

KANGAROO RAT FORAGING IN PROXIMITY TO A
COLONY OF REINTRODUCED BLACK-TAILED PRAIRIE
DOGS

By

Kirsten Marie Fulgham

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SIGNED: _____

APPROVAL BY THESIS COMMITTEE

This thesis has been approved on the date shown below:

John L. Koprowski
Professor of Wildlife Ecology

Date

Steven R. Archer
Professor of Rangeland and Forest Resources

Date

Lisa K. Elfring
Associate Professor, Molecular and Cellular Biology

Date

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ABSTRACT

A majority of the arid grasslands in the western U.S. have been dramatically altered by anthropogenic influences resulting in degradation and desertification. Within the arid grasslands of North America a guild of burrowing herbivorous rodents that includes kangaroo rats (*Dipodomys* spp.) and prairie dogs (*Cynomys* spp.) is often considered integral to arid grassland maintenance. As part of the larger guild of burrowing herbivorous rodents, kangaroo rats are considered to be an important keystone guild whose role as ecosystem engineers and habitat modifiers complements that of prairie dogs. Together these species organize and structure arid grassland ecosystems and the biodiversity therein, by providing a mosaic of microhabitat patches, thus increasing overall heterogeneity. In an area where black-tailed prairie dogs (*C. ludovicianus*) were reintroduced, I used Giving-up Density (GUD) to assess the indirect effects black-tailed prairie dogs might have on the foraging patterns of resident kangaroo rats (*D. spectabilis* and *D. merriamii*). My objective was to compare and contrast kangaroo rat foraging GUD within and along the boundary of a recently established black-tailed prairie dog colony with that in the surrounding unmodified native habitat. This enabled assessment of whether black-tailed prairie dogs had an influence on the perceived quality of the habitat by kangaroo rats. Kangaroo rats visited off-colony feeding trays more frequently, and collected a greater mean mass of seed per tray as well. This indicates that the kangaroo rats perceived the area off the prairie dog colony as having a lower foraging cost than on the colony or along the colony edge. I conclude that from the perspective of the seed-

eating kangaroo rat, the colony is not viewed as high quality habitat. What impact the reintroduction and management of one keystone species might have on another keystone species deserves additional consideration as we attempt to restore arid grassland ecosystems.

CHAPTER 1: INTRODUCTION

Grasslands are one of the world's largest ecosystems, covering almost a quarter of the Earth's land surface, and once comprised the largest natural biotic community in North America (Bock and Bock, 2005). In southern and central Arizona and southwestern New Mexico grasslands historically covered nearly 4.5 million ha (Gori and Enquist, 2003). A majority of the arid grasslands in the western U.S. have been dramatically altered by anthropogenic influences resulting in the encroachment of shrubs and woody plants (Reynolds, 1954; Kerley and Whitford, 2000; Van Auken, 2000; Bock and Bock, 2005). As early as the 1940s rapid mesquite encroachment in the grasslands was already being noted with mesquite increasing from 160 to 248 trees/ha on the Santa Rita Experimental Range in southern Arizona between 1932 and 1948 (Reynolds and Glendening, 1949). The Nature Conservancy estimates that 37% of historic grasslands in southern and central Arizona and southwestern New Mexico have been permanently degraded (Gori and Enquist, 2003).

A North American guild of burrowing herbivorous rodents that includes kangaroo rats (*Dipodomys* spp.) and prairie dogs (*Cynomys* spp.) is often considered integral to arid grassland maintenance (Brown and Heske, 1990; Miller et al., 1994; Valone et al., 1995; Kotliar et al., 1999; Kotliar, 2000; Kerley and Whitford, 2009). The foraging behaviors, mound building, burrowing and nutrient cycling activities of both genera result in a mosaic of microhabitat patches within the larger landscape (Davidson and Lightfoot, 2006). However, since the 1960s a significant component of the guild, black-tailed prairie dogs (*Cynomys ludovicianus*), has been absent from

southern Arizona grasslands (Arizona Game and Fish Department, 2012). Government poisoning programs reduced populations throughout the western U.S. because prairie dogs were considered to have a negative impact on agriculture and rangelands (Koford, 1958). The eventual extirpation of the species from Arizona was driven by the same factors (Underwood and Van Pelt, 2008).

Prairie dog reintroduction efforts began at the Las Cienegas National Conservation Area in southern Arizona in October 2008 with multiple goals of increasing ecosystem health, biodiversity, and improving rangeland conditions (Bureau of Land Management, 2003; Underwood and Van Pelt, 2008).

Prairie dogs and kangaroo rats have been recognized as keystone species and ecosystem engineers (Davidson and Lightfoot, 2006). Keystone species are defined as those that have a disproportionately large impact on the ecosystem relative to their abundance (Power et al., 1996). Ecosystem engineers are organisms whose activities alter, maintain or create habitat (Jones et al., 1994). Although studies have examined the individual and combined keystone aspects of these two genera (Davidson and Lightfoot, 2006), little has been done to assess the impact one reintroduced keystone species might have on another similarly influential resident.

I examined the indirect effects that reintroduced black-tailed prairie dogs might have on resident kangaroo rats. My objective was to determine if kangaroo rat foraging behavior on a recently established black-tailed prairie dog colony would differ from that occurring in the immediately surrounding native habitat. This enabled assessment of whether black-tailed prairie dogs had an influence on kangaroo rat perceptions of habitat quality.

CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in Appendix A, which has been formatted for submission to the journal *The Southwestern Naturalist*. The following is a summary of the major findings.

Artificial food trays were placed around the perimeter of a recently established black-tailed prairie dog colony in the Las Cienegas National Conservation Area over five seasons (wet summer, autumn, winter, spring and dry summer). The trays were placed in concentric rings around the colony: the innermost ring of trays was in the colony interior (hereafter, on-colony), the middle ring was near the colony perimeter (hereafter, edge), and the outermost ring was off the colony (hereafter, off-colony).

Kangaroo rats showed a greater foraging preference off-colony in three of the five seasons (winter, spring and dry summer): more trays were visited and a greater mass of seed was collected from the off-colony trays. No significant differences were found in the number of visits or the mass of seed collected from any location during the wet summer and autumn seasons. Previous studies found more kangaroo rat burrows, evidence of activity and captures in the transition zone between prairie dog colonies and the dense grasslands surrounding colonies than on the prairie dog colonies themselves (Curtin, 2008). My study complements these previous findings and indicates that seed-eating kangaroo rats perceive the off-colony area as higher quality habitat than on or along the edge of the colony.

