Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert

Edward J. Heske*, James H. Brown, Qinfeng Guo

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

Received: 27 November 1991 / Accepted: 19 April 1993

Abstract. Long-term (1977–90) experimental exclusion of three species of kangaroo rats from study plots in the Chihuahuan Desert resulted in significant increases in abundance of a tall annual grass (Aristida adscensionis) and a perennial bunch grass (Eragrostis lehmanniana). This change in the vegetative cover affected use of these plots by several other rodent species and by foraging birds. The mechanism producing this change probably involves a combination of decreased soil disturbance and reduced predation on large-sized seeds when kangaroo rats are absent. Species diversity of summer annual dicots was greater on plots where kangaroo rats were present, as predicted by keystone predator models. However, it is not clear whether this was caused directly by activities of the kangaroo rats or indirectly as a consequence of the increase in grass cover. No experimental effect on species diversity of winter annual dicots was detected. Our study site was located in a natural transition between desert scrub and grassland, where abiotic conditions and the effects of organisms may be particularly influential in determining the structure and composition of vegetation. Under these conditions kangaroo rats have a dramatic effect on plant cover and species composition.

Key words: Keystone species – Dipodomys – Plant-animal interactions – Chihuahuan Desert – Species diversity

Not only do abiotic conditions and vegetation affect the animal species present in an area, but certain animal species in turn may greatly influence the biogeochemical processes that determine the characteristics of the habitat and the composition of the plant and animal species that occupy it (e.g., Naiman 1988). In some cases, biotic interactions of certain animal species can have effects that cascade throughout the trophic web, drastically changing community structure. In other cases, physical activities (soil movement, dam building, etc.) of animals can affect basic ecosystem processes and alter whole landscapes (Estes and Palmisano 1974; Carpenter et al. 1985; Castilla and Duran 1985; Carpenter and Kitchell 1988; Huntley and Inouye 1988; Naiman et al. 1988; Pastor et al. 1988). Species whose presence or absence dramatically alter the structure and dynamics of ecological systems are known as "keystone species" (Paine 1966).

Rodents can have significant effects on species diversity and abundance of the plant community (e.g., Huntly and Inouye 1988; Whickler and Detling 1988; Martinsen et al. 1990; Swihart 1991). These effects may be a direct result of consumption of plants by rodents, or an indirect consequence of physical disturbance due to rodent activity.

In this paper, we examine the effects of kangaroo rat (genus Dipodomys) exclusion from replicated study plots in the Chihuahuan Desert, southeastern Arizona, USA on vegetative structure and especially on grass cover. A brief description of these effects appears in Brown and Heske (1990). We also examine the effects of kangaroo rat exclusion on species diversity of grasses and of summer and winter ephemeral dicots. Kangaroo rats are predators on the seeds of flowering plants, and decreased diversity among competing prey species when keystone predators are removed is predicted by some models (Paine 1966; Caswell 1978; Vance 1978; Dayton 1984). Decreased species diversity in herbaceous plants could also be caused if the decreased soil disturbance owing to the absence of burrowing and surface activity by kangaroo rats reduced the spatial heterogeneity that promotes the persistence of "fugitive" species (sensu Hutchinson 1951; Connell 1978).

Materials and methods

Study site and experimental treatments

The study was conducted on the Cave Creek Bajada, 6.5 km east and 2 km north of Portal, Cochise County, AZ USA (elevation
1330 m). The habitat is upper elevation Chihuahuan Desert scrub (Brown 1982), and varies from open areas dominated by widely spaced shrubs (primarily *Flourensia cernua*, *Ephedra trifurca*, *Lycium torreyi*, and *Prosopis glandulosa*) to dense stands of arborescent shrubs (primarily *Acacia greggi*, *Acacia neovernicosa*, and *P. glandulosa*) along the usually dry watercourses that dissect the study site in several places. A small-statured, relatively short-lived perennial shrub, *Gutierrezia sarothrae*, is common throughout the area. The soil is a mixture of alluvial boulders mixed with and overlaid by finer particles. The entire 20-ha study site has been enclosed since July 1977 with a barbed-wire fence to exclude livestock.

