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Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory?

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Abstract Graminivory by kangaroo rats (*Dipodomys* spp.) was investigated as a potential mechanism for the keystone role of these rodents in the dynamics of desert grasslands. Experiments confirmed that Ord's kangaroo rats (*Dipodomys ordii*) cut and consumed a large proportion of the tillers of three Chihuahuan Desert tussock-forming grass species. Field observations indicated that the characteristically cut grass tillers were absent from all-rodent and medium-sized kangaroo rat exclosures, but were frequent in large-sized kangaroo rat and rabbit exclosures, indicating that the medium-sized kangaroo rats (*D. ordii*, *D. merriami*) were responsible for grass cutting. Tiller waste as a percentage of peak standing crop ranged from 7% in grassland habitats to 0.7% in *Flourensia cernua* shrubland. Of the 13 species of perennial, tussock-forming grasses measured, only one, *Muhlenbergia porteri*, had no tillers cut by kangaroo rats. This study demonstrates that the keystone role of kangaroo rats in Chihuahuan Desert grassland ecosystems is probably the result of their graminivory.

Key words Graminivory · Keystone species · *Dipodomys* · Grass populations · Chihuahuan Desert

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Introduction

Brown and Heske (1990) and Heske et al. (1993) showed that kangaroo rats (genus *Dipodomys*: Heteromyidae) were functioning as a keystone guild in North American desert grasslands, affecting the density and composition of the grass community, particularly tall tussock-forming grasses. Brown and Heske (1990) and Heske et al. (1993) speculated that the observed impact of kangaroo rats might be explained in terms of granivory or soil disturbance by kangaroo rats, but did not quantify either of these effects, nor provide any direct mechanisms for the grasses being affected.

Both the granivory and the soil disturbance mechanisms for the impact of kangaroo rats on desert grasses mentioned above are problematical, as suggested by Heske et al. (1993). The role of kangaroo rats as granivores, and the consequences for desert rodent community ecology and desert ecosystem functioning, has received considerable attention (e.g., Brown et al. 1979). There is clear evidence for the selection of large seeds by kangaroo rats (Brown and Davidson 1977). One of the grass species that showed the largest increase in the absence of kangaroo rats (Heske et al. 1993) has very small seeds (i.e., *Eragrostis lehmanniana*) which are unlikely to be selected by the medium-sized kangaroo rats (*Dipodomys ordii*, *D. merriami*). In addition, *D. merriami* consumes limited amounts of grass seed (7.5% of total seed in the diet; Reichman 1975). The alternative mechanism presented by Brown and Heske (1990), whereby unquantified soil disturbance by kangaroo rats hinders the establishment of grasses is contradicted by the observation of increased germination of both cached (Reynolds and Glendening 1949; McAuliffe 1990; McAdoo et al. 1983; Longland 1995) and uncached seeds (i.e., wind-dispersed seeds trapped in open cache pits – Steinberger and Whitford 1983) where kangaroo rat soil disturbance is present. *Aristida adscensionis*, the tall summer annual grass discussed by Brown and Heske (1990) and Heske et al. (1993), is generally recognized as colonizing disturbed sites (Allred 1993), so it is not clear why this species should increase in the absence of soil disturbance by kangaroo rats. An alternative mechanism for the increase of grasses in the absence of kangaroo rats is needed.

Kangaroo rats are not exclusively granivorous; they consume a significant proportion of green foliage (Kerley and Whitford 1994), with seasonal peaks in foliage consumption (e.g., Flake 1973). We observed large quantities of freshly cut tillers of several species of grass in the desert grasslands of southern New Mexico. Close inspection of the soil around the grass clumps from which these cuttings originated revealed "tail drags" characteristic of kangaroo rats. These observations led us to hypothesize that kangaroo rats were responsible for these grass cuttings. If kangaroo rats cut grass tillers this could provide a mechanism for the observed impact of kangaroo rats on desert grasslands. We further hypothesized that fresh tillers have a higher nitrogen content than senescent tillers, thereby contributing directly to nutrient cycling in these ecosystems. We also investigated the impacts of grass cutting by kangaroo rats on grass biomass and seed production, and grass community structure.

