

## Burrowing activities of kangaroo rats and patterns in plant species dominance at a shortgrass steppe-desert grassland ecotone

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**Abstract.** Our objective was to evaluate the effects of burrowing activities by banner-tail kangaroo rats (*Dipodomys spectabilis* Merriam) on plant community structure and species dominance for two patch types at the ecotone between shortgrass steppe and desert grassland in New Mexico, USA. 10 mounds produced by kangaroo rats were selected in patches dominated by *Bouteloua gracilis* (the dominant in shortgrass steppe communities) and 10 mounds were selected in patches dominated by *B. eriopoda* (the dominant in Chihuahuan desert grasslands). Plant cover and density by species were sampled from three locations associated with each mound: the mound proper, the edge of the mound in the transition area, and the off-mound vegetation. Similar cover of *B. eriopoda* for the edges of mounds in both patch types indicates the ability of this species to respond to animal disturbances regardless of the amount of cover in the surrounding undisturbed vegetation. By contrast, cover of *B. gracilis* was low for all mounds and mound edges in patches dominated by this species. Much higher cover of *B. eriopoda* on mound edges compared to the undisturbed vegetation in *B. gracilis*-dominated patches indicates that kangaroo rats have important positive effects on this species. Lower cover of perennial grasses and higher cover of forbs, shrubs, and succulents on the edges of mounds in *B. eriopoda*-dominated patches compared to patches dominated by *B. gracilis* indicate the importance of surrounding vegetation to plant responses on disturbed areas.

Our results show that kangaroo rats have important effects on both species dominance and composition for different patch types, and may provide a mechanism for small-scale dominance patterns at an ecotone; thus providing further support for their role as keystone species in desert grasslands.

**Keywords:** *Bouteloua*; Chihuahuan desert; *Dipodomys spectabilis*; Disturbance; Dominant species; Kangaroo rat.

**Nomenclature:** Stubbendieck et al. (1992).

### Introduction

Naturally-occurring small-scale disturbances are an important component of many ecosystems (Pickett & White 1985). Although specific effects vary, all disturbance events result in an alteration of resource availability and ecosystem structure. Disturbances also result in mortality for some plants and establishment for others, thus creating a mosaic of successional and undisturbed microsites across the landscape (Bormann & Likens 1979; Denslow 1980; Lavorel et al. 1994). Each disturbance microsite undergoes its own successional dynamics through time that is influenced by plant life history traits interacting with disturbance characteristics, such as intensity and size (Klinkhamer & de Jong 1988; Chambers 1995; McIntyre et al. 1995; Wiegand et al. 1997). At the scale of the landscape, vegetation dynamics are not only determined by microsite-level processes, such as competition, but also by larger-scale characteristics including plant community composition of the landscape and transfer of materials (notably seeds) among microsites (Gibson 1989; Coffin & Lauenroth 1994; Milton et al. 1997).

For landscapes that consist of a number of different patch types defined by their dominant species, such as at ecotones between biome types, the effects of disturbances on vegetation dynamics are expected to depend upon the vegetation characteristics of each patch. Our use of the term ecotone follows Curtis (1959), and is based on phytogeographical transition zones with strong temporal fluctuations in climate across the boundary; this differentiates ecotones from ecoclines (van der Maarel 1990). Soil texture, topography, and other edaphic and microclimatic factors are important in producing patches of variable size and species composition at ecotones (Neilson 1991; Gosz 1992, 1993; Brown 1994; Breck & Jenkins 1997). Small-scale disturbances interacting with patch characteristics may also be important,

especially for patterns in dominant species that are not explained well by uniform soil properties, although to our knowledge this has not been tested. Our hypothesis is that small-scale disturbances have different effects on vegetation dynamics and patterns in species dominance depending on the patch characteristics and life history traits of plants responding to disturbances. Furthermore, at ecotones, these disturbances may be important in determining small-scale patterns in species dominance from adjacent biomes.

The burrowing activity of banner-tail kangaroo rats (*Dipodomys spectabilis* Merriam) is one type of small-scale animal disturbance that affects small-scale to landscape-scale patterns in plant community structure (Heske et al. 1993; Guo 1996). Banner-tail kangaroo rats are heteromyid New World rodents, occurring primarily in arid shrublands and grasslands, that construct complicated subterranean chambers and tunnels (Van der Wall 1990). Each burrow is capped by a large mound, sometimes over 1 m high and 1.5–4.5 m in diameter (Van der Wall 1990). Mounds are long-lived (>30 yr; Chew & Whitford 1992) and differ in vegetation and soil properties from the surrounding habitat (Guo 1996). Kangaroo rats are agents of soil and plant disturbance as a result of constructing these burrows, digging tunnels, disturbing surrounding soil as they forage for seeds, and building seed caches (Reichman et al. 1985). Their mounds create disturbance gaps by killing plants, and contribute to local species diversity by forming microhabitats that support diverse plant and animal communities (Hawkins & Nicoletto 1992; Guo 1996). Many studies have shown that plant cover tends to be lower and species diversity higher on mounds than in adjacent, off-mound areas due to lower soil water and higher nitrogen contents on mounds (Moroka et al. 1982; Moorhead et al. 1988; Mun & Whitford 1990).

