

## A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosotebushes (*Larrea tridentata*)

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### Introduction

Several studies have shown the effects of the mounds of the banner-tailed kangaroo rat (*Dipodomys spectabilis* Merriam) on desert annuals. There can be effects on density, biomass and composition of the herbaceous assemblage (Moroka *et al.*, 1982; Mun & Whitford, 1989). As a result of a long-term study of a site in south-eastern Arizona, we observed a positive effect of these mounds on the growth, flowering and fruiting, and survival of creosotebush, which is the dominant woody perennial of the community. This effect became obvious at this site long after the kangaroo rats disappeared from the system, probably as a result of invasion of creosotebushes and other shrubby vegetation into what was previously a desert grassland system. Whereas creosotebushes had a negative effect on the kangaroo rat population, the mounds created by these rodents have had a residual positive effect on the creosotebushes.

A number of measurements were made to examine the nature of this unusual, if not unique, relationship, and to provide some basis for speculation as to the cause(s) of the positive effect.

### Study site

The site is a 9.3-ha cattle enclosure, established in 1958, in the San Simon Valley, 8 km north of Portal, Cochise County, Arizona. The site is at 1370 m on a very gentle slope (1.8%) of alluvium, largely derived from limestone. The soil is shallow over hard caliche. The vegetation is Chihuahuan desert scrub formed by degradation of semidesert grassland (Chew & Chew, 1965). The dominant plants are creosotebush (*Larrea tridentata* [D.C.] Coville), fluff grass (*Tridens pulchellus* [H.K.B.] Hitchc.), and snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby).

When the study site was established, the creosotebush population appeared to be in good condition; flowering, fruiting and shoot elongation seemed normal in 1958–9. It was speculated that there would be a gradual reduction in density, with survival of the larger shrubs and disappearance of smaller ones (Chew & Chew, 1965). This did not occur, as shown by measurements of sizes of individual creosotebushes, and shrub densities, done at 10-year intervals along permanently marked transects established in 1958. At first there

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was an increase in the size of small shrubs, a decrease in the size of large shrubs, and a maintenance of size of medium sized shrubs, while density was unchanged (Chew, unpubl. observations). When the last measurements were made (1988), it was obvious that all shrubs were declining in size and vigor, and had a high proportion of dead stems, except in the immediate vicinity of old mounds of the banner-tailed kangaroo rat and several other microsites. This was particularly obvious in the spring of 1989, and again in summer, when only shrubs around mounds flowered and set fruit (unpubl. observations). At this time, selected measurements were made on these islands of shrubs that were maintaining their growth and vigor.

## Methods

### *Soil nitrogen*

On 1 August 1988, ten pairs of soil samples were taken for analysis of soil nitrogen. Soil was removed with a corer to a depth of 15 cm from under a large or medium sized creosotebush immediately adjacent to a kangaroo rat mound and from a nearby smaller creosotebush that was beyond the zone of influence of the mound. Samples were put into plastic bags and immediately taken to the laboratory for analysis. An initial measurement was made of ammonia, nitrite and nitrate N ( $\text{mg kg}^{-1}$ ) in sieved subsamples.

After sieving (2-mm mesh), 25-g soil samples were incubated at 35°C in 50-ml plastic vials covered with 0.5 mil (0.0125 mm thick) polyethylene film to permit aeration and reduce moisture loss (Bremner & Douglas, 1971; Westermann & Crothers, 1980). Moisture content was adjusted to field capacity ( $0.1 \text{ g g}^{-1}$ ) using a syringe to add water through a small hole in the polyethylene film. The hole in the polyethylene also improved aeration. Moisture content was adjusted every 7 days during the incubation and subsamples were removed for inorganic N determination at days 28 and 56.

Inorganic N ( $\text{NH}_4\text{-N}$  and  $\text{NO}_3 + \text{NO}_2\text{-N}$ ) was determined in 2.0 M KCl extracts with a 10 : 1 ratio of soil to KCl (Keeney & Nelson, 1982). An automated salicylate procedure (Wall & Gehrke, 1975; Nelson, 1983) was used to measure  $\text{NH}_4\text{-N}$  in the extracts, and  $\text{NO}_3 + \text{NO}_2\text{-N}$  was measured by an automated Cd reduction procedure (Henriksen & Selmer-Olsen, 1970).

