important roles in creating and maintaining a shifting mosaic of habitat patches that supported a diversity of species within grassland ecosystems of the North American Great Plains (Axelrod, 1985; Knapp et al., 1999). Although the importance of both fire and native grazing vertebrates has declined in most regions of the Plains, growing interest in restoration of grassland ecosystems and the conservation of native biodiversity have led to much research into the important roles that native grazers may play in these efforts (Truett et al., 2001). American bison (*Bison bison*) and the colonial prairie dogs (*Cynomys* spp.) have received considerable attention in this regard because of the central role they formerly played in prairie ecosystems due to their incredible abundance; during the early nineteenth century an estimated 30 million or more bison grazed the

Great Plains (McHugh, 1972), including at least 40 million ha of grasslands occupied by prairie dog colonies (Marsh, 1984). Although populations of both bison and prairie dogs today represent only a remnant of these past numbers, these herbivores still maintain the potential to greatly affect habitat structure and species composition often earning them the label of keystone species (Knapp et al., 1999; Kotliar et al., 1999, 2006; Truett et al., 2001).

Keystone species are those that through their actions influence ecosystem structure, composition, and function in a significant manner, particularly relative to their abundance (Power et al., 1996). American bison, for example, historically supported large populations of predators and scavengers, and through their grazing, trampling, and wallowing strongly influenced the structure and composition of tall- and mixed-grass prairie systems creating habitat diversity that enhanced species diversity at large spatial scales (Knapp et al., 1999; Truett et al., 2001). The effects of prairie dogs are even more profound and occur over a broader range of habitats as these species act not only as food sources for a wide range of predators, and as abundant grazers, but also as ecosystem engineers that create unique habitat components and greatly

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modify ecosystem processes (Bangert and Slobodchikoff, 2004; Kotliar et al., 1999, 2006). Prairie dogs not only affect vegetation through consumption but also clip vegetation of all types throughout colonies without consuming it. The primary function of this action is to reduce vegetation height to facilitate predator detection (Hoogland, 1995), but it also, in conjunction with grazing, often results in the suppression of woody plants, increased nutritional content of re-growth, reduced overall plant height, coverage, and biomass, and an increase in exposed bare soil (Reviewed in Detling, 2006; Whicker and Detling, 1988). Further, the intensive disturbance and soil movement generated by the burrowing actions of prairie dogs creates important microhabitats where annual forbs that compete poorly against dominant perennial grasses may survive, and can also indirectly affect vegetation by altering hydrology and nutrient cycling (Detling, 2006; Whicker and Detling, 1988). Finally, the burrows and tunnel systems themselves can act as breeding dens or refugia for a variety of vertebrate and invertebrate species (Reviewed in Kotliar et al., 1999).

Given their many ecological impacts and apparent roles as keystone species, there is little doubt that these grazers, particularly the focus of this paper, black-tailed prairie dogs (*Cynomys ludovicianus*), can exert a great influence on grassland ecosystems and biodiversity. However, how these activities affect species diversity or composition, how these effects vary across the range of grassland types, and how much particular species depend on these activities for their persistence are questions that remain unresolved (Kotliar et al., 1999, 2006; Stapp, 1998). For example, researchers have typically reported greater breeding bird species richness and total abundance on prairie dog colonies compared to adjacent uncolonized grassland habitats (Agnew et al., 1986; Barko et al., 1999; O'Meilia et al., 1982; Smith and Lomolino, 2004). In similar studies involving mammals, however, results have been more equivocal with some documenting greater total abundance and/or species richness on colonies (Agnew et al., 1986; Shipley and Reading, 2006), but most documenting little difference in total abundance and, often, lower species richness on colonies (Lomolino and Smith, 2003; McCaffrey et al., 2009; Pruett et al., 2010; Shaughnessy and Cifelli, 2004). At the species level, these patterns are further complicated by the fact that many studies have also identified individual species that respond negatively to prairie dog activities, or have identified species that show a positive response in some locations or seasons, but a negative or neutral response in others (Kotliar et al., 1999, 2006). If the keystone role of prairie dogs is to be used to justify recolonization or other conservation efforts (e.g., federal protection), additional research is needed to better understand the manner in which prairie dog activities influence native diversity over a broad range of taxa and grassland environments.

I used line-transect surveys and distance sampling (Buckland et al., 2001) to study the effects of black-tailed prairie dog colonies on grassland bird and mammal communities within a large, shortgrass prairie study area in northeastern New Mexico, U.S.A. This site had experienced prairie dog restoration efforts for over a decade such that prairie dog colonies covered over 2000 ha of grassland at the start of the study in 2008. Although American bison were also present within this system, bison were grazed at relatively low densities (See 2.1. Study area below) and roamed freely within large paddocks such that they were not restricted to colonized or uncolonized areas. My specific objectives were to compare breeding bird and day-active mammal species composition, as well as basic habitat and vegetative characteristics, on areas of shortgrass prairie occupied by prairie dog colonies versus associated uncolonized prairie. I also hoped to identify species that were strongly benefitted by, and/or species that were negatively

impacted by, prairie dog activities within the poorly studied shortgrass prairie ecosystem of New Mexico.