In Chihuahuan desert plant communities of the southwestern U.S., areas affected by banner-tail kangaroo rat mounds are large (>20 m<sup>2</sup>/mound) and mounds occur at sufficient densities (2 to >10/ha) to result in >10% of a site being affected by mounds (Wood 1969). Kangaroo rats have a major impact on vegetation structure in a number of patch types or landscape units including those dominated by various species of grasses and shrubs (Moroka et al. 1982). As a result of these large effects on the vegetation relative to their low abundance, banner-tail kangaroo rats have been identified as keystone species – *sensu* Power et al. (1996) – (Brown & Heske 1990).

At the ecotone between Chihuahuan desert grasslands and shortgrass steppe communities in central New Mexico, kangaroo rats affect patches dominated by *Bouteloua eriopoda* (black grama), the dominant grass in Chihuahuan desert grasslands, or *B. gracilis* (blue grama), the dominant grass in shortgrass steppe com-

munities. These two species differ in their life history traits, especially in response to disturbances that may affect their ability to dominate in the presence of small disturbances, such as mounds produced by banner-tail kangaroo rats. *B. eriopoda* is a short-lived grass that may respond rapidly to disturbance through the production of long stolons (Nelson 1934; Wright & Van Dyne 1976). By contrast, *B. gracilis* is a long-lived, slow-growing bunchgrass with limited ability to respond to disturbance either vegetatively or through seedling establishment (Samuel 1985; Coffin et al. 1996). Differences in species or life-form composition of patches dominated by one or the other *Bouteloua* species (Kröel-Dulay et al. 1997) may result in patch-specific patterns in vegetation associated with mounds.

Our overall objective was to determine the role of banner-tail kangaroo rats in generating small-scale patterns in vegetation at a desert grassland-shortgrass steppe ecotone. We had two specific objectives associated with the activities of kangaroo rats: (1) to evaluate effects of burrowing activity on species dominance by *B. eriopoda* and *B. gracilis*; and (2) to evaluate effects of burrowing activity on life-form composition for mounds in patches dominated by either *B. eriopoda* or *B. gracilis*.

## Study area

The study was conducted at the Sevilleta National Wildlife Refuge (SNWR; 34.5°N, 106.9°W) located ca. 75 km south of Albuquerque, New Mexico, USA. The SNWR is a 100 000-ha wildlife refuge established in 1973 and managed by the U.S. Fish and Wildlife Service; the refuge is also a Long-Term Ecological Research site (<http://sevilleta.unm.edu>). Grazing by cattle has been excluded from the SNWR since 1973, although grazing by native herbivores, such as pronghorn antelope and rabbits, occurs at a low intensity.

The climate of the SNWR is semi-arid to arid with high temporal and spatial variability. Long-term (65 yr) mean annual precipitation was 231 mm/yr (*sd*=70.4) and annual temperatures averaged 14.2°C (*sd*=0.7). Precipitation during the year of the study (1997) was 325 mm with above-average amounts during the growing season (April through September). Average monthly temperature in 1997 was 12.9°C with average temperatures occurring during the growing season. The location selected for this study was the McKenzie Flats (1450 m elevation) where vegetation is typical of the Chihuahuan desert grasslands-shortgrass steppe transition zone. Patches of variable size (<10 m<sup>2</sup> to >1000 m<sup>2</sup>) and shape may be dominated or codominated by *B. eriopoda* or *B. gracilis* at this location (Gosz 1995; Gosz & Gosz 1996;

Kröel-Dulay et al. 1997). Other associated species of annual and perennial grasses and forbs, cactus, and shrubs can be found in all patch types. The specific area is located near the 'Deep Well' intensive study site and meteorological station maintained by the LTER.

## Methods

### Mound selection

Mounds of banner-tail kangaroo rats were selected from within patches dominated by either *Bouteloua eriopoda* or *B. gracilis* where dominance was based on average cover > 75% of total plant cover. We identified eight patches, four dominated by each *Bouteloua* species, from within a 400m × 1000m area; each patch was ca. 200 m × 200m in size. From within each patch, we identified five active kangaroo rat mounds where activity was determined by unobstructed entrances to burrows and/or fresh fecal material near a mound. Only active mounds were used in this study in order to minimize variation in vegetation and soil properties due to recovery processes that begin after a mound is abandoned (Mun & Whitford 1990; Hawkins & Nicoletto 1992). Although mound age could not be determined, mounds are sufficiently long-lived (> 30yr; Chew & Whitford 1992) that differences in age are unlikely to affect vegetation dynamics. We then randomly selected a total of ten mounds to be sampled in each patch type. The area of each mound was estimated by measuring its outer length in two cardinal directions (north-south, east-west), and assuming an elliptical shape. Because average mound size was similar in *B. eriopoda* (11.3 m<sup>2</sup>) and *B. gracilis* (12.0 m<sup>2</sup>), mound size was not needed as a covariate in our analyses.