### *Mound geography*

In the spring of 1989, when creosotebushes were flowering, maps were drawn to scale for each mound ( $n = 16$ ) showing the size and relationship of the areas of: (1) the zone of influence of the mound, as defined by a polygon around the shrubs that were in flower; (2) the mound remnant within this zone; and (3) the open space, generally around the mound, within this zone. The current usage of each mound by packrats (*Neotoma albigula* Hartley) and Merriam's kangaroo rat (*Dipodomys merriami* Mearns), and the state of deterioration of the mound, were noted. One mound and its zone of influence, was mapped in detail to show position and size of each creosotebush.

### *Soil depth*

In spring and summer of 1989, soil depth measurements were made across the zone of influence of 10 mounds, and along 17, 30-m shrub measurement transects where there were no mounds. Soil depth was measured by driving a steel rod (15 mm diameter, 120 cm length), into the soil until it was stopped by indurated caliche. Repeat measurements were

made when there was suspicion that the rod had been stopped by a rock rather than caliche. Depths were measured at 1 or 2 m intervals along a tape line.

*Soil moisture measurements:* In summer, 1990, soil cores were taken at points along transects across three zones of influence, and soil moisture content was measured by oven-drying the samples at 60°C. Water contents of soil cores at different points were estimated.

## Results

### *Soil nitrogen*

In all cases, the initial concentration of mineral nitrogen (N in ammonia + nitrite + nitrate) was greater in the soil from under creosotebushes in the zone of influence of the mound than in that from under creosotebushes beyond the zone. The same was true after 4 weeks of incubation in the laboratory (Table 1). After 8 weeks, one pair of samples (mound B0, Table 1), had a greater value for the soil beyond the zone of influence. After 8 weeks of incubation, mineralization in samples from within the zone of influence, was an average of 141% of that of samples beyond the zone: 41.63 mg N kg<sup>-1</sup> soil near mounds vs. 29.45 mg N kg<sup>-1</sup> soil away from mounds (Table 1).