Materials and methods

Experimental demonstration of kangaroo rat graminivory

In order to test for graminivory by kangaroo rats we established an experimental study using *D. ordii* (Ord's kangaroo rat). Eight experimental chambers, 109 × 40 cm and 45 cm deep, were prepared and placed out-of-doors. Each chamber was filled with soil, to a depth of about 25 cm, from the area where the grasses and kangaroo rats were obtained. Each chamber was provided with an artificial burrow of 1-cm-mesh wire that was 45 cm long by 10 cm diameter and extended to about 15 cm depth. The entire chamber was covered with 1-cm wire mesh under about 2 cm of soil to discourage burrowing but to provide sufficient soil for dust bathing and food caching activities. The burrow entrance was placed at one end of the chamber and a 20-cm opening for a pot containing a grass plant was placed at the opposite end. Each chamber was covered with 1-cm wire mesh.

Eight *D. ordii* (four males, four females) were live-trapped and placed individually in the experimental chambers. Rolled sorghum (*Sorghum bicolor*) was provided ad libitum to the rats. No free water was provided. Each rat was weighed at capture and prior to release, 10–14 days later. All animals maintained weight during the experimental interval. After the trials, each animal's artificial burrow was excavated and any stored plant and other material was removed and examined.

Three species of Chihuahuan Desert perennial tussock-forming grasses (*Bouteloua eriopoda*, black grama; *Sporobolus flexuosus*, mesa dropseed; and *Bothriochloa saccharoides*, silver bluestem) were established in 20-cm pots, and maintained out-of-doors in the same area as the experimental chambers. All plants were in good condition with green, growing tillers and seed heads. Individual grass plants were presented to the rats for 1–4 days. Each morning the plants were checked, cut green tillers were counted, and grass tiller, leaf and seedhead cuttings were removed and placed in paper bags for weighing, and grass plants replaced if necessary. Grass cuttings were oven dried at 60°C for 24 h and weighed. We collected and weighed all cut material, live and dead, but, for simplicity, counted only cut green tillers. Biomass consumption was estimated by clipping whole grass plants and obtaining average dry weight per green tiller for each species tested. As with grass cuttings, we dried and weighed the entire plants but counted only green tillers. Our estimates of biomass cut and consumed are, therefore, composites of live and dead material.

Field evidence of kangaroo rat graminivory

We tested the hypothesis that kangaroo rats were responsible for the observed grass cuttings by measuring the frequency of grass tussocks with grass cuttings at J.H. Brown's long-term experimental plots at Portal, Arizona (Brown and Munger 1985; Brown and Heske 1990; Heske et al. 1993), during November 1991. These exclosures are constructed with differential permeability for different taxa. Treatments include control (access to all rodents and ants, $n = 4$), rodent exclosure ($n = 4$), rodent and ant exclosure ($n = 2$), medium-sized kangaroo rat (*D. merriami* and *D. ordii*, $n = 4$) exclosure, medium-sized kangaroo rat and ant exclosure ($n = 4$), large-sized kangaroo rat (*D. spectabilis*, $n = 2$) exclosure and ant exclosure ($n = 4$) (Brown and Heske 1990; Heske et al. 1993). As we were interested in the activity of rodents, we pooled treatments with regard to rodent access: control + ant exclosure ($n = 8$); rodent + rodent and ant exclosure ($n = 6$); medium-sized kangaroo rat + ant and medium-sized kangaroo rat exclosure ($n = 8$) and large-sized kangaroo rat exclosure ($n = 2$). Within each treatment we sampled the frequency of cutting of tall tussock-forming grasses, attempting to sample at least 50 grass tussocks (in two plots we could locate only 34 and 37 tussocks). Tussocks were recorded as being with or without grass cuttings. Frequencies were arcsine transformed for comparison between treatments by ANOVA (Zar 1984).

