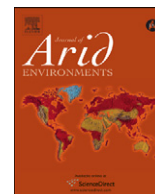




Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Engineering rodents create key habitat for lizards

A.D. Davidson*, D.C. Lightfoot, J.L. McIntyre

Department of Biology, University of New Mexico, Albuquerque, NM 87131-0001, USA

ARTICLE INFO

Article history:

Received 16 June 2008

Accepted 7 July 2008

Available online 12 August 2008

Keywords:

Banner-tailed kangaroo rats

Ecosystem engineers

Gunnison's prairie dogs

Keystone species

Rodent mounds

ABSTRACT

There is growing recognition among ecologists that ecosystem engineers play important roles in creating habitat for other species, but the comparative and combined effects of co-existing engineers are not well known. Here, we evaluated the separate and interactive effects of two burrowing rodents, Gunnison's prairie dogs (*Cynomys gunnisoni*) and banner-tailed kangaroo rats (*Dipodomys spectabilis*), on lizards in the Chihuahuan Desert grassland (USA). We found that the mounds and burrow systems of both rodent species provided important habitat for lizards, with lizard abundance being 2 to 4-fold higher on mounds than in adjacent areas without mounds. Kangaroo rat mounds supported greater numbers of lizards than prairie dog mounds, but the prairie dog colony with kangaroo rats supported 2-times more lizards than the landscape with only kangaroo rats. A greater number of mound habitats were available for lizards where prairie dogs and kangaroo rats co-occurred, and the rodents created unique structural mound types with different spatial distributions on the landscape. Our results demonstrate the importance of burrowing rodents in creating habitat for other animals, and that the combined effect of ecosystem engineers, especially those with large ecological roles, can be complementary and additive in areas where they co-occur.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Ecosystem engineers physically create, maintain, and modify their environment (Jones et al., 1994). By doing so, these organisms form unique patches of modified habitat and alter community structure and ecosystem processes. Ecosystem engineers are found in most, if not all, ecosystems and produce effects through a broad range of activities on a wide diversity of resources (Jones et al., 1994; Wright and Jones, 2006). While the effects of some engineers can be small, others can have profound impacts on their environment. Beavers (*Castor canadensis*), for example, engineer dams, which create important riparian habitat for plants and other animals, and elephants (*Loxodonta africana*) maintain open, wooded grasslands by damaging and consuming trees, providing habitat for many other species (Jones et al., 1994; Pringle, 2008). Burrowing mammals such as gophers (*Geomys* and *Thomomys* spp.), plains vizcachas (*Lagostomus maximus*), prairie dogs (*Cynomys* spp.), banner-tailed kangaroo rats (*Dipodomys spectabilis*), plateau zokors (*Myospalax fontanierii*), and Siberian marmots (*Marmota sibirica*), are especially well known ecosystem engineers; their mound building transforms grassland landscapes, creating unique habitats for many other species (Branch et al., 1999; Ceballos et al., 1999; Davidson and Lightfoot, 2006, 2007, 2008; Guo, 1996; Huntly and Inouye, 1988; Lomolino and Smith, 2003; Van Staaldunin and Werger, 2007; Zhang et al., 2003).

* Corresponding author. Current address: Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo Postal 70-275, México D.F. 04510, México. Tel.: +52 555 6229004; fax: +52 555 56229004.

E-mail address: davidson@unm.edu (A.D. Davidson).

Prairie dogs and banner-tailed kangaroo rats are often considered keystone species and ecosystem engineers of grassland ecosystems (Davidson and Lightfoot, 2006; Kotliar et al., 1999, 2006; Valone et al., 1995). Prairie dogs alter grassland landscapes by grazing grass and constructing numerous mounds with extensive burrow systems (Whicker and Detling, 1988, Fig. A1a). Within their colonies, prairie dogs maintain a low, dense turf of rapidly growing plants dominated by forbs and grazing-tolerant grasses, forming a mosaic of unique open habitat patches within the greater grassland landscape (Whicker and Detling, 1988). Banner-tailed kangaroo rats alter grassland landscapes through their selective seed harvesting and engineering of large, resource-rich mounds that are conspicuously dispersed across the landscape (Brown and Heske, 1990; Guo, 1996; Mun and Whitford, 1990; Fig. A1b). As grasslands provide open habitats lacking natural refuges like trees and boulders, the burrows made by prairie dogs and kangaroo rats are especially important habitats for a wide diversity of animals (Bangert and Slobodchikoff, 2006; Davidson and Lightfoot, 2007; see also citations in Kotliar et al., 2006; Valone et al., 1995). They provide refuge from predators, shelter from weather, and add another dimension of available habitat with entirely different microclimatic conditions. While many animals are attracted to the habitats prairie dogs and kangaroo rats create in grasslands, little is known about their combined impacts on other animals in areas where these rodents co-exist, and how the ecological roles of these generally similar species compare. In this study, we evaluate the comparative and interactive effects of prairie dogs and kangaroo rats on lizards.