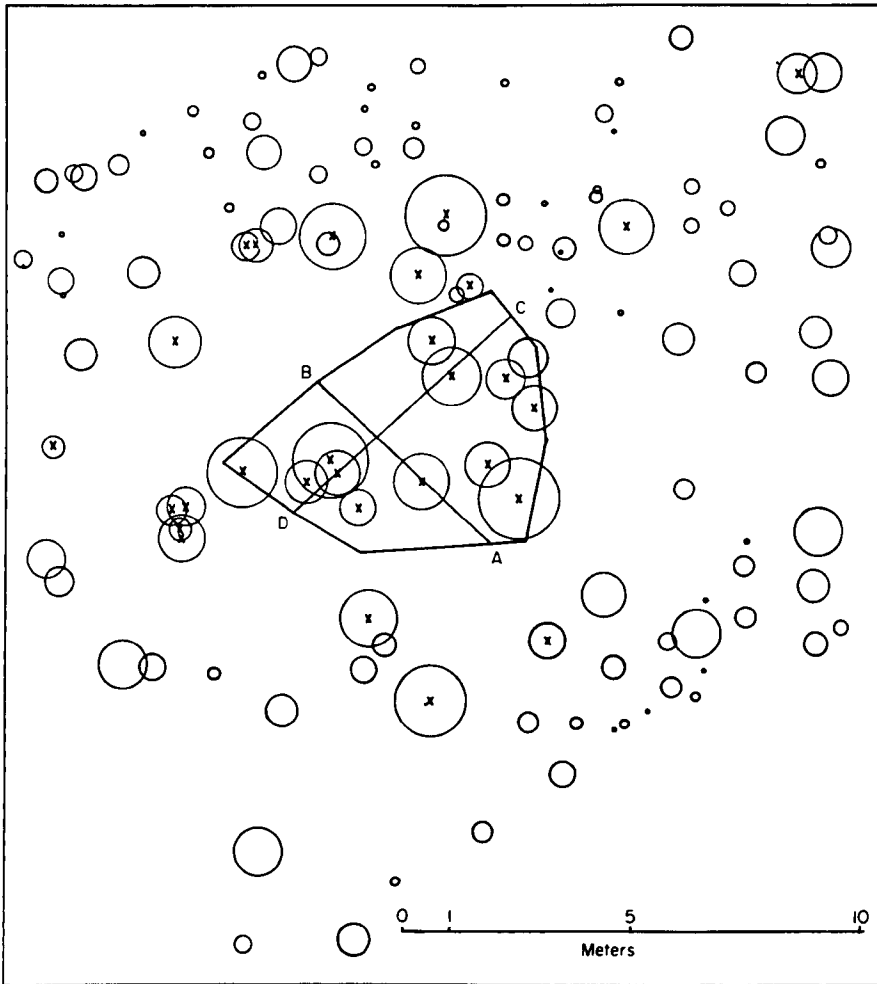
### *Mound geography*

Figure 1 shows the details of one mound (A1). The canopy coverage of each creosotebush is plotted as that of a circle, although canopies were usually elliptical. Canopies marked with an X in the centre are for shrubs that were in flower at the time. The zone of influence for this mound, as defined by a polygon around the outermost flowering shrubs (except for the one outlying shrub to upper right), was 94.4 m<sup>2</sup>. The size and vigor of creosotebushes (as defined by the proportion of dead stems), fell off sharply beyond the zone of influence. The area of discernible remaining mound, which was actively being used by *D. merriami* at the time, defined by the polygon in Fig. 1, was 27.8 m<sup>2</sup>. This mound is somewhat unusual in the number of shrubs that are established on the mound (rather than overlapping it with their canopies). A contiguous open area within the zone of influence had an area of 12.6 m<sup>2</sup>; about one-third of the open area overlaps the mound.

**Table 1.** Mineral nitrogen contents (the sum of NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup>) (mg kg<sup>-1</sup>) for soil under creosotebushes growing near mounds and bushes growing away from mounds. Initial values, and values after 8 weeks of incubation in the laboratory

Mound	Initial values		After 8 week incubation		Mineralization	
	Near mound	Away from mound	Near mound	Away from mound	Near mound	Away from mound
B0	2.9	2.2	36.8	39.9	33.9	37.7
D0	6.4	0.5	47.6	29.7	41.2	29.2
E2	4.4	3.9	91.5	44.9	81.1	41.0
E3	4.2	2.0	62.7	42.6	58.5	40.6
D4	3.3	1.4	60.5	44.4	57.2	43.0
E4	5.9	1.1	36.7	29.3	30.8	28.2
E5	15.0	1.2	44.9	15.2	29.8	14.0
C6	1.7	0.9	24.5	18.2	22.8	17.3
B4	3.7	1.4	28.2	24.6	24.5	23.2
B1	4.1	2.0	40.6	22.3	36.5	20.3

In paired comparison, with values converted to logarithms, the difference between near-mound soils and away-from-mound soils is highly significant for initial values, values at 8 weeks, and increase during 8 weeks (mineralization) ( $p < 0.005$ ).



**Figure 1.** Map of the vicinity of Mound A1. Circles show the location of creosotebushes and their relative coverages, ⊗ = blooming shrubs; blooming shrubs show the zone of influence of the old banner-tail mound on shrub vigor. Polygon outlines extent of old mound; A-B and C-D are soil depth transect lines.

The 16 mounds that were mapped averaged ( $\bar{x} \pm \text{S.D.}$ )  $83.7 \pm 37.7 \text{ m}^2$  for the zone of influence,  $13.5 \pm 8.3 \text{ m}^2$  for the discernable mound, and  $15.2 \pm 12.0 \text{ m}^2$  for open area. Collectively, the 16 zones of influence were 2.4% of the area that was surveyed ( $5.57 \text{ ha}$ , i.e.  $2.87 \text{ mounds ha}^{-1}$ ).

Of the 16 mound areas, 12 were still actively used: seven by *D. merriami*, four by *D. merriami* and *N. albigula*, and one by *N. albigula* alone. One mound was still apparent, but not inhabited; and in three cases, the old mound area was completely flattened by erosion and no rodent burrows were present.

