

Can kangaroo rat graminivory contribute to the persistence of desertified shrublands?

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ABSTRACT

Medium-sized kangaroo rats (*Dipodomys* spp. Gray) function as keystone species in the dynamics of desert bunchgrasses. We tested the hypothesis that kangaroo rat graminivory leads to reduced grass growth and inflorescence production, and that kangaroo rat grass consumption reflects their preferences for open microhabitats. We excluded kangaroo rats from grasses, and measured tiller loss, leaf and tiller growth and inflorescence production. We recorded the extent of tiller loss in grasses varying in tussock size or the extent of surrounding cover. Consumption of tillers by kangaroo rats was extensive, peaking in late summer. Grasses protected from kangaroo rat graminivory showed elevated leaf and tiller growth and inflorescence production. Grass tussocks protected by surrounding vegetation or large grass tussocks suffered lower graminivory than tussocks in the open or small tussocks. Our data demonstrate that the mechanism of the keystone role of kangaroo rats is through direct graminivory. We hypothesize that kangaroo rat graminivory may contribute to the persistence of desertified shrublands by limiting grass recruitment and abundance. Medium-sized kangaroo rats prefer open microhabitats and increase in abundance as such microhabitats increase, suggesting a positive feedback, with kangaroo rats increasing in abundance in overgrazed, desertified landscapes, and then contributing to their persistence through graminivory.

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1. Introduction

Medium-sized kangaroo rats (*Dipodomys merriami* Mearns and *Dipodomys ordii* Woodhouse) are keystone species in the dynamics of North American desert bunchgrasses. When these kangaroo rats are excluded from desert grasslands, grasses increase in abundance (Norris, 1950; Brown and Heske, 1990; Heske et al., 1993). This finding is highly relevant to understanding the dynamics and the management of North American desert grasslands that are undergoing, or have undergone, extensive desertification, apparently as a result of overgrazing by domestic livestock (Hastings and Turner, 1965; Frederickson et al., 1998; Kerley and Whitford, 2000). Brown and Heske (1990) speculated that granivory or soil disturbance by kangaroo rats could be the mechanism whereby kangaroo rats suppress grasses. However, experimental evidence confirms that direct herbivory of the grasses (graminivory) is the mechanism

involved (Kerley et al., 1997). Observations indicate that kangaroo rats bite off and consume part of the tiller and discard the remainder at the base of the tussock (Kerley et al., 1997; Sipos et al., 2002).

Understanding this process of kangaroo rat graminivory is critical to understand the dynamics of desert grasses, as well as the contribution to the larger phenomenon of desertification. The major causal factors of desertification are overgrazing and drought. Both drought and overgrazing reduce the density and size of perennial grass tussocks (Whitford, 2002). If graminivory by kangaroo rats is higher on small grass tussocks and tussocks in bare areas, this behaviour can suppress grass recovery, even in the absence of livestock grazing. Fortunately, there is a considerable body of information on the ecology and behaviour of the medium-sized kangaroo rats. Here we develop a number of hypotheses dealing with the interactions between kangaroo rats and grasses, and test predictions arising from these in order to contribute to the understanding of kangaroo rat graminivory. We then use these findings to discuss the possible contribution of kangaroo rat graminivory to the persistence of desertified systems.

Based on observations of kangaroo rat graminivory (Norris, 1950; Kerley et al., 1997), we hypothesized that it depresses grass

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growth and seed production. Predictions arising from this hypothesis are that grasses protected from kangaroo rat graminivory would have elevated growth, tiller production and seed production. We therefore measured grass growth and tiller and inflorescence production in individual grass tussocks exposed to or protected from kangaroo rat graminivory.

Numerous studies have demonstrated that the medium-sized kangaroo rats prefer to forage in open patches (e.g., Price, 1978); hence we hypothesized that grass tussocks in open patches are more likely to be subjected to kangaroo rat graminivory, compared to those surrounded by other plants. We furthermore predicted that large grass tussocks (which represent covered patches within themselves), will be less impacted than small tussocks. We measured kangaroo rat graminivory in a range of grass tussock sizes relative to surrounding plant cover. We further assessed how general this process was by recording the variety of plant species at our sites that exhibited signs of kangaroo rat herbivory.

2. Methods

2.1. Study site

This study was conducted at a livestock–rabbit enclosure on the Jornada Experimental Range and at a Lehmann's lovegrass (*Eragrostis lehmanniana* Nees)–black gramma (*Bouteloua eriopoda* Torr.) grassland on a montane piedmont on the adjacent Chihuahuan Desert Rangeland Research Centre, approximately 40 km NE of Las Cruces, New Mexico, USA. These sites are within an arid ecotone of the grasslands and shrublands of the northern Chihuahuan Desert. Precipitation at the enclosure site averages 240 mm (73 years, 1927–2000), 53% of which occurs as late summer (July–September) convective storms.

2.2. Grasses

We used three grass species in our study, all of which were used by kangaroo rats (Kerley et al., 1997). These included the indigenous *Sporobolus flexuosus* (Thurb.) Rydb. which was the dominant perennial tussock-forming grass in the livestock–rabbit enclosure; the invasive alien perennial tussock-forming *E. lehmanniana* which occurred in areas of high grass cover needed for our experimental design (see later); and the indigenous annual *Panicum hirticaule* Presl, which represented a species occurring in a variety of plant cover situations.

2.3. Kangaroo rat graminivory and *S. flexuosus* growth and seed production

We used experimental enclosures to determine the effects of kangaroo rat graminivory on growth and flowering tiller production of individual *S. flexuosus*. Within the rabbit- and livestock enclosure in a mesquite coppice dune habitat, we selected 72 individual grass tussocks that varied between 20 and 90 cm² in basal area. Tussocks were randomly allocated to control (kangaroo rat access, $n = 36$) or kangaroo rat enclosure ($n = 36$) treatments. Two of the enclosure plants died during the experimental period, hence the sample size was reduced to 34 for the enclosure treatments. Enclosure treatments comprised individual enclosures made of 12 × 12 mm welded mesh, 61 cm high and 98 cm circumference. The enclosures were buried to a depth of 5 cm, and topped with 10 cm of aluminium flashing to prevent access by rodents. The enclosures were installed on 19 March 1998, prior to the appearance of any current growth, and were maintained until November 1998, by which time the grasses were exhibiting dieback.

The perennial vegetation within the experimental area was characterised by measuring plant cover to the nearest cm along six 50 m transects (Mueller-Dombois and Ellenberg, 1974) during September 1998. Rainfall data, both long term (73 years) and for the study period were obtained from a rain gauge within 100 m of the study site.

The rodent community within the experimental area, as well as the unfenced areas immediately adjacent to the rabbit enclosure, was characterised through live-trapping with Sherman traps (7.5 × 9 × 23 cm), set in a 5 × 6 trap configuration with traps 10 m apart. Traps were baited with mixed bird seed, set at dusk and checked and closed at dawn, for three nights during March 1998. Captured animals were identified to species, sexed, weighed, marked and released at the point of capture.

Green leaf length and tiller length of the *S. flexuosus* were measured at monthly intervals, as the average of the lengths of four randomly selected green leaves and tillers on each plant. The phenology of each plant and the appearance of flowering tillers were recorded monthly. Kangaroo rat graminivory is characterised by cleanly bitten-off tillers (Kerley et al., 1997; Sipos et al., 2002); these were counted (monthly from March to June, and weekly from July to November), and expressed as total monthly offtake. Cut tillers that had already developed inflorescences (flowering tillers) were identified. Two-way repeated measures ANOVA was used to compare monthly leaf and tiller length between the control and enclosure treatments. The total number of cut tillers, and flowering tillers remaining on the control and enclosure tussocks, were compared using the Mann–Whitney Rank Sum Test. Regrowth of tillers that had been bitten-off by kangaroo rats was monitored from August to November, for a sample of 12 tillers, from four additional tussocks not used in the above treatments. After labeling the bitten-off tillers, the tussocks were protected with enclosures as described above.

2.4. Influence of *E. lehmanniana* tussock size and surrounding plant cover on kangaroo rat graminivory

We experimentally manipulated the density of vegetation around *E. lehmanniana* tussocks of four different size classes and monitored the extent of graminivory. This was conducted in a paddock from which livestock had been excluded since in 1971. Surrounding vegetation density treatments were: (i) surrounding vegetation in direct contact with focal tussock, (ii) surrounding vegetation in direct contact with half of the focal tussock, with an open space of at least one kangaroo rat length (20 cm) around the remainder, (iii) an open space of one kangaroo rat length around the focal tussock, (iv) an open space gap of two kangaroo rat lengths (40 cm) around the focal tussock. Each size class in each treatment was represented by five replicate tussocks.

These manipulations were set up on 5 August 1998 and tiller production and characteristic kangaroo rat tiller removal (of flowering and non-flowering tillers) were monitored weekly ($n = 6$) from 17 August until 21 September, and summed for this period. A two-way ANOVA was used to test for the effects of tussock size and surrounding vegetation density on the proportion (arcsine transformed – Zar, 1984) of tillers produced that were cut by kangaroo rats over this period.

Although jackrabbits and cottontail rabbits were present at this site, they do not produce the characteristic grass cuttings measured here (Kerley et al., 1997). The small mammal community at this site was characterised through trapping, as described above, for three nights during August 1998. The perennial vegetation of this site was characterised by measuring plant cover to the nearest cm along three 30 m transects (Mueller-Dombois and Ellenberg, 1974) during September 1998.

2.5. Influence of surrounding plant cover on kangaroo rat graminivory on *P. hirticaule*

We measured the extent of kangaroo rat graminivory in relation to the degree of cover (provided by other plants) within a circular area (diameter = 40 cm) around a sample of 100 *P. hirticaule*. This was conducted in the same area as the *E. lehmanniana* experiments. We estimated the cover of plants growing immediately around the individual *P. hirticaule*, and recorded the number of cut tillers and remaining flowering tillers on each plant, on 24 September 1998. The relationship between cover and tiller offtake was described through fitting a logistic regression model (Zar, 1984).

2.6. Other plant species foraged on by kangaroo rats

We recorded all plant species encountered during searches of the study sites which had characteristic kangaroo rat cuttings, in addition to those recorded by Kerley et al. (1997).

3. Results

3.1. Kangaroo rat graminivory and *S. flexuosus* growth and flowering tiller production

This site comprised 72.5% bare ground, and the perennial vegetation was dominated by *Prosopis glandulosa* (Swartz) DC (11.2%), *Dasyochloa pulchella* (H.B.K) Hitchc. (2.6%), *Atriplex canescens* (Pursh) Nutt. (2.3%) and *Gutierrezia sarothrae* (Pursh) Britt. and Rusby (1.6%). *S. flexuosus* cover was 0.7%, and this was the most abundant perennial tussock-forming grass. Rodent species trapped in March included *D. ordii*, *D. merriami*, *Onychomys arenicola* Mearns and *Chaetodipus penicillatus* Woodhouse. Although our trapping was not spatially quantitative, eight medium-sized kangaroo rats (*D. ordii* and *D. merriami*) were captured in an area of approximately 0.3 ha, in a ratio of about 2:1 *D. ordii*: *D. merriami*. The rodent community within the rabbit enclosure was comparable to that outside it. Observations of tracks through the fence, and the recapture of individuals inside the rabbit enclosure that had been marked outside, indicate that the medium-sized kangaroo rats moved through the rabbit-proof fence. There was no evidence of rodent activity (tracks, feces, etc) within any of the experimental rodent enclosures. Invertebrate herbivores, including the large pallid-winged grasshopper *Trimerotropis pallidipennis* Saussure, were able to access them. Total rainfall for the study period (March–November 1998, 186 mm) represented 91% of the 73-year long term average for these months, with five of the nine months having below average rainfall (Fig. 1d).

3.2. *Sporobolus* phenology and response to exclusion of kangaroo rats

Sporobolus plants were dormant during February, and produced the first green leaves in March (Fig. 1a). During the period April to mid-July, the site received very little rainfall (Fig. 1d) and after a significant rain in July, leaf growth was rapid. For the control plants, leaf length peaked in July and declined thereafter. In contrast, leaf length of the grass tussocks protected from kangaroo rats continued to increase until August and only showed major dieback in November (Fig. 1a). Leaf lengths differed between treatments and months, with a significant treatment by month effect (Table 1). Tukey's *post hoc* comparisons showed that leaf length did not differ between control and enclosure treatments during March–June, but did differ for July–November (Fig. 1a).

Tiller growth showed similar trends, with the first tillers recorded in April (Fig. 1b) and the first flowering tillers observed on

11 August. Mean tiller length remained relatively short in the control plants, but was up to six times greater in the enclosure treatments (Fig. 1b), and differed significantly between treatments and months, with a significant treatment by month effect (Table 2). Tukey's *post hoc* comparisons showed that tiller length did not differ between control and enclosure treatments during March–July, but did differ for August–November (Fig. 1b).

3.3. Kangaroo rat graminivory

Grasses from which kangaroo rats were excluded showed no loss of tillers characteristic of kangaroo rat graminivory, whereas control plants exposed to kangaroo rats had an average of 48.0 ± 22.5 (mean \pm SD, range: 5–83) tillers cut by kangaroo rats in the period March–November. This loss varied monthly, peaking in August (Fig. 1c) when 77% of the total cutting (March–November) were observed, and an average of 37.7 ± 18.0 tillers were cut per plant. Only 22 (1.25%) of the 1756 cut tillers recorded here were flowering (i.e., had inflorescences), indicating that the kangaroo rats were not cutting these tillers in order to access the inflorescences or seeds.

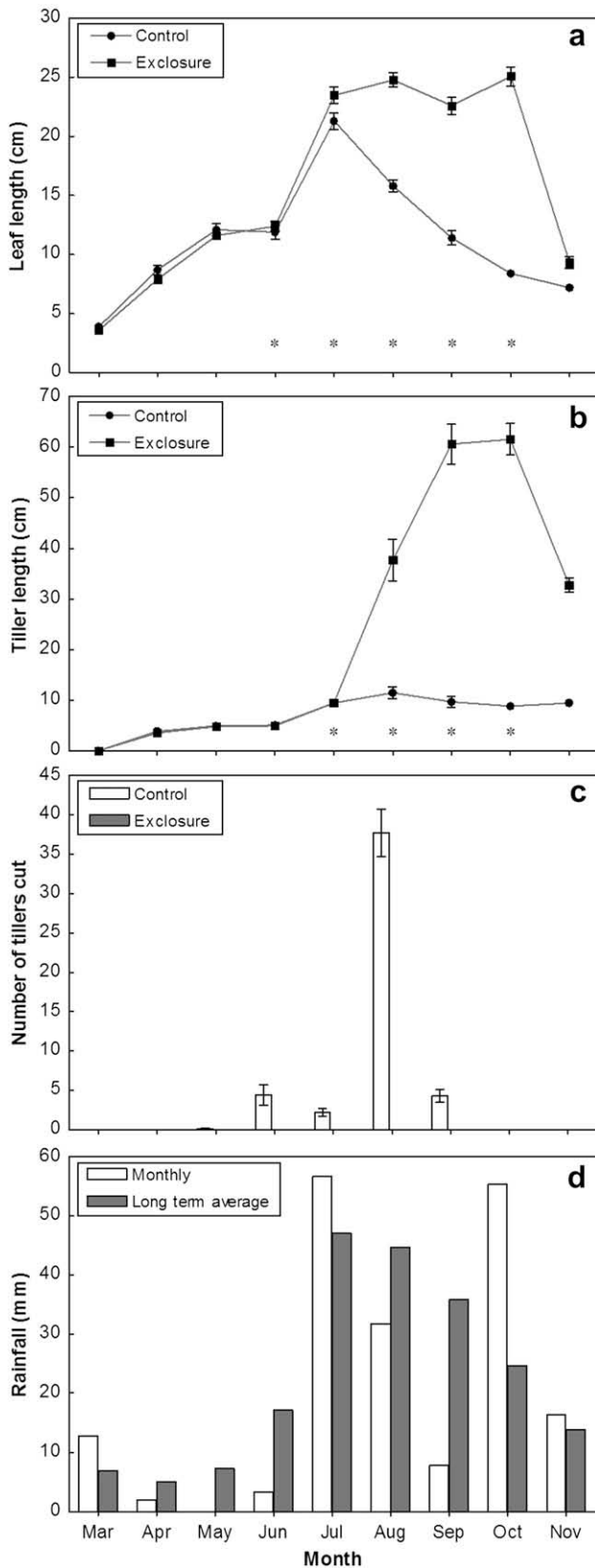
There is evidence for compensatory tiller production, with defoliated grasses producing significantly ($t = 7.58$, $df = 68$, $p < 0.001$) more tillers (49.0 ± 22.1 , cut tillers + tillers that were not cut) than the enclosure plants (16.4 ± 12.2 , flowering tillers). The number of flowering tillers produced by the grasses differed significantly between treatments (Mann–Whitney $t = 1771.5$, $p < 0.001$), with a mean of 0.25 ± 0.91 flowering tillers produced by the control plants (range: 0–5). Thus, on average, grass tussocks protected from kangaroo rat graminivory produced 65 times more inflorescences than those tussocks accessible to kangaroo rats.

The mean defoliated tiller length observed here for *S. flexuosus* was 3.5 ± 1.32 cm ($n = 12$). Tillers that had been cut by kangaroo rats showed some growth when protected from further kangaroo rat graminivory, but this was not sustained and all showed dieback from mid-September (Fig. 2, and cf. Fig. 1b for tiller lengths of uncut tillers). None of these tillers produced inflorescences, and only one of the 12 cut tillers produced a new tiller, but this did not grow longer than 2.0 cm before the November dieback. This lack of recovery occurred despite good rainfall in October (Fig. 1d).

3.4. *Eragrostis* cover and size and kangaroo rat graminivory

This site comprised 75.8% bare ground. The perennial vegetation was dominated by *E. lehmanniana* (12.5%), *B. eriopoda* (7.3%), *Opuntia phaeacantha* Haw. (2.4%) and *Pleuraphis mutica* Buckl. (1.1%). Rodents trapped during August included two individuals each of *D. merriami* and *Neotoma albigula* Hartley.

Tiller cutting from *E. lehmanniana* was a function of both the size of the tussock, and the surrounding density of vegetation (Table 3), but there was no significant interaction effect. Thus tiller cutting differed significantly between tussocks of different size (Table 4), and Tukey's *post hoc* test indicated that small tussocks differed from the large and the largest tussocks, but not from the medium-sized tussocks. None of the tussocks with total cover suffered any kangaroo rat cutting, and the extent of cutting increased with increasing exposure (Table 4). Similarly, the impact of kangaroo rat cutting decreased with increasing tussock size, although trends were less clear between the two larger size classes (Table 4). Of the total of 180 tillers recorded as being cut by kangaroo rats, only 55.6% were flowering (i.e., had inflorescences), indicating that the kangaroo rats were not cutting these *E. lehmanniana* tillers in order to access the inflorescences or seeds.



3.5. Influence of surrounding plant cover on kangaroo rat graminivory on *P. hirticaule*

The *P. hirticaule* plants had a mean of 2.2 ± 1.6 flowering tillers, and had had a mean of 6.1 ± 4.5 tillers cut by kangaroo rats. The extent of cutting varied between 0 and 100% of the tillers produced by *P. hirticaule*, and all tillers were removed from plants growing in open patches (cover < 30%). Tiller loss declined with an increase in cover provided by other plants growing around the *P. hirticaule* (logistic regression model in Fig. 3, $R^2 = 0.62$, $df = 98$, $p < 0.05$). None of the *P. hirticaule* growing under 100% cover suffered any kangaroo rat graminivory (Fig. 3), comparable to the situation for the totally surrounded *E. lehmanniana* tussocks (cf. Table 4).

3.6. Other species cut

A total of 19 grass and six forb species were found to be subjected to characteristic kangaroo rat herbivory (Table 5).

4. Discussion

4.1. Defoliation impacts on the grasses

The exclosures demonstrated that the medium-sized kangaroo rats were responsible for the extensive cutting of grass tillers from the *S. flexuosus* plants, supporting earlier observations (Kerley et al., 1997; Sipos et al., 2002). Because there were no differences in leaf and tiller growth of the control and exclosure plants prior to the major defoliation by kangaroo rats in August, we conclude that the experimental protocol was not responsible for these differences, which can therefore be attributed to the defoliation by the kangaroo rats. Also, because kangaroo rat cutting was recorded for a total of 19 grass and six forb species, this largely unrecognised phenomenon is not restricted to a few grass species, nor is it restricted to monocotyledons (cf. Meehan et al., 1977), but is in fact reasonably general.

The lack of recovery (growth) of cut tillers was due to the loss of the apical meristem, which controls tiller elongation (Briske, 1991). The limited growth observed in defoliated tillers is attributable to the growth of existing cells in the undefoliated section (Briske, 1991). For grasses, further tiller formation from the basal axillary buds is stimulated by the loss of the apical meristem (McClaran, 1995). Since the majority of carbohydrate reserves for regrowth of grasses after defoliation originates in the remaining undefoliated plant tissue, the amount of remaining undefoliated tissue is the best predictor of regrowth potential (McClaran, 1995). Thus the height of tiller defoliation may be critical in determining the ability of the grass to recover from defoliation. An important feature of kangaroo rat graminivory may be that the defoliation occurs close to the base of the tiller, thereby limiting the ability of the defoliated tiller to recover.

Defoliated *S. flexuosus* plants showed significantly reduced leaf and tiller growth. As a large proportion of photosynthesis in grass occurs in the distal tiller portion (McClaran, 1995), and hence their

Fig. 1. Phenology of leaf and tiller length, and kangaroo rat cutting of *Sporobolus flexuosus* in relation to rainfall for the period March–November 1998. (a) Monthly *S. flexuosus* mean (\pm SE) leaf length for the control ($n = 36$) and exclosure ($n = 34$) plants. Data points marked with * differ ($p < 0.05$) within months according to *post hoc* comparisons. (b) *S. flexuosus* mean tiller length (\pm SE) for the control and exclosure plants. Data points marked with * differ ($p < 0.05$) within months according to *post hoc* comparisons. (c) Monthly mean number (\pm SE) of tillers bitten off the *S. flexuosus* for the control plants. Note that there were no cuttings for exclosure plants. (d) Monthly rainfall for the period of the study, together with the 73-year long term average for this site.

Table 1

Summary of the results of a two-way repeated measures ANOVA comparing monthly *Sporobolus flexuosus* leaf length between the control and enclosure treatments. See Fig. 1a for the outcomes of the monthly Tukey's *post hoc* comparisons of control vs enclosures.

Source of variation	DF	SS	MS	F	p
Treatment	1	3065.7	3065.7	104.20	<0.001
Tussock (treatment)	68	2000.7	29.4		
Month	8	21097.4	2637.2	402.95	<0.001
Treatment × month	8	5566.3	695.8	106.31	<0.001
Residual	544	3560.3	6.6		
Total	629	34966.7	55.6		

loss is expressed as reduced vigor of the plant. Loss of vigor reduces the survival of these plants. Our study provides a mechanistic explanation for the observations of perennial grass biomass increases of 230 kg ha⁻¹ (Norris, 1950), and increased cover of tussock-forming grasses (Brown and Heske, 1990) when kangaroo rats are excluded.

The significant effect of tussock size on graminivory demonstrated here has further implications for grass demography, as selective defoliation of smaller plants will affect grass recruitment. Rodent graminivory was found to remove most of the flowering tillers of grasses in paddocks subjected to overgrazing by livestock (Roth et al., 2009). The surviving grass tussocks in the overgrazed paddock were approximately 75% smaller than the grass tussocks in the ungrazed paddocks. Rodent graminivory removed only a small fraction of the tillers of grasses in the ungrazed paddocks. It was concluded that rodent graminivory was largely responsible for the lack of grass recovery in the overgrazed paddocks more than 7 years after the cessation of livestock grazing (Roth et al., 2009).

Estimates of the impact of kangaroo rats as seed predators, suggest that they account for between 37 and 86% of seed production in desert shrublands (Chew and Chew, 1970; Sohlt, 1973). Although they may affect tillering, medium-sized kangaroo rats consume relatively few grass seeds (7.5% of seed in the diet of *D. merriami*; Reichman, 1975). Conservatively assuming that the seed production per flowering tiller of defoliated grasses is the same as that of undefoliated grasses, then the effect of kangaroo rat graminivory was to reduce average seed production by a factor of 65 (i.e., 65 times as many flowering tillers on enclosure plants vs control plants). This is probably an underestimate, since the observed loss of vigor is probably also expressed in reduced seed production. This supports the hypothesis (Kerley et al., 1997) that kangaroo rat graminivory may have major effects on seed dynamics of desert grasses, in addition to their impact on desert shrub seeds through direct granivory. The observed differences between the proportions of tillers cut from *S. flexuosus* and *E. lehmanniana* also support the hypothesis (Kerley et al., 1997) that the species-specific response of grasses to kangaroo rat exclusion shown by Brown

Table 2

Summary of the results of a two-way repeated measures ANOVA comparing monthly (April–November) *Sporobolus flexuosus* tiller length between the control and enclosure treatments. See Fig. 1b for the outcomes of the monthly Tukey's *post hoc* comparisons of control vs enclosures.

Source of variation	DF	SS	MS	F	p
Treatment	1	50881.964	50881.964	158.63	<0.001
Tussock (treatment)	68	21812.17	320.77		
Month	7	87838.86	12548.41	186.81	<0.001
Treatment × month	7	64759.75	9251.39	137.73	<0.001
Residual	476	31973.434	67.17		
Total	559	253137.684	452.84		

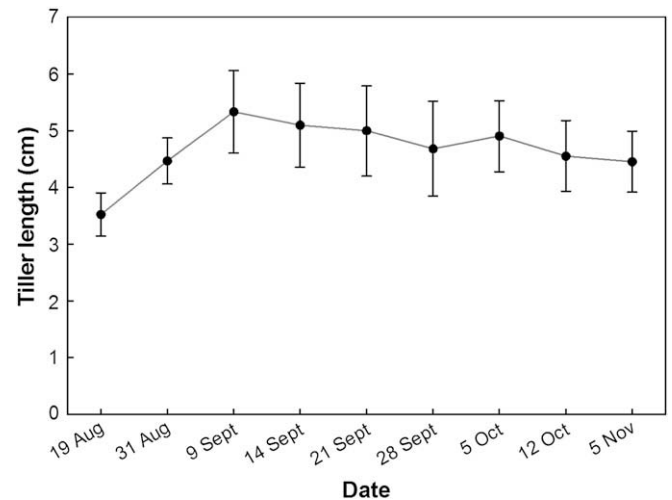


Fig. 2. Recovery of *Sporobolus flexuosus* tillers (mean tiller length ± SE) subsequent to graminivory by kangaroo rats (cf. enclosure tiller lengths in Fig. 1b for uncut tiller lengths).

and Heske (1990) is a reflection of selective graminivory by kangaroo rats.

4.2. Patch specific graminivory

Both the *E. lehmanniana* and *P. hirticaule* data support the hypothesis that kangaroo rat graminivory is higher in open habitat patches. This is consistent with observations that the medium-sized kangaroo rats spend more time and forage more in these open patches (Price, 1978). This, combined with observations of higher graminivory of small grasses, suggests that seedling grasses recruiting in open patches may suffer disproportionately high defoliation by kangaroo rats. The consequences in terms of desert grass dynamics are that effective grass recruitment may be largely limited to those seedlings that establish in the shelter of, or proximity of, other plants, with further implications in terms of competition for resources between the plants. Roth et al. (2009) showed that grasses that escaped loss of tillers by graminivory grew through the canopies of snakeweed (*G. sarothrae*), which served as nurse plants.

4.3. Why do kangaroo rats cut grasses?

Kangaroo rat graminivory occurs before flower production, and overall less than half of the cut tillers had inflorescences or seeds (1.25% for *S. flexuosus* and 56% for *E. lehmanniana*). Typically, those cut tillers were discarded with the inflorescence intact (Kerley et al., 1997). Thus kangaroo rats are clearly not cutting the tillers to access the inflorescences or the seed (cf. Reichman, 1975). We noted (but

Table 3

Summary of the results of a two-way ANOVA comparing proportional tiller cutting (asin transformed) among the size and exposure treatments for *Eragrostis lehmanniana*. See Table 4 for the outcomes of the Tukey's *post hoc* comparisons within size and exposure treatments.

Source of variation	DF	SS	MS	F	p
Tussock size	3	1.576	0.525	5.08	0.003
Exposure	3	3.878	1.293	12.50	<0.001
Size × exposure	9	1.474	0.164	1.584	0.140
Residual	64	6.617	0.103		
Total	79	13.545	0.171		

Table 4

Relationship between tussock size and degree of exposure for *Eragrostis lehmanniana* and the extent of kangaroo rat graminivory, expressed as the proportion (%) of tillers produced that were cut off the plants. Treatments marked with different letters across rows (size effects), or down the column (exposure effects) differ significantly within that row or column according to Tukey's *post hoc* comparison of asin transformed data.

Tussock size		Small	Medium	Large	Largest
Mean basal area \pm SD		3.3 \pm 1.8	13.3 \pm 4.6	43.7 \pm 11.3	119.7 \pm 48.7
Exposure treatment	Exposure effects	Size effects			
40 cm gap	A	73.2	48.9	22.4	7.2
20 cm gap	AC	31.7	32.4	7.1	10.5
Half cover	BC	27.9	9.8	1.1	12.9
Total cover	B	0	0	0	0

did not quantify) that the tillers were typically cut at the internode, hence the kangaroo rats may be consuming part of the intercalary meristem, a region of high cell growth and division (Briske, 1991). The consumption of green vegetation has been linked to reproduction in *D. merriami* (Beatley, 1969, 1976; Bradley and Mauer, 1971; Van de Graaff and Balda, 1973; Soholt, 1973, 1977; Reichman and Van de Graaff, 1975), and both *D. merriami* and *D. ordii* have been recorded consuming up to 35% grass and other green foliage (Flake, 1973; Soholt, 1973). *D. ordii* grass consumption peaks at the onset of reproductive activity in late summer/fall (Duke, 1944; McCulloch and Inglis, 1961; Flake, 1973). The August peak of graminivory therefore coincides with the reproductive activity of these kangaroo rats, and they may be obtaining critical nutrients from these grasses. In addition to preformed water, one such resource may be 6-MBOA, an estrogenic phytochemical that occurs in the new growth of grasses, and which boosts reproductive activity in *D. ordii* (Rowsemitt and O'Connor, 1989).

4.4. Graminivory and invasion by *E. lehmanniana*

E. lehmanniana is one of the grasses to show a major response to kangaroo rat exclusion in Brown and Heske's (1990) study and is an invasive exotic species (Anable et al., 1992). Although *E. lehmanniana* is subject to low levels of kangaroo rat graminivory, this is obviously not sufficient to prevent the establishment and spread of this species. Although small *E. lehmanniana* tussocks, and tussocks growing in the open are vulnerable to graminivory by kangaroo rats, Lehmann lovegrass may escape graminivory by growing under

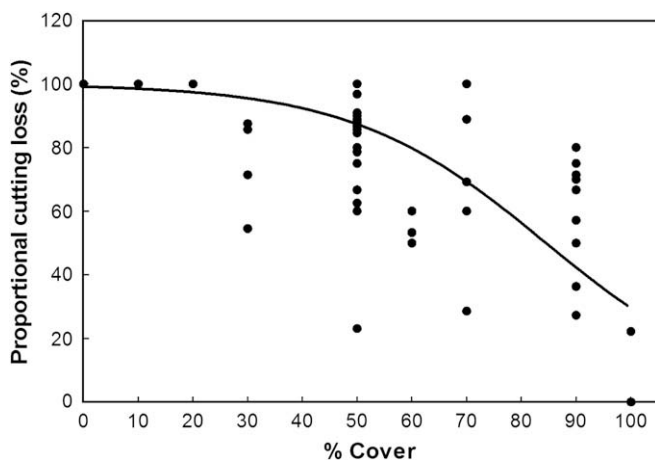


Fig. 3. The relationship between the proportional offtake of tillers by kangaroo rats and the extent of plant cover surrounding *Panicum hirticaule*.

Table 5

Records of plant species exhibiting signs of typical kangaroo rat foraging behaviour in the Chihuahuan Desert (*recorded by Kerley et al., 1997). See Kearney and Peebles (1960) and Allred (1993) for dicotyledon and monocotyledon authorities, respectively.

Monocotyledons		Dicotyledons	
<i>Muhlenbergia porteri</i>	Bush muhly	<i>Croton pottsii</i>	Leatherweed
<i>Dasyochloa pulchella</i>	Fluffgrass	<i>Eriogonum annuum</i>	Annual buckwheat
<i>Panicum hirticaule</i>	Mexican witchgrass	<i>E. abertianum</i>	Buckwheat
* <i>Digitaria californica</i>	Arizona cottontop	<i>Cassia bahinioides</i>	Two-leaf senna
* <i>Bothriochloa barbinodis</i>	Cane bluestem	<i>Bahia absinthifolia</i>	Hairyseed bahia
* <i>Sporobolus airoides</i>	Alkali sacaton	<i>Boerhaavia spicata</i>	Spiderling
* <i>S. flexuosus</i>	Mesa dropseed	<i>Tidestromia lanuginosa</i>	Woolly tidestromia
* <i>S. giganteus</i>	Giant dropseed		
* <i>S. cryptandrus</i>	Sand dropseed		
* <i>Setaria leucopila</i>	Bristle grass		
* <i>Aristida ternipes</i>	Spider grass		
* <i>A. purpurea</i>	Purple threeawn		
* <i>Bouteloua curtipendula</i>	Sideoats gramma		
* <i>B. eriopoda</i>	Black gramma		
<i>B. barbata</i>	Six-weeks' gramma		
<i>B. aristoides</i>	Six-weeks' gramma		
* <i>Pleuraphis mutica</i>	Tobosa		
* <i>Eragrostis lehmanniana</i>	Lehmann's lovegrass		

nurse plants (cf. Roth et al., 2009). Also, once *E. lehmanniana* becomes established it forms dense grass stands (Anable et al., 1992). Dense grasslands represent unfavourable habitat for *D. ordii* and *D. merriami* (Pulliam and Brand, 1975), and therefore exclude these species, further reducing their impact on this invasive grass.

4.5. Conceptual model of kangaroo rat graminivory and the persistence of desertified habitats

North American desert grasslands have relatively low densities and diversities of small mammals (e.g., Whitford, 1976; Pulliam and Brand, 1975): this can be considered the predesertified state (*sensu* Milton et al., 1994). However, overgrazing leads to a reduction in grass cover and an increase in shrub cover and the proportion of open spaces (Kerley and Whitford, 2000), habitats favoured by the medium-sized kangaroo rats (Price, 1978). This leads to an increase in the abundance of *D. ordii* and *D. merriami* (Alberico, 1978; Kerley and Whitford, 2000). Thus desertification brings about an increase in the abundance of those kangaroo rats that exhibit graminivory. The relative extent of kangaroo rat graminivory increases with decreasing grass density (Kerley et al., 1997), in more open patches and with smaller tussock size (this study). This is sufficient to significantly reduce grass vigor in areas of low grass cover (this study) and reduce grass seed production (this study) and grass establishment (Norris 1950; Brown and Heske, 1990). We therefore hypothesize that kangaroo rat graminivory acts to inhibit the establishment of grasses on overgrazed desertified landscapes. This is consistent with state and transition models of semi-arid landscape functioning (Westoby et al., 1989; Milton et al., 1994), with the transition to the desertified state being brought about through overgrazing, and the desertified stable state being maintained, at least in part, by kangaroo rat graminivory.

The impacts of the medium-sized kangaroo rats in maintaining desertified landscapes are compounded by their role as granivores. We have shown elsewhere that rodent granivory (chiefly by the

kangaroo rats) increases in desertified shrublands compared to grasslands (Kerley and Whitford, 2000), and suggests that elevated levels of granivory may also influence seed-based plant regeneration in desertified landscapes. The combined impacts (graminivory and granivory) of the medium-sized kangaroo rats provide the mechanisms for their status as keystone species (*sensu* Brown and Heske, 1990) in the Chihuahuan Desert.

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References

- Alberico, M.S., 1978. Species diversity of nocturnal rodents in disturbed desert-grassland habitats. Ph.D. dissertation, New Mexico State University.
- Allred, K.W., 1993. A Field Guide to the Grasses of New Mexico. New Mexico State University Agricultural Experimental Station, Las Cruces.
- Anable, M.E., McLaren, M.E., Ruyle, G.B., 1992. Spread of Lehmann lovegrass *Eragrostis lehmanniana* Nees. in southern Arizona, USA. *Biological Conservation* 61, 181–188.
- Beatley, J.C., 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50, 721–724.
- Beatley, J.C., 1976. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. *Oecologia* 24, 21–42.
- Bradley, W.G., Mauer, R.A., 1971. Reproduction and food habits of Merriam's kangaroo rat, *Dipodomys merriami*. *Journal of Mammalogy* 52, 497–507.
- Briske, D.D., 1991. Developmental morphology and physiology of grasses. In: Heitschmidt, R.K., Stuth, J.W. (Eds.), *Grazing Management: an Ecological Perspective*. Timber Press, Portland, pp. 85–108.
- Brown, J.H., Heske, E.J., 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250, 1705–1708.
- Chew, R.M., Chew, A.E., 1970. Energy relations of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecological Monographs* 40, 1–21.
- Duke, K.L., 1944. The breeding season in two species of *Dipodomys*. *Journal of Mammalogy* 25, 155–160.
- Flake, L.D., 1973. Food habits of four species of rodents on a short-grass prairie in Colorado. *Journal of Mammalogy* 54, 636–647.
- Frederickson, E., Havstad, K.M., Estell, R., Hyder, P., 1998. Perspectives on desertification: southwestern United States. *Journal of Arid Environments* 39, 191–207.
- Hastings, J.R., Turner, R.M., 1965. *The Changing Mile: an Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semiarid Region*. University of Arizona Press, Tucson.
- Heske, E.J., Brown, J.H., Guo, Q., 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95, 520–524.
- Kearney, T.H., Peebles, R.H., 1960. *Arizona Flora*. University of California Press, Berkeley.
- Kerley, G.I.H., Whitford, W.G., 2000. Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores and granivory. *American Midland Naturalist* 144, 78–91.
- Kerley, G.I.H., Whitford, W.G., Kay, F.R., 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia* 111, 422–428.
- McClaran, M.P., 1995. Desert grasslands and grasses. In: McClaran, M.P., van Devender, T.R. (Eds.), *The Desert Grassland*. University of Arizona Press, Tucson, pp. 1–30.
- McCulloch, C.Y., Inglis, J.M., 1961. Breeding periods of the Ord kangaroo rat. *Journal of Mammalogy* 42, 337–344.
- Meehan, T.E., Rundell, P.W., Ambrose, R., Baker, G., Rappapora, A., 1977. The influence of intense selective browsing by pocket mice (*Perognathus*) on the spatial distribution of *Polygala deserticum* in Baja, California. *American Midland Naturalist* 97, 489–495.
- Milton, S.J., Dean, W.R.J., du Plessis, M.A., Siegfried, W.R., 1994. A conceptual model of arid rangeland degradation: the escalating costs of declining productivity. *BioScience* 44, 70–76.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York.
- Norris, J.J., 1950. Effect of rodents, rabbits and cattle on two vegetation types in semidesert rangeland. *Agricultural Experimental Station. New Mexico College of Agriculture and Mechanical Arts Bulletin* 353, 1–23.
- Price, M.V., 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59, 910–921.
- Pulliam, H.R., Brand, M.R., 1975. The production and utilization of seeds in plains grasslands of south western Arizona. *Ecology* 65, 1158–1166.
- Reichman, O.J., 1975. Relation of desert rodent diets to available resources. *Journal of Mammalogy* 56, 731–751.
- Reichman, O.J., Van de Graaff, K.M., 1975. Association between ingestion of green vegetation and desert rodent reproduction. *Journal of Mammalogy* 56, 503–506.
- Roth, G.A., Whitford, W.G., Steinberger, Y., 2009. Small mammal herbivory: feedbacks that help maintain desertified ecosystems. *Journal of Arid Environments* 73, 62–65.
- Rowsemitt, C.N., O'Connor, A.J., 1989. Reproductive function in *Dipodomys ordii* stimulated by 6-methoxybenzoxazolinone. *Journal of Mammalogy* 70, 805–809.
- Sipos, M.P., Andersen, M.C., Whitford, W.G., Gould, W.R., 2002. Graminivory by *Dipodomys ordii* and *Dipodomys merriami* on four species of perennial grasses. *SouthWestern Naturalist* 47, 276–281.
- Soholt, L.F., 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecological Monographs* 43, 357–376.
- Soholt, L.F., 1977. Consumption of herbaceous material and water during reproduction and development of Merriam's kangaroo rat *Dipodomys merriami*. *American Midland Naturalist* 98, 445–457.
- Van de Graaff, K.M., Balda, R.P., 1973. Importance of green vegetation for reproduction in the kangaroo rat *Dipodomys merriami*. *Journal of Mammalogy* 54, 509–512.
- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42, 266–274.
- Whitford, W.G., 1976. Temporal fluctuations in density and diversity of desert rodent populations. *Journal of Mammalogy* 57, 351–369.
- Whitford, W.G., 2002. *Ecology of Desert Systems*. Academic Press, London.
- Zar, J.H., 1984. *Biostatistical Analysis*, second ed. Prentice-Hall, New Jersey.