## 2. Materials and methods

### 2.1. Study area

I conducted this study during spring (May–June) 2008–2010 within a 16,190 ha shortgrass prairie study area located on the 233,603 ha Vermejo Park Ranch (VPR) in northeastern New Mexico (36° 31'N, 104° 43'W). VPR is a privately-owned property that extends mostly across the Sangre de Cristo Mountains of western Colfax and eastern Taos counties. Although most of VPR consists of mixed-coniferous forests typical of higher elevations (>2200 m), the study area was located at lower elevations (1800–2000 m) on the southeastern edge of the ranch within Colfax County, just northeast of the town of Cimarron. Climate of the region is semi-arid, averaging ~410 mm of precipitation with most falling during spring and summer. Long-term mean precipitation during spring (Mar–Jun) in this region is 110 mm, but totaled 66, 30, and 127 mm during spring 2008, 2009, and 2010, respectively (all climate data from Cimarron 4 SW station, U.S. National Oceanographic and Atmospheric Administration). Habitat of the study area consisted primarily of perennial shortgrasses, particularly blue grama (*Bouteloua gracilis*), interspersed with other grasses, forbs, dwarf shrubs, and cacti, particularly purple three-awn (*Aristida purpurea*), fringed sage (*Artemisia frigida*), broom snakeweed (*Gutierrezia sarothrae*), winterfat (*Eurotia lanata*), prickly-pear cactus (*Opuntia* spp.), and cane cholla (*Cylindropuntia imbricata*). The study area also contained large areas dominated by shrubs, mostly green rabbitbrush (*Chrysothamnus viscidiflorus*) and four-winged saltbush (*Atriplex canescens*), and was transected by three stream systems supporting narrow strips of woody riparian habitat, particularly dense willow (*Salix* spp.).

Management efforts on VPR have focused on ecosystem restoration with the goal of restoring native biodiversity since its purchase by the current owner in 1996. American bison were reintroduced in the late-1990s, and during the study 500–700 adult bison and calves were rotated among fenced allotments within the study area such that some areas were actively-grazed during the spring. Black-tailed prairie dog restoration efforts have been underway since 1999 (Long et al., 2006), increasing the number and coverage of colonies in the study area from 8 colonies totaling <200 ha in 1997 to 45–50 colonies totaling ~2200 ha in 2008, ~2800 ha in 2009, and ~3200 ha in 2010. Additional restoration efforts restoring black-footed ferrets (*Mustela nigripes*) starting in 2007 have made the vertebrate community present at this site unusually complete.

### 2.2. Bird and mammal surveys

To evaluate the effects of prairie dog colonies on bird and mammal diversity I conducted morning surveys along paired 600 m linear transects established within prairie dog colonies and within associated shortgrass prairie habitats that were uncolonized by prairie dogs (hereafter, control habitats). Colony transects were positioned somewhat centrally within larger colonies (>25 ha) to ensure that they were >150 m from the colony edge for their entire length. Control transects were located within 1 km of the associated colony, but were located in habitats with no sign of current or past prairie dog activities within at least 150 m of their entire length.

During spring 2008, I established and surveyed 6 paired colony/control transects, and added 6 additional pairs of transects in spring 2009 for a total of 12 paired transects surveyed in 2009 and 2010.

Sampled prairie dog colonies ranged in size from 29 to 118 ha in 2008, 41–483 ha in 2009, and 58–431 ha in 2010. During all 3 years I used the same survey methods: I surveyed bird and mammal abundance by slowly walking each transect within 3 h after sunrise on calm, rain-free days while listening and scanning with  $8 \times 42$  binoculars. Obviously, this methodology limited my sampling effort to diurnal or crepuscular species, and in the case of mammals, mostly larger species. For consistency of effort, I covered the 600 m length in 30 min, and counted all individual adult birds or mammals detected within 100 m of the transect, by species, recording them within 4 distance categories (0–10 m, 11–30 m, 31–60 m, and 61–100 m) based on their perpendicular distance from the transect. I used distance categories instead of trying to estimate exact distance for each individual to reduce the time needed in documenting each individual, and to reduce errors associated with distance estimation. Because American bison were often present in large herds when encountered, I recorded only presence or absence for this species. I surveyed each transect three times during spring (once each during the last two weeks of May, first two weeks of June, and last two weeks of June), varying the order of visitation.

### 2.3. Habitat sampling

To compare basic habitat features between treatments (i.e., colonies and control), during early June each year I sampled habitat and vegetation characteristics at 7 points located systematically every 100 m along each transect line. Within a 5 m radius of each point, I visually estimated percentage of ground covered by bare soil, live forb/dwarf shrub (this category included herbaceous forbs and perennial dwarf shrubs, mainly broom snakeweed and fringed sage), live woody shrub, or grass (live, dormant, or dead combined). I combined living, dormant, and dead grasses as one cover category because this combination best described overall importance of grass at a site regardless of the level of spring precipitation when sampled. I estimated mean vegetation height by measuring the maximum canopy height of vegetation at 12 systematically located points within the 5 m radius of each main sampling point. Finally, I measured density of cholla, a tall, branching cactus, and woody shrubs, mainly winterfat and four-winged saltbush, by counting stems within an 11.3 m radius (0.04 ha) of each point.