Field evidence for other species as harvesters

We tested alternate hypotheses that species besides kangaroo rats (e.g., rabbits, other rodents) may be responsible for the grass cuttings by searching for cuttings in rabbit-proof exclosures, as well as in a wide variety of habitats (grasslands, mesquite dunefields, creosote shrublands, tarbush shrublands and playa communities) on the Jornada Experimental Range, north-west of Las Cruces, New Mexico. In addition, in December 1996, the proportion of cut tillers on 50 *S. flexuosus* plants was recorded in a rodent plus rabbit exclosure, a rabbit only exclosure and a control area on a Jornada Long Term Ecological Research (LTER) study site.

Extent and effect of grass harvesting

In order to estimate the extent of these grass cuttings in desert habitats, we collected all cuttings in 15 × 15 m quadrats in grassland, mesquite dunefield, creosote shrubland and tarbush shrubland communities within the Jornada Basin during October 1991. We used quadrats that had been previously established as part of the Jornada LTER project, selecting these randomly within each habitat. We sampled six quadrats in each habitat, except for the grassland site, where the sheer mass of material forced us to sample only three quadrats. Cuttings were oven-dried at 50°C for 48 h and weighed in the laboratory.

We counted the proportion of cut and intact stalks in a random sample of 60 *S. flexuosus* tussocks at the Jornada, and recorded the proportion of cut stalks which had their fruiting heads intact in a random sample of 50 freshly cut stalks of *S. flexuosus*. Species-specific frequencies (proportion of tussocks with cuttings) of grass cuttings were recorded for 13 species of tussock-forming grass in the Jornada Basin and at the Portal study site.

Table 1 Graminivory by *Dipodomys ordii*, Ord's kangaroo rat, in experimental chambers. Values are presented as Mean (±SE). Mean tiller weight of *B. saccharoides* was based on a single pooled sample of 4 plants, that of *B. eriopoda* and *S. flexuosus* was based on 10 individual plants of each species

Grass species	*n*	Number tillers cut	Tiller mass (g)	Remnant mass (g)	Biomass cut (g)	Biomass consumed (g)	% Consumed
Bothriochloa saccharoides	3	11 (±2.3)	0.72	2.24 (±1.03)	7.84 (±1.53)	5.61 (±2.48)	71.5
Bouteloua eriopoda	4	18 (±1.5)	0.12 (±0.02)	2.90 (±0.21)	2.26 (±0.2)	1.22 (±0.18)	53.7
Sporobolus flexuosus	4	9 (±2.0)	0.48 (±0.05)	2.90 (±0.69)	4.12 (±1.02)	1.52 (±0.46)	34.3

Table 2 Frequency of tall grass tussocks with grass cuttings (mean ± SE) in rodent exclosures, kangaroo rat exclosures and control plots at Portal, Arizona

Treatment	*n*	Proportion of tussocks with cuttings (%)	Mean number of tussocks sampled per treatment
Control plots	8	58.25 ± 5.64	48
Rodent exclosures	8	0.67 ± 0.58	50
Dipodomys exclosures	6	0.25 ± 0.29	50
D. spectabilis exclosures	2	49.50	42

Table 3 Dry mass of grass cuttings (mean ± SE) collected in different habitats in the Jornada Basin, New Mexico

Habitat	*n*	Mass of cut grass g ha^{-1}	Grass production g ha^{-1a}	Proportion of production (%)
Grassland	3	9822 ± 3528	139 500	7
Mesquite dunefield	6	1134 ± 441	24 000	4.7
Creosote shrubland	6	533 ± 235	27 500	1.9
Tarbush shrubland	6	338 ± 231	46 333	0.7

[a] Measured as standing crop of tall grasses at the peak of summer growth period, October 1991. Data courtesy of L. Huenneke and the Jornada LTER

Results and discussion

Confirmation of kangaroo rat graminivory

Do kangaroo rats harvest grass?