#### Soil depth

For 184 measurements along 17, 30-m transects, mean soil depth ( $\bar{x} \pm \text{S.D.}$ ) was  $29.47 \pm 10.77 \text{ cm}$ . Means of individual transects ranged from 13.5 cm to 43.2 cm. Depth

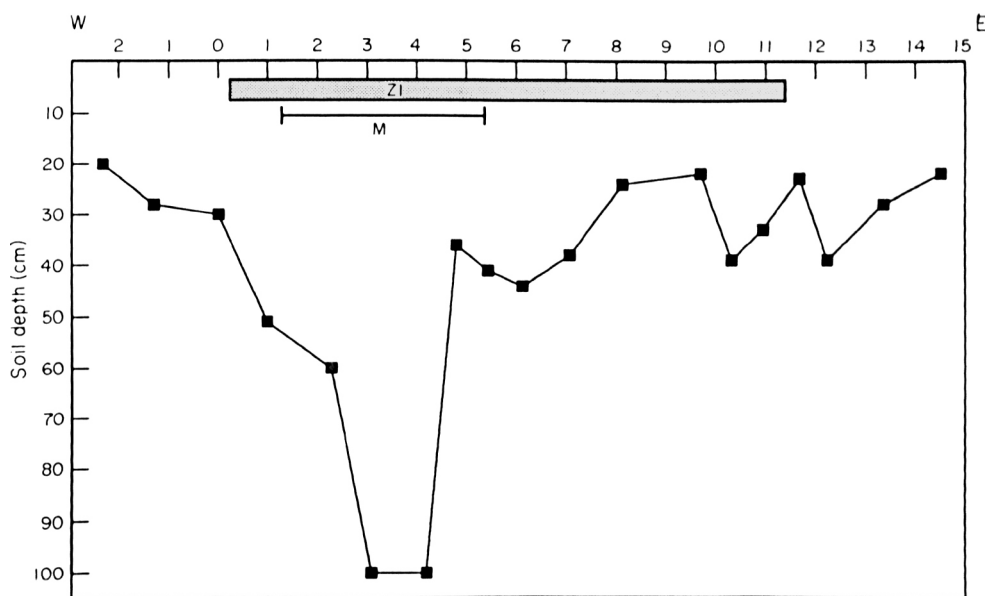
was somewhat greater in eight transects which were along a pattern of very shallow drainage channels that terminated in an area of soil deposition from sheet washing. Depth along these eight transects averaged 36.0 cm, as compared to 23.2 cm in the nine transects outside this drainage area.

In comparison, for 118 depth measurements within 10 zones of influence of mounds: mean depth was 43.08 cm (median 60), and for 48 measurements within old mounds themselves, mean depth was 50.82 cm (median 53).

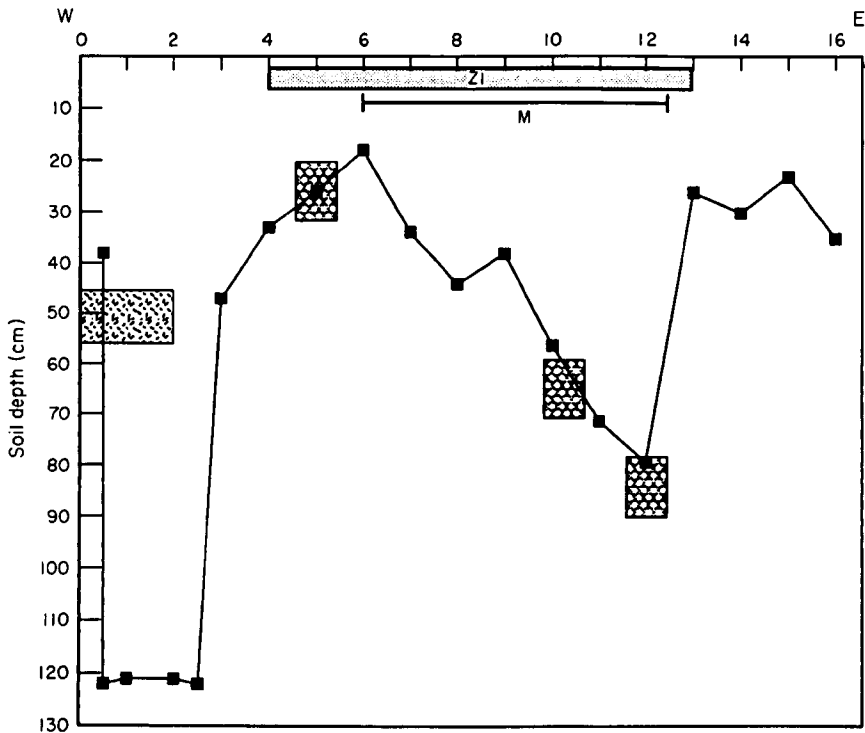
*Depth profile across zones of influence:* For ten zones, six had a profile similar to Figure 2 (mound D0, with shallow edges and a deep centre within the mound. That is, there was a basin of deeper soil within the zone of influence. For four mounds, there was a deep centre, but also an apparently anomalously deep edge, as in Figure 3 (mound C8). Excavation along the transect for mound C8 showed that the apparently deep soil at the edge actually had fine soil, impregnated with calcium carbonate, beginning at about 45 cm depth. Because of the fineness of the soil, the steel measuring rod was able to penetrate to greater depth (with more force than usual, however). At three other points, as shown in Figure 3, the soil contained enough fine gravel, cemented with calcium carbonate, to stop penetration of the measuring rod. For the ten transects, the maximum soil depth in the basin under the old mound averaged  $77.7 \pm 18.87$  cm. In two mounds the basin passed entirely through the indurated caliche.