Annual precipitation (approximately 35 cm) at this site is distributed bimodally. A winter rainy season occurs from approximately December through March, followed by a late spring-early summer drought. A summer monsoon season, accounting for approximately two-thirds of the annual total rainfall, begins in July and continues through early September. As a result of this pattern, there are two flushes of annual and short-lived perennial plants. One group of species flowers in late spring; another, which includes most of the species of grasses at our site, flowers in the summer and early fall (Davidson et al. 1985; Samson et al. 1992).

Within the livestock enclosure arc 24 total plots, each enclosed by a fence of fine wire mesh topped with 15 cm of aluminum flashing. The fences contain holes of different sizes at ground level that provide access to selected plots by rodents of different species. Manipulations of the granivore community, consisting of removal of some or all rodent and ant species in a 2 by 2 factorial design, were initiated in September 1977; details of the enclosure design and experimental manipulations have been described elsewhere (Munger and Brown 1981; Brown and Munger 1985; Davidson et al. 1985).

Eight plots were initially assigned to four seed (millet) addition treatments, but the effects of these treatments on the rodent, ant, or plant communities at this site were not significant (Brown and Munger 1985; Davidson et al. 1985; Guo and Brown unpublished), and seed additions were discontinued in 1985. Subsequent attempts to manipulate annual plant densities on some of these plots by selective application of an herbicide in 1986–1987 were ineffective (Samson et al. 1992). These previous treatments had no detectable effects on the plant measures used in this study (Hesk et al. unpublished data). In January 1988, the eight seed addition plots were reassigned as new replicates of the rodent and ant removal experiments (Hesk et al. in press). When the present study was conducted, in September 1989, we could detect no consistent differences between these plots and unmanipulated controls [previous studies found that rodent or ant removal has substantial effects on the annual plant community, but only after several years (Inouye et al. 1980; Brown et al. 1986)].

Despite these shortcomings in our analysis, greatly increased the power of our tests (there were only two completely unmanipulated plots), these eight former seed addition plots were grouped with unmanipulated plots as “controls.”

**Data collection and statistical analyses**

Numbers of annual and short-lived perennial ephemeral plants were censused each spring and fall on a fixed grid of 16 0.25-m² quadrats on each plot (Samson et al. 1992). From 4 to 16 September 1989, additional measurements were taken to better characterize the plant community, particularly grass species composition and cover. All plant species (or bare ground) were counted at 10-cm intervals (point-intercept method) along eight transect lines associated with each plot. Four transects began 8 m from the center of each plot and ran outward toward each corner. Four additional transects continued for another 25 m immediately outside of each plot after a gap of 2 m from the fence.

The effect of rodent and ant removals on the abundance of grasses and other plant groups was determined by analysis of variance (ANOVA), using summed data from the four transects within each plot to avoid pseudoreplication (Hurlbert 1984). When other significant differences between treatments were found,
grass" for analysis by ANOVA. Shrubs and “half-shrubs” (Gutierrezia, Haplopappus, and Zinnia) were also considered general categories.

Four measures of species diversity or abundance were calculated for both summer and winter annual and perennial ephemeral dicots on each plot, using data from the ephemeral plant censuses: 1) mean number of individuals per sample quadrat, 2) mean number of species per sample quadrat, 3) mean species diversity per sample quadrat (Shannon-Weaver H, see Ludwig and Reynolds 1988), and 4) mean species evenness per sample quadrat (J, see Ludwig and Reynolds 1988). For the summer ephemeral dicots, we used data from the 1990 summer census, which was conducted at the same time as the grass transects. The amount of rainfall in the winter of 1989–90 was the lowest recorded at our site during the 12 years of the study, and the number of ephemeral plants counted the following spring was the lowest in any spring census (including zero values for many quadrats); we therefore used data from the 1989 spring census (instead of 1990) to measure diversity of the winter ephemerals. Because the sample quadrats used in the ephemeral plant censuses did not contain sufficient numbers of individuals to provide good estimates of the abundances of many grasses, particularly the perennial bunch grasses, data from the within-plot line transects were used to calculate the four diversity indices for grasses. ANOVA was then used to determine differences between treatments in these values, with sample quadrats or transects nested within plots.