### 2.4. Statistical analyses

I used survey data to estimate relative abundance of all bird and mammal species detected, and to calculate density estimates for common species using distance sampling (Buckland et al., 2001). Relative abundance values, i.e., the number of individuals detected within 100 m of each 600 m transect, were calculated for all species as a means to provide coarse information about species composition on colony and control sites. Prior to calculating annual means for a given treatment, relative abundance values were first calculated for each species on each transect by averaging detections from the 3 replicate surveys in a given year. Finally, for each survey I also calculated the total number of individual birds detected by summing across all species, and determined bird species richness, the number of different bird species detected per survey, as an added means to broadly compare the bird communities. For these two variables, I used two-way ANOVA performed using the statistical package SPSS Statistics 18 (IBM Corporation, Somers, NY) to compare means by treatment and year. Mammals were not detected frequently enough to warrant similar community-level analyses.

Because relative abundance estimates can be misleading due to differences in detectability, both among species and among

habitats (Norvell et al., 2003), I used Program DISTANCE Version 6.0, Release 2 (Thomas et al., 2009) to derive treatment-specific density estimates and associated confidence intervals to compare abundance of common species on colony versus control sites. DISTANCE calculates the density of each species by fitting the frequency of detection, as a function of perpendicular distance from the transect line, into a series of theoretical models that can be compared for fit and parsimony (Buckland et al., 2001). I limited these analyses to 2009 and 2010 surveys only, the two years during

**Table 1**

Mean relative abundance estimates for bird and mammal species detected within 100 m of twelve 600 m transects in prairie dog colonies, and twelve 600 m transects in associated uncolonized shortgrass prairie habitats (controls). Means represent the mean number of detections per survey, i.e., the number of individuals detected within 100 m of the 600 m transect, averaged over the 12 transects per treatment, and over 3 years, 2008–2010.

Species	Relative abundance estimates	
	Prairie dog colonies	Uncolonized controls
	Mean (SE)	Mean (SE)
<b>Birds:</b>		
Killdeer ( <i>Charadrius vociferous</i> )	0.04 (0.02)	0.02 (0.02)
Mountain plover ( <i>C. montanus</i> )	0.91 (0.19)	0.04 (0.02)
Long-billed curlew ( <i>Numenius americanus</i> )	0.02 (0.02)	0.12 (0.06)
Turkey vulture ( <i>Cathartes aura</i> )	0.03 (0.02)	0.04 (0.03)
Red-tailed hawk ( <i>Buteo jamaicensis</i> )	0.06 (0.03)	0.02 (0.02)
Swainson's hawk ( <i>B. swainsoni</i> )	0.02 (0.02)	0.02 (0.02)
Ferruginous hawk ( <i>B. regalis</i> )	0.13 (0.04)	0.00
American kestrel ( <i>Falco columbarius</i> )	0.00	0.02 (0.02)
Prairie falcon ( <i>F. mexicanus</i> )	0.02 (0.02)	0.04 (0.02)
Scaled quail ( <i>Callipepla squamata</i> )	0.01 (0.01)	0.00
Mourning dove ( <i>Zenaidura macroura</i> )	0.08 (0.04)	0.10 (0.09)
Burrowing owl ( <i>Athene cunicularia</i> )	1.12 (0.19)	0.01 (0.01)
Common nighthawk ( <i>Chordeiles minor</i> )	0.00	0.03 (0.02)
Western kingbird ( <i>Tyrannus verticalis</i> )	0.02 (0.02)	0.01 (0.01)
Say's phoebe ( <i>Sayornis saya</i> )	0.02 (0.02)	0.00
Horned lark ( <i>Eremophila alpestris</i> )	17.76 (1.03)	18.57 (1.27)
Violet-green swallow ( <i>Tachycineta thalassina</i> )	0.13 (0.08)	0.08 (0.05)
N. rough-winged swallow ( <i>Stelgidopteryx serripennis</i> )	0.04 (0.03)	0.11 (0.07)
Cliff swallow ( <i>Hirundo pyrrhonota</i> )	0.23 (0.09)	0.11 (0.05)
Barn swallow ( <i>H. rustica</i> )	0.01 (0.01)	0.08 (0.04)
Chihuahuan raven ( <i>Corvus cryptoleucus</i> )	0.67 (0.12)	0.73 (0.15)
Loggerhead shrike ( <i>Lanius ludovicianus</i> )	0.02 (0.02)	0.01 (0.01)
Northern mockingbird ( <i>Mimus polyglottos</i> )	0.23 (0.06)	0.30 (0.12)
Curve-billed thrasher ( <i>Toxostoma curvirostre</i> )	0.18 (0.07)	0.02 (0.02)
Vesper sparrow ( <i>Poecetes gramineus</i> )	0.08 (0.04)	1.06 (0.16)
Lark sparrow ( <i>Chondestes grammacus</i> )	0.02 (0.02)	0.26 (0.09)
Cassin's sparrow ( <i>Aimophila cassinii</i> )	0.08 (0.04)	1.78 (0.52)
Brewer's sparrow ( <i>Spizella breweri</i> )	0.00	0.08 (0.06)
Lark bunting ( <i>Calamospiza melanocorys</i> )	0.07 (0.04)	0.16 (0.09)
Western meadowlark ( <i>Sturnella neglecta</i> )	0.37 (0.07)	3.68 (0.37)
Brown-headed cowbird ( <i>Molothrus ater</i> )	0.00	0.12 (0.06)
Lesser goldfinch ( <i>Carduelis psaltria</i> )	0.00	0.02 (0.02)
<b>Mammals:</b>		
Desert cottontail ( <i>Sylvilagus audubonii</i> )	1.28 (0.23)	0.02 (0.02)
Black-tailed jackrabbit ( <i>Lepus californicus</i> )	0.06 (0.03)	0.17 (0.07)
13-lined ground squirrel ( <i>Spermophilus tridecemlineatus</i> )	0.07 (0.03)	0.00
Coyote ( <i>Canis latrans</i> )	0.17 (0.05)	0.19 (0.07)
American badger ( <i>Taxidea taxus</i> )	0.12 (0.23)	0.01 (0.01)
Elk ( <i>Cervus elaphus</i> )	0.06 (0.06)	0.00
Pronghorn ( <i>Antilocapra americana</i> )	1.43 (0.24)	0.88 (0.16)
American bison ( <i>Bison bison</i> ) <sup>a</sup>	0.16	0.10

<sup>a</sup> Because of their tendency to be present in large (>50 individuals) herds, bison were recorded simply as present or absent on each survey. Numbers represent the proportion of surveys in each treatment at which bison were present. The proportion of surveys at which bison were present did not differ between colony and control transects (G-test of independence:  $G = 1.25$ , 1 df,  $P = 0.26$ ).

which I surveyed all 12 sites, and only attempted analyses for species with at least 60 total detections over both years. For each species, I selected among three monotonic, decreasing key functions (uniform, half-normal, or hazard-rate), with possible cosine adjustment terms. I also fitted models that included year as a covariate for the detection function. I used Akaike's Information Criterion (AIC, Burnham and Anderson, 1998) to identify the best-approximating model and evaluate whether the year covariate improved model fit. For most species, small numbers of detections on at least one treatment required me to use all detections combined in calculating a global detection function. I then used this function to estimate density (individuals/km<sup>2</sup>) and 95% confidence intervals for each treatment. For species with >50 detections on both treatments, I also performed similar analyses allowing the detection function to vary by stratum (i.e., treatment) to potentially allow for a better fit if detectability varied between colony and control sites. For these species, stratum models were compared with global models, and the best model was chosen based on the lowest AIC. Densities of individual species were considered to be different between colonies and controls when there was a lack of overlap of the 95% confidence intervals.

To obtain information from less frequently detected species, I also used basic survey data to identify species with strong associations with either prairie dog colonies or uncolonized control habitats. For all species with at least 12 total detections over all 3 years, I calculated the proportion of detections on colony sites versus control sites. I classified species for which >80% of total detections occurred on only one treatment as "strong associates" of that treatment.

Finally, during each year I summarized habitat characteristics for each transect by averaging values from the 7 sample points, and used two-way ANOVA to compare means for each habitat variable by treatment and year. Data for variables that were percentages were arcsine-square root transformed prior to analyses to better meet the assumptions of this parametric test.

**Table 2**  
Overall density estimates, 95% confidence intervals, and other associated statistics acquired using program DISTANCE for common (>60 total detections) bird and mammal species detected on 12 prairie dog colony transects (Treatment = colony) and 12 uncolonized, shortgrass prairie transects (Treatment = control) surveyed during spring 2009 and 2010.

Species	Model <sup>a</sup>	G.O.F. <i>P</i> -value <sup>b</sup>	Treatment	<i>n</i> <sup>c</sup>	Density estimates (indivs./km <sup>2</sup> )			%CV <sup>d</sup>
					Mean	Lower 95% CI	Upper 95% CI	
<i>Birds:</i>								
Mountain plover	un + cos	0.70	Colony	74	10.1	5.2	20.0	32.3
			Control	4	0.6	0.2	1.9	58.1
Burrowing owl	un + cos	0.21	Colony	75	8.6	5.3	13.8	21.9
			Control	1	0.2	0.1	0.9	67.4
Horned lark	hn + cos	<0.001 <sup>e</sup>	Colony	1313	214.3	166.6	259.9	9.4
			Control	1412	337.7	271.4	420.2	10.3
Chihuahuan raven	un + cos	0.20	Colony	55	6.0	3.8	9.5	21.1
			Control	60	6.8	4.0	11.5	24.2
Vesper sparrow	un + cos	0.06	Colony	4	0.5	0.1	2.1	76.9
			Control	67	7.9	4.9	12.7	21.9
Cassin's sparrow	hn + cos	0.21	Colony	7	1.7	0.6	4.8	50.9
			Control	145	33.4	13.5	82.9	43.4
Western meadowlark	un + cos	0.83	Colony	26	3.7	2.2	6.1	23.2
			Control	273	37.1	26.7	51.5	15.7
<i>Mammals:</i>								
Pronghorn	un + cos	0.14	Colony	104	11.7	6.8	19.9	24.8
			Control	66	7.4	4.6	12.0	22.3
Desert cottontail	un + cos	0.20	Colony	67	9.1	5.0	16.5	29.1
			Control	0	0.0			

<sup>a</sup> Preferred model based on AIC: un + cos = uniform key function with cosine series expansion; hn + cos = half-normal key function with cosine series expansion.  
<sup>b</sup> *P*-value from a chi-square goodness of fit test evaluating model fit.  
<sup>c</sup> *n* = total number of detections across both years.  
<sup>d</sup> % coefficient of variation of the estimated density.  
<sup>e</sup> For horned lark, a model that allowed the detection function to vary by treatment was preferred over a global model due to differences in detectability among habitat types (See 3.1, Bird and mammal surveys).

### 3. Results

#### 3.1. Bird and mammal surveys

Over all 3 years, I recorded 4505 detections among 32 bird species, and 835 detections among 8 mammal species (excluding black-tailed prairie dogs). Of these totals, I detected 27 bird and 8 mammal species on prairie dog colony transects, and 28 bird and 6 mammal species on control transects (Table 1). Horned larks (See Table 1 for scientific names) made up the majority of bird detections for both colony (79.1%) and control (67.5%) sites. Besides horned larks, the next four most commonly detected bird species on colony transects were burrowing owl, mountain plover, Chihuahuan raven, and western meadowlark, whereas on control transects they were western meadowlark, Cassin's sparrow, vesper sparrow, and Chihuahuan raven (Table 1). Because of the nocturnal nature and small size of most mammals, only pronghorn, desert cottontails, and American bison were detected frequently, with pronghorn accounting for 43.0% and 64.2% of mammal detections on colony and control sites, respectively (Table 1).

Based on relative abundance data, on average I detected more total individual birds per survey on control (mean = 27.6, SE = 1.0) than colony transects (mean = 22.5; SE = 1.1; *F* = 9.22; 1, 54 df; *P* = 0.004). Mean total individual birds per survey also varied by year (*F* = 4.93; 2, 54 df; *P* = 0.01), however, the pattern showing greater abundance on control sites was consistent across all three years (i.e., there was no significant treatment by year interaction). Bird species richness per survey was low overall for both treatments, but tended to be greater on control sites (mean = 4.6 species/survey; SE = 0.3) than on colonies (mean = 3.8; SE = 0.2; *F* = 3.67; 1, 54 df; *P* = 0.06).

Nine species (7 birds and 2 mammals) were detected frequently enough to estimate and compare densities (Table 2). In all cases, including year in the model did not improve model fit so I pooled detection distances across the two years for the detection function.

**Table 3**

Habitat associations of birds or mammals with at least 12 detections during surveys of prairie dog colonies and uncolonized shortgrass prairie control habitats, northeastern New Mexico, 2008–2010. Species were considered to be strongly associated with colonies or controls when >80% of detections occurred on only that treatment. Number in parentheses following each species is the total number of detections during surveys over all 3 years.

	Birds	Mammals
Strongly associated with prairie dog colonies	mountain plover (83), ferruginous hawk (12), burrowing owl (102), curve-billed thrasher (18)	desert cottontail (117), American badger (12)
Strongly associated with uncolonized control habitats	long-billed curlew (13), vesper sparrow (102), lark sparrow (25), Cassin's sparrow (168), western meadowlark (364)	none
No strong association	mourning dove (16), horned lark (3269), violet-green swallow (19), northern rough-winged swallow (14), cliff swallow (31), Chihuahuan raven (126), northern mockingbird (48), lark bunting (20).	black-tailed jackrabbit (20), coyote (32), pronghorn (208), American bison (NA) <sup>a</sup>

<sup>a</sup> Because of their herding behavior, bison were recorded simply as present or absent on each survey transect. Overall, bison were present on 23 surveys (14 on prairie dog colonies and 9 on uncolonized sites).

For most species, the preferred model fit the detection data well based on chi-square goodness of fit tests ( $P > 0.15$ ). The horned lark was an exception, however this was primarily due to a very large sample size (i.e., high power) and the small number of distance groups used (Buckland et al., 2001); the graph of the detection data visually fit the detection function reasonably well for both treatments. Based on 95% confidence intervals, densities of mountain plovers, burrowing owls, and desert cottontails were greater on colonies than on control habitats, while densities of horned larks, Cassin's sparrows, vesper sparrows, and western meadowlarks were greater on control habitats than on colonies (Table 2). For the horned lark, a model that allowed the detection function to vary by stratum (i.e., treatment), was preferred over the global model (AIC = 7261.7;  $\Delta$ AIC = 53.0) due to differences in detectability ( $p_a$ ) among habitat types ( $p_a = 0.71$  on colony transects,  $p_a = 0.48$  on control transects).

Of 17 bird species with at least 12 detections over all 3 years, 4 species were strongly associated with prairie dog colonies, 5 were strongly associated with control habitats, while the 8 remaining species showed no association (Table 3). Of 6 mammal species with at least 12 detections, 2 species were strongly associated with prairie dog colonies while the remainder showed no association (Table 3).

### 3.2. Habitat sampling

Habitat structure differed greatly between colony and control transects with controls sites, on average, having significantly less bare ground and forb/dwarf shrub cover, but greater grass and shrub cover, greater shrub density, and greater vegetation height (Table 4). Annual variation in habitat structure was apparent for vegetation height, and for bare ground and forb/dwarf shrub cover (Table 4); mean vegetation height was significantly greater in 2008 than in 2009 or 2010, whereas mean forb cover was significantly greater in 2010 than in 2009 or 2008, apparently at the expense of

bare ground cover which decreased in 2010. All year effects, however, were consistent on both colony and control sites.

## 4. Discussion

Prairie dogs brought about major changes to habitat structure and resource availability within the shortgrass prairie of this study area so it is unsurprising that their presence and activities had large effects, both positive and negative, on bird and mammal species composition. What was surprising in this study was the manner in which many of my results, particularly in regards to the bird communities, differed from past research in other locations. For example, based on past studies (Agnew et al., 1986; Barko et al., 1999; O'Meilia et al., 1982; Smith and Lomolino, 2004), I expected overall bird abundance and species richness to be greater on colonies, but observed the opposite patterns. Uncolonized shortgrass prairie had significantly more total individual birds per survey than colonies, and tended to have greater species richness at the level of the transect. When one considers the lower detection probability of horned larks in uncolonized sites revealed by distance sampling analyses, this difference in total abundance was apparently even more substantial than indicated by relative abundance estimates.

Because different species often exhibit differing responses to ecosystem change, patterns of abundance of individual species are probably more instructive than community-level patterns (Kotliar et al., 2006), and once again I found several species that exhibited unexpected responses based on past research. Kotliar et al. (1999, 2006) used existing literature to identify species that depend, at least to some degree, on prairie dogs based on them fitting at least one of four criteria; 1) abundance is higher at prairie dog colonies than elsewhere; 2) individuals use features that are specific to colonies, like burrows; 3) populations increase (or decrease) when prairie dog populations increase (or decrease), and; 4) survivorship or reproduction is higher at colonies than elsewhere. Horned larks

**Table 4**

Mean habitat characteristics of bird and mammal survey transects on 12 prairie dog colonies and 12 associated, uncolonized control sites in shortgrass prairie habitats in northeastern New Mexico, 2008–2010.

Habitat characteristic	Prairie dog colony mean (SE)	Control mean (SE)	$P_{\text{YR}}^a$	$P_{\text{TRT}}^a$
Ground cover (%):				
Grass (green, dormant, and dead)	25.02 (2.20)	62.64 (1.91)	0.16	<0.001
Live forb/dwarf shrub	14.38 (2.52)	4.75 (0.94)	<0.001	<0.001
Live shrub	0.15 (0.05)	1.15 (0.36)	0.83	0.003
Bare ground	60.42 (2.24)	30.21 (1.90)	0.03	<0.001
Mean vegetation height (cm)	3.72 (0.59)	11.66 (2.10)	<0.001	<0.001
Live shrubs per 0.04 ha	0.17 (0.11)	3.86 (1.62)	0.26	0.05
Cholla cacti per 0.04 ha	0.29 (0.08)	0.66 (0.27)	0.70	0.30

<sup>a</sup>  $P$ -values from 2-way ANOVA comparing means across years (YR) and treatments (TRT).

and western meadowlarks made this list based primarily on studies indicating that they fit criterion 1; greater abundance on prairie dog colonies (Agnew et al., 1986; Barko et al., 1999; Smith and Lomolino, 2004). Horned larks are ground nesting species that are often associated with short vegetation and ample bare ground, and have often been documented as having higher densities in more heavily grazed areas (Beason, 1995; Bock and Webb, 1984). On my study site, horned larks were abundant on prairie dog colonies, but had greater densities on uncolonized prairie. This result highlights a limitation of using relative abundance estimates to compare abundance among habitat types. Based on relative abundance data, horned larks appeared to be of similar abundance on colonies and controls. Detectability was substantially greater on colonies, however, probably due to the shorter, sparser vegetation and my dependence on visual detection for this relatively quiet species. When this fact was incorporated into density estimates, it became apparent that horned lark densities were greater on uncolonized habitats. Perhaps in shortgrass prairie, the relatively short vegetation and abundant bare ground that is present even in undisturbed or lightly-grazed habitats represent ideal nesting and foraging conditions for this species.

Western meadowlarks, on the other hand, may not belong on Kotliar et al.'s (2006) list of prairie dog dependent species. Western meadowlarks use a variety of grassland habitat types but tend to prefer habitats with denser vegetation and considerable grass and litter cover for nest sites (Lanyon, 1994). In my study area, meadowlark densities were 10 times greater on control sites, likely due to the more complex vegetation structure relative to prairie dog colonies. Control habitats had taller, denser vegetation, including, in many areas, numerous shrubs suitable for singing perches. During years with low spring rainfall (2008 and 2009), the central regions of prairie dog colonies where my transects were located provided few areas of dense vegetation for concealment of nests. Of interest, meadowlark use of prairie dog colonies appeared to increase slightly during the very wet spring of 2010; during the three-year study, 58% of meadowlark detections on prairie dog colony transects occurred in 2010. By late June 2010, vegetation had become quite tall and dense on many colonies, primarily as a result of the rapid growth of annual forbs and dwarf shrubs, providing better habitat for breeding meadowlarks. Perhaps Smith and Lomolino (2004), who also worked in shortgrass habitats, detected a significant positive association of meadowlarks with prairie dog colonies because their surveys continued later into the summer (mid-May to August) than mine, or included more areas near the edges of colonies where meadowlarks had access to adjacent denser vegetation. Agnew et al. (1986) and Barko et al. (1999) also found meadowlarks to be common on prairie dog colonies, but found similar numbers of this species in associated uncolonized prairie.

American bison and pronghorn were also included on Kotliar et al.'s (2006) list of prairie dog dependent species because they are often more abundant on colonies, apparently because prairie dog activities enhance foraging opportunities. Bison prefer to forage on the younger edges of colonies because the grazing and clipping activities of prairie dogs enhance the digestibility, protein content, and productivity of their preferred grasses (Coppock et al., 1983; Kreuger, 1986). Pronghorn prefer to forage on the older portions of prairie dog colonies as these sites support greater abundance of their preferred forb foods (Kreuger, 1986; Wydeven and Dahlgren, 1985). My results neither supported nor refuted the value of prairie dog colonies for these species. Both of these large grazers regularly used both colony and control habitats in my study area, but neither was significantly more abundant on colonies. That said, both species showed a pattern of greater abundance or presence on colonies. Ungulate selection for prairie dog colonies may be difficult to detect as patterns can vary by season, precipitation levels, or be influenced by territorial behaviors (Wydeven and Dahlgren, 1985).

#### 4.1. Species positively impacted by prairie dog colonies

Although to this point I have emphasized the exceptions, my results also strongly supported the inclusion of several species identified on Kotliar et al.'s (2006) list of prairie dog dependent species. Burrowing owls, mountain plovers, ferruginous hawks, and badgers were all either more abundant on, or at least strongly associated with, prairie dog colonies in my study area. Mountain plovers and burrowing owls were both common on colonies and were rarely encountered elsewhere; in fact, all but one of the few detections of both species on control transects consisted of individuals in flight, as opposed to on the ground using the habitat. Mountain plovers prefer areas with very short vegetation and a high proportion of bare soil, and have often been positively associated with prairie dog activities, especially in mixed- or tall-grass habitats (Knopf and Wunder, 2006). Burrowing owls are well known for their use of prairie dog colonies where they benefit from the availability of burrows for nesting and protection, and may also prefer the shorter vegetation both in terms of predator detection and foraging efficiency (Haug et al., 1993). Both ferruginous hawks and badgers benefit largely from the prairie dogs themselves as prey (Cook et al., 2003; Findley, 1987). Both of these species were encountered infrequently during surveys, but were almost exclusively detected on colonies. Of importance, three of these species (burrowing owl, mountain plover, and ferruginous hawk) have been designated as Species of Greatest Conservation Need in New Mexico; species of low or declining abundance that are important indicators of the diversity and health of New Mexico ecosystems (New Mexico Department of Game and Fish, 2006). In addition, the mountain plover has recently been considered for federal listing as threatened due to range-wide declines associated greatly with declines in prairie dog abundance and distribution, although this listing was denied (U.S. Fish and Wildlife Service, 2011).

Two additional species not listed by Kotliar et al. (2006) were strongly associated with prairie dog colonies on my study site; desert cottontail (although eastern cottontail [*Sylvilagus floridanus*] was listed) and curve-billed thrasher. Desert cottontails were significantly more abundant on prairie dog colonies, likely because of the availability of burrows as protective cover. Unlike black-tailed jackrabbits which depend on high-speed running to escape predators and were often observed in control habitats, cottontails depend on concealment or a short run to protective cover to evade predators (Findley, 1987). When disturbed on surveys, it was common for cottontails to seek the cover of a nearby burrow. Others have also noted a greater abundance of this species on prairie dog colonies relative to other habitat types (Hansen and Gold, 1977; Shipley and Reading, 2006). Curve-billed thrashers were not encountered often but were also found almost exclusively on prairie dog colonies. This species depends primarily on cholla for nest sites in this region, but given that cholla abundance did not differ between treatments the apparent preference by this species for prairie dog colonies is difficult to explain. Curve-billed thrashers are ground foragers (Tweit, 1996) that may prefer the shorter vegetation and more open nature of colonies for foraging and predator detection, but I could find no other studies strongly associating this species with prairie dogs.

#### 4.2. Species negatively impacted by prairie dog activities

Any disturbance that brings about changes in an ecosystem at the scale and intensity of prairie dog activities is likely to improve habitat quality for some species, but also reduce quality for others. Although none of the mammal species I studied appeared to be negatively impacted by prairie dog activities, my methods sampled

just a small portion of the mammal community, primarily larger, generalist species that were active, at least to some degree, by day. Other studies have indicated that populations of many small, nocturnal rodent species, species which tend to have more specific habitat requirements, are reduced by prairie dog activities (Lomolino and Smith, 2003; McCaffrey et al., 2009; Pruett et al., 2010). Prairie dog activities may have also had this negative effect on small mammal species on my study area. My study, however, was not designed to sample this group of species.

Songbirds also tend to have very specific habitat requirements and, thus, it is not surprising that I found that prairie dog activities reduced habitat suitability for a suite of grassland bird species. I have already discussed western meadowlarks and horned larks, but Cassin's sparrows and vesper sparrows were also significantly more abundant on control sites, while long-billed curlews and lark sparrows, although less frequently encountered, showed strong associations with control habitats. All six of these species have recently exhibited declining population trends (McCracken 2005; Peterjohn and Sauer, 1999). For all three-sparrow species, the preference for control sites was likely explained by the greater vegetative cover and greater density of shrubs. Vesper sparrows, for example, favor grasslands with patchy herbaceous vegetation and low to moderate shrub cover (Jones and Cornely, 2002). Cassin's sparrows prefer sites with taller, denser vegetation and, typically, a considerable shrub component (Dunning et al., 1999) and have previously been found to avoid prairie dog colonies (Smith and Lomolino, 2004). Lark sparrows also show an affinity for open habitats with a shrub or woodland component (Martin and Parrish, 2000), but have variously been positively (Sharps and Uresk, 1990; Smith and Lomolino, 2004) or negatively (Barko et al., 1999) associated with prairie dog colonies.

Like lark sparrows, the association between long-billed curlews and prairie dogs remains unclear. For nesting, long-billed curlews favor habitats of short, sparse grasses, avoiding areas with high shrub densities, but tend to rear young in areas with taller, denser vegetation (Dugger and Dugger, 2002). Curlews have been positively associated with prairie dog colonies in other locations (Sharps and Uresk, 1990; Smith and Lomolino, 2004). In my study area, I encountered nesting curlews and young solely in uncolonized grasslands where there was taller grass cover, but also observed adult curlews feeding on colonies on numerous occasions outside of surveys. Perhaps this species benefits from a landscape that contains both colonized and uncolonized grasslands to meet its reproductive and foraging needs.

## 5. Conclusions

In shortgrass prairie of northeastern New Mexico, prairie dog colonies provide unique habitats and habitat elements that benefit many bird and mammal species, including several rare or declining species, but they also tend to eliminate vegetative conditions that are preferred by several declining grassland bird species. Although this appears to present a management dilemma, when one considers the history of persecution of prairie dogs, and the positive effects that remaining colonies have on grassland biodiversity when measured at larger spatial scales, this dilemma is readily resolved. Prairie dogs are natural and important components of grassland ecosystems that have shared a long evolutionary history with many grassland species, forming in some cases such a close association that prairie dogs truly have become keystone species. Given the massive declines of prairie dog populations over the past two centuries, the somewhat restrictive habitat requirements of the species (Long et al., 2006), and the persistent negative attitudes towards these species among western rural land owners (Lamb et al., 2006), there is currently little risk of managing for too

many prairie dogs. For example, in my study pasture, prairie dog restoration efforts have increased colony coverage ten-fold to over 3000 ha in less than 15 years. Yet there is little danger of prairie dogs homogenizing this system at the expense of western meadowlarks or Cassin's sparrows as large areas of the pasture remain either too rocky, too sloped, and/or too vegetated to allow prairie dog colonization. Further, given that this 16,000 ha pasture is surrounded to the north, east, and south by tens of thousands of additional ha of shortgrass prairie managed primarily for cattle, and often controlled for prairie dogs, the value of these restoration efforts become more clear. Prairie dog colonies represent islands of unique habitat where mountain plovers, burrowing owls, and ferruginous hawks can thrive. Ultimately, biodiversity is maximized in this landscape by maintaining a mixture of colonized and uncolonized habitats.

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