Lizards are ectotherms that tend to have specific habitat requirements, largely determined by microhabitats for thermoregulation, accessibility of predator escape space, and food resource availability (Pianka, 1986). Soil texture, spatial heterogeneity, rodent burrow availability, and vegetation cover are known to be key factors for structuring desert lizard communities and species diversity (Pianka, 1966; Shenbrot et al., 1991). Therefore, the habitats that prairie dog and kangaroo rat mounds provide, the availability of burrows as refuges, and the high abundance of arthropods found in prairie dog and kangaroo rat burrows (Davidson and Lightfoot, 2007) may influence the structure of desert grassland lizard communities. Recent research has shown that black-tailed prairie dogs (*C. ludovicianus*) increase beta diversity of herpetofauna in shortgrass prairie systems (Shiple and Reading, 2006). Certain species prefer the open grassland habitat of prairie dog colonies, while others prefer uncolonized, denser grassland habitat (Shiple and Reading, 2006). Some lizard species also associate with the mounds of prairie dogs and kangaroo rats (Davis and Theimer, 2003; Hawkins and Nicoletto, 1992). Yet, what is known is based on a small number of studies in areas where prairie dogs and kangaroo rats occur alone (Davis and Theimer, 2003; Hawkins and Nicoletto, 1992; Kretzer and Cully, 2001; Shiple and Reading, 2006). Little is known about how the mound, burrow, and overall landscape conditions formed by the rodents impact lizards, and how the combined effects of these rodents interplay with lizard habitat use in areas where they co-occur. Our recent research in the northern Chihuahuan Desert where prairie dogs and banner-tailed kangaroo rats co-occur, demonstrated that they have distinctive effects on plants and arthropods and that their combined effects are additive and complementary (Davidson and Lightfoot, 2006, 2007, 2008), suggesting that they may have similar effects on lizard communities.

To understand how the roles of prairie dogs and kangaroo rats separately and together interact with other local, vertebrate taxonomic groups, we evaluated the impacts of Gunnison's prairie dogs (*C. gunnisoni*) and banner-tailed kangaroo rats on lizards in Chihuahuan Desert grassland. We hypothesized that mounds and burrows of the two rodent species would provide distinctive and important habitat for lizards, and given the results from our previous work, that they would have complementary, additive effects on the lizard community. To test this hypothesis, we focused on the association of lizards with prairie dog and kangaroo rat mounds in an area where the animals co-occurred, and conducted complementary research to understand how their combined activities affected lizards on the greater landscape.

2. Materials and methods

2.1. Study site

Our research was conducted at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA, 90 km south of Albuquerque, in Socorro County (NAD-27: 34° 24' N, 106° 36' W, 1600 m elevation). Long-term mean annual precipitation was 243 mm, about 60% of which occurred during the summer. Long-term mean monthly temperatures for January and July were 1.5 and 25.1 °C, respectively. Gunnison's prairie dogs colonized the study site in 1998, occurring within a 13 ha area during our study, and the site had been long inhabited by kangaroo rats. The area represents typical northern Chihuahuan Desert grassland with deep clayey loam soils, and burrograss (*Scleropogon brevifolius*), sand dropseed (*Sporobolus cryptandrus*), and black grama (*Bouteloua eriopoda*) as the dominant vegetation.

2.2. Mound-scale plots

To measure lizard species composition and abundance associated with mound disturbance patches, we established replicate mound-scale plots consisting of paired mound and non-mound control plots, a design similar to that used by Davidson and Lightfoot (2007), Hawkins and Nicoletto (1992), and others (Fig. B1). Mound-scale plots were located in areas occupied by: (1) both species of rodents (Pdog+Krat plot) and (2) only kangaroo rats (Krat plot) (Fig. B1). Mounds that were at least 10 m from other mounds of the same type were chosen in order to minimize impacts from adjacent mounds on the sampling points. Paired non-mound sampling points represented areas with minimal rodent disturbance (i.e., no rodent

mound), systematically positioned 10 m from each study mound. Measurements were taken from 20 prairie dog mounds and 20 kangaroo rat mounds on the Pdog+Krat plot, and around 20 kangaroo rat mounds on the Krat plot, as well as on paired non-mounds. Five-meter transects were located along the four cardinal directions centered on each mound.

2.3. Landscape-scale plots

While the focus of our study was on the mound-scale impacts of prairie dogs and kangaroo rats, we also established complementary landscape-scale plots to help us address effects of prairie dogs and kangaroo rats on lizard use of the greater landscape. Lizards were sampled on the Pdog+Krat and Krat landscape-scale plots. Each landscape plot was 180 m × 180 m with a 5 × 5 grid, and transects were separated by 30 m intervals (Fig. B1). Historic extermination of prairie dogs at what is now the SNWR was extensive, leaving most of the grasslands inhabited only by kangaroo rats, and making it impossible to locate replicate sites (study plots) occupied by both species, exclusively by prairie dogs, or by neither species.

2.4. Lizard Sampling

Sampling for lizards was conducted on the mound and landscape-scale study plots during the mid-morning hours when lizards tended to be most active and easily observed, and only on clear, sunny days with little or no wind. One person walked slowly along transect lines, recording the species of individual lizards observed, their initial location, and the end location of each lizard if it ran away from the observer. For mound-scale sampling, lizards were visually sampled along 5 m × 5 m strip transects running both north to south and east to west on each mound and non-mound plot. Lizards were identified to species, and their initial location and end location (on mound or in open grassland) within the 25 m² area around the mounds were recorded. Sampling occurred throughout the spring and summer (May–August) of 2000–2002, for a total of 17 sample periods, but kangaroo rat mounds and non-mounds were sampled on the Pdog+Krat plot only in late summer of 2001 and spring 2002. On the landscape-scale plots, lizards were visually sampled along 30 m × 3 m strip transects. Individuals were identified to species and their initial and end location (on mound or in open grassland) and the approximate distance they ran to mounds were recorded. Sampling occurred throughout the spring and summer (May–August) of 2000–2002, for a total of 17 sample periods.

2.5. Statistical analyses

Data were analyzed using non-parametric statistics due to the non-normal distribution of the data, and all analyses were performed using SAS version 8.2 (SAS Institute, 2001). Wilcoxon–Mann–Whitney tests were used to analyze differences in abundance of lizards between the Pdog+Krat and Krat plots, and between mound types within the Pdog+Krat plot. The landscape plots were not replicated, so interpretation of all results from these plots is limited to the differences between the two plots. Paired sign tests were used to compare lizard abundance patterns between the paired mound and non-mound plots. Mound-scale data were pooled when analyzing across sample periods ($n = 20$). Chi square tests were used to compare the frequency of lizards on the 25 m² mound plots observed: (1) on mounds and stayed on mounds; (2) on mounds that ran off mounds to open grassland; (3) in open grassland that ran to mounds; and (4) in open grasslands that stayed in open grassland.

3. Results

Six lizard species were observed during this study: New Mexico whiptail (*Aspidoscelis neomexicanus*), little striped whiptail (*Aspidoscelis inornatus*), collared lizard (*Crotaphytus collaris*), lesser earless lizard (*Holbrookia maculata*), pygmy short horned lizard (*Phrynosoma douglasii*), and round-tailed lizard (*Phrynosoma modestum*). However, the two whiptail species and the lesser earless lizard were the only species sufficiently abundant and conspicuous for conducting the line transect surveys, so our results focus on the associations of these lizards with the activities of prairie dogs and kangaroo rats. Additionally, during the breeding season (May) *A. inornatus* and *A. neomexicanus* were sometimes difficult to identify species because of similar body colors and patterns (Christiansen et al., 1971), in which case they were identified as *Aspidoscelis* sp.

3.1. Mound-scale plots

Lizard abundance was two and three times greater on prairie dog and kangaroo rat mounds, respectively, than lizard abundance off mounds (Sign-test: Prairie dog mounds $M = 6$, $P = 0.01$; Kangaroo rat mounds on Krat plot $M = 9$, $P < 0.0001$; Kangaroo rat mounds on Pdog+Krat plot $M = 6$, $P < 0.008$) (Fig. 1). More lizards associated with the kangaroo rat mounds ($n = 81$) compared to the prairie dog mounds ($n = 56$) on the Pdog+Krat plot (during late summer 2001 and spring 2002, only), although differences were not significant ($P < 0.05$) for all sample periods (Fig. 1). The three dominant lizard species were 2–4 times more abundant on kangaroo rat mounds on the Krat plot ($P < 0.002$, for all tests). On the Pdog+Krat plot, however, while all three species were consistently more abundant on both the kangaroo rat and prairie dog mounds,

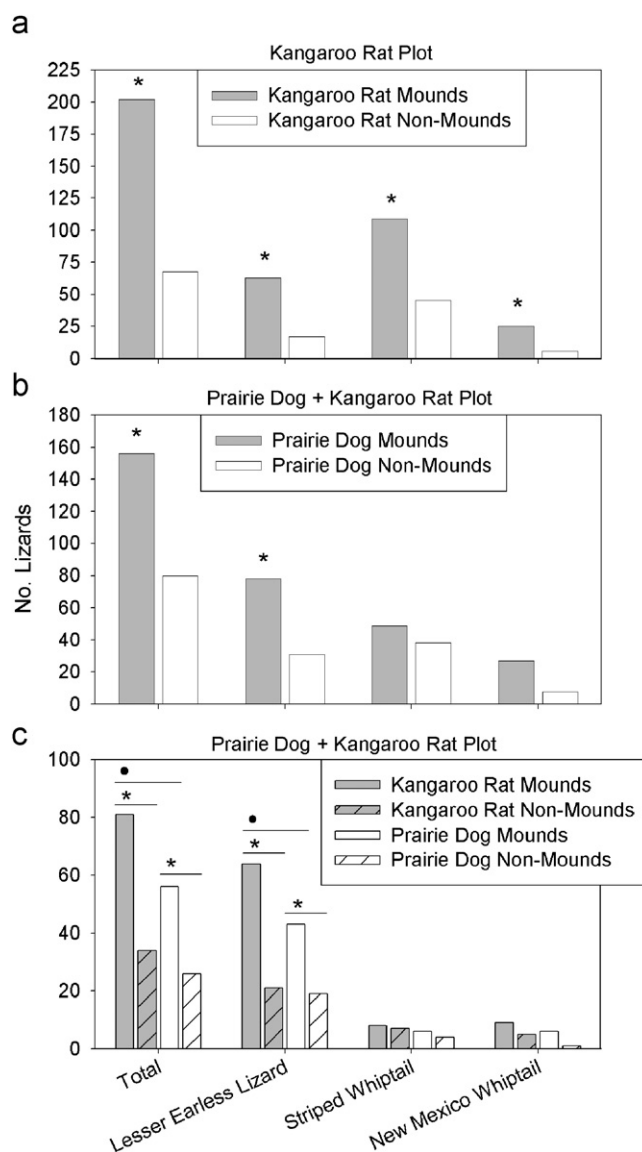


Fig. 1. Total number of the lesser earless lizard, little striped whiptail, New Mexico whiptail, and all three lizard species combined on (a) kangaroo rat mounds and paired non-mounds on the kangaroo rat plot from 2000 to 2002, (b) prairie dog mounds and paired non-mounds on the prairie dog plot from 2000 to 2002, and (c) both rodent mounds and paired non-mounds on the prairie dog+kangaroo rat plot from 2001 to 2002. * $P < 0.05$ over all sample periods. • $P < 0.05$ during one or more sample periods.

only the lesser earless lizard was statistically (2–3 times) more abundant on the mounds (Sign-test: Prairie dog mounds $M = -5.5$, $P = 0.01$, Kangaroo rat mounds $M = -6$, $P = 0.0042$). The lesser earless lizard was consistently more common on the kangaroo rat mounds compared to prairie dog mounds, although differences were not significant for all sample periods (Fig. 1).

Lizard behavior demonstrated strong use of the mounds for protection and habitat (Figs. 2 and C1). Of those lizards found initially on kangaroo rat mounds (on the Krat plot), 90% of them stayed on the mounds, while only 10% ran off. Of those lizards initially observed off the mounds in the open grassland, 100% of them ran onto the kangaroo rat mounds (chi square test: $\chi^2 = 7.3$, $P = 0.007$). Similar patterns were observed for lizards associated with the kangaroo rat mounds on the Pdog+Krat plot with 97% of those on mounds staying on mounds, and only 3% running off. However, of the lizards found off the kangaroo rat mounds on the Pdog+Krat plot, slightly fewer of them ran onto the mounds (68%) and relatively more of them stayed in the off mound areas (32%) compared to those on the Krat plot (chi square test: $\chi^2 = 11.86$, $P = 0.0006$). Of the lizards found initially on prairie dog mounds, 77% stayed on the mounds, while 23% ran into the open grassland. Of those found off the prairie dog mounds in the open grassland, 45% of them ran onto the mounds, while the rest stayed in the open grassland (chi square test: $\chi^2 = 11.06$, $P = 0.0009$).

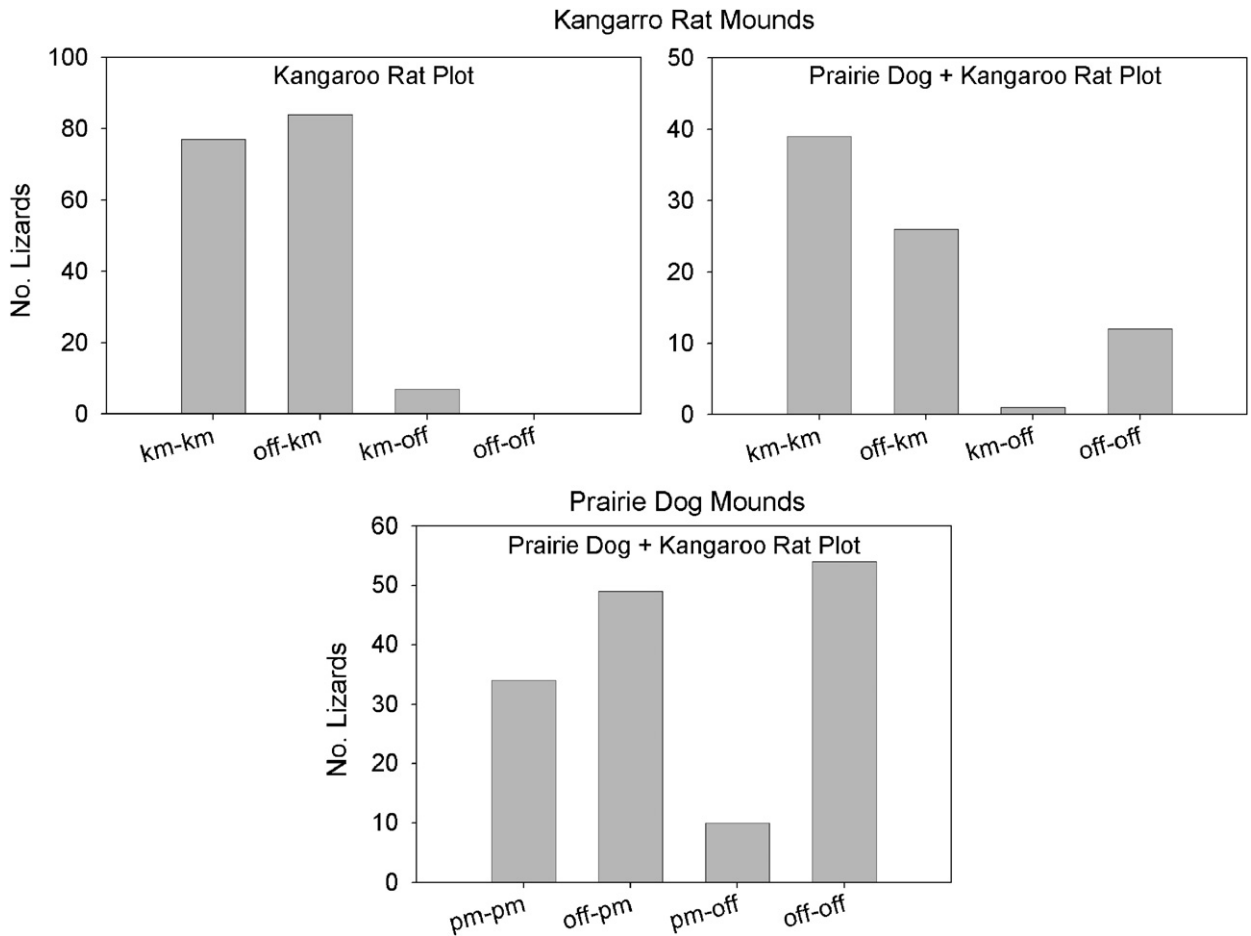


Fig. 2. The start and end location of lizards sampled within the 25 m² area around the mounds on the prairie dog+kangaroo rat and the kangaroo rat plots. Locations are indicated according to whether lizards were first spotted on a kangaroo rat mound (km), prairie dog mound (pm), or non-mound area (off), and then where they ran to, or if they remained at the same location (km, pm, or off) after being approached (e.g., lizard first spotted on kangaroo rat mound and then ran off mound: km-off).

3.2. Landscape-scale plots

Lizard abundance was two-fold greater on the Pdog+Krat plot than the Krat plot (Wilcoxon: $W_{42} = 1409.5$, $P < 0.001$) (Fig. 3). The whiptail species together were more abundant on the Pdog+Krat plot than the Krat plot (Wilcoxon: $W_{42} = 1564$, $P = 0.048$). Most of this difference was due to the New Mexico whiptail species, which was ca. 4 times more abundant on the Pdog+Krat plot (Wilcoxon: $W_{42} = 1464.5$, $P = 0.0012$), while the little striped whiptail showed no difference in abundance between the landscape plots. The lesser earless lizard showed the most striking difference, being almost 7-times more common on the Pdog+Krat plot than the Krat plot (Wilcoxon: $W_{42} = 1299.5$, $P < 0.0001$). All three lizard species commonly ran 1–5 m from open grassland to prairie dog and kangaroo rat mounds, and many ran up to 10 and even 20 m (Fig. 4).

4. Discussion

Our results demonstrate that both prairie dogs and kangaroo rats provided important habitats for lizards. The combination of two structurally different types of rodent mounds and burrows, and the overall increased numbers of rodent mounds provided not only more open soil and burrow habitats on the grassland landscape, but also an architecturally more diverse environment for lizards. The distinctive spatial distributions and densities of prairie dog and kangaroo rat mounds on the landscape differentially affected lizard abundance and behavior, resulting in a 2-fold increase in lizard abundance where prairie dogs and kangaroo rats co-occurred.

Lizard abundance on both prairie dog and kangaroo rat mounds was impressively 2- to 4-fold higher than lizard abundance in the surrounding grassland. The strong association of lizards with the mounds of both prairie dogs and

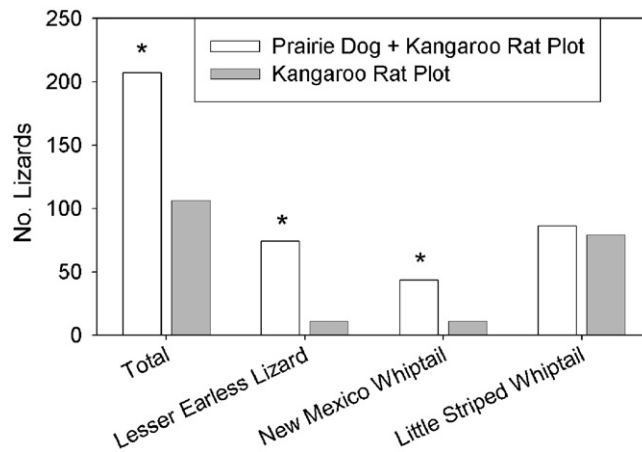


Fig. 3. Total number of lizards per 1 m × 30 m area on the prairie dog+kangaroo rat and kangaroo rat plots from spring 2000 to late summer 2002. * $P < 0.05$ over all sample periods.

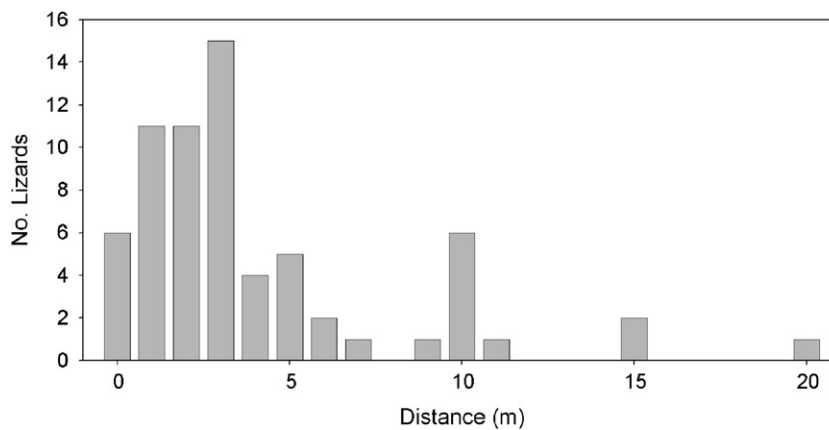


Fig. 4. Distance lizards traveled to reach prairie dog and kangaroo rat mounds.

kangaroo rats appeared to be in large part because mounds provided important escape space from predators, as demonstrated by the large percentages of lizards that ran to the mounds and often also into the burrows when approached by a human observer (Figs. 2 and C1). Some individuals ran up to 20 m to reach a mound. Davis and Theimer (2003) also found that lesser earless lizard abundance was correlated with Gunnison's prairie dog mound density and that burrows were used as refuge from predators. The landscape of fear concept (Laundre et al., 2001; Ripple and Beschta, 2004) postulates that the presence of predators can affect resource and habitat use by prey species. The lizards that we observed clearly were utilizing both prairie dog and kangaroo rat mounds and associated burrow entrances to escape from us, and apparently also to escape from natural predators such as hawks, burrowing owls, coyotes, foxes, and others. Therefore, prairie dog and kangaroo rat mounds and burrows appear to be providing key habitat and escape refugia from predators, and, by doing so, they are changing lizard behavior, use of the landscape, and likely increasing their overall abundance and survivorship.

Although all three species of lizards in our study showed an association with the mounds, the lesser earless lizards associated most strongly with the mounds. The mounds provided open habitat for basking, which the lizards, especially the lesser earless lizards, were commonly observed doing when spotted on mounds (Fig. C1). The burrows of both prairie dog and kangaroo rat mounds also provide cool, moist microclimates and harbor large numbers of arthropods, the lizards' principle prey (Davidson and Lightfoot, 2007; Kay and Whitford, 1978), so the lizards may also have associated strongly with the mound habitats for temperature regulation and the abundance of prey. Indeed, others have shown that rodent burrows are used as thermal and escape refugia and the mounds as basking sites for lizards (Cooper, 2000; Davis and Theimer, 2003).

Lizards associated more strongly with kangaroo rat mounds than prairie dog mounds, but were 2-times more abundant on the landscape with prairie dogs than where only kangaroo rats occurred. Kangaroo rat mounds are much larger, being 3–5 m in diameter, compared to prairie dog mounds that are generally 1–2 m in diameter (Best, 1988; Hoogland, 1995). These larger mounds honeycombed with numerous escape tunnels likely provided the lizards with an increased surface

area that could support a greater number of lizards compared to the smaller prairie dog mounds. However, prairie dog burrows were far more numerous on the landscape, at 30 mounds per ha compared to five kangaroo rat mounds per ha at our study site (Davidson and Lightfoot, 2008). The greater density of prairie dog mounds provided a contiguous network of basking sites for thermoregulation, foraging locations, and refuges for lizards across the landscape, likely resulting in more favorable habitat and higher survivorship at the landscape-scale. These findings are consistent with others that have found lizard abundance correlated with the availability of rodent burrows (Davis and Theimer, 2003; Shenbrot et al., 1991).

Differences in the structure of vegetation on the different landscape patches occupied by prairie dogs and kangaroo rats likely influenced lizard species abundance and distribution. The landscape where both prairie dogs and kangaroo rats co-occurred was much more open, with greater soil disturbance and lower vegetation height and cover compared to where only kangaroo rats occurred, largely resulting from prairie dog grazing and the abundance of mounds by both species (Davidson and Lightfoot, 2008). New Mexican whiptails and especially lesser earless lizards prefer such open, more disturbed grassland habitat (Christiansen et al., 1971; Degenhardt et al., 1996), and were four and seven times more abundant, respectively, on the prairie dog colony where both rodents co-occurred. Lesser earless lizards consistently have been found in strong association with prairie dog colonies (Davis and Theimer, 2003; Kretzer and Cully, 2001; Shipley and Reading, 2006). In contrast, the little striped whiptail prefers denser grassland habitat (Christiansen et al., 1971), and did not differ in abundance between the two landscape patches. Interestingly, however, all three lizard species strongly associated with the kangaroo rat mounds in the denser grassland habitat where only kangaroo rats occurred, but on the prairie dog colony, only the lesser earless lizard strongly associated with the kangaroo rat mounds. Further, the kangaroo rat mounds on the prairie dog colony had two times more lizards than those on the kangaroo rat site. These patterns demonstrate: (1) that the surrounding habitat matrix and density of mounds play an important role in structuring lizard communities, in addition to the individual mound and burrow complexes, and (2) that the engineering impacts from both rodent species occurring together produce compounding interactions between the rodents and the lizard community.

The varied spatial distributions and densities of the prairie dog and kangaroo rat mounds had differential effects on lizards. Consistent with our findings on plant and arthropod community structure from the same and different study sites (Davidson and Lightfoot, 2007, 2008), the overall pattern here was that kangaroo rats created larger, more localized disturbance patches on the landscape, while prairie dog disturbances were more widespread. So while both prairie dog and kangaroo rat mounds support greater numbers of arthropods, lizards, and certain plants, compared to the surrounding grassland, those numbers were typically higher on kangaroo rat mounds than prairie dog mounds (Davidson and Lightfoot, 2007, 2008). However, the overall prairie dog colony where both animals co-occurred had greater numbers of those same plants, arthropods, and lizards that associate with the mound disturbance patches compared to areas where only kangaroo rats occurred (Davidson and Lightfoot, 2007, 2008).

Such differences in the kinds of habitats that prairie dogs and kangaroo rats create translate into more heterogeneous landscapes and increased biodiversity where the animals co-occur, as also demonstrated by our work on plants and arthropods (Davidson and Lightfoot, 2006, 2007). Although we were not able to evaluate patterns in species composition and richness since we only studied three species of lizards (out of a community of six species), the abundances and behaviors of the lizard species did differ between the different mound types and between the landscape patches, demonstrating that prairie dogs and kangaroo rats individually and collectively offer unique resources to lizard communities. Further, similar to our results with Gunnison's prairie dogs, others have found that different assemblages of herpetofauna are found on black-tailed prairie dog (*C. ludovicianus*) colonies compared to off colony areas, resulting in increased biodiversity on the greater grassland landscape (Shipley and Reading, 2006).

Burrowing mammals are important ecosystem engineers of grasslands throughout the world (Whitford and Kay, 1999; Wright et al., 2006). Our research provides insights into how these animals create important habitats for species at multiple taxonomic levels, and demonstrates that engineering species play non-replaceable roles in these systems (see also Davidson and Lightfoot, 2006, 2007, 2008). Additionally, we have shown that burrowing rodents increase habitat heterogeneity for lizards, and have additive, complementary effects where they co-occur. Burrowing activities also are known to alter soil properties and nutrient cycling, and many burrowing rodents are key prey for predators (Kotliar et al., 2006; Valone and Brown, 1995; Whitford and Kay, 1999). Yet, much remains to be explored, as most of the research on the roles of burrowing mammals is limited to studies of only a few species, especially of those in North American grasslands. Many burrowing species in grasslands around the world have experienced drastic declines due to habitat loss, over-hunting, and control efforts to reduce their competition with domestic livestock. The loss of these burrowing mammals from grasslands may have cascading effects throughout the entire system, as has been demonstrated by the decline of some of the better-studied species, such as prairie dogs and kangaroo rats (Brown and Heske, 1990; Kotliar et al., 2006; Miller et al., 1994; Whitford, 1997). Given the transformative effects and often keystone roles that these animals play in grasslands, there is a great need to better understand their ecological impacts on both the surrounding landscape and the biota that may depend on them.

Acknowledgements

We thank Patrick Jantz for assistance with fieldwork, and E. Bedrick for valuable statistical advice. Marcus Hamilton provided helpful comments on a previous version of this manuscript. This research was supported by the National Science Foundation Grants DEB-9411976, DEB-0080529, DEB-0217774, and is Publication no. 430 of the Sevilleta LTER.

Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2008.07.006

References

- Bangert, R.K., Slobodchikoff, C.N., 2006. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* 67, 100–115.
- Best, T.L., 1988. *Dipodomys spectabilis*. *Mammalian Species* 311, 1–10.
- Branch, L.C., Hierro, J.L., Villarreal, D., 1999. Patterns of plant species diversity following local extinction of the plains vizcacha in semi-arid scrub. *Journal of Arid Environments* 41, 173–182.
- Brown, J.H., Heske, E.J., 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250, 1705–1707.
- Ceballos, G., Pacheco, J., List, R., 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* 41, 161–172.
- Christiansen, J.L., Degenhardt, W.G., White, J.E., 1971. Habitat preferences of *Cnemidophorus inornatus* and *C. neomexicanus* with reference to conditions contributing to their hybridization. *Copeia* 1971, 357–359.
- Cooper, W.E.J., 2000. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* 137, 1299–1315.
- Davidson, A.D., Lightfoot, D.C., 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29, 755–756.
- Davidson, A.D., Lightfoot, D.C., 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* 30, 515–525.
- Davidson, A.D., Lightfoot, D.C., 2008. Burrowing rodents increase landscape heterogeneity in a Desert Grassland. *Journal of Arid Environments* 72, 1133–1145.
- Davis, J.R., Theimer, C., 2003. Increased lesser earless lizard (*Holbrookia maculata*) abundance on Gunnison's prairie dog colonies and short term responses to artificial prairie dog burrows. *American Midland Naturalist* 150, 282–290.
- Degenhardt, W.G., Painter, C.W., Price, A.H., 1996. *Amphibians and Reptiles of New Mexico*. University of New Mexico Press, Albuquerque.
- Guo, Q., 1996. Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia* 106, 247–256.
- Hawkins, L.K., Nicoletto, P.F., 1992. Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a Semiarid Grassland. *Journal of Arid Environments* 23, 199–208.
- Hoogland, J.L., 1995. *The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal*. University of Chicago Press, Chicago.
- Huntly, N., Inouye, R., 1988. Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38, 786–793.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Kay, F.R., Whitford, W.G., 1978. The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in Southcentral New Mexico. *American Midland Naturalist* 24, 177–192.
- Kotliar, N.B., Baker, B.W., Whicker, A.D., 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24, 177–192.
- Kotliar, N.B., Miller, B.J., Reading, R.P., Clark, T.W., 2006. The prairie dog as a keystone species. In: Hoogland, J.L. (Ed.), *Conservation of the Black-Tailed Prairie Dog: Saving North America's Western Grasslands*. Island Press, Washington, DC, pp. 53–64.
- Kretzer, J.E., Cully Jr., J.F., 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. *Southwestern Naturalist* 46, 171–177.
- Laundre, J.W., Hernandez, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park. *USA Canadian Journal of Zoology* 79, 1401–1409.
- Lomolino, M.V., Smith, G.A., 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Biological Conservation* 115, 89–100.
- Miller, B., Ceballos, G., Reading, R., 1994. The prairie dog and biotic diversity. *Conservation Biology* 8, 677–681.
- Mun, H.T., Whitford, W.G., 1990. Factors affecting annual plants assemblages on banner-tailed kangaroo rat mounds. *Journal of Arid Environments* 18, 165–173.
- Pianka, E.R., 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47, 155–159.
- Pianka, E.R., 1986. *Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton.
- Pringle, R.M., 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* 89, 26–33.
- Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 54, 755–766.
- SAS Institute, 2001. *SAS System for Microsoft Windows*. SAS Institute Inc., Cary, North Carolina.
- Shenbrot, G.I., Rogovin, K.A., Surkov, A.V., 1991. Comparative analysis of spatial organization of desert lizard communities in Middle Asia and Mexico. *Oikos* 61, 157–168.
- ShIPLEY, B.K., Reading, R.P., 2006. A comparison of herpetofauna and small mammal diversity on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and non-colonized Grasslands in Colorado. *Journal of Arid Environments* 66, 27–41.
- Valone, T.J., Brown, J.H., 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science* 267, 880–883.
- Valone, T.J., Brown, J.H., Jacobi, C.L., 1995. Catastrophic decline of a desert rodent, *Dipodomys spectabilis*: insights from a long-term study. *Journal of Mammalogy* 76, 428–436.
- Van Staalduijn, M.A., Werger, M.J.A., 2007. Marmot disturbances in a Mongolian steppe vegetation. *Journal of Arid Environments* 69, 344–351.
- Whicker, A.D., Detling, J.K., 1988. Ecological consequences of prairie dog disturbances: prairie dogs alter grassland patch structure, nutrient cycling, and feeding-site selection by other herbivores. *Bioscience* 38, 778–785.
- Whitford, W.G., 1997. Desertification and animal biodiversity in the desert grasslands of North America. *Journal of Arid Environments* 37, 709–720.
- Whitford, W.G., Kay, F.R., 1999. Bioperturbation by mammals in deserts: a review. *Journal of Arid Environments* 41, 203–230.
- Wright, J.P., Jones, C., 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience* 56.
- Wright, J.P., Jones, C.G., Boeken, B., Shachak, M., 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology* 94, 815–824.
- Zhang, Y., Zhang, Z., Liu, J., 2003. Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mammal Review* 33, 284–294.