Kangaroo rats clearly gnawed off and consumed tillers of all three grass species offered (Table 1). Grass tillers cut by kangaroo rats had cleanly severed ends that were either perpendicular or at a slight angle to the stem. The rats cut both live (green) and dead tillers. Biomass cut by the rats in the experiment approached 100% of that available. Six of the eight rats tested, three males and three females, cut and consumed portions of all of the tillers on each grass plant, irrespective of species, presented to them. A male that was presented only with *S. flexuosus* never harvested more than five tillers from a plant. A female that was presented with *B. eriopoda*, and *B. saccharoides* harvested between 6 and 17 *B. eriopoda* tillers and all of the *B. saccharoides* tillers (16). None of the rats was found to have cached appreciable amounts of grass or sorghum. Our estimates of consumption (Table 1) suggest that graminivory by kangaroo rats can have a substantial impact on desert grass tussocks.

We did not quantify sorghum use, but noted signs of foraging and consumption of the grain by all of the rats. Little use of sorghum was noted until the rats were deprived of grass plants for one or more nights.

Field evidence of species responsible for grass harvesting

The frequency of grass tussocks with cuttings differed between kangaroo rat access treatments ($F_{3,20} = 90.99$, $P < 0.0005$). Cuttings were virtually absent from rodent and medium-sized kangaroo rat exclosures (Table 2), which did not differ in the frequency of cuttings according to Tukey's range test ($P > 0.05$). However, cuttings were common in the control and large-sized kangaroo rat plots (Table 2), which did not differ in the frequency of cuttings according to Tukey's range test ($P > 0.05$). This suggests that it is the medium-sized kangaroo rats (*D. merriami* and *D. ordii*) which are responsible for these grass cuttings.

We could rule out jackrabbits *Lepus californicus* and cottontail rabbits *Sylvilagus auduboni* as the species responsible for these grass cuttings, as cuttings were found inside rabbit-proof exclosures on the Jornada LTER site. There were no cut stalks in a sample of 50 *S. flexuosus* tussocks in a rabbit plus rodent exclosure on the LTER site, 48% of tussocks had cut tillers in a rabbit exclosure, and 56% in a control area. The cuttings were also observed in a wide range of habitats on the Jornada Basin, including grasslands, mesquite dunefields, creosote shrublands, tarbush shrublands and playa communities. This would suggest that the grass cuttings are not the work of grass specialists such as the cotton rat *Sigmodon hispidus*, which is largely restricted to high grass cover grasslands and is abundant only during periods of above average rainfall (Wood 1969; Whitford 1976).

Extent of harvesting

The amount of grass cuttings (characteristic of those discarded by the kangaroo rats) averaged about 2 kg ha^{-1} dry mass over the four habitats (Table 3), but varied markedly between the habitats ($F_{3,17} = 10.23$, $P = 0.005$) from a maximum of nearly 10 kg ha^{-1} in the grasslands to about 0.3 kg ha^{-1} in the tarbush shrubland. The mass of grass cuttings was significantly higher in the grasslands than the other habitats (Tukey's range test, $P < 0.05$).

Impact of kangaroo rat graminivory

Impact on grass biomass

The cuttings represent an average of about 3.6% of grass biomass in the habitats studied, with the maximum of 7.0% being recorded in the grassland habitat (Table 3). Our estimates of grass harvested are conservative compared to those of Norris (1950). He reported that exclusion of rodents from pastures on the Jornada resulted in perennial grass biomass increases of 230 kg ha^{-1}. There is a trend towards a negative relationship between grass standing crop and the proportion of grass cut by kangaroo rats in the shrubland habitats in our study. Our observations suggest that as grasses become sparser within shrublands, they are more likely to be impacted by kangaroo rat graminivory. Unfortunately, our limited sample size of three shrublands habitats precluded testing this relationship.