### Vegetation sampling

Average mound radius was used to locate the center of each mound. Vegetation was sampled in July along four transects radiating within 5° of the four cardinal directions from the center of each mound, and extending to a distance of 25m away in vegetation considered typical of the patch type between mounds. Variation in the direction was necessary to avoid nearby mounds. Data were collected using a 2.0-m<sup>2</sup> quadrat placed at nine locations along each transect (in m from the mound center): 0.0, 1.5, 3.0, 5.0, 7.5, 10.0, 15.0, 20.0, and 25.0.

Distance between quadrats was short near the mound to allow intense sampling of this area and to increase sample size; most of the length of each transect was contained in the typical patch vegetation, thus longer distances between quadrats were used. Each quadrat

was recorded as occurring at one of three locations: on the mound ('mound') at the edge of the mound in the transition area ('edge'), or off the mound in typical vegetation between mounds ('off-mound'). Locations were defined based upon the frequency and intensity of burrowing activities of kangaroo rats as well as the amount of bare ground (based on the disturbance gradient of Guo 1996). Mound locations were characterized by frequent, unobstructed entrances to burrows, predominantly bare ground, and elevated topography. Edges were defined as the transitional area surrounding mounds that contained few burrows with an intermediate amount of bare ground. Off-mound vegetation was characterized by no burrowing activity and low amounts of bare ground.

For each quadrat, canopy cover only (to the nearest 1 %) was estimated for bare ground and litter combined, and by species for perennial grasses where vegetative spread by tillers or stolons makes identification of individuals difficult, thus density estimates are imprecise. Data were collected by species for *B. eriopoda*, *B. gracilis*, and other frequently-occurring grasses including *Hilaria jamesii*, *Sporobolus flexuosus* and *Aristida purpurea*; all other perennial grasses were combined into one cover estimate for each quadrat. Canopy cover (%) and density (no./2 m<sup>2</sup>) were estimated for species where individual plants are easily determined, including shrubs (*Gutierrezia sarothrae*, *Ephedra viridis*) and succulents (*Yucca glauca*, *Opuntia* spp.). Cover and density of annual and perennial forbs and subshrubs including:

<i>Astragalus</i> spp.	<i>Chaetopappa ericoides</i>
<i>Cryptantha crassiseppala</i>	<i>Glandularia wrightii</i>
<i>Hymenopappus filifolius</i>	<i>Kraschninnikovia lanata</i>
<i>Machaeranthera pinnatifida</i>	<i>Plantago patagonica</i>
<i>Psilostrophe tagetina</i>	<i>Salsola kali</i>
<i>Solanum elaeagnifolium</i>	<i>Sphaeralcea</i> spp.

were determined as a group for each quadrat due to low frequencies of occurrence. Because sampling was conducted in the middle of the growing season (July), cover of all species are likely underestimates of peak growth for that year.

### Statistical analyses

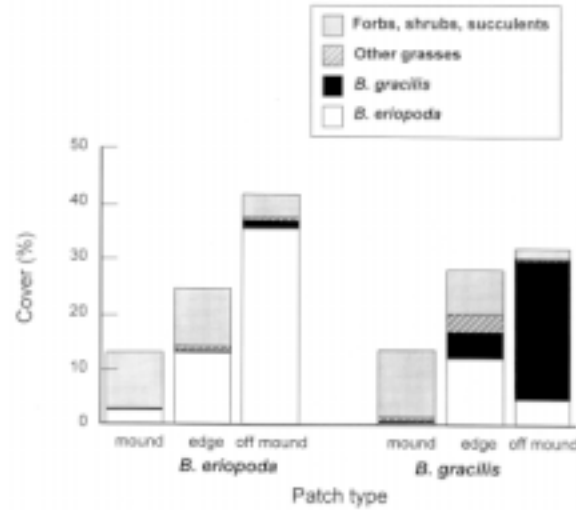
The data were analysed using analysis of variance to test for the significance of patch type (*B. eriopoda*- or *B. gracilis*-dominated) and sampling location (mound, edge, off-mound) on cover or density of the vegetation. The design included patch type as the between subjects factor and location as the within subject factor. Dependent variables were analysed separately, and included cover of five species or species-groups: (1) *B. eriopoda*; (2) *B. gracilis*; (3) other grasses combined; (4) forbs,

shrubs and succulents combined; and (5) the total. Species-groups were used for grasses other than the two *Bouteloua* species, and for forbs, shrubs and succulents due to small sample sizes for individual species. Density of the forbs, shrubs, and succulents group was also analysed. Least significant difference (LSD) means comparison tests were used to identify significantly different means at the 0.05 level. Two separate means comparisons tests were conducted for each response variable. Effects of patch type were determined by comparing cover or density of each species or group within the three locations. A similar analysis was conducted for determining effects of location on cover or density within each patch type.