#### Soil moisture

Table 2 shows the water stored within the soil at several positions with respect to the zone of influence (ZI) of an old *D. spectabilis* mound. The samples were taken during the summer rainy season. At this time the amount of water in the soil was not different between outside the zone influence, ZI, and at the inner edge of the large creosotebushes



**Figure 2.** Typical soil-depth profile across an old banner-tailed kangaroo rat mound. Bar at top marked ZI is the width of the zone of influence of the mound, as defined by the outer edges of canopies of blooming/fruited creosotebushes. M is the width of the old mound within ZI.



**Figure 3.** A typical soil-depth profile across an old banner-tailed kangaroo rat mound. Depth to left, outside zone of influence of the mound (ZI) is much deeper than usual. M is the width of the old mound. Fine-grained box on left shows depth at which fine soil, impregnated with calcium carbonate, was first encountered on excavation. The three boxes with coarser grain show depth at which carbonate-cemented gravel was first encountered.

**Table 2.** Grams of water within a soil core of 8.0 cm diameter, from the surface down to indurated caliche, at depth ( $\times$  cm), at different points in relation to the zone of influence (ZI) of an old *D. spectabilis* mound

	Mound D0	Mound A6	Mound C3
Date measured	5 Aug. 1990	14 Aug. 1990	23 Aug. 1990
Rainfall since June 4	79.5 mm	93.0 mm	187.5 mm
Open area outside ZI		189 g (27 cm)	175 g (30 cm)
Inner edge of <i>L. tridentata</i> canopy, within ZI	197 g (25 cm)	118 g (21 cm)	191 g (30 cm)
Open area of ZI, but not on mound	222 g (46 cm)		
On highest point of mound, within ZI	(a) 215 g (57 cm) (b) 487 g (120 cm)	169 g (51 cm) 203 g (64 cm)	262 g (73 cm) 410 g (120 cm)

(a) Values as measured to depth of soil core taken.

(b) Values estimated down to actual depth of caliche, assuming that the water content of the soil at lowest measured depth continues unchanged down to caliche (soil corer could not penetrate all the way).

within ZI. However, the deep soil under the mounds within ZI did store much more water. The samples taken on 14 and 23 August showed the lack of effect of a large single rain of 9.09 cm, which occurred between these dates. Most of this rain apparently ran off down slope. There is no indication that it penetrated the soil even under the large creosotebushes.

*Other areas of good growth of creosotebushes:* In addition to the zones of influence around mounds, there were other situations in which creosotebushes showed healthy growth: (1) an area in the north-east corner of enclosure where there was obvious soil deposition from sheet washing of water. There were no old mounds of *D. spectabilis* in this area; (2) isolated large, nonflowering shrubs, associated with active *D. merriami* mounds; (3) one situation in which there was a long, narrow open area, edged by medium and large shrubs, flowering and nonflowering. Soil depth ranged from 26 to 81 cm. Because of the long, narrow shape of the central open area, we judged this was not an area of a disappeared *D. spectabilis* mound; (4) outside the enclosure, along major drainage channels, there was vigorous growth and flowering of creosotebushes.