Interactions between location and season were significant; a greater mass of seed was collected from the off-colony trays in the dry summer period than any

location during any other season. This indicates that the kangaroo rats perceive the off-colony area as having a lower foraging cost than on the edge or on-colony areas. My findings suggest that from the perspective of the seed-eating kangaroo rat, the colony is not viewed as high quality habitat.

Both prairie dogs and kangaroo rats have been described as keystone modifiers in grassland ecosystems. What impact the reintroduction and management of one keystone species might have on another keystone species deserves additional consideration as we attempt to restore arid grassland ecosystems.

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APPENDIX A: KANGAROO RAT FORAGING IN PROXIMITY TO A COLONY OF REINTRODUCED BLACK-TAILED PRAIRIE DOGS

ABSTRACT

We examined the indirect effects of reintroduced black-tailed prairie dogs (*Cynomys ludovicianus*) on resident kangaroo rat (*Dipodomys*) populations. We used Giving-up Density (GUD) to quantify kangaroo rat foraging on a black-tailed prairie dog colony versus foraging near the colony edge or in the surrounding native habitat. This enabled assessment of whether black-tailed prairie dogs had an influence on kangaroo rat perceptions of habitat quality. Our results showed a greater foraging preference off-colony in most seasons. Kangaroo rats visited off-colony feeding trays more frequently and collected a greater mean mass of seed as well. This indicated that kangaroo rats perceived the area off the prairie dog colony as having a lower foraging cost than the on-colony or colony edge locations. Our data suggest that from the perspective of the seed-eating kangaroo rat, the colony is not viewed as high quality habitat. Both prairie dogs and kangaroo rats have been described as keystone modifiers in grassland ecosystems. What impact the reintroduction and management of one keystone species might have on another keystone species deserves additional consideration as we attempt to restore arid grassland ecosystems.

INTRODUCTION

Grasslands are one of the world's largest ecosystems, covering almost a quarter of the Earth's land surface, and comprised historically the largest biotic community in North America prior to farming, urbanization and desertification (Bock

and Bock, 2005). In southern and central Arizona and southwestern New Mexico grasslands covered nearly 4.5 million ha in recent history (Gori and Enquist, 2003).

A majority of the arid grasslands in the Western U.S. have been dramatically altered by anthropogenic influences resulting in the encroachment of shrubs and woody plants (Reynolds, 1954; Kerley and Whitford, 2000; Van Auken, 2000; Bock and Bock, 2005). As early as the 1940s rapid mesquite encroachment in southwestern grasslands was already being noted with mesquite on the Santa Rita Experimental Range in southern Arizona increasing from 160 to 248 trees/ha between 1932 and 1948 (Reynolds and Glendening, 1949). The Nature Conservancy estimates that 37% of historic grasslands in southern and central Arizona and southwestern New Mexico have been permanently degraded (Gori and Enquist, 2003).

Restoration efforts for grasslands currently focus on ecological improvements for biotic communities as well as human uses (Gottfried, 2004; Bock and Bock, 2005; Ostoja, 2008). Such restoration efforts need to be informed by an understanding of the ecosystem. A North American guild of burrowing herbivorous rodents that includes kangaroo rats (*Dipodomys*) and prairie dogs (*Cynomys*) is often considered integral to arid grassland maintenance (Brown and Heske, 1990; Miller et al., 1994; Valone et al., 1995; Kotliar et al., 1999; Kotliar, 2000; Kerley and Whitford, 2009). Both genera have been suggested as potential agents for grassland restoration (Sjoberg et al., 1984; Underwood and Van Pelt, 2008).

Much like prairie dogs, kangaroo rats were once viewed as pests having a deleterious impact on the condition of the rangelands, and were oftentimes exterminated (Vorhies and Taylor, 1922; Wood, 1965; Schroeder, 1967; Whitford,

2002). In recent years the desertification due to drought and non-existent or poor livestock grazing management has been exacerbated in part due to the seed caching activities of kangaroo rats, which can promote shrub encroachment (Duval et al., 2005; Kerley and Whitford, 2009; Eldridge et al., 2009). However, this shrub encroachment can be countered, in part, by kangaroo rat herbivory on shrub seedlings (Valone and Thornhill, 2001). In healthy grasslands, and in good seed years, the caching activities of kangaroo rats can serve as a seed dispersal mechanism for many other native perennial plants promoting biodiversity and grassland health (Reynolds, 1958; Eldridge et al., 2009). Digging and burrowing activity increase soil permeability, thus promoting greater moisture retention and aid in germination of cached seeds (Reynolds, 1958). The actions of kangaroo rats help to naturally maintain a healthy ecosystem by increasing the survivorship of native seedlings (Sjoberg et al., 1984; Whitford and Kay, 1999).

Important concepts to the function of ecosystems are the roles of keystone species and ecosystem engineers. Keystone species are defined as those who have a disproportionately large impact on the ecosystem relative to their abundance (Power et al., 1996). Ecosystem engineers are those organisms whose activities alter, maintain or even create habitat (Jones et al., 1994). In other words, the biotic effects of organisms define their keystone status, whereas the causal mechanisms that produce those effects define the ecosystem engineering role (Van Nimwegen et al., 2008). Organisms whose activities result in unique habitat patches being created within a larger, different landscape are considered to be habitat modifiers (Davidson and Lightfoot, 2008).

As part of the larger guild of burrowing herbivorous rodents, kangaroo rats are considered to be an important keystone guild whose role as ecosystem engineers and habitat modifiers complements that of prairie dogs. Together these genera effect the organization and structure of arid grassland ecosystems and the biodiversity therein by providing a mosaic of microhabitat patches and increasing overall heterogeneity (Heske et al., 1993; Guo, 1996; Fields et al., 1999; Brock and Kelt, 2004; Davidson and Lightfoot, 2006, 2007, 2008; Kelt, 2011). Kangaroo rats are considered ecosystem engineers due to their foraging methods, mound building, burrowing, and nutrient cycling activities (Hawkins and Nicoletto, 1992; Longland, 1995; Guo, 1996; Davidson and Lightfoot, 2006). They fulfill the role of a keystone guild by having a large-scale influence on vegetative composition and diversity as well as the species dominance structure of various patch types in desert grasslands (Brown and Heske, 1990; Heske et al., 1993; Fields et al., 1999; Valone and Thornhill, 2001). Granivory and graminivory both factor into the keystone status of kangaroo rats (Kerley et al., 1997). As keystone species, their engineering effects (burrowing and digging) combine with non-engineering effects (population density), but are more influential than their non-engineering effects (Prugh and Brashares, 2012). These effects persist for years after burrows have been vacated (Bowers and Brown, 1992; Chew and Whitford, 1992).

