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

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**ABSTRACT**—We examined the indirect effects of reintroduced black-tailed prairie dogs (*Cynomys ludovicianus*) on resident kangaroo rat (*Dipodomys*) populations. We used the Giving-up Density theory to quantify kangaroo rat foraging on a black-tailed prairie dog colony vs. foraging near the colony edge or in the surrounding native habitat. This approach allowed us to assess the influence of black-tailed prairie dogs on kangaroo rat foraging activity. 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.

**RESUMEN**—Examinamos los efectos indirectos de perros de las praderas de cola negra (*Cynomys ludovicianus*) reintroducidos en poblaciones residentes de ratas canguro (*Dipodomys*). Utilizamos la teoría de la Densidad de Abandono para cuantificar el forrajeo de las ratas canguro dentro de una colonia de perros de las praderas de cola negra contra el forrajeo cerca del borde de la colonia o en el hábitat nativo circundante. Este enfoque nos permitió evaluar la influencia de los perros de las praderas de cola negra en la actividad de forrajeo de la rata canguro. Nuestros resultados mostraron una preferencia de forrajeo mayor fuera de la colonia en la mayoría de las estaciones. Las ratas canguros visitaron las bandejas de alimentación fuera de la colonia más frecuentemente y también colectaron una masa promedio mayor de semillas. Esto indicó que las ratas canguros percibieron el área fuera de la colonia de los perros de las praderas como la que tenía un costo de forrajeo más bajo que los sitios en la colonia o al borde de la colonia. Nuestros datos sugieren que desde la perspectiva de las ratas canguros, que se alimentan de semillas, la colonia no es vista como hábitat de alta calidad. Tanto los perros de las praderas como las ratas canguros han sido descritos como modificadores clave en ecosistemas de pastizal. Qué impacto podría tener la reintroducción y manejo de una especie clave sobre otra especie clave merece consideración adicional conforme intentamos restaurar ecosistemas de pastizales áridos.

Grasslands are one of the world's largest ecosystems, covering almost a quarter of the Earth's land surface, and they historically comprised the largest biotic community in North America prior to farming, urbanization, and desertification (Bock and Bock, 2005). A majority of the arid grasslands in the western United States have been dramatically altered by anthropogenic influences, resulting in the encroachment of shrubs and woody plants (Kerley and Whitford, 2000; Van Auken, 2000). Restoration efforts for grasslands currently focus on ecological improvements for biotic communities as well as on human uses (Gottfried, 2004; Ostoja, 2008). A North American guild of burrowing herbivorous rodents that includes kangaroo rat (*Dipodomys*) and prairie dog

(*Cynomys*) species is often considered integral to arid grassland maintenance (Brown and Heske, 1990; Miller et al., 1994). Both genera have been suggested as potential agents for grassland restoration (Sjoberg et al., 1984).

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 affect the organization and structure of arid grassland ecosystems and the biodiversity therein by providing a mosaic of microhabitat patches and increasing overall heterogeneity (Fields et al., 1999; Davidson and Lightfoot, 2006, 2008). 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). They fulfill the role of a keystone guild by having a large-scale influence on vegetative composition and diversity as well as on the species dominance structure of various patch types in desert grasslands (Heske et al., 1993; Fields et al., 1999). 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 nonengineering effects (population density) but are more influential than their nonengineering 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 (*Dipodomys merriami*), and Ord's kangaroo rats (*Dipodomys 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 has been absent. 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 (Oakes, 2000). 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 (U.S. Department of the Interior, in litt.).

Long-term research (Curtin, 2008) has found that reintroduction of prairie dogs had 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 the Giving-up Density (GUD) theory 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 was 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 because 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 vs. 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 foraging activity.

**MATERIALS AND METHODS—Study Area**—We conducted this study at the Mud Springs prairie dog colony reintroduction site (hereafter referred to as the colony) within the Las Cienegas National Conservation Area (31°46'39.89''N, 110°34'43.28''W) from August 2013 to May 2014. The Las Cienegas National Conservation Area, near Sonoita, Arizona, is managed by the Bureau of Land Management as an actively grazed ranch and is open to dispersed public recreation.