## Results

Life-form composition based on species-groups on mounds and for the off-mound vegetation had similar patterns for *B. eriopoda* and *B. gracilis*-dominated patches. Vegetation on all mounds sampled was dominated by forbs, shrubs, and succulents (>77% of the total) whereas most cover of the off-mound vegetation was attributed to the dominant species of the patch, either *B. eriopoda* (85%) or *B. gracilis* (78%) (Fig. 1). Vegetation on edges of mounds in both patch types was dominated by *B. eriopoda* (>43% of the total) and forbs, shrubs and succulents (>28%). Edges of mounds in *B. gracilis* patches also had large cover of *B. gracilis* and other grasses that was not evident for edges in *B. eriopoda* patches. For both patch types and all locations, *Hilaria jamesii* had the highest proportion of cover in the other grasses group (>0.20) and *Gutierrezia sarothrae* had the highest proportion (0.20 to 0.48) for the forbs, shrubs, and succulents group.

Cover of *B. eriopoda* was lowest on mounds and increased as distance increased from the edge to the off-



**Fig. 1.** Cover of *Bouteloua eriopoda*, *B. gracilis*, and two species-groups for three locations in patches dominated by either *B. eriopoda* or *B. gracilis*.

mound vegetation in patches dominated by this species (Table 1). By contrast, in patches dominated by *B. gracilis*, cover of *B. eriopoda* was significantly higher in edge locations compared to mounds or off-mound vegetation. Furthermore, cover of *B. eriopoda* was similar in edge locations for both patch types whereas cover of this species was significantly higher for mounds and off-mound vegetation in patches dominated by this species compared to the corresponding locations in *B. gracilis*-dominated patches.

Different spatial patterns were found for cover of *B. gracilis* vs. *B. eriopoda*. For both patch types, *B. gracilis* cover was lowest on mounds with insignificant differences between patch types, and it increased as distance from mounds increased into the off-mound vegetation (Table 1). Cover of *B. gracilis* was significantly

**Table 1.** Average and standard error of canopy cover (%) and/or density (no./m<sup>2</sup>) for *Bouteloua eriopoda*, *B. gracilis*, two species-groups, and the total for two patch types and three locations<sup>1</sup>.

Species or group		<i>B. eriopoda</i> patch			<i>B. gracilis</i> patch		
		Mound	Edge	Off-mound	Mound	Edge	Off-mound
<i>Bouteloua eriopoda</i>	cover	2.9 <sup>c</sup> <sub>a</sub> (0.6)	13.4 <sup>b</sup> <sub>a</sub> (1.2)	35.7 <sup>a</sup> <sub>a</sub> (0.7)	0.7 <sup>c</sup> <sub>b</sub> (0.3)	12.7 <sup>a</sup> <sub>a</sub> (1.3)	4.9 <sup>b</sup> <sub>b</sub> (0.6)
<i>Bouteloua gracilis</i>	cover	0.02 <sup>b</sup> <sub>b</sub> (0.02)	0.1 <sup>b</sup> <sub>b</sub> (0.1)	1.4 <sup>a</sup> <sub>b</sub> (0.3)	0.2 <sup>c</sup> <sub>a</sub> (0.1)	4.5 <sup>b</sup> <sub>a</sub> (0.6)	25.0 <sup>a</sup> <sub>a</sub> (0.6)
Other grasses	cover	0.2 <sup>c</sup> <sub>a</sub> (0.1)	1.0 <sup>a</sup> <sub>b</sub> (0.2)	0.5 <sup>b</sup> <sub>a</sub> (0.1)	0.8 <sup>b</sup> <sub>a</sub> (0.3)	3.3 <sup>a</sup> <sub>a</sub> (0.5)	0.6 <sup>c</sup> <sub>a</sub> (0.1)
Forbs, shrubs, succulents	cover	10.1 <sup>a</sup> <sub>a</sub> (0.8)	10.4 <sup>a</sup> <sub>a</sub> (0.6)	4.4 <sup>b</sup> <sub>a</sub> (0.3)	12.2 <sup>a</sup> <sub>a</sub> (1.2)	8.0 <sup>b</sup> <sub>b</sub> (0.9)	1.7 <sup>c</sup> <sub>b</sub> (0.2)
	density	6.7 <sup>a</sup> <sub>a</sub> (0.5)	6.8 <sup>a</sup> <sub>a</sub> (0.4)	2.9 <sup>b</sup> <sub>a</sub> (0.2)	4.2 <sup>a</sup> <sub>b</sub> (0.3)	4.3 <sup>a</sup> <sub>b</sub> (0.4)	1.0 <sup>b</sup> <sub>b</sub> (0.1)
Total cover		13.2 <sup>c</sup> <sub>a</sub> (1.0)	24.9 <sup>b</sup> <sub>b</sub> (1.1)	42.0 <sup>a</sup> <sub>a</sub> (0.6)	13.8 <sup>c</sup> <sub>a</sub> (1.3)	28.5 <sup>b</sup> <sub>a</sub> (1.2)	32.1 <sup>a</sup> <sub>b</sub> (0.6)