Impact on litter production

The desert tussock-forming grasses tend to decompose as standing dead material, with small fragments being added to the litter pool by wind and physical trampling by domestic and indigenous ungulates. We observed that tillers clipped by rodents contributed much of the litter in these desert habitats, thereby accelerating the rate of input of this material into the litter pool.

Grass stalks that had been cut off were actively growing flowering\seeding stalks, and not senescent material. We measured the nitrogen and phosphorous content of actively growing grass stalks (i.e., comparable to those cut) and compared these to levels in naturally senesced material from the same sites on the Jornada.

The nitrogen content of grass stems cut by rodents differed from that of standing senesced material for both the grassland (8.9 ± 0.3 g kg^{-1} and 5.5 ± 0.9 g kg^{-1}, respectively, $t = 3.1$, $P < 0.05$, $n = 5$) and mesquite sites (12.6 ± 3.0 g kg^{-1} and 5.2 ± 0.7 g kg^{-1}, respectively, $t = 3.8$, $P < 0.05$, $n = 4$). Although the phosphorus content of the cut material was slightly higher on average, there were no differences in the phosphorus content of fresh and senesced stalks for the grassland (0.9 ± 1 g kg^{-1} and 0.7 ± 0.5 g kg^{-1}, $P > 0.05$, $n = 5$) or mesquite sites (1.2 ± 0.3 g kg^{-1} and 0.5 ± 0.1 g kg^{-1}, $P > 0.05$, $n = 4$). These data confirm our hypothesis that graminivory by kangaroo rats generates litter with an elevated nitrogen status compared to that provided by naturally senesced grass. The nitrogen content of tillers which senesce naturally may be resorbed by the plant, so cutting the stalks while still green prevents the plant from resorbing these nutrients.

We conclude therefore that graminivory by kangaroo rats influences the quantity and quality of litter produced in desert habitats. The grass cuttings discarded on the soil surface increase the availability of this material to termites, one of the most important species breaking down litter (Whitford et al. 1982). Litter consumed by subterranean termites does not contribute to soil organic matter or soil nitrogen stores (Nash and Whitford 1995). Wind redistribution of clippings results in burial of a portion of this material in rodent cache pits (Steinberger and Whitford 1983). Buried litter is decomposed by biological processes at a higher rate than exposed material (Santos et al. 1984) and contributes to nutrient cycling while organic material on the surface decomposes primarily by abiotic processes.

Plant fragments on the soil surface are decomposed primarily by ultraviolet light combined with high temperatures that break down the lignins (MacKay et al. 1994). Thus grass fragments that are not buried contribute virtually nothing to soil organic matter and most of these fragments are consumed by termites (Whitford 1991). However litter that is, for instance, buried, or trapped in rodent cache pits, decomposes rapidly, contributes the recalcitrant fraction of the litter to the soil organic carbon pool, and contributes directly to nitrogen cycling (Parker et al. 1984; Fisher et al. 1990). The higher nitrogen content of freshly cut tillers reduces or eliminates the nitrogen immobilization phase in decomposing buried fragments thereby contributing to the supply of available nitrogen by mineralization (Whitford et al. 1987). Thus, kangaroo rat graminivory contributes directly to nutrient cycling in desert grassland ecosystems.

Impact on seed production

An important effect of kangaroo rat graminivory is the loss of seed production of grasses subjected to cutting of flowering\seeding tillers. In a desert shrubland on the Jornada that is similar to the Portal site, an average of 59% of tillers had been cut from a sample of 60 *S. flexuosus*. On a Jornada grassland site, 12% of the tillers from a sample of 50 *S. flexuosus* plants were cut. This suggests that a considerable amount of the reproductive effort of these grasses was lost to graminivory.