Within the grasslands of southeast Arizona, the burrowing granivorous rodent guild is composed primarily of banner-tailed kangaroo rats (*Dipodomys spectabilis*), Merriam's kangaroo rats (*D. merriami*), and Ord's kangaroo rats (*D. ordii*) (Hoffmeister, 1986). Historically, this area was in the range of the black-tailed prairie

dog (*Cynomys ludovicianus*). However, since the 1960s this significant component of the guild had been absent (Arizona Game and Fish Department, 2012). Government poisoning programs reduced populations throughout the West because prairie dogs were considered to have a negative impact on agriculture and rangelands (Koford, 1958). The eventual extirpation of the species from Arizona was driven by the same factors (Underwood and Van Pelt, 2008). Reintroduction of black-tailed prairie dogs began at the Las Cienegas National Conservation Area in October 2008 with the goals of increasing ecosystem health, biodiversity, and the rangeland conditions (Bureau of Land Management, 2003; Underwood and Van Pelt, 2008).

Long-term research (Curtin, 2008; Davidson and Lightfoot, 2010) has found that reintroduction of prairie dogs has significant impacts on kangaroo rat populations that reside in an area of reintroduction. In an area where black-tailed prairie dogs were reintroduced, we used Giving-up Density (GUD) to assess the indirect effects black-tailed prairie dogs might have on the foraging patterns of resident kangaroo rats. Seed trays were used as artificial resource patches. The premise behind the methodology is that as a forager harvests from a patch, the density of the resource is reduced. A point exists wherein the costs of continuing to forage from the patch (e.g., energy expended, predation risk, missed opportunities) begin to outweigh the benefits of continuing to forage on an ever-dwindling resource. At this point, termed the giving-up density, the forager will abandon the patch (Brown, 1988; Bouskila, 1995). GUD can be used to compare the relative costs of different patches in terms of habitat quality (Hernandez, 2000; Sullivan et al., 2001). The longer an animal forages in a patch the less seed will remain, which results in a lower GUD. Therefore GUDs will

be higher in riskier areas than in safer ones as individuals spend less time and thus collect less seed (Brown and Kotler, 2004). This method has been used to explore kangaroo rat foraging response to variations in habitat associated with roadside verges versus adjacent grazing lands (Stapp and Lindquist, 2007), topography (Sullivan et al., 2001), and shrub cover (Hernandez, 2000).

Our objective was to determine if kangaroo rat foraging behavior on a recently established black-tailed prairie dog colony would differ from that occurring in the immediately surrounding native habitat. This enabled assessment of whether black-tailed prairie dogs had an influence on kangaroo rat perceptions of habitat quality.

MATERIALS AND METHODS

Study Area

The study was conducted on the Las Cienegas National Conservation Area near Sonoita, Arizona. The temperature of the area ranges from a winter average high of 16°C and average low of -2°C, to a summer average high of 33°C and average low of 16°C. Precipitation falls mainly as rain, ranging from 26 cm to 74 cm with an annual average of ~46 cm, more than half of which occurs during summer monsoon (National Climate Data Center. 2015. <http://www.ncdc.noaa.gov/cag/> Accessed 04/24/2015). In Arizona, summer is bisected by a rainy monsoon (mid-June through September). This effectively yields two distinct summer seasons: pre-monsoon dry summer (hereafter, dry summer) and monsoon summer (hereafter, wet summer).

The Las Cienegas National Conservation Area is managed by the Bureau of Land Management as an actively grazed ranch and is open to dispersed public recreation (Bureau of Land Management, 2003). On a broad landscape scale the

vegetation can be defined as desert grassland, mixed shrub-succulent or xeromorphic tree savanna with two distinct areas. The northern hills (30 cm to 41 cm annual precipitation) have rocky soils and are potentially prone to losses in perennial grass cover and shrub encroachment. The southern bottomlands (30 cm to 51 cm annual precipitation) have loamy soils and are potentially prone to soil erosion and invasive grass and mesquite encroachment (Gori and Schussman, 2005). For more details on vegetation and soils see Gori and Schussman (2005).

We conducted this study from August 2013 to May 2014 at the Mud Springs prairie dog colony reintroduction site (31°46'39.89"N, 110°34'43.28"W) hereafter referred to as the colony. The colony was situated at the boundary of the northern hills and the southern bottomlands areas in the Las Cienegas National Conservation Area (Gori and Schussman, 2005). The colony and west side were generally clay loam, while the north, east and south sides were generally loamy uplands (Soil Survey Staff, NRCS, USDA). On the colony and along its perimeter the grass genera included *Bouteloua*, *Panicum*, *Muhlenburgia*, *Eragrostis*, *Chloris*, *Aristida*, *Bothriochloa*, *Digitaria*, *Setaria*, *Psilostrophe*, and *Sporobolus*. Forb genera included *Lepidium*, *Chenopodium*, *Proboscidea*, *Ambrosia*, *Amaranthus*, *Cucurbita*, *Solanum*, *Datura*, *Asclepias*, *Oenothera*, and *Calochortus*. Small shrubs (all <30 cm except for one *Yucca* that was >1m in height) included *Prosopis*, *Mimosa*, *Isocoma* and *Yucca*. Off the colony the species composition was generally the same, but the velvet mesquites (*Prosopis velutina*) were generally shrubs and small trees ranging from <1 m to > 4 m in height.

The Arizona Game and Fish Department (AZGFD) established the colony in October 2009 in the Las Cienegas National Conservation Area following mesquite removal and installation of 25 artificial burrows. Sixty-eight prairie dogs were initially introduced into the colony in October 2009 and were augmented in each of the following two years. At the time of the study there were over 35 prairie dogs in the colony (H. Hicks, personal comm.). Commercial herbivore chow pellets (Mazuri ADF 16 - Regional, PMI Nutrition Int'l, LLC., Brentwood, MO) were provided by AZGFD as supplemental food for the prairie dogs from early March through late July in both years of study.

No obvious active or abandoned kangaroo rat mounds were found on colony, but several were found along the edge of the colony and in the surrounding environment. It is possible that any kangaroo rat burrows within the colony boundaries prior to establishment by AZGFD could have been destroyed by the construction process. Kangaroo rats might be displaced by reintroduced prairie dog colonies (Curtin, 2008), and during the course of the study we observed prairie dogs invading and excavating active kangaroo rat burrows along the colony boundary.