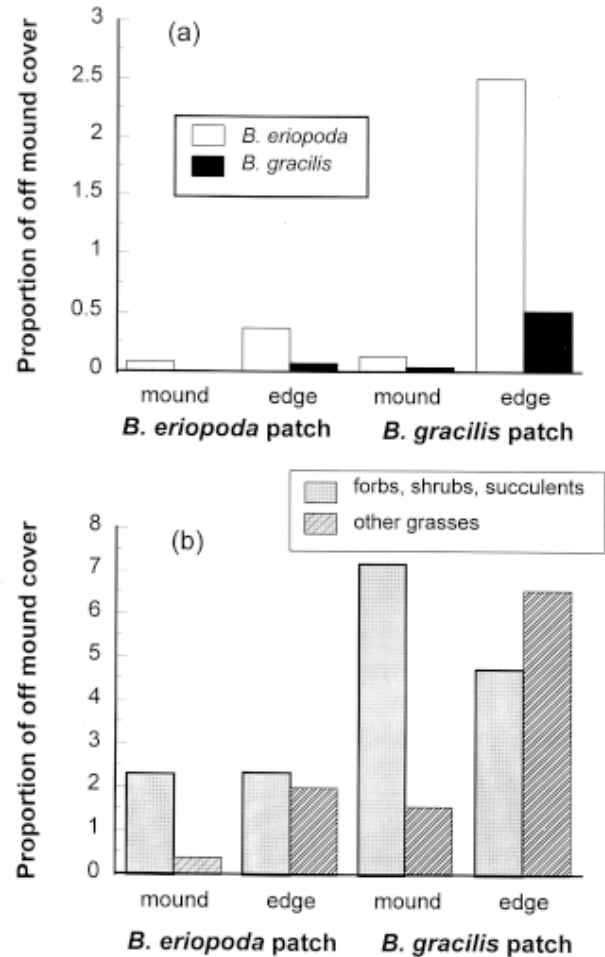
<sup>1</sup>Different superscripts indicate significantly different means ( $P < 0.05$ ) between locations and within patch types. Different subscripts indicate significantly different means ( $P < 0.05$ ) between patch types and within locations.

higher for edge and off-mound locations in patches dominated by this species compared to corresponding locations in *B. eriopoda*-dominated patches.

Cover of grasses other than the two *Bouteloua* species was highest in the edge locations for both patch types with the largest cover of all locations occurring in edges of *B. gracilis*-dominated patches (Table 1). Cover of this group was significantly higher in *B. gracilis*-dominated patches compared to patches dominated by *B. eriopoda* for both locations affected by kangaroo rats (mounds, edges). In most cases for both patch types, cover and density of forbs, shrubs, and succulents were similar for both locations affected by kangaroo rats and significantly higher than the corresponding off-mound vegetation (Table 1). Except for similarly high cover on mounds, cover and density of this group were significantly higher for each location in *B. eriopoda*-dominated patches compared to corresponding locations in *B. gracilis*-dominated patches. Spatial patterns in total cover were the same as for *B. gracilis*: lowest total cover was found on mounds and highest cover occurred in the off-mound vegetation (Table 1). Similar total cover was found within each location and between patch types for mounds and edges; significantly higher total cover was found in off-mound vegetation of *B. eriopoda*-dominated patches compared to patches dominated by *B. gracilis*.