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, accessed 24 April 2015, <http://www.ncdc.noaa.gov/cag/>). In Arizona, summer is bisected by a rainy monsoon (mid-June through September). This effectively yields two distinct summer seasons: premonsoon dry summer (hereafter, dry summer) and monsoon summer (hereafter, wet summer).

On a broad landscape scale, the vegetation of the Las Cienegas National Conservation Area can be defined as desert grassland, mixed shrub-succulent, or xeromorphic tree savanna with two distinct areas. The northern hills (30–41 cm annual precipitation) have rocky soils and are potentially prone to losses in perennial grass cover and shrub encroachment. The southern bottomlands (30–51 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).

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, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey, accessed 24 April 2015, <http://websoilsurvey.nrcs.usda.gov/>). On the colony and along its perimeter the grass genera included *Bouteloua*, *Panicum*, *Muhlenbergia*, *Eragrostis*, *Chloris*, *Aristida*, *Bothriochloa*, *Digitaria*, *Setaria*, *Psilostrophe*, and *Sporobolus* species. Forb genera included *Lepidium*, *Chenopodium*, *Proboscidea*, *Ambrosia*, *Amaranthus*, *Cucurbita*, *Solanum*, *Datura*, *Asclepias*, *Oenothera*, and *Calochortus*. Small shrubs (all <30 cm except for one *Yucca* species that was >1 m 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 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 preparation of the site for reintroduction of prairie dogs. On colony, the herbaceous vegetation height was  $\leq 10$  cm for four of the five collection dates (autumn, winter, spring, and dry summer) due to a combination of mowing by Arizona Game and Fish Department (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  $\leq 10$  cm for most of the colony to over 100 cm in low-lying areas where rainwater ponding occurred.

The 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 2 y. At the time of the study there were over 35 prairie dogs in the colony (H. Hicks, pers. comm.). Commercial herbivore chow pellets (Mazuri® ADF 16 Regional, PMI Nutrition International, LLC, Brentwood, Missouri) 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 may 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.

Prior to initiating the foraging study, kangaroo rat populations were inventoried over 4 nights (1 June 2013 to 4 June 2013) to confirm the presence of kangaroo rats on the study site (Stapp and Lindquist, 2007). Sherman live traps were baited with rolled oats and peanut butter with an equal number of traps placed both on and off the colony. 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).

**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; that 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  $\sim 30$ -m intervals in each of the cardinal directions ( $n = 3$  to 6, depending on the length of the N, S, E, W perimeter segments). The trays were situated 10 m outside the colony perimeter (hereafter, off-colony), the second tray 10 m inside the colony perimeter (hereafter, edge) and the third tray 20 m inside the colony perimeter (hereafter, on-colony) to establish a grid of uniform density of trays around the 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 replicate trays), another location was distinctly off the colony

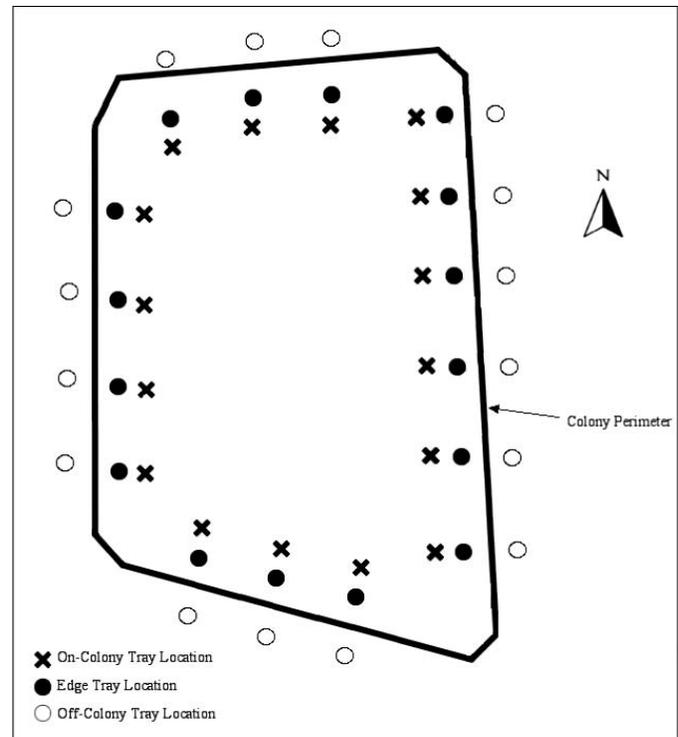


FIG. 1—Seed tray locations (x = on-colony, • = edge, o = off-colony) on black-tailed prairie dog (*Cynomys ludovicianus*) colony at Mud Springs (31°46'39.89"N, 110°34'43.28"W), Las Cienegas National Conservation Area, Pima County, Arizona (study conducted from August 2013 to May 2014). The thick solid 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  $\sim 30$  m).