Kangaroo rat populations were inventoried over 4 nights (1 June 2013 to 4 June 2013) using Sherman live traps baited with rolled oats and peanut butter both on and off the colony prior to initiating the foraging study. Handling methods followed the American Society of Mammalogists (Sikes and Gannon, 2011) and University of Arizona Institutional Animal Care and Use Committee guidelines (Protocol # 11-251). A total of 200 trap-nights with 5 banner-tailed kangaroo rats and 13 Merriam's kangaroo rats caught over the 4 nights yielding a trapping success rate of 9.0%, which

was consistent with other kangaroo rat trapping rates (9.1%) around the same time in the other three prairie dog colonies in Las Cienegas National Conservation Area (S. Hale, personal comm.). Although three species of kangaroo rats are known to be present in the Las Cienegas National Conservation Area (Hoffmeister, 1986), no Ord's kangaroo rats were caught or observed during any session.

Placement of Seed Trays

We established a transect around the entire perimeter of the prairie dog colony, which we defined as 10 m distant from the outermost active prairie dog burrows, which is considered to be the distance beyond the influence of a prairie dog burrow (Davidson and Lightfoot, 2006, 2008). Artificial food patches (hereafter trays) were arrayed around the colony perimeter at ca. 30 m intervals so as to provide replicates in each of the cardinal directions ($n = 3$ to 6, depending on the length of the N, S, E, W perimeter segments). The replicate trays were situated 10 m outside the colony perimeter (hereafter, off-colony), the second tray 10 m inside the colony perimeter (hereafter, edge) and 20 m inside the colony perimeter (hereafter, on-colony). This generated a total of 48 trays per night, and effectively created three distinct location transects (hereafter known as the locations). One location was distinctly on the colony (16 trays), another location was distinctly off the colony (16 trays) and a third location was along the line of the outermost burrows (16 trays) to assess an effect of edge (Fig. 1). Trays were placed out after sunset when prairie dogs retreat to their burrows.

The vegetation conditions on the colony differed from the surrounding environment in that all velvet mesquite trees on the colony had been removed in 2008

as part of the preparation of the site for reintroduction of prairie dogs. On colony, the herbaceous vegetation height was ≤ 10 cm for four of the five collection dates (autumn, winter, spring, and dry summer) due to a combination of mowing by AZGFD in mid-September after monsoon rains, cattle grazing and prairie dog foraging and felling. On the wet summer collection date the height ranged from ≤ 10 cm for most of the colony to over 100 cm in low-lying areas where rainwater ponding occurred. All on-colony trays were in open areas of mixed grasses and forbs. Trays off-colony were in a shrub and grassland mix and outside the mowed area. Edge trays were in an area of transition from open herbaceous cover to mixed grass-shrub cover. Thirteen edge trays were in mowed areas and three were not.

Lunar Cycle and Seasonality

Moonlight has a demonstrated negative effect on foraging behavior of kangaroo rats (Lockard and Owings, 1974; Kaufman and Kaufman, 1982; Kotler, 1984; Bowers, 1988). In order to control for the effect of moonlight, we conducted all trials within four consecutive nights of the new moon (Hernandez, 2000). We conducted foraging trials in five seasons (wet summer, autumn, winter, spring, and dry summer), defined by meteorological and phenological events.

We collected wet summer data in early August 2013. This season was mid-monsoon and the area was dense with green vegetation undergoing luxuriant growth with some plants flowering. Thurber's peppergrass (*Lepidium thurberi*), velvet mesquite and Palmer amaranth (*Amaranthus palmeri*) were producing seeds but grass seeds were not yet present. We collected autumn data in early October 2013 after the monsoon. There was little green vegetation, except on colony, which had been mown

in September by AZGFD and grazed by cattle and prairie dogs. In unmown areas, the grasses *Bouteloua*, *Panicum*, *Muhlenburgia*, *Eragrostis*, *Chloris*, *Aristida*, *Bothriochloa*, *Digitaria*, *Setaria*, *Sporobolus* were producing seed, and mesquite pods and forb fruits were dry. We collected winter data in late December 2013 and early January 2014 during the dormant season; winter rain had not yet refreshed vegetation. Some grass seeds were still present. We collected spring data in late March and early April 2014 during the period when new basal growth on grasses and green forbs was underway. Little to no seeds remained on grass plants at this time and AZGFD had begun supplemental feeding of prairie dogs. We collected dry summer data in late May 2014. This season was pre-monsoon, with minimal green vegetation that had declined since the previous season. Only the bases of some grasses were still green. Peppergrass forbs and mesquite shrubs were flowering and no seeds from the previous season remained on grass plants. Supplemental feeding of prairie dogs was still occurring.

Giving-up Density Assessments

Prior to the 4-night data collection in each season, we conducted a 1-2 night habituation period to allow the kangaroo rats to acclimate to the trays. The trays consisted of aluminum pans (46 X 33 X 3 cm) filled with a smoothed, uniform mixture of 4.1 g of hulled oat seed and 2 L of sifted sand obtained from near the colony. The surface of the mixture was smoothed and all seeds were below the surface to minimize the likelihood of seed loss to harvester ants (*Pogonomyrmex*), birds or other non-target animals. We documented the location of each tray with a Global Positioning System (GPS) (Garmin GPSMAP 60 CSx, Garmin Ltd., Olathe,

KS). Prior to sunrise we examined trays for evidence of kangaroo rat visitation (footprints, tail drag marks, digging) and categorized each as either visited or not visited. A tray was considered visited if signs of kangaroo rats or a combination of kangaroo rats and other small mammals were present. Trays displaying signs of visitation by only other small mammals were considered not visited (Sullivan et al., 2001). We sifted the substrate and seed mixture from each tray visited by kangaroo rats, removed debris and weighed remaining seed. We also collected and processed at least five trays each night with no signs of visitation as control trays. We did this to account for any gain or loss of mass that occurred due to changes in humidity through the night (Stapp and Lindquist, 2007). The mean percentage mass gained or lost by the controls was used to adjust the mass of the remaining seeds in visited trays. If the controls trays gained mass, the percentage gained was subtracted from the visited trays mass; if the control trays lost mass, the percentage lost was added to the visited trays mass. We re-deployed replenished trays at all locations each evening prior to sunset.

Camera Traps

During the first two seasons we found evidence of kangaroo rat activity near trays that showed no visitation activity. We were able to supplement our seed collection data using 12 camera traps (Stealth Cam Nomad IR, GSM Outdoors, Grand Prairie, TX) positioned at randomly selected trays along each transect each night in the December 2013/January 2014 winter season. We added another 12 cameras (Bushnell MP Trophy Cam Standard Edition, Overland Park, KS) for the final two seasons.