## Discussion

Disturbances created by the activities of animals are important in generating and maintaining spatial and temporal heterogeneity in various types of plant communities (e.g. Platt 1975; Collins & Barber 1985; Coffin & Lauenroth 1988; Hobbs & Mooney 1995; Milton et al. 1997; Weltzin et al. 1997). Responses of vegetation to these small, patchy disturbances has been attributed to both the life history traits of colonizing plants and the characteristics of the disturbance (Denslow 1980; Chambers 1995; McIntyre et al. 1995; Wiegand et al. 1997). Our results indicate that disturbances created by banner-tail kangaroo rats have important effects on species dominance at an ecotone due to differences in life history traits of the dominant species, and provide further support for keystone status by kangaroo rats in desert grasslands (Brown & Heske 1990; Heske et al. 1993; Kerley et al. 1997). Furthermore, our results conducted in different patch types defined by the dominant species support previous studies showing that the vegetation surrounding a disturbed area is another important component of the recovery process (Gibson 1989).



**Fig. 2.** Cover for two locations affected by kangaroo rats as a proportion of cover in the surrounding undisturbed vegetation for patches dominated by either *Bouteloua eriopoda* or *B. gracilis*; **a.** cover of *B. eriopoda* and *B. gracilis*; **b.** perennial grasses other than the two *Bouteloua* species and forbs, shrubs, and succulents.

### Response by dominant species

Similar cover of *B. eriopoda* for edges of kangaroo rat mounds in patches dominated by either *B. eriopoda* or *B. gracilis* indicates the ability of this species to respond to soil disturbances regardless of the amount of its cover in the surrounding off-mound vegetation, the most likely source of propagules for recovery. By contrast, cover of *B. gracilis* was low for all areas affected by burrowing activities of kangaroo rats in both patch types reflecting a reduced ability to colonize disturbed areas. Differences in life history traits may explain these species-specific responses to disturbance. *B. eriopoda* is a short-lived perennial (35-40 yr; Wright & Van Dyne 1976) with a fast vegetative growth rate through the production of stolons (Nelson 1934). *B. gracilis* is a long-lived perennial (ca. 400 yr; Coffin & Lauenroth

1990) with a slow rate of spread through the production of tillers (Samuel 1985). Thus, these vegetative traits would be expected to allow *B. eriopoda* to invade disturbed areas more quickly than *B. gracilis*. Recovery through seedling establishment is an alternative explanation if seeds are available to the areas affected by kangaroo rats, either through abiotic (wind) or biotic dispersal mechanisms (i.e., caching by kangaroo rats, Vorhies & Taylor 1922; Reichman et al. 1985). Recent simulation analyses indicate that precipitation and temperature amount and seasonality at the SNWR favor *B. eriopoda* establishment more frequently than *B. gracilis* establishment (Minnick & Coffin in press). However, specific microenvironmental conditions associated with soil properties on and around mounds were not simulated. Another alternative hypothesis is that the two *Bouteloua* species differ in their palatability or in their response to herbivory by *D. spectabilis*, but this has not been tested.

Furthermore, much higher cover of *B. eriopoda* on edges around kangaroo rat mounds compared to the off-mound vegetation in patches dominated by *B. gracilis* (2.5×; Fig. 2a) suggests that this species is positively affected by kangaroo rat activity; similar beneficial responses were not observed for *B. gracilis* in either patch type (Fig. 2a). Processes that determine dominance by one or the other *Bouteloua* species at their ecotone are not well-understood; patterns in dominance are only partly explained by soil properties (J.R. Gosz pers. observ.) and patterns of resource use (Coffin 1997). Species-specific responses to small, patchy disturbances or herbivory by kangaroo rats may provide an alternative mechanism to explain local patterns in dominance by *B. eriopoda* at this site. Because the two *Bouteloua* species differ in their ability to withstand prolonged drought and heavy grazing by large herbivores (Lauenroth & Milchunas 1991; Schmutz et al. 1991), processes that shift the plant community towards one species or another have important consequences for system stability; thus our results provide further support for the role of kangaroo rats functioning as keystone species in desert grasslands (Brown & Heske 1990; Heske et al. 1993; Kerley et al. 1997).

#### Importance of patch type

Vegetation on kangaroo rat mounds located in patches dominated by *B. eriopoda* was similar in some aspects, yet different in others, to mounds located in patches dominated by *B. gracilis*. Dominance of vegetative cover by non-grasses (forbs, shrubs, and succulents) on all mounds in our study, regardless of patch type, is similar to previous studies showing an increase in annuals on mounds created by small animals compared to off-

mound vegetation dominated by perennial grasses (Platt 1975; Coffin & Lauenroth 1989). Our results also confirm previous studies of effects of kangaroo rat mounds on vegetation (Moroka et al. 1982; Mun & Whitford 1990; Guo 1996). Increase in annuals on mounds has been attributed to higher nitrate and total nitrogen contents of mound soils compared to undisturbed areas (Moorhead et al. 1988).