Of the *S. flexuosus* stalks on the Jornada desert shrub site that had been cut by kangaroo rats, 90% ($n = 50$) still had their fruiting heads intact. It appears that the kangaroo rats cut-off and consume only the lower green stems of these grasses, exhibiting dietary selection similar to that of *S. hispidus*, which in its consumption of the lower green stems of grasses selects for plant parts with high soluble carbohydrate content and short handling time (Randolph et al. 1991). The impact of graminivory on seed production is in addition to the contribution by rodents to seed dynamics through granivory, the latter being normally calculated on the basis of the contribution of seeds in the diet towards satisfying the energy requirements of the rodent populations. Such estimates of seed consumption vary from 37 to 86% of seed production in desert shrublands (Chew and Chew 1970; Soholt 1973), with a single estimate of 0.8% in desert grasslands (Pulliam and Brand 1975). The impact of rodent graminivory on seed dynamics demonstrated here augments that of direct granivory, potentially by several orders of magnitude. The estimate of Pulliam and Brand (1975) of the consumption of 0.8% of annual seed production by rodents in desert grasslands needs to be adjusted by the loss of seed production via graminivory. Such an adjustment could potentially raise the value to the levels estimated for desert shrublands.

Composition of the grass community

Brown and Heske (1990) and Heske et al. (1993) reported that the extensive increase of grass cover in their kangaroo rat exclosures could largely be attributed to the introduced African Lehmann's love grass, *Eragrostis lehmanniana*. We hypothesized that this increase in a specific grass species could be due to selective graminivory by kangaroo rats, and compared species specific frequencies of cuttings (Table 4). The frequency of cuttings differed markedly between species ($\chi^2 = 113.7$, $df = 12, P < 0.001$), ranging between 88 and 0% of tussocks (Table 4). *E. lehmanniana* is relatively infrequently cut by kangaroo rats, with only 34% of tussocks having cuttings.

We suggest that those species which are subjected to high graminivory by kangaroo rats such as *Digitaria californica*, *Bothriochloa saccharoides*, *Sporobolus* sp., *Aristida ternipes* and *Setaria* sp. are at a competitive disadvantage compared to other, less eaten grasses. The fact that *Bouteloua curtipendula*, *B. eriopoda*, *Hilaria mutica* and *Muhlenbergia porteri* do not dominate these habitats despite limited graminivory must be due to other factors. For example, at these study sites *H. mutica* is restricted to heavy, clay soils and *B. curtipendula* is specific to arroyo-edge habitats. *Muhlenbergia porteri* establishes beneath shrubs and does not readily colonize open areas, while *B. eriopoda* is the only stoloniferous grass among the tall grasses that we sampled. The two *Bouteloua* species decreased in response to removal of kangaroo rats (Brown and Heske 1990; Heske et al. 1993), which suggests that these species are affected in some other fashion. *Dipodomys spectabilis* and *D. ordii* are both known to cut and utilize entire seed heads of *Bouteloua* sp. (Vorhies and Taylor 1922). These kangaroo rats may actually contribute to the spread and germination of *Bouteloua* by burying seed heads in scattered caches. Such burying of seed heads may provide protection from invertebrate seed predators (McAuliffe 1990).

Table 4 Species-specific frequencies of grass tussocks with grass cuttings for different grass species in the Chihuahuan Desert

Species	Cuttings present	Cuttings absent	% With cuttings
Digitaria californica	44	6	88.0%
Bothriochloa barbinodis	14	3	82.4%
Sporobolus airoides	41	9	82.0%
Aristida ternipes	45	11	80.4%
Setaria leucophila	43	14	75.4%
Sporobolus flexuosus	39	11	78.0%
Sporobolus cryptandrus	31	22	58.5%
Aristida purpurea	18	32	36.0%
Eragrostis lehmanniana	17	33	34.0%
Bouteloua curtipendula	13	37	26.0%
Hilaria mutica	8	42	16%
Bouteloua eriopoda	1	49	2.0%
Muhlenbergia porteri	0	50	0.0%
Mean ± SE for all species (n = 13)			50.7 ± 9.1%