Results

Rodent exclusion treatments and controls showed significant differences in the relative cover of several annual grasses (Aristida adscensionis, Bouteloua aristidoides, B. barbata) and one perennial bunch grass (Poa lehmanniana) (all P-values < 0.05). No significant differences due to ant removal treatments were detected in any vegetation category; ant removal treatments were therefore lumped with controls or appropriate rodent exclusion treatments in subsequent analyses.

Pairwise Tukey’s Studentized Range Tests indicated that the four kangaroo rat exclusion plots and the four total rodent exclusion plots did not differ significantly in any vegetation category, but one or both treatments differed from the 14 plots with kangaroo rats present in the vegetation categories noted above, and always in the same direction. The two banner-tailed kangaroo rat exclusion plots were intermediate between these two groups in many vegetative categories and will not be considered further. Subsequent analysis therefore compared vegetative characteristics between two groups: eight plots where kangaroo rats were absent and 14 plots where they were present.

Comparisons of vegetative cover on transects inside and outside of plots where kangaroo rats were present and absent are shown in Fig. 1. The perennial bunch grass, E. lehmanniana, and a tall annual grass, A. adscensionis, were significantly more abundant inside than outside of plots where kangaroo rats were excluded, but these species were equally abundant inside or outside of plots where kangaroo rats were present. In contrast, two short-statured annual grasses, B. aristidoides and B. barbata, were relatively more abundant outside than inside the kangaroo rat exclusion plots. B. aristidoides was also more abundant outside than inside plots where kangaroo rats were present, but the difference was much less pronounced.

Half-shrubs were more abundant outside than inside of all plots. Gutierrezia is known to be relatively impalatable and to increase when grazing is intense (Stoddard and Smith 1975). We suggest that differential herbivory by larger mammals such as jackrabbits and javelina, which are partially or completely excluded by the fences surrounding the plots, may be responsible for this fence effect.

Differences in plant species diversity associated with kangaroo rat activity were detected only for summer annual dicots, which were significantly more abundant and diverse on plots where kangaroo rats were present (Fig. 2). Abundance of summer short-lived ephemeral perennial dicots did not differ significantly among treatments, but the small number of species limits the power of this analysis. Summer grasses were more abundant but not
more diverse in species on exclusion plots. Similarly, winter ephemeral plants were more abundant but not more diverse in species on kangaroo rat exclusion plots (Fig. 2). Differences between treatments for winter annual dicots, grasses, and short-lived perennial dicots could not be compared because of the small sample sizes in the latter two groups (only 1 grass and 3 perennials).

Discussion

At our study site, three species of kangaroo rats composed a keystone rodent guild whose activity had significant effects on both the physical structure of the plant community and its species diversity. In the absence of kangaroo rats, grass cover increased, primarily as a result of increased density of the introduced bunchgrass *Eragrostis lehmanniana* and the native tall annual *Aristida adscensionis* (see also Samson et al. 1992). This produced an obvious change in the vegetative structure on these plots, which was reflected in the increased use of these plots by several species of grassland-prefering rodents (*Sigmodon hispidus*, *S. fulviventris*, *Baiomys taylori*, and *Reithrodontomys spp.*; Brown and Heske 1990, Heske et al., in press) and decreased use by seed-foraging birds (Thompson et al. 1991). The similarity in response by vegetation on kangaroo rat and total rodent exclusion plots indicates that other species of small rodents at our site did not compensate for the absence of kangaroo rats.

The mechanisms producing this shift in grass cover are uncertain. Kangaroo rats are both seed predators and a major cause of small-scale physical disturbance in this environment. The seeds of *A. adscensionis* are relatively large (Samson et al. 1992) and commonly found in kangaroo rat cheek pouches (Heske, personal observation); thus, reduced seed predation may contribute to its increase on exclusion plots. However, the seeds of *E. lehmanniana* are tiny and probably not a preferred food item. During their burrowing, foraging, and food catching activities, kangaroo rats turn over a large amount of soil and create numerous shallow pits and small mounds. Decreased soil disturbance can be a factor promoting the success of perennial grasses (Martinsen et al. 1990).

Kangaroo rats can affect the relative abundances of many species of annual dicots (Inouye et al. 1980; Davidson et al. 1985; Brown et al. 1986; Samson et al. 1992), but their overall impact on species diversity has not been measured. Because kangaroo rats apparently prey selectively on competitively dominant (large-seeded) species, we expected plant species diversity to be higher on the plots where kangaroo rats were present than on those where they were excluded (Paine 1966). This prediction was upheld only for summer annual dicots (Fig. 2); the number of individuals, the number of species, and two diversity indices (H and J) were all significantly higher per 0.25 m² sample quadrat on plots where kangaroo rats were present than on kangaroo rat exclusion plots. In contrast, summer grasses and winter dicots were more abundant in the absence of kangaroo rats (see also Davidson et al. 1985).

Because the effects of differential seed predation by kangaroo rats on the relative abundances of large-versus small-seeded plants have been well-documented in the winter annual community at our site, our inability to detect an effect on species diversity in this group was surprising. Our analysis of diversity was based only on numbers of species; however, and did not consider changes in either the identities or rank order of those species. Samson et al. (1992) have shown that several species of winter ephemerals increased in abundance in the absence of kangaroo rats, whereas others decreased; these changes in relative abundance may have balanced each other in our calculations of H and J. It is uncertain whether continued decreases in certain small-seeded species due to competition with large-seeded species will result in their local extinction. After 12 years of kangaroo rat exclusion, however, we did not detect a net loss of diversity.

The lack of a treatment effect on the diversity of winter annual dicots makes us question the mechanism resulting in higher diversity on control plots for the summer annual dicots, especially since summer dicots are generally small-seeded and the evidence for differential seed predation by kangaroo rats is much less clear (Samson et al. 1992). An alternative hypothesis is that the abundance and species diversity of the summer annual dicots was only indirectly affected by the presence of kangaroo rats, through the direct effects of kangaroo rat activity on the summer grasses. Numerical responses of the summer grasses to the experimental treatments were opposite in direction from those of the summer annual dicots, suggesting a competitive interaction. Further, only a few species of winter grasses occur at our site, and these are uncommon; no similar effect is thus expected in the winter plant community.

Our study site lies in a natural transition zone between Chihuahuan Desert scrub and grassland habitat, so the composition of local vegetation may be sensitive to small shifts in abiotic and biotic conditions. Similar manipulations in other desert habitats may not produce as strong a response (but see Norris 1950). Finally, our results show that at this site the presence or absence of kangaroo rats had dramatic effects on the structure and composition of vegetation, whereas the presence or absence of livestock grazing has much less influence. Heske and Campbell (1991, substantiated by more recent results of Guo and Valone, unpublished) found no significant differences in vegetative cover inside and outside of the livestock fence surrounding the entire study site. While it is important to emphasize that the kangaroo rat effects were observed only where livestock has also been excluded, these results show that large grazing mammals are not the only animals that can profoundly influence the vegetation in the arid habitats of southwestern North America.

Acknowledgements. We thank L. Valle, P.M. Mazzolini, and K. Ernest for help in the data collection, and S. Mistry for help with the statistical analyses. J. Brown and S. Robinson made helpful comments on an earlier draft of the manuscript. This research was supported by National Science Foundation Grant BSR-8718139 to JHB.

References

Castilla JC, Duran LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on Concholepas concholepas (Gastropoda). Oikos 45: 391–399
Norris JJ (1950) Effect of rodents, rabbits, and cattle on two vegetation types in semidesert range land. Bull 353 Agr Exp Sta New Mexico College of Agriculture and Mechanical Arts, Las Cruces