Lower cover of perennial grasses other than the two *Bouteloua* species and higher cover of forbs, shrubs, and succulents on edges of mounds in *B. eriopoda*-dominated patches compared to *B. gracilis*-dominated patches supports previous studies indicating the importance of surrounding vegetation to areas affected by small animals (Gibson 1989), although one study did not find an effect of vegetation type on plant responses to kangaroo rat mounds (Moroka et al. 1982). In our study, stronger effects of patch type can be seen by comparing cover by species-group on mounds or edges as a proportion of the surrounding off-mound vegetation. Within each location, cover of each group as a proportion of its respective off-mound cover was higher in *B. gracilis*-dominated patches compared to *B. eriopoda* patches (Fig. 2b). This increased response in subordinate species on mounds and edges in *B. gracilis*-dominated patches likely reflects differences in characteristics of the off-mound patches rather than differences associated with areas affected by kangaroo rats. High cover of *B. eriopoda* within patches dominated by *B. gracilis* are common at this ecotone, and result in lower cover of other species. Patches dominated by *B. eriopoda* have little or no *B. gracilis*, but high cover of other grasses and forbs (Kröel-Dulay et al. 1997). Thus, disturbed and undisturbed areas in *B. gracilis* patches are less similar than corresponding areas in *B. eriopoda*-dominated patches.

Small animals such as kangaroo rats have important effects on spatial and temporal heterogeneity in vegetation through their consumption and redistribution of seeds and plant parts as well as by soil disturbance (Brown & Heske 1990; Heske et al. 1993; Guo 1996; Kerley et al. 1997). In our study, mounds of kangaroo rats were found to differentially affect the dominant plant species of Chihuahuan desert grasslands (*B. eriopoda*) and shortgrass steppe communities (*B. gracilis*), likely due to differences in their life history traits. These species-specific responses are expected to have important consequences for patterns in species dominance by these two species in that soil disturbance by kangaroo rats may provide favorable microsites for the continued dominance by the short-lived, yet fast growing, *B. eriopoda*. Conditions that promote the dominance by one of these congeneric species are not well-understood, and our study provides one possible explanation for patterns in dominance at their ecotone.

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## References

- Bormann, F.H. & Likens, G.E. 1979. *Pattern and process in a forested ecosystem*. Springer, New York, NY.
- Breck, S.W. & Jenkins, S.H. 1997. Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. *Ecography* 20: 253-263.
- Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J. Veg. Sci.* 5: 641-656.
- Brown, J.H. & Heske, E.J. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Chambers, J.C. 1995. Disturbance, life history strategies, and seed fates in alpine herbfield communities. *Am. J. Bot.* 82: 421-433.
- Chew, R.M. & Whitford, W.G. 1992. A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). *J. Arid Environ.* 22: 375-386.
- Coffin, D.P. 1997. Plant species dominance and soil water resources at a grassland-shrubland ecotone. *Bull. Ecol. Soc. Am.* 78: 70.
- Coffin, D.P. & Lauenroth, W.K. 1988. The effects of disturbance size and frequency on a shortgrass plant community. *Ecology* 69: 1609-1617.
- Coffin, D.P. & Lauenroth, W.K. 1989. Small scale disturbances and successional dynamics in a shortgrass community: Interactions of disturbance characteristics. *Phytologia* 67: 258-286.
- Coffin, D.P. & Lauenroth, W.K. 1990. A gap dynamics simulation model of succession in the shortgrass steppe. *Ecol. Model.* 49: 229-266.
- Coffin, D.P. & Lauenroth, W.K. 1994. Successional dynamics of a semiarid grassland: effects of soil texture and disturbance size. *Vegetatio* 110: 67-82.
- Coffin, D.P., Lauenroth, W.K. & Burke, I.C. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. *Ecol. Appl.* 6: 538-555.
- Collins, S.L. & Barber, S.C. 1985. Effects of disturbance in mixed-grass prairie. *Vegetatio* 64: 87-94.
- Curtis, J.T. 1959. *The vegetation of Wisconsin. An ordination of plant communities*. The University of Wisconsin Press, Madison, WI.
- Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia (Berl.)* 46: 18-21.
- Gibson, D.J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. *Am. Midl. Nat.* 121: 144-155.
- Gosz, J.R. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hanson, A.J. & di Castri, F. (eds.) *Landscape boundaries: consequences for biotic diversity and ecological fluxes*, pp. 55-75. Springer-Verlag, New York, NY.
- Gosz, J.R. 1993. Ecotone hierarchies. *Ecol. Appl.* 3: 369-376.
- Gosz, J.R. 1995. Edges and natural resource management: Future directions. *Ecol. Int.* 22: 17-34.
- Gosz, R.J. & Gosz, J.R. 1996. Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eriopoda*) to fire and herbivory. *J. Arid Environ.* 34: 101-114.
- Guo, Q. 1996. Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia (Berl.)* 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. *J. Arid Environ.* 23: 199-208.
- 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 (Berl.)* 95: 520-524.
- Hobbs, R.J. & Mooney, H.A. 1995. Spatial and temporal variability in California annual grassland: results from a long-term study. *J. Veg. Sci.* 6: 43-56.
- Kerley, G.I.H., Whitford, W.G. & Kay, F.R. 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia (Berl.)* 111: 422-428.
- Klinkhamer, P.G.L. & de Jong, T.J. 1988. The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. *J. Ecol.* 76: 383-392.
- Kröel-Dulay, G., Hochstrasser, T. & Coffin, D.P. 1997. Compositional comparison of grass-dominated patches at a semiarid-arid grassland ecotone. *Bull. Ecol. Soc. Am.* 78: 272.
- Lauenroth, W.K. & Milchunas, D.G. 1991. Short-grass steppe. In: Coupland, R.T. (ed.) *Natural grasslands: Introduction and western hemisphere*, pp. 183-226. Ecosystems of the World, 8A. Elsevier, Amsterdam.
- Lavorel, S., O'Neill, R.V.O. & Gardner, R.H. 1994. Spatio-temporal dispersal strategies and annual plant species coexistence in a structured landscape. *Oikos* 71: 75-88.
- McIntyre, S., Lavorel, S. & Tremont, R.M. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 83: 31-44.
- Milton, S.J., Dean, W.R.J. & Klotz, S. 1997. Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *J. Veg. Sci.* 8: 45-54.
- Minnick, T. J. & Coffin, D.P. In press. Geographic patterns of simulated establishment of two *Bouteloua* species: Impli-