(16 replicate trays), and a third location was along the line of the outermost burrows (16 replicate trays) to assess an effect of edge (Fig. 1). Trays were placed out after sunset when prairie dogs retreated to their burrows.

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; 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), as defined by meteorological and phenological events.

**Giving-up Density Assessments**—Prior to the 4-night data collection in each season, we conducted a 1- to 2-night habituation period to allow the kangaroo rats to acclimate to the trays. The trays consisted of aluminum pans (46 × 33 × 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 nontarget animals. We documented the location of each tray with a Global Positioning System (Garmin GPSMAP 60 CSx, Garmin Ltd., Olathe, Kansas). 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, those 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 control 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, Texas) 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, Kansas) 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 verify which species visited trays and whether trays were approached but not entered.

We used a chi-square ( $\chi^2$ ) test to compare visitation rates of kangaroo rats (Sullivan et al., 2001) and an analysis of variance (ANOVA) to compare the mean 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 honest significant difference (HSD) was used to test for significant difference between means (Jacob and Brown, 2000).

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 rat tracks within the tray but with tracks around the tray.

TABLE 1—Tukey's HSD comparing the mean ( $\pm$ SE) giving-up density (GUD) for kangaroo rats (*Dipodomys*) at a prairie dog (*Cynomys*) colony in Pima County, Arizona across locations and across seasons. GUD was reported as grams of remaining seed in seed tray. Values are ranked from highest to lowest. 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 that do not share the same superscripted letter are different at  $P < 0.05$ .

Location	Least square mean $\pm$ SE (g of remaining seed)
On-colony <sup>A</sup>	3.89 $\pm$ 0.059
Edge <sup>A</sup>	3.82 $\pm$ 0.085
Off-colony <sup>B</sup>	3.46 $\pm$ 0.137
Season	
Winter <sup>A</sup>	4.05 $\pm$ 0.031
Autumn <sup>A</sup>	4.01 $\pm$ 0.039
Wet summer <sup>A</sup>	3.78 $\pm$ 0.103
Spring <sup>A</sup>	3.66 $\pm$ 0.148
Dry summer <sup>B</sup>	3.13 $\pm$ 0.199

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**—A total of 200 live trap-nights prior to seed tray placement caught 5 banner-tailed kangaroo rats and 13 Merriam's kangaroo rats over the 4 nights, yielding a trapping success rate of 9.0%. This rate 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, pers. 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 of our study.

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), 6% by other small mammals only, and 73% were not visited by any organism.

The lowest GUD, or greatest seed collection, was in the off-colony trays (two-way ANOVA: location  $F_{2,225} = 6.48$ ,  $P = 0.002$ ; Tukey's HSD:  $P < 0.05$ ; Table 1), with the GUD being lowest from trays in dry summer (pooled mean = 3.13 g) and highest in autumn (pooled mean = 4.01 g) and winter (pooled mean = 4.05 g; two-way ANOVA: season  $F_{4,225} = 9.91$ ,  $P < 0.001$ , Fig. 2; Tukey's HSD:  $P < 0.05$ ; Table 1). There was no interaction between location and season.