Data Analyses

For each trial night we recorded the following information: ambient air temperature, relative humidity, cloud cover, and wind speed near sunrise and sunset. We identified which trays were visited by kangaroo rats based on the identification of their unique bipedal tracks, size of footprints, and tail drags in trays (Hoffmeister, 1986; Elbroch, 2003). We weighed the amount of seed recovered to the nearest 0.1 g from any tray with evidence of activity and the controls. We examined video footage from cameras to help determine which species visited trays and whether trays were approached but not entered.

We used a chi-square test to compare visitation rates of kangaroo rats (Sullivan et al., 2001) and an analysis of variance (ANOVA) to compare the mass of remaining seeds for location (on-colony, edge, and off-colony) season (wet summer, autumn, winter, spring, and dry summer) and their interaction (Sullivan et al., 2001; Stapp and Lindquist, 2007). Tukey's HSD was used to test for significant difference between means.

We ran two-way ANOVAs in order to assess the extent of influence of other small mammals on the mean GUD. There was no difference in the models ($p < 0.001$ for each), therefore the effects of other small mammals visiting trays had a negligible effect on the data and were not considered in the study.

All trays, visited by kangaroo rats or not, were included in the ANOVAs because many trays were observed with no kangaroo rats tracks within the tray but with tracks around the tray. Camera images confirmed that some trays were being inspected and rejected; others appeared to not be found by kangaroo rats. We could

not reliably tell which trays were being rejected, resulting in a high GUD, and which trays were never visited. So, to avoid undercounting high GUD trays, we included the mass of remaining seeds in all of the trays in the ANOVAs.

RESULTS

We monitored 960 tray-nights (48 trays/night, 4 nights/season, 5 seasons) creating 192 data points per season. Over the entire study, 21% of the trays were visited by kangaroo rats (8% *Dipodomys* alone, 13% *Dipodomys* and other small mammals), and by 6% other small mammals; 73% were unvisited by any organism. The low visitation rate is consistent with the low trapping success rate discussed earlier.

Seed collection was highest in the off-colony trays (Two-way ANOVA: location $F_{(2,945)} = 19.8$, $P < 0.001$) with collection being greatest from trays in dry summer (pooled mean = 3.13 g), and lowest in autumn (pooled mean = 4.01g) and winter (pooled mean = 4.05 g) (Two-way ANOVA: season $F_{(4,945)} = 30.3$, $P < 0.001$) with an interaction between location and season (Two-way ANOVA: $F_{(8,945)} = 5.2$, $P < 0.001$). More seed was collected from the off-colony trays in the dry summer than any other location during any season (Tukey's HSD: $P < 0.05$ - Table 1).

Wet summer (ANOVA: $F_{(2,189)} = 0.184$, $P = 0.832$) and autumn (ANOVA: $F_{(2,189)} = 0.56$, $P = 0.572$) were similar in that the amount of seed collected from any of the three locations did not differ. Conversely, winter (ANOVA: $F_{(2,189)} = 9.6$, $P < 0.001$), spring (ANOVA: $F_{(2,189)} = 13.7$, $P < 0.001$) and dry summer (ANOVA: $F_{(2,189)} = 9.8$, $P < 0.001$), were similar in that we found more seed was collected from off-colony trays for each of the three seasons (Fig. 2).

The number of visits by kangaroo rats did not differ among locations during the wet summer ($\chi^2 = 0.237$, $df = 2$, $P = 0.888$) and autumn seasons ($\chi^2 = 2.5$, $df = 2$, $P = 0.293$). We found the number of trays visited was greatest at the off-colony location during the winter ($\chi^2 = 26.0$, $df = 2$, $P < 0.001$), spring ($\chi^2 = 13.7$, $df = 2$, $P = 0.001$) and dry summer ($\chi^2 = 9.8$, $df = 2$, $P = 0.008$, Fig. 3).

DISCUSSION

Kangaroo rats visit off-colony trays more frequently and collect a greater mass of seed from these trays. They appear to perceive the area off the prairie dog colony to have a lower foraging cost than on the colony or along the edge. From the perspective of the seed-eating kangaroo rat, the colony is not viewed as high quality habitat.

Giving-Up Density to Assess Foraging Decisions

GUD is a method to approximate the Quitting Harvest Rate (QHR) of an organism because it is difficult to directly measure QHR (Brown, 1988; Brown and Kotler, 2004). A QHR is the point at which the various costs of feeding from a food patch exceed the benefits that remain in the food patch. Brown (1988) defined the quitting harvest rate in the following formula:

$$\textit{Quitting Harvest Rate} = \textit{Metabolic Cost} + \textit{Predator Cost} + \textit{Missed Opportunity Cost}.$$

This formula has been used to examine the various costs involved in GUDs (Brown, 1988; Brown and Kotler, 2004). Metabolic costs are the energetic costs involved in finding and harvesting seeds, predator costs are the risks of being exposed to predators, and missed opportunity costs are those incurred from not engaging in activities necessary to the health of the individual or the species (Brown, 1988;

Brown and Kotler, 2004). We use these components to frame the discussion of the costs that kangaroo rats might have been encountering in order to assess the relative value of prairie dog influenced habitats to kangaroo rats.

Metabolic cost of foraging— The metabolic cost of foraging is influenced by, but not limited to, seed availability and time spent reaching food patches (Brown, 1988; Bouskila, 1995). Kangaroo rats use areas away from shrub cover mostly for transit (Thompson, 1982; O'Farrell and Uptain, 1987) and spend up to 85% of their foraging time under the cover of shrubs (Thompson, 1982), perhaps because seed density has been found to be up to five times greater under desert shrubs than in the surrounding areas (Nelson and Chew, 1977). This might explain why kangaroo rats might perceive the more open habitat of the colony as poor foraging habitat.

Kangaroo rat activity in an area decreases in the presence of prairie dogs (Davidson and Lightfoot, 2006; Davidson et al., 2010). Kangaroo rats are displaced by reintroduced prairie dog colonies and generally found just off the colonies where vegetation density is lower than the surrounding area but where there are also few prairie dogs (Curtin, 2008). During the course of our study we observed two banner-tailed kangaroo rat mounds along the edge transect become inhabited by prairie dogs resulting in the abandonment of at least one of the mounds by kangaroo rats. The off-colony trays were closer to kangaroo rat burrows, which were primarily along the edge and off-colony, and were harvested at a greater rate perhaps because the cost of travel was less. The kangaroo rats might have perceived the on-colony location to be too costly to visit because of distance and quality of habitat.

Predator cost— Even though most of the food trays were well within the nightly travel range of kangaroo rats (Schroder, 1979; Best, 1988; Jones, 1989), on-colony trays were visited less. Clearly, costs other than metabolic costs might have had a role in the kangaroo rat foraging decisions. Open, low vegetation areas present greater predator risk than brushy areas for kangaroo rats and GUDs are higher in open versus brushy habitats (Kotler et al., 1988). Kangaroo rat foraging habits will shift in response to risk of predation, and when risk of predation from owls increases, kangaroo rats will avoid foraging in open areas and instead forage under cover (Brown et al., 1988). Great-horned owl (*Bubo virginianus*) attacks on Merriam's kangaroo rats were ~7 times greater in open habitat than brushy on new moon nights increasing to ~40 times greater on full moon nights (Longland and Price, 1991). On-colony sites, through the combined actions of prairie dogs, cattle grazing and mowing, were much more open with shorter vegetation (generally ≤ 10 cm during our study period) than edge or off-colony locations and might have been perceived as more risky by the kangaroo rats and visited less. We documented frequent vocalizations and sightings of great horned owls and coyotes (*Canis latrans*). During the wet summer session only, we also observed one western diamond-backed (*Crotalus atrox*) and three Mojave (*C. scutulatus*) rattlesnakes located near prairie dog or kangaroo rat burrows either on the colony or near the perimeter. Prairie dog colonies attract carnivores such as coyotes, foxes (*Urocyon* and *Vulpes*), badgers (*Taxidea taxus*), rattlesnakes (*Crotalus*), burrowing owls (*Athene cunicularia*), great horned owls and several hawk (*Buteo*) species (Ceballos et al., 1999; Kretzer and Cully, 2001; Lomolino and Smith, 2004). Kangaroo rats comprised 16% of all food

items and 19% of all vertebrate prey in the diets of coyotes in active rangelands (Fitch, 1948). Also, travel time to a food patch might be an issue. The farther a kangaroo rat travels the more likely it is to incur predation costs (Daly et al., 1990).

Missed opportunity costs— As with foraging costs, the distance of a burrow from a food patch also affects the missed opportunity costs because of the time involved in reaching energy rich food patches (Brown, 1988). Time spent traveling to forage might take a kangaroo rat away from doing other things such as burrow maintenance, seeking a mate, or dust bathing. Kangaroo rats dust bathe for pelage maintenance and conspecific communication (Eisenberg, 1963; Laine and Griswold, 1976). The farther away a banner-tailed kangaroo rat is from its burrow the less time spent stationary with as little as 20% of that time spent foraging (Schroder, 1979).

Cattle were present at various locations throughout the study period. Soil disturbances created by cattle, resulting in bare earth patches, are used as dust bathing areas by kangaroo rats (Braun, 1985; Stangl et al., 1992). Off-colony locations were threaded by well-used cattle trails where cattle were restricted in their movements by tall mesquite shrub and tree cover. The passage of many hooves created the fine textured soils preferred by kangaroo rats for dust bathing. The trails showed substantial evidence of kangaroo rat activity (tracks, tail drags, dust bathing). They also provide clear pathways, which could be easily and speedily negotiated by kangaroo rats over long distances. Kangaroo rats use trails to achieve maximum speed to evade predators (O'Farrell and Uptain, 1987). On-colony, had few distinct cattle trails because livestock were able to spread out freely over the colony, had few good dust bathing patches, and showed much less obvious kangaroo rat activity (e.g.

fewer kangaroo rat tracks and tail drag marks). It is reasonable to consider that the cattle trails reduced missed opportunity costs in the off-colony locations.

Seasonality

Kangaroo rat foraging behavior changes in response to quality of habitat, resulting in a high GUD in good seed years, and a low GUD in bad seed years (Bouskila, 1995). Seasonal differences in GUD can likewise be attributed to variations in seed naturally available. The peak of grass seed production in southeastern Arizona grasslands is after the wet summer season, with seed availability typically beginning in mid-September and ending in early January (Pulliam and Brand, 1975). The lowest GUDs were in seasons with the least naturally available seed: spring and dry summer. The months with the lowest levels of stored seed by kangaroo rats are in the seasons with the least seed naturally available (Monson, 1943).

Implications

Kangaroo rats prefer not to forage on-colony for most of the year, which might explain in part the decline of kangaroo rats from re-established prairie dog colonies elsewhere (Curtin, 2008). What is unknown is if this is a short-term result of the construction of the prairie dog colony only a few years ago, or if this will persist. Perhaps this is how a newly created relationship between two keystone species emerges. While prairie dog reintroduction appears to initially displace kangaroo rats, in the long-term prairie dog colony boundaries seem to facilitate kangaroo rat activity (Curtin, 2008). Prairie dogs and kangaroo rats are known to coexist but probably compete for some resources (Davidson and Lightfoot, 2006). When found together,

the densities of prairie dogs and kangaroo rats are less than when either is found alone, but the overall heterogeneity of the area increases because of the unique ecosystem impact of each keystone species (Davidson and Lightfoot, 2006). A decrease in population density of kangaroo rats might cause a decrease in the non-engineering component of their keystone effect. It is the compounded engineering and non-engineering effects of kangaroo rats on the ecosystem that results in an increased biodiversity and abundance of organisms (Prugh and Brashares, 2012). On a larger scale the resulting mosaic might indirectly benefit the other species within the guild (Curtin, 2008) as well as enhancing the resilience of the system as a whole.

Monitoring the status of both black-tailed prairie dogs and banner-tailed kangaroo rats is of special concern to natural resource management agencies. Both are listed as species of Greatest Conservation Need by the Arizona Game and Fish Department (2012) and as Sensitive Species by the Bureau of Land Management (2010). What impact the reintroduction and management of one keystone species might have on another keystone species deserves additional consideration as we attempt to restore arid grassland ecosystems.

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TABLES AND FIGURES

Table 1--Tukey's HSD comparing the mean (\pm SE) Giving-up Density (GUD) across locations and seasons (values ranked from highest to lowest). GUD is measured by the grams of remaining seed in seed tray. On-colony locations were 20 m inside the prairie dog colony perimeter, edge locations were 10 m inside the colony perimeter and off-colony locations were 10 m outside the colony perimeter. Locations and seasons that do not share the same letter are different at $p < 0.05$.