- cations for distributions of dominants and ecotones. *J. Veg. Sci.* 10
- Moorhead, D.L., Fisher, F.M. & Whitford, W.G. 1988. Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan desert grassland. *Am. Midl. Nat.* 120: 443-447.
- Moroka, N., Beck, R.F. & Pieper, R.D. 1982. Impact of burrowing activity of the bannertail kangaroo rat on southern New Mexico desert rangelands. *J. Range Manage.* 35: 707-710.
- Mun, H. & Whitford, W.G. 1990. Factors affecting annual plant assemblages on banner-tailed kangaroo rat mounds. *J. Arid Environ.* 18: 165-173.
- Neilson, R.P. 1991. Climatic constraints and issues of scale controlling regional biomes. In: Holland, M.M., Naiman, R.J. & Risser, P.G. (eds) *Role of landscape boundaries in the management and restoration of changing environments*, pp. 31-51. Chapman & Hall, New York, NY.
- Nelson, E.W. 1934. *The influence of precipitation and grazing upon black grama grass range*. United States Department of Agriculture Techn. Bull. 409, Washington, DC.
- Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Inc., Orlando, FL.
- Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol. Monogr.* 45: 285-305.
- Power, M.E., Tilman, T., Estes, J.A., Menge, B.A., Bond, W. J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. 1996. Challenges in the quest for keystones. *BioScience* 46: 611-620.
- Reichman, O.J., Wicklow, D.T. & Rebar, C. 1985. Ecological and mycological characteristics of caches in the mounds of *Dipodomys spectabilis*. *J. Mammol.* 66(4): 643-651.
- Samuel, M.J. 1985. Growth parameter differences between populations of blue grama. *J. Range Manage.* 38: 339-342.
- Schmutz, E.M., Smith, E.L., Ogden, P.R., Cox, M.L., Klemmedson, J.O., Norris, J.J. & Fierro, L.C. 1991. Desert grassland. In: Coupland, R.T. (eds) *Natural grasslands: introduction and western hemisphere*, pp. 337-362. *Ecosystems of the World*, 8A. Elsevier, Amsterdam.
- Stubbendieck, J., Hatch, S.L. & Butterfield, C.H. 1992. *North American range plants*. University of Nebraska Press, Lincoln, NE.
- van der Maarel, E. 1990. Ecotones and ecoclines are different. *J. Veg. Sci.* 1: 135-138.
- Van der Wall, S.B. 1990. *Food-hoarding mammals*. University of Chicago Press, Chicago, IL.
- Vorhies, C.T. & Taylor, W.P. 1922. Life history of the kangaroo rat, *Dipodomys spectabilis spectabilis* Merriam. USDA Bull. 1091, Washington, DC.
- Weltzin, J.F., Archer, S. & Heitschmidt, R.K. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78: 751-763.
- Wiegand, T., Dean, W.R.J. & Milton, S.J. 1997. Simulated plant population responses to small-scale disturbance in semi-arid shrublands. *J. Veg. Sci.* 8: 163-176.
- Wright, R.G. & Van Dyne, G.M. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwest. Nat.* 21: 259-274.
- Wood, J.E. 1969. *Rodent populations and their impact on rangelands*. Bull. 555. Agricultural Experiment Station, New Mexico State University, Las Cruces, NM.

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