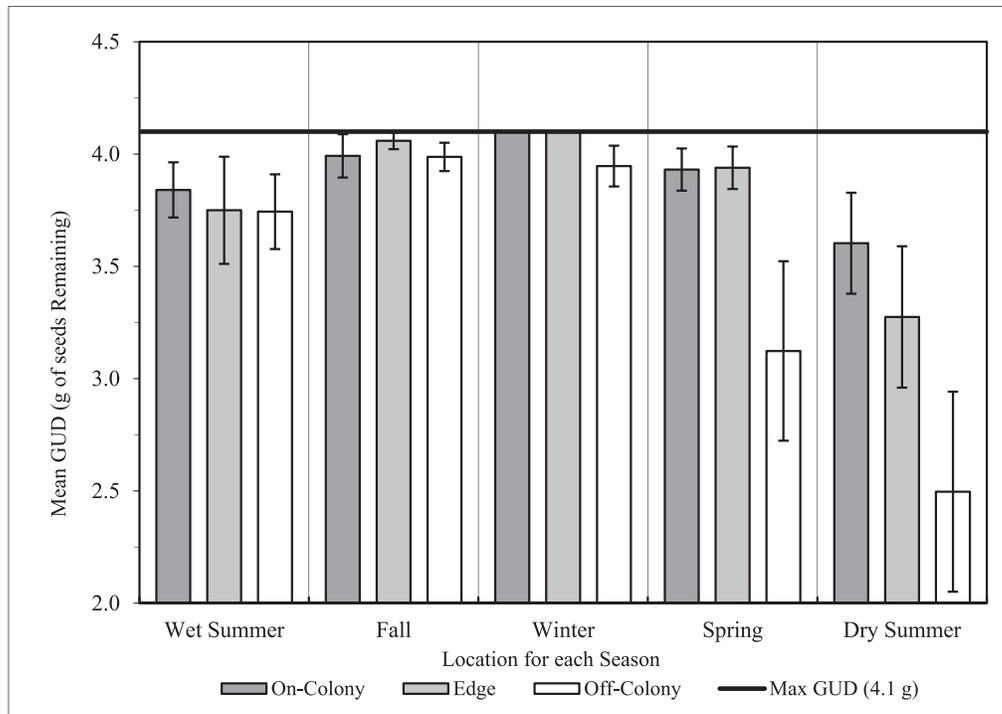


FIG. 2—Mean ( $\pm$ SE;  $n = 64 = 16$  trays  $\times$  4 nights) Giving-up Density (GUD, grams of seed remaining) at different locations for each season on black-tailed prairie dog (*Cynomys ludovicianus*) colony, (31°46'39.89''N, 110°34'43.28''W), Las Cienegas National Conservation Area, Pima County, Arizona (study conducted from August 2013 to May 2014). 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.

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, creating a lower GUD. 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, this colony in the Las Cienegas National Conservation Area 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. The QHR presumes a balance between the benefits vs. the costs of foraging. High GUDs indicate high costs, low GUDs indicate low costs. Based on the QHR formula we would expect GUD to be lowest where the cumulative costs of foraging are lowest. Where our results show the

lowest GUDs, generally off colony, indicates the lowest total costs of foraging. Brown (1988) defined the quitting harvest rate in the following formula:

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

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

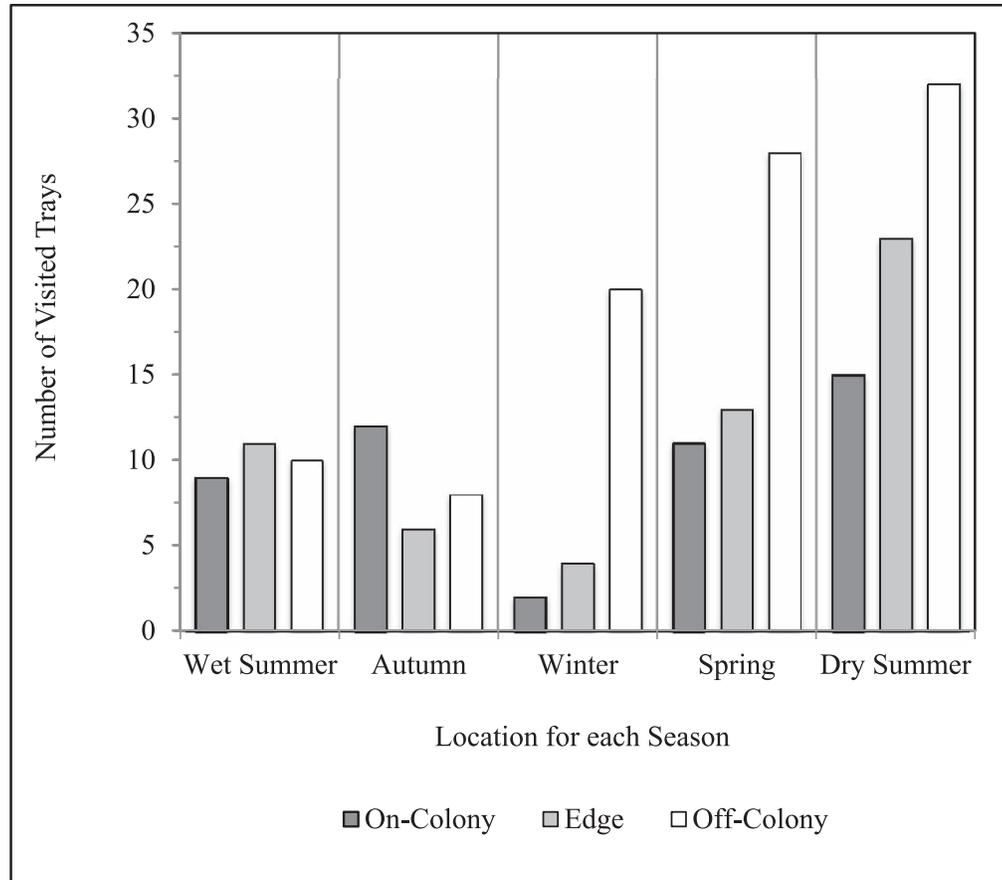


FIG. 3—Number of seed trays visited by *Dipodomys* at different locations for each season on black-tailed prairie dog (*Cynomys ludovicianus*) colony, (31°46'39.89"N, 110°34'43.28"W), Las Cienegas National Conservation Area, Pima County, Arizona, August 2013 to May 2014. Each count is relative to 64 total trays (16 trays  $\times$  4 nights).

surrounding areas (Nelson and Chew, 1977). This might explain why kangaroo rats might perceive the more-open habitat of this colony in the Las Cienegas National Conservation Area as poor foraging habitat and why the GUDs of on-colony seed trays were higher than off-colony seed trays.

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, creating lower GUDs 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 on this colony in the Las Cienegas National Conservation Area.

*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 do brushy areas for kangaroo rats, and GUDs are higher in open vs. 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  $\sim 7$  times greater in open habitat than in brushy habitat on new moon nights, increasing to  $\sim 40$  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  $\leq 10$  cm during our study period) than were the edge or off-colony locations and might have been perceived as more risky by the kangaroo rats and visited less, creating higher GUDs on this colony in the Las Cienegas National Conservation Area. We documented frequent vocalizations and sight-

ings 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 (*Crotalus 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 provided 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, there were few distinct cattle trails because livestock were able to spread out freely over the colony, resulting in few good dust-bathing patches, and these sites 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 at this colony in the Las Cienegas National Conservation Area. It may be that GUDs were lower in off-colony trays because the kangaroo rats already spent more of their time there for other behaviors besides foraging.

*Seasonality*—Kangaroo rat foraging behavior changes in response to the 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). We found the highest GUDs throughout all locations in the study site during fall and winter when seed was plentiful and there was little need to forage in any of the artificial patches. 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). GUDs in all locations (off, edge, and on-colony) were lower during these periods of lowest stored seed and least naturally available seed, though significantly lowest in off-colony locations. When faced with such conditions, it may be that kangaroo rats, given the opportunity to forage in artificial seed patches, were willing to pay the assorted costs involved in foraging in areas that under other conditions were assessed as low-quality foraging sites.

*Implications*—Kangaroo rats prefer not to forage on-colony for most of the year in the Las Cienegas National Conservation Area, which might explain in part the decline of kangaroo rats from re-established prairie dog colonies elsewhere (Curtin, 2008). What is unknown is if the decline is a short-term result of the construction of the prairie dog colony only a few years ago or if it will persist. Perhaps this is how a newly created relationship between two keystone species emerges. While prairie dog reintroduction appeared 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 nonengineering component of their keystone effect. It is the compounded engineering and nonengineering 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 (in litt.) and as Sensitive

Species by the U.S. Department of the Interior's Bureau of Land Management (in litt.). 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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