Location	Season		Least Square Mean (g of remaining seed)	Standard error
on-colony	Winter	A	4.10	0.00
edge	Winter	A	4.10	0.00
edge	autumn	A	4.06	0.06
on-colony	autumn	A	3.99	0.02
off-colony	autumn	A	3.99	0.07
off-colony	Winter	A	3.95	0.05
edge	Spring	A	3.94	0.06
on-colony	Spring	A	3.93	0.06
on-colony	wet summer	A	3.84	0.13
edge	wet summer	A B	3.75	0.10
off-colony	wet summer	A B	3.74	0.14
on-colony	dry summer	A B C	3.60	0.17
edge	dry summer	B C	3.28	0.14
off-colony	Spring	C	3.12	0.20
off-colony	dry summer	D	2.49	0.22

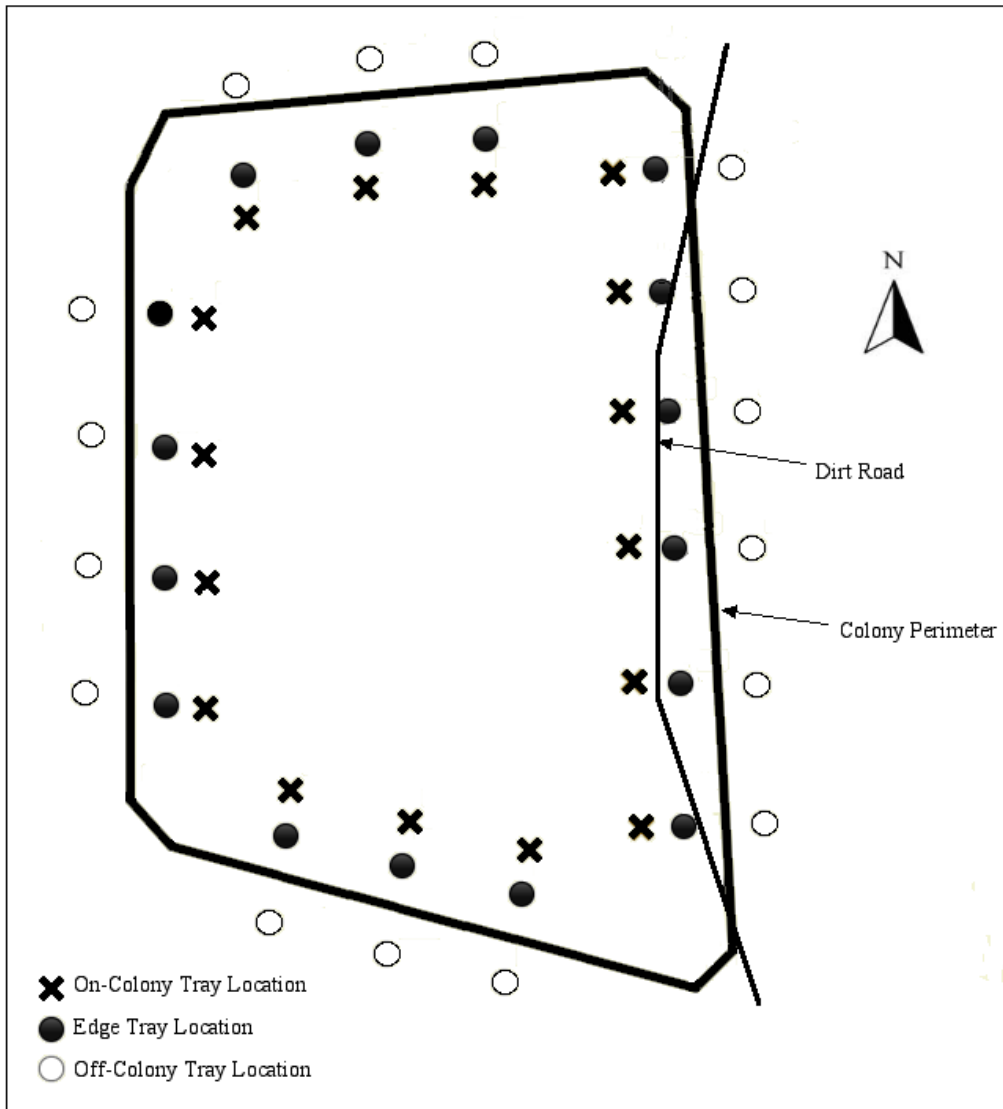


FIG. 1--Seed tray locations (x = on-colony, ● = edge, ○ = off-colony) on black-tailed prairie dog (*Cynomys ludovicianus*) colony at Mud Springs (31°46'39.89"N, 110°34'43.28"W), Las Cienegas National Conservation Area, Pima County, Arizona. The thick solid line represents the perimeter (defined by the location of the outermost burrows). The on-colony and edge locations were 20 m and 10 m, respectively, inside the perimeter of the colony; off-colony locations were 10 m outside the perimeter (map not to scale; distance between trays arrayed around the perimeter circumference was ca. 30 m). A ranch road (thin solid line) traversed the eastern perimeter of the colony.