### Discussion

A variety of data exists for a reasonable scenario to explain the present observations of creosotebushes and banner-tailed kangaroo rats:

#### *Characteristics of Dipodomys spectabilis.*

This species is locally common in grasslands in south central and south-eastern Arizona, New Mexico (except for the north-eastern one-third), and part way down into Sonora and Chihuahua, Mexico (Hall & Kelson, 1959). The banner-tailed kangaroo rat is the largest seed-feeding mammal in the communities of southeastern Arizona; among herbivores, it is exceeded in weight only by woodrats (*Neotoma* spp.) and lagomorphs (*Sylvilagus* spp. and *Lepus* spp.). This kangaroo rat builds large, conspicuous mounds which have a multilayered complex of tunnels and chambers (Vorhies & Taylor, 1922). The mounds vary considerably in size, ranging up to 1.2 m high and 4.6 m in diameter (Hall & Kelson, 1959). Ten occupied mounds measured in a grassland 8.5 km south-east of the study site averaged  $38.8 \pm 3.08$  cm high, with mean elliptical dimensions of  $4.42 \text{ m} \times 3.95 \text{ m}$ , giving an average area coverage of  $14.29 \text{ m}^2$  (unpubl. observations). If this average coverage is extrapolated to the density of mounds in this site,  $8.22 \text{ mounds ha}^{-1}$  (Wasser, unpubl. data), then the mounds cover about 1.2% of the habitat. Moroka *et al.* (1982) described an area with 7–10 mounds  $\text{ha}^{-1}$ , with mounds covering 2% of the habitat.

*D. spectabilis* mounds are a long-term feature of the habitat. Individual rats have a high fidelity to one burrow, with 60–70% of individuals remaining in the same burrow throughout adult life (Jones, 1987). Juvenile rats require an already made burrow system for survival, and hence, disperse to vacant mounds (Jones, 1988). Vacant mounds may also be used by *N. albigula*, *D. merriami* and antelope ground squirrels, *Ammospermophilus harrisi* (Bryant).

*D. spectabilis* and shrub cover: The banner-tailed kangaroo rat, like other species of kangaroo rats, is associated with sparseness of vegetation (Rosenzweig & Winakur, 1969). *D. spectabilis* is probably like *D. merriami* in avoiding areas that naturally, or by experimental manipulation, have thick cover (Rosenzweig, 1973). Limited data for radio-tracked individuals showed that *D. spectabilis* avoided shrubs in their foraging, and generally included in their home range only sparsely shrub-covered area; their mounds were far more common in shrub-free grassy situations (Shroeder, 1987).

Thus, it is reasonable to conclude that banner-tailed kangaroo rats gradually left the present study site as it changed from a desert-grassland community to one dominated by shrubs, principally creosotebush. The oldest creosotebushes in the study site were established about 1890–1900, the greatest period of establishment was 1939–49 (Chew & Chew, 1965). This pattern of spread of creosotebushes into grassland is similar to that on the Jornada Experimental Range, New Mexico, 210 km east north-east of Portal (Buffington & Herbel, 1965). No *D. spectabilis* was live-trapped on the site during 12 monthly periods of trapping in 1958–59 (Chew & Chew, 1970). Only one transient male was caught, at an old mound site, in subsequent years (1967) (Chew, unpubl. data). The old mounds were used by other rodents, as in results.

*Mounds as nitrogen-rich microsites:* Moorhead *et al.* (1988), have shown that occupied banner-tailed kangaroo rat mounds are high-nitrogen patches in the environment. They found a nitrogen mineralization potential of  $43.4 \text{ mg N kg}^{-1}$  of soil from occupied mounds, as compared to  $15.2 \text{ mg kg}^{-1}$  for intermound soil. As shown in Table 1, old mound locations persist as N-rich patches with elevated nitrogen mineralization potential long after the banner-tailed kangaroo rats have left the community.

The available nitrogen in mounds can have several sources: (1) *D. spectabilis* cache exceptional amounts of seeds and other plant parts in their dens — up to  $5.67 \text{ kg}$  in a mound (Vorhies & Taylor, 1922). This material may be eaten within the mound, decay within the mound, