

## Reintroduced prairie dog colonies change arthropod communities and enhance burrowing owl foraging resources

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### Abstract

In the western United States, human activities have decreased black-tailed prairie dog (*Cynomys ludovicianus*) populations to <10% of their historic extent. These animals are ecosystem engineers that radically alter soil physical and chemical characteristics and plant communities on their colonies. We tested the hypothesis that prairie dogs have an impact on higher levels of grassland ecology by measuring the differences in arthropod community structure and burrowing owl foraging on those arthropods, between reintroduced colonies and adjacent grassland in southern New Mexico, USA. Arthropod communities differed between colonies and grassland in both number of taxa and abundance. Burrowing owls foraged more on colonies, and caught more prey on colonies compared to grasslands. Pursuit times of burrowing owls in grassland were longer than pursuits on colonies. Burrowing owls nesting on the edge of colonies foraged extensively on colonies, and edge and center-nesting owls delivered similar proportions of prey captured on colonies to their nests. This study suggests that prairie dogs play a vital role in structuring arthropod communities and provide foraging resources for other grassland species.

### Keywords

arthropod communities; *Athene cunicularia*; *Cynomys ludovicianus*; ecosystem engineering; grassland conservation.

### Development

Black-tailed prairie dogs have long been appreciated as important engineers in arid grassland systems. Here, we show that prairie dog colonies host significantly different vegetation structure and arthropod communities compared to surrounding grassland, and an associated species, burrowing owls, preferentially feed on that unique arthropod prey base. These results show a mechanism for why burrowing owls are often associated with prairie dogs, other than simply habitat.

### Introduction

Grasslands in the southwestern United States have undergone radical changes since the expansion of anthropogenic activity in late 19<sup>th</sup> century (1,2). Coincident with the introduction of cattle were efforts to eliminate livestock predators and perceived herbivore competitors (3,4). Black-tailed prairie dogs (*Cynomys ludovicianus*) were extensively targeted for elimination, and have been reduced to <10% of their historic extent by human activities (5). Because prairie dog colonies are commonly observed to host a suite of associated species, extensive research has been devoted to their role in grassland systems and the impact of their extirpation (5-10). Black-tailed prairie dogs fit the definition of allogenic ecosystem engineers because they “change the environment by transforming living or non-living materials from one physical state to another, via

mechanical or other means" (11, p. 374). Black-tailed prairie dogs reduce vegetation height and cover, and create subterranean burrows that may be 1 m deep and 15 m long (6,8,12,13). In addition, these animals are colonial, and even small colonies can occupy ~1 ha (8,10). The presence of black-tailed prairie dog colonies within grassland mosaics thus provides unique habitat and contributes to environmental heterogeneity.

Colonies are characterized by reduced vegetation height and increased bare ground compared with adjacent grassland patches, but the significance of these landscape traits for associated fauna is not clear. The abundance and community structure of vertebrates differs between colonies and undisturbed grassland (14-19). However, the increased presence of some vertebrates on colonies has only been attributed to colony physical structure and the use of prairie dogs as prey (15,17,20,21). If colonies support different communities and abundances of arthropods, this could be a mechanism for the increased presence of arthropagous vertebrates on colonies. However, results from investigations of invertebrate response to prairie dog activity are equivocal. Harvester ant (*Pogonomyrmex* spp.) diversity was not different between colony and grassland sites in Kansas, but abundance was higher off colonies (22). Grasshoppers were sampled in greater abundance off colonies in one study (23), but denser populations of grasshoppers have been reported on colonies (24). Other studies report both higher arthropod densities in grassland compared to colonies (25) and reduced arthropod diversity on colonies (26).

The association of burrowing owls (*Athene cunicularia*) with fossorial mammals provides a model system to examine the impact of colonies on prey resources for other species (27,28). Burrowing owls are small (23-27 cm, ~150 g), cavity-nesting raptors that commonly nest in black-tailed prairie dog burrows (15,27). While burrowing owls use burrows of other grassland mammals, Desmond and Savidge (15) found that nest densities were higher on black-tailed prairie dog colonies than in areas where badger (*Taxidea taxus*) burrows were the only available nesting sites. The greater availability of nest burrows for owls on colonies may partially explain this observation (29). However, burrowing owl preference for colonies may be due to enhanced prey availability or increased predator detection capability afforded by prairie dog alarm calls, two suggested yet untested hypotheses (15). Burrowing owls feed primarily on arthropods (30-32). Prairie dog colonies reduce vegetation complexity compared to grassland, and because burrowing owls utilize auditory and visual cues to hunt, they may

forage more efficiently on colonies (33,34). If burrowing owls forage extensively on colonies, this could suggest that black-tailed prairie dogs enhance prey resources for them.

In this study, we test the hypothesis that reintroduced black-tailed prairie dog colonies support unique arthropod communities, and those communities are a prey resource for burrowing owls. Specifically, we ask: (a) Do prairie dog colonies support different arthropod communities compared to adjacent grassland patches? (b) Do burrowing owls nesting on colonies consume more prey items from colony arthropod communities? (c) Do burrowing owls have higher foraging success on black-tailed prairie dog colonies than in grassland?

## Materials and methods

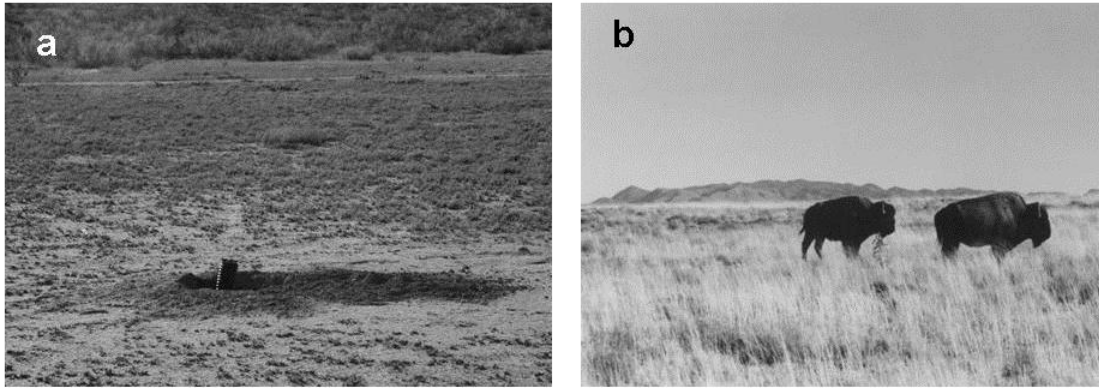
### Study site

We conducted our research at the Armendaris Ranch, a 146,000 ha tract of Chihuahuan desert grassland ~40 km northeast of Truth or Consequences, New Mexico, USA (Figure 1). The Armendaris is dominated by burro grass (*Scleropogon brevifolius*), alkali sacaton (*Sporobolus airoides*), and tobosa (*Pleuraphis mutica*) grasses, interspersed with opuntia (*Opuntia* spp.), honey mesquite (*Prosopis glandulosa*) and ephedra (*Ephedra torreyana*) shrubs (35). Bison (*Bison bison*) production is the principal operation of the ranch. Black-tailed prairie dogs were reintroduced to the Armendaris in 1994 as part of a commitment to grassland conservation and restoration. Prairie dogs were introduced into areas with low-lying, sandy loam soils, characteristic of areas that they historically colonized in the western United States (8). The colonies sampled were Burro Grass I (BGI), Burro Grass II (BGII), Lava Flow (LFC), Red Lake (RLC) and S-Curve (SCC).

### Data Collection

#### *Arthropod communities and vegetation structure*

We collected arthropods on five black-tailed prairie dog colonies and paired grassland sites. Colonies ranged in size from 1.97-11.07 ha. We installed a series of pitfall traps in an "X" orientation, with one in the center and 4 traps installed in cardinal directions, 25 m from the center trap. Since the area sampled by pitfall traps varies with species of arthropod and is indeterminate, a small number of widely spaced traps provide sufficient information on relative abundance and species composition for comparisons of modified and



**Figure 1.** a) Pictures of a representative reintroduced prairie dog colony, and b) an adjacent (50m away) grassland undisturbed by prairie dog activity. Vegetation foliar cover and height were significantly higher in grassland sites than on colonies. Picture is from colony BGI, Armendaris Ranch, New Mexico.

unmodified habitats. In addition, use of 5 traps per colony and grassland comparison should not have reduced the population of arthropods sufficiently to change the behavior of the owls. Furthermore, this number of pitfalls is sufficient to document temporal community changes based on previous work in the region (36). We installed grassland pitfall trap grids in the same design, 100 m from the edge of each colony, starting from a randomly generated compass bearing. We emptied pitfalls weekly during four, six week sampling periods. Arthropods were identified to the finest possible taxonomic resolution using keys and reference collections from the New Mexico State University Arthropod Museum (37-39). The level of identification varied across groups, but all specimens were identified to at least family. Hereafter groups are referred to as operational taxonomic units (OTU).

Using a random compass bearing, an “X” consisting of two perpendicular 100 m transects was generated in the center of the arthropod sampling grids to quantify the vegetation structure of the sites. A 0.5 m<sup>2</sup> frame with 10 cm x 10 cm squares was overlaid every 10 m along each 100 m transect to estimate percent cover of vegetation (40), and height measurements were taken within each frame by recording the height of the first three plants within the center row of the frame grid.

#### *Burrowing owl behavior & diet*

While the Armendaris represents intact desert grassland, burrowing owls were rarely observed before the introduction of black-tailed prairie dogs. One year following reintroduction, all of the five colonies used in this study were home to at least one nesting pair of burrowing owls (J. Truett, unpublished data). At the

time of our study, the mean density of owls was  $2.88 \pm 0.80$  (SE) ha<sup>-1</sup> for the five study colonies, and no owls were found nesting in adjacent grassland. To quantify burrowing owl foraging behavior, we made preliminary observations on 5 and 6 June 2004 to standardize observations between researchers and locate two nesting pairs of burrowing owls per colony. Using flagging on a metal pin, we then marked one nest in the center of each colony and one nest near a colony edge for observation. Only nests that were being used by discernible males and females were chosen for our observations. We identified individual owls based on plumage differences between males and females, assuming that the high degree of nest fidelity exhibited by both adult males and females while they are breeding and fledging their chicks ensured that we were indeed observing the same owls on repeated visits to colonies.

We observed burrowing owls from a vehicle approximately 25 m from the edge of colonies, for a minimum of two hours across three time periods during twilight and daylight hours. No observations were made at night because we were unable to differentiate males from females. We arrived at colonies 30 minutes before sunrise for early observations, and began data collection as soon as there was enough light to recognize individual owls. Midday observations took place from 13:00–15:00. Evening observations were two hours before sunset until it became too dark to observe owls. We began recording observations 5-10 min after arriving at the study colony to allow birds to return to normal behavior. Each owl was observed four separate times per time period (12 observation periods, >24 h of observation time per owl) between 7 June and 25 July 2004, which represented the 2004

nesting season. We chose this period to maximize our observations during a time when owls would be provisioning nestlings, and need to be most efficient when foraging.

Data collected during the owl observations were: the duration of flights, if pursuits were successful (did the owl return with a prey item), if the flights occurred on or off of their nesting colony, and the sex of the bird. One observer was assigned to the center nest and the other to the edge nest, and observers were responsible for the same nests throughout the study to minimize error in observations.

Burrowing owls regurgitate pellets of non-digestible prey remains such as fur, bones, and insect exoskeletons. We collected pellets from each colony every two weeks in the summer of 2003 and spring 2004, and every week in summer 2004. A total of 308 pellets were collected during the study. Burrowing owls migrate south in the winter, so no pellets were not collected in our winter sampling period. Individual pellets were dissolved in 30 ml of 8.0% NaOH for 24 h to reduce the quantity of fur and soil, air dried for 24 h and then dissected. Prey remains were removed from individual pellets and sorted to the finest taxonomic resolution possible. We were conservative in estimating prey abundance per pellet, by comparing single and paired body parts when available, and we assumed single individuals unless there was unambiguous evidence for more than one. The resulting data set consisted of prey OTU abundance for each colony during the summer 2003, spring 2004 and summer 2004 sampling periods.

#### Data analysis

Vegetation data were analyzed by comparing height and foliar cover differences between colonies and grassland with the Wilcoxon signed rank test. Relationships between height and cover were elucidated with correlation analysis. We used all data to examine overall patterns between height and cover, but also analyzed each site independently (cover vs. height per colony and grassland) to ensure that no one site drove our results.

Arthropod abundance data for OTU sampled on colonies and in grassland were analyzed with repeated measures ANOVA, to account for sampling the same colonies during four different seasons. We utilized a two way model to determine effects of the treatment (colony vs. grassland), season and their interaction, and used individual colonies as the error term in the model. Repeated measures was also used to delineate

differences in owl flight times between colonies and grassland, as well as differences in prey capture by owls on colonies versus grassland, and we used individual owls as the error term in this model. We used the AOV function in R, based on the repeated measures model (41).

A data matrix consisting of the abundance of each arthropod OTU per site per sampling period was converted into a similarity matrix using 4<sup>th</sup> root transformations and Bray-Curtis similarity coefficients with the PRIMER (Version 5) statistical package (42). We used non-metric multidimensional scaling (NMDS) ordination based on the abundance of OTU for each sampling grid to evaluate the degree of community overlap between colonies and grassland and the similarity of sites across seasons. NMDS is an ordination technique that uses ranked differences between individual points to create a dimensionless plot, and is robust against multivariate non-normal data (43). Replicating colonies and grassland plots provides a robust estimate of differences in arthropod communities due to prairie dog activity.

Hypotheses regarding the differences in community structure between study sites, colony versus grassland plots, and sampling dates were tested with the ANOSIM function of PRIMER (44). Within PRIMER, the routine SIMPER calculated the percent dissimilarity of arthropod assemblages between colonies and grassland, and the percent dissimilarity of each pair-wise comparison of seasonal colony and grassland assemblages. The routine also calculated the percent dissimilarity between two assemblages attributable to specific OTU.

Burrowing owl behaviors (flight times, prey captures) were compared between nests (center and edge) and male and female birds, employing the Wilcoxon signed rank test to account for the paired nature of those comparisons. Burrowing owl use of colonies as a prey resource was determined by calculating the similarity of the owl diet to arthropod communities on colonies versus grassland. The Morisita-Horn Index ( $C_{mH}$ ), a metric considering abundance and richness, was calculated and the index was compared between colonies and grassland (45).  $C_{mH}$  values were compared across sites and treated as paired samples in a *t*-test.

All statistical analyses other than the multivariate approach to quantify community structure were performed in R and JMP. All parametric tests are homogeneous for variance, and non-parametric tests are employed in cases of heteroscedasticity.

**Table 1.** Dominant grass species on prairie dog colonies and adjacent grassland sites, for each study site, Armendaris Ranch, New Mexico. Percent basal cover and height (cm) of vegetation is given for all vegetation,  $\pm$  SE.

Colony	Treatment	Dominant species	Height (cm)	Foliar cover (%)
BGI	colony	<i>Scleropogon brevifolius</i>	3.09 $\pm$ 0.27	2.90 $\pm$ 0.40
	grassland	<i>S. brevifolius</i>	10.13 $\pm$ 0.60	16.48 $\pm$ 0.96
BGII	colony	<i>S. brevifolius</i>	3.70 $\pm$ 0.21	4.42 $\pm$ 0.62
	grassland	<i>S. brevifolius</i>	9.24 $\pm$ 0.54	17.13 $\pm$ 1.75
LFC	colony	<i>S. brevifolius</i>	3.99 $\pm$ 0.39	4.53 $\pm$ 0.76
	grassland	<i>S. brevifolius, Hilaria mutica</i>	10.89 $\pm$ 1.14	12.58 $\pm$ 1.77
RLC	Colony	<i>H. mutica</i>	6.89 $\pm$ 0.82	1.54 $\pm$ 0.31
	grassland	<i>H. mutica</i>	3.58 $\pm$ 1.98	0.70 $\pm$ 0.42
SCC	Colony	<i>H. mutica</i>	5.86 $\pm$ 1.36	3.24 $\pm$ 0.80
	grassland	<i>S. brevifolius</i>	14.09 $\pm$ 2.32	6.43 $\pm$ 1.44

## Results

### Vegetation structure

Mean height and percent foliar cover of vegetation were both significantly lower on prairie dog colonies (4.70  $\pm$  0.36 cm, 3.32  $\pm$  0.29% cover) than adjacent grassland patches (9.59  $\pm$  0.74 cm, 10.66  $\pm$  0.87%) (Table 1; Wilcoxon signed rank,  $Z = 4.16$ ,  $P < 0.001$ ;  $Z = 4.96$ ,  $P < 0.001$ ). Vegetation height and basal cover were strongly correlated on colonies and in grassland (Spearman's Rank Correlation,  $n = 20$ ,  $r_s = 0.71$ ,  $P < 0.001$ ), and were significantly correlated within each site.

### Arthropod assemblages

We identified a total of 178 arthropod OTU from our pitfall survey. Thirty-seven OTU were sampled at only one site, 19 on colonies and 18 in grassland. For OTU sampled from more than one site, 11 were exclusively sampled on colonies and 10 in grassland.

There was no difference in arthropod abundance between colonies and grassland (Repeated Measures ANOVA,  $F_{1,4} = 1.36$ ,  $P = 0.31$ ). There were differences between seasons, with more arthropods collected during the summer months than other times of the year (Figure 2, RM-ANOVA,  $F_{1,3} = 6.67$ ,  $P < 0.01$ ), but there was not an interaction between the treatment and sampling season that explained arthropod abundance (RM-ANOVA,  $F_{1,3} = 0.54$ ,  $P = 0.64$ ). It is notable that during the winter of 2003-04, arthropods were sampled in greater abundance on each colony compared to adjacent grassland (Figure 3). Arthropod abundance was not correlated with either vegetation height ( $n = 10$ ,  $r = 0.02$ ,  $P = 0.48$ ) or vegetation basal cover ( $r = 0.11$ ,  $P = 0.42$ ).

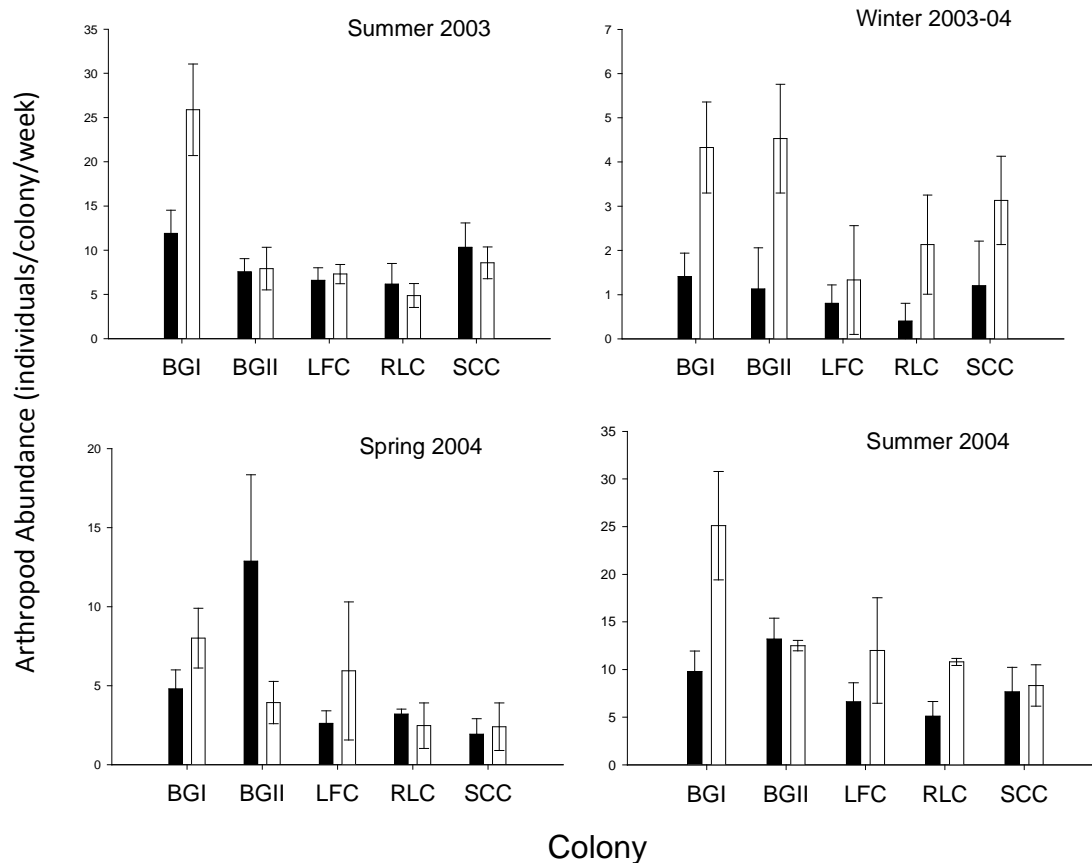
Arthropod community similarity determined by NMDS did not differ across sites (Global  $R = -0.001$ ,  $P =$

0.47). The trend for community differences between colonies and grassland was weak (Global  $R = 0.05$ ,  $P = 0.06$ ), but the SIMPER function calculated 83.0% dissimilarity between these plots (Figure 3). Community structure differed between sampling periods, and pair-wise ANOSIM comparisons between sampling periods were significantly different (Global  $R = 0.72$ ,  $P < 0.001$ ). Seasonal arthropod assemblages differed at both grassland and colony sites (grassland, Global  $R = 0.65$ ,  $P < 0.001$ ; colony, Global  $R = 0.83$ ,  $P < 0.001$ ), and NMDS clusters suggest a temporal community gradient across sites (Figure 4). All pair-wise comparisons between seasons were significant (all  $P < 0.01$ ).

Differences in abundance of ants in the genera *Cremastogaster* and *Solenopsis* accounted for 12.9% and 11.7% of the total dissimilarity between the colonies and grassland sites, with *Cremastogaster* sampled in higher numbers on colonies and *Solenopsis* sampled in greater abundance in grassland. Pair-wise comparisons of communities by season ranged from 70.3%–90.3% dissimilarity for colony sites and 73.9% - 97.2% dissimilarity in grassland (all pair-wise comparisons  $P < 0.05$ ). Seasonal comparisons were strongly influenced by differences in *Cremastogaster* and *Solenopsis* abundance across seasons, and only three other taxa (*Dorymyrmex* ants, Pyralid moths, and the spider *Micaria*) accounted for >10% of the total dissimilarity for any pair-wise seasonal comparisons between different taxa.

### Burrowing owl diet

We identified 1874 individual prey items representing 41 OTU from burrowing owl pellets. We found no significant differences in the similarity (mean  $C_{mH}$ ) of owl diet with colony versus grassland arthropod assemblages (Wilcoxon signed rank,  $Z = 1.02$ ,  $P = 0.31$ ). However, 1293 individuals (70%) were from four families of arthropods: Carabidae, Formicidae,

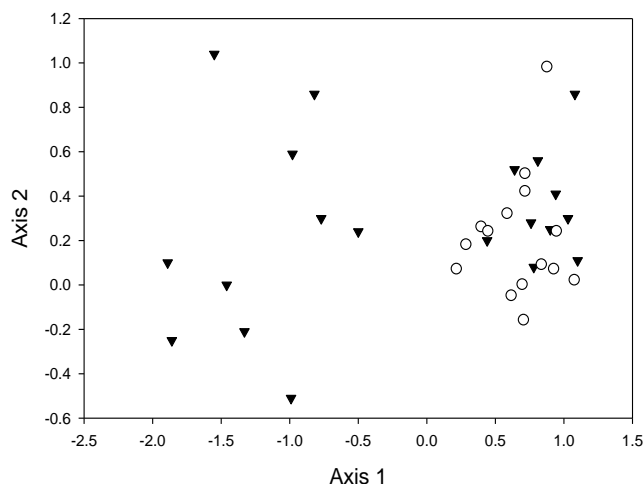


**Figure 2.** Mean abundance ( $\pm$  SE) of arthropods captured per week, for seasonal sampling periods per black-tailed prairie dog colony (white bars) and adjacent grassland patch (black bars), Armendaris Ranch, New Mexico. Colony abbreviations are explained in the Methods.

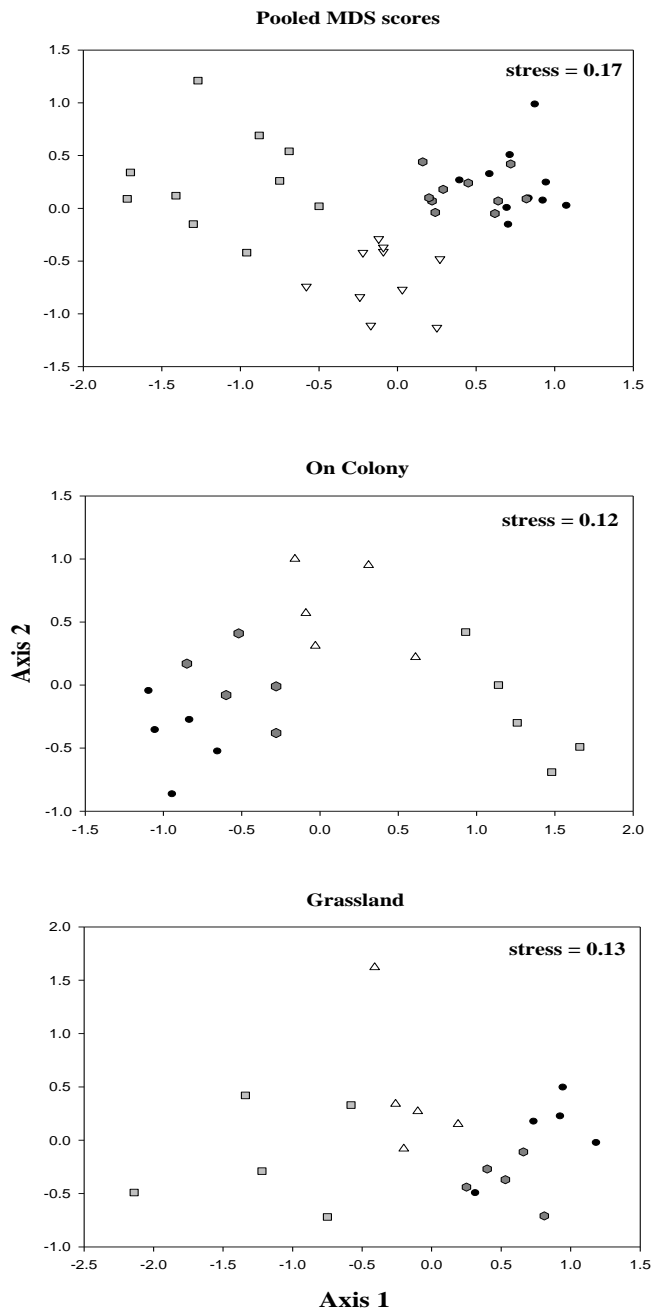
Eremobatidae and Tenebrionidae. Carabids, Eremobatids and Tenebrionids were sampled on colonies in significantly greater numbers than in adjacent grassland patches across seasons in which burrowing owls were present (Figure 5). Small mammals were present in the burrowing owl's diet, but accounted for only 9.9% of the identified prey items from pellets. The presence of small mammals in the burrowing owl diet did not differ across sampling periods (ANOVA,  $F_{2, 137} = 1.30$ ,  $P = 0.28$ ).

#### Burrowing owl foraging behavior

Burrowing owls foraged more often on prairie dog colonies than in grassland (RM-ANOVA,  $F_{1,43} = 6.16$ ,  $P = 0.017$ ). A two-way model including sex showed no differences between males and females, and there was no interaction between foraging on colonies and sex. The time burrowing owls foraged on colonies was significantly less than owl pursuits in adjacent



**Figure 3.** Arthropod community structure on black-tailed prairie dog colonies (black triangles) versus adjacent grassland patches (open circles), per site per season, determined by NMDS scores, Armendaris Ranch, New Mexico. Each symbol represents a specific colony or grassland arthropod assemblage across a given seasonal sampling period.



**Figure 4.** NMDS scores for seasonal differences in arthropod communities on prairie dog colonies and in adjacent grasslands. Season symbols are as follows: Summer 2003, closed circles; Winter 2003-04, open triangles; Spring 2004, grey squares; Summer 2004, dark grey hexagons. Each symbol represents colony or grassland arthropod assemblages across a given seasonal sampling period.

grassland, for both male and females (RM-ANOVA,  $F_{1,26}=40.06$ ,  $P < 0.001$ ) (Figure 6). Successful pursuits, which we defined as an owl returning to the nest with a prey item, were significantly shorter when conducted on colonies than off (Wilcoxon signed rank,  $Z = 4.14$ ,  $P <$

0.001), and successful pursuits by male owls were longer than those by their female nest-mates (Wilcoxon signed rank,  $Z = -2.08$ ,  $P = 0.037$ ). There was a non-significant trend for more successful pursuits to occur on colonies opposed to grassland by both sexes (Wilcoxon signed rank,  $Z = 1.44$ ,  $P=0.14$ ). There were no differences in the mean time of pursuits by owls nesting on the edge compared to the interior of colonies (RM-ANOVA,  $F_{1,26} = 0.001$ ,  $P = 0.97$ ).

Successful burrowing owl foraging pursuits were significantly longer in duration compared to unsuccessful pursuits (RM-ANOVA,  $F_{2,27} = 16.21$ ,  $P < 0.001$ ). Center and edge nesting owls delivered similar proportions of prey from on colony sources (Table 2). It is interesting to note that edge-nesting owls had a higher proportion of on colony pursuits than interior nesters, (Table 2).

## Discussion

### Arthropod communities on colonies

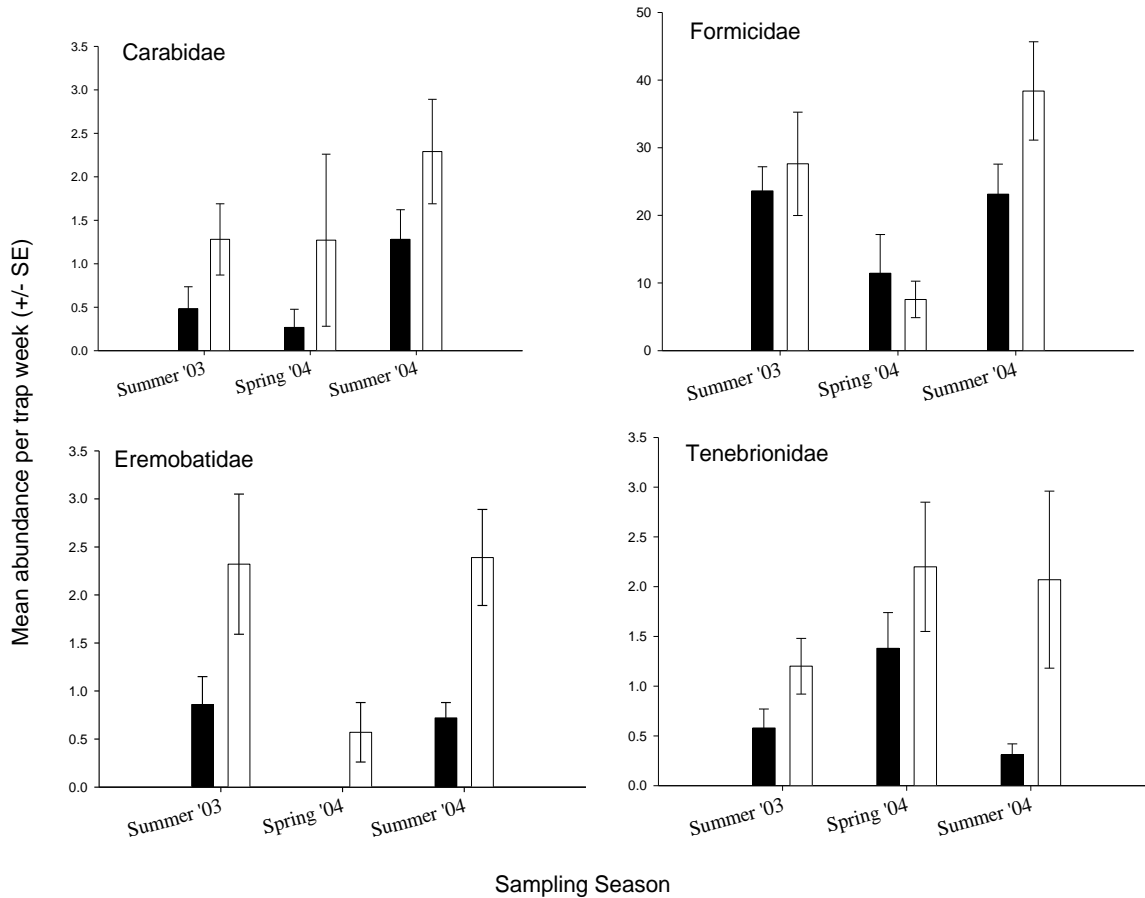
Reintroduced black-tailed prairie dog colonies support unique assemblages of arthropods compared to adjacent grassland patches. Abundances of arthropods did not differ between colonies and grassland, but ~10% of OTU sampled were found exclusively on colonies or in grassland. These OTU were rare taxa, but these observations suggest that black-tailed prairie dog colonies support and/or exclude certain groups of arthropods. While colonies are likely preferable habitat for some taxa, colonies may be suboptimal patches for arthropods dependent on greater vegetation height and cover (24) and predators of those taxa (46).

The pattern of vegetation clumps on colonies exhibits a fractal, homogeneous distribution (34). The concentration of burrows may serve as habitat for arthropods, and the even distribution of small vegetation clumps may concentrate foraging resources such as seeds and detritus for some arthropods (34,47). Furthermore, important predatory arthropods such as camel spiders were sampled on both colonies and in grassland but their abundance was higher on colonies, providing a biological feedback that may enhance community differences (48, 49).

Prairie dog burrows provide climatic micro sites that may explain differences between arthropod communities on colonies and grassland. A common adaptation by animals to environmental stress in deserts like extreme temperatures, precipitation fluxes and intense solar radiation is avoidance of these pressures (50). In the summer months, soil surface temperatures in the Chihuahuan desert can reach 60°C, but substrates as

**Table 2.** Proportion of pursuits conducted on colony, proportion of total pursuits resulting in prey delivery to the nest, and the proportion of prey deliveries in which the prey item was captured on colony for male and female burrowing owls (n = 20 owls) nesting in the interior and on the edge of black-tailed prairie dog colonies, Armendaris Ranch, New Mexico. Proportions are given as mean proportion of on colony pursuits, averaged per owl, per colony  $\pm$  SE.

Sex	Nest position	Pursuits On Colony	Prey Deliveries	% Prey Deliveries From Colonies
Female	Interior	0.72 $\pm$ 0.05	0.10 $\pm$ 0.04	0.86 $\pm$ 0.08
	Edge	0.81 $\pm$ 0.04	0.25 $\pm$ 0.05	0.80 $\pm$ 0.20
Male	Interior	0.53 $\pm$ 0.07	0.17 $\pm$ 0.08	0.49 $\pm$ 0.06
	Edge	0.73 $\pm$ 0.09	0.18 $\pm$ 0.08	0.45 $\pm$ 0.20



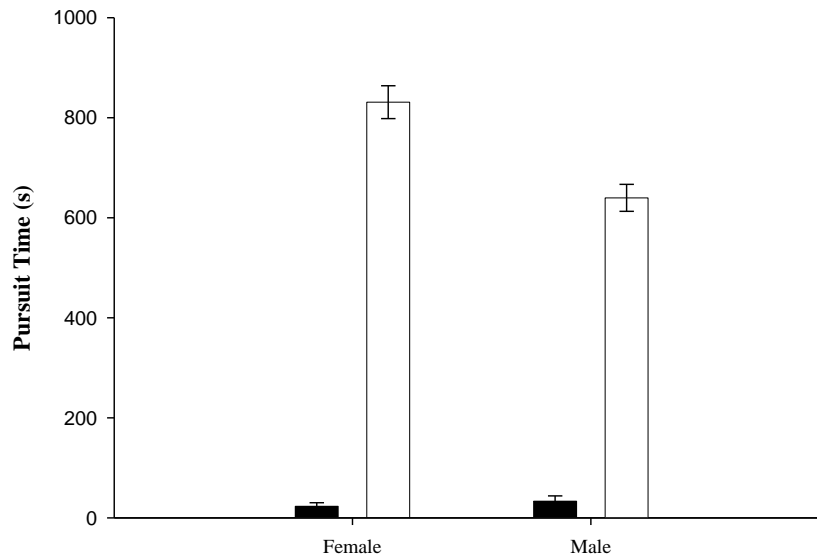
**Figure 5.** Mean abundance ( $\pm$  SE) of four most numerous burrowing owl prey items sampled on black-tailed prairie dog colonies (white bars) and adjacent grassland patches (black bars). These taxa represent the majority of burrowing owl prey and were sampled in significantly greater quantities on colonies during summer of 2003.

little as 10 cm above the surface or 5 cm below the surface can be 30°C cooler (51). Some ground-dwelling arthropods like burrowing spiders avoid desert extremes by creating their own refugia, but others such as Tenebrionid beetles cannot, and can benefit from the climatic relief provided by prairie dog burrows. Therefore, it is likely that even with greatly reduced vegetation, colonies are preferred habitat for some grassland arthropods due to the refugia provided by prairie dog burrows.

#### Burrowing owl use of colonies

Our results suggest that burrowing owls forage more often on colonies. Three of the four dominant components of the owl's diet were sampled in greater abundance on colonies than grassland (Figure 5). It is unlikely that more prey could persist in an area amenable to their detection without that area being suitable habitat for the prey species (33,52). While nearly 10% of burrowing owl pellets contained small





**Figure 6.** Mean foraging pursuit time  $\pm$  SE (sec/flight) of male and female burrowing owls on prairie dog colonies (black bars) and in adjacent grassland. Means are from pooling samples.

mammal remains, all remains were identified as the genus *Perognathus*, or bones of similar size, and adults of these small pocket mice range from 6-10 g (53). In comparison, one of the most prevalent prey items, *Elodes* sp. (Tenebrionidae) beetles, have an average mass of 0.6 g (54). Therefore, 10-15 beetles equal the biomass of a small mouse and owls are likely gaining an important dietary component from colony dwelling arthropods. The use of colonies by burrowing owls for foraging provides evidence that prairie dogs are indeed important engineers in grasslands given that they regulate food resources for other organisms (11).

An unexpected result from this study is that burrowing owls nesting on the edges of colonies did not engage in foraging pursuits into grassland more than center nesters (Table 2). Despite the short distance edge nesting owls had to travel to access adjacent grassland, those birds foraged preferentially on black-tailed prairie dog colonies. Sergio *et al.* (55) report that black kites (*Milvus migrans*) nesting closer to lakes, their preferred foraging areas, forage more efficiently and exhibit increased fitness compared to kites nesting further from lakes. In the context of this study, the owls were nesting within their preferred foraging areas, and it is expected that the spatial orientation of their nests within the colony should not influence their foraging behavior. Indeed, this hypothesis is bolstered by the observation that edge-nesting owls did not forage in grassland more than center nesters.

#### Significance of reintroduced colonies

Our data suggest that black-tailed prairie dog colonies are ecologically valuable patches to certain arthropods and an important habitat and foraging resource for burrowing owls within a desert grassland mosaic. The significant vegetation structure differences between black-tailed prairie dog colonies and adjacent grassland likely play a pivotal role in modulating resources between the patches and the foraging success of owls on colonies. Burrowing owl use of black-tailed prairie dog colonies as nesting areas has been established (15,29), but data presented here support the hypothesis that this preference is also related to increased prey abundance on colonies.

There are important implications for land managers and conservation biologists from this study. First, recently (<10 y) reintroduced black-tailed prairie dog colonies support a structurally unique flora, which in turn changes patch-level arthropod community structure. Secondly, our observation that burrowing owls forage extensively on colonies emphasizes that black-tailed prairie dog colonies are a foraging habitat for associated species. Finally, the greater implication of patch value differences between colonies and grassland is that species that forage on arthropods, and prefer open areas with low vegetation to hunt, will profit from the presence of these patches on the landscape. Thus, in terms of importance to other grassland taxa, black-

tailed prairie dog colonies represent a benefit in the form of habitat and food for a subset of associated organisms.

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