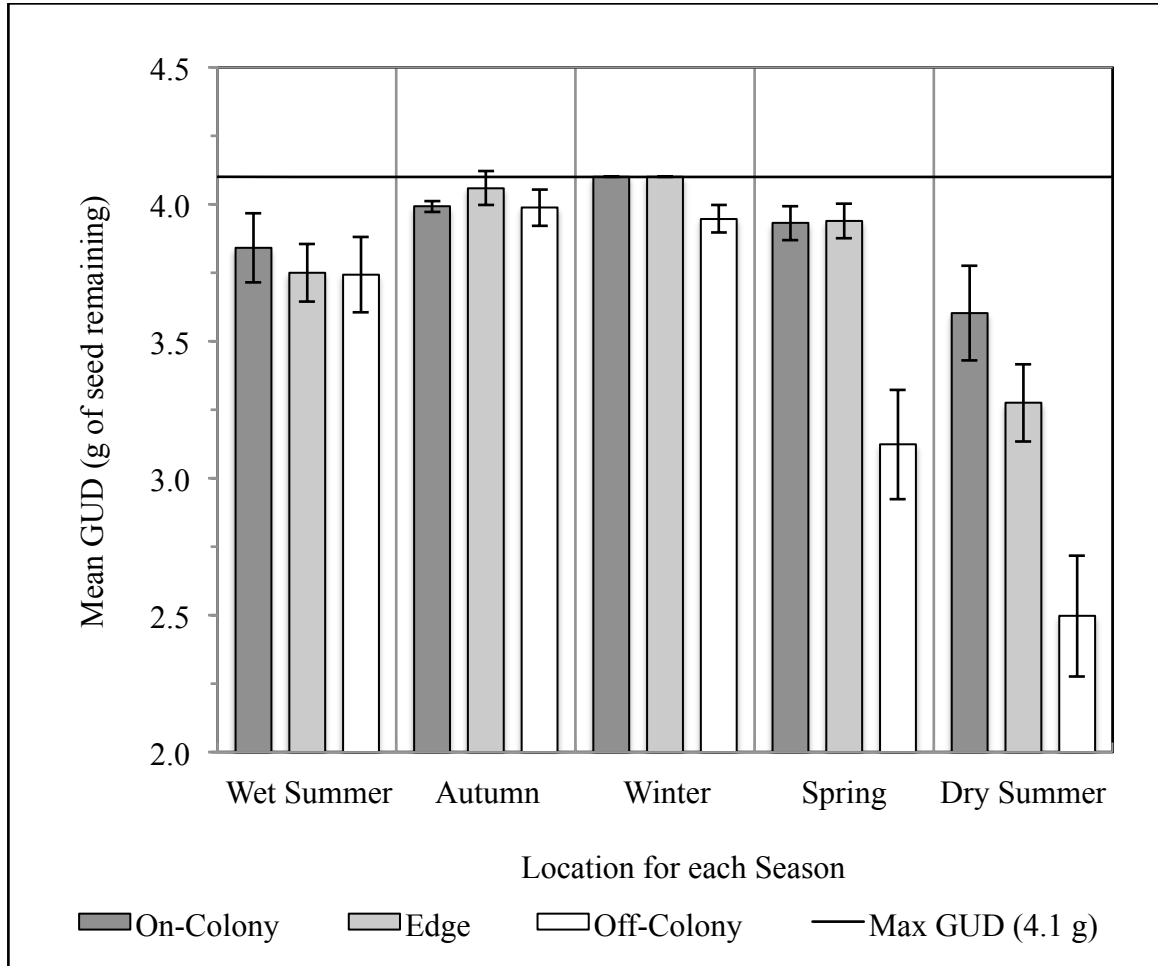


FIG. 2--Mean (\pm SE; $n=64=16$ trays \times 4 nights) Giving-up Density (GUD, grams of seed remaining) at different locations for each season on black-tailed prairie dog (*C. ludovicianus*) colony, ($31^{\circ}46'39.89''N$, $110^{\circ}34'43.28''W$), Las Cienegas National Conservation Area, Pima County, Arizona. All trays, visited or not, were included in the mean (see text for details). Winter on-colony and edge location trays had no loss of seed from any tray, therefore the GUD = 4.1 for all trays and the SE = 0.0 for both locations.

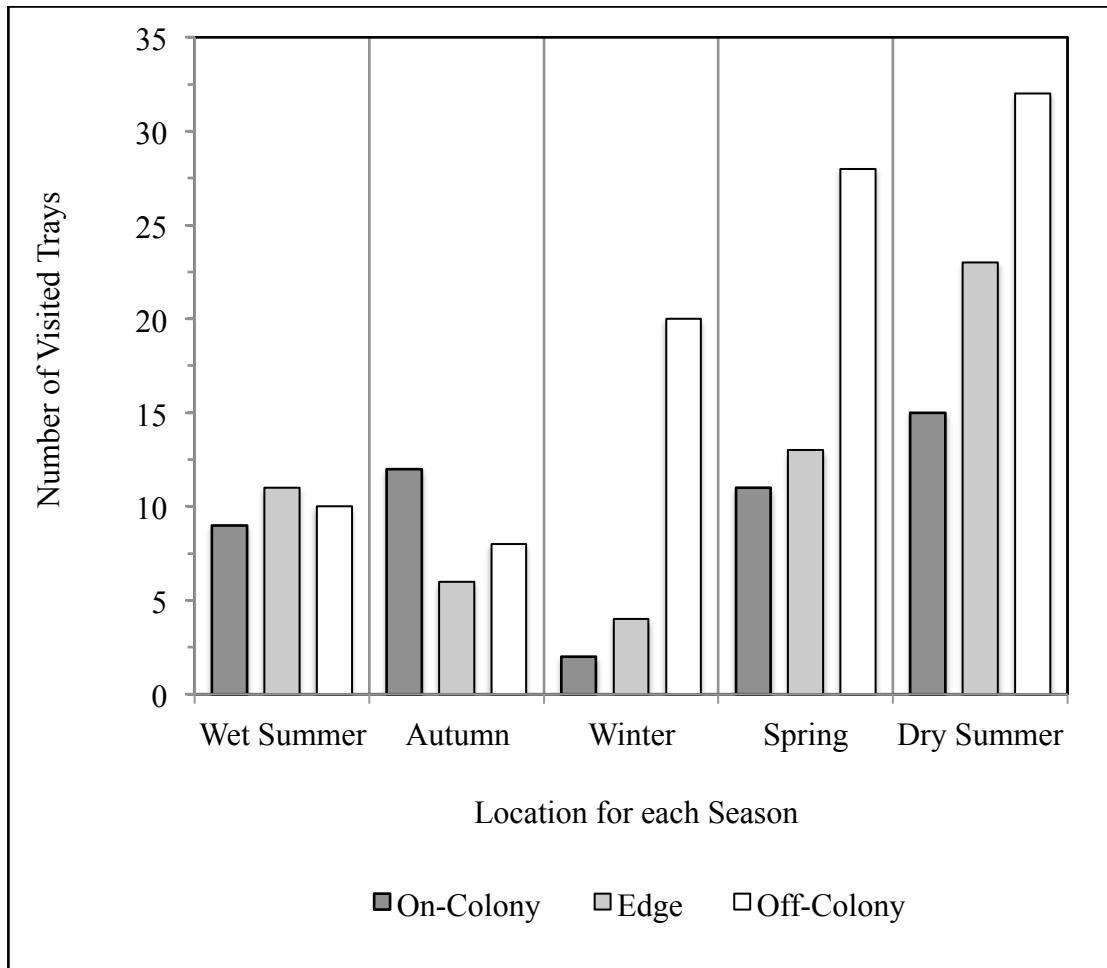


FIG. 3--Number of seed trays visited by *Dipodomys* at different locations for each season on black-tailed prairie dog (*C. ludovicianus*) colony, (31°46'39.89"N, 110°34'43.28"W), Las Cienegas National Conservation Area, Pima County, Arizona. Each count is relative to 64 total trays (16 trays x four nights).