We therefore hypothesize that the reason that *E. lehmanniana* has exhibited such extensive population increase at the Portal study site is due to a competitive advantage over other seed-producing grasses outside the treatment areas (where this species is dominant, personal observations), and consequent domination of the seed bank within the treatment areas (where the removal of kangaroo rat graminivory allows the tall grasses to flourish). These findings on the potential mechanism for the invasion of this grass have more widespread relevance than the increase of tussock-forming grasses at this site, as *E. lehmanniana* has spread aggressively throughout southern Arizona since its introduction in 1932 (Anable et al. 1992).

The consumption of green grass is not unusual for either *D. ordii* or *D. merriami*. The diets of both species have been recorded to be comprised of up to 35% grass and green foliage (Flake 1973; Soholt 1973). Consumption of green vegetation has been correlated with reproduction in desert rodents, including *D. merriami* (Beatley 1969, 1976; Bradley and Mauer 1971; Van De Graaff and Balda 1973; Reichman and Van De Graaff 1975; Soholt 1973, 1977). Flake (1973) recorded a peak in grass consumption by *D. ordii* during late summer/fall, with grass recorded in the diet of this species throughout the year. The peak of grass consumption recorded by Flake (1973) corresponds very well with onset of reproductive activity in *D. ordii* (Duke 1944; McCulloch and Inglis 1961). *D. ordii* has been shown to respond positively to ingestion of 6-MBOA, an estrogenic phytochemical that occurs in the new growth of grasses (Rowsemitt and O'Connor 1989). This suggests a role in addition to nutrition for grass consumption in *D. ordii* and *D. merriami*.

Mechanism for keystone status

Our observations of grass cutting by kangaroo rats provide an alternative explanation for the impact of these rats on grass dynamics to that based on seed predation and soil disturbance proposed by Brown and Heske (1990) and Heske et al. (1993). Graminivory by kangaroo rats provides a direct mechanism to explain their impact on the abundance of tall tussock-forming grasses. Furthermore, the selective nature of this graminivory provides a basis for an understanding of why a specific grass should have increased so dramatically in the absence of kangaroo rats.

Our postulated scenario to explain the changes in grass cover observed by Brown and Heske (1990) and Heske et al. (1993) in response to the removal of kangaroo rats therefore has two components. Firstly, the increase in the tall grass guild may be a result of the removal of kangaroo rat graminivory of the tillers of these grasses. Presumably such grass cutting would depress those grass populations. Secondly, the specific increase in *E. lehmanniana* may due to a competitive advantage that this species has over the other tall grasses, as it is subjected to less kangaroo rat graminivory.

In the past the role of desert rodents as granivores has received considerable attention. The present study shows that these species are playing a much broader role in desert environments, affecting the production of grasses and their seed, litter production and possibly the composition of grass communities. The analogous observation by Meehan et al. (1977) that *Perognathus* sp. were affecting the numbers and distribution of the perennial shrub *Polygala deserticum* in the southern Mohave Desert through direct herbivory, indicates that the impact of herbivory by desert rodents is not limited to grasses. This process is also not restricted to the North American deserts. In a description of the ecology of *Dipus sagitta*, Fenuik and Kazantzeva (1936, p. 416) wrote "While feeding, the jerboas show the wastefulness common to the majority of wild animals, for they sever a stalk and eat a bit of it, only to repeat the whole process".

Conclusion

We agree with Brown and Heske (1990) and Heske et al. (1993) that kangaroo rats are keystone species in Chihuahuan desert ecosystems. We do however suggest that this keystone role is due not only to kangaroo rat granivory, but also to their graminivory. The previous emphasis on kangaroo rat granivory has probably masked other important animal/plant interactions and their contribution to ecosystem processes. The implications of kangaroo rat graminivory for maintenance and restoration of grasslands and ecosystem processes need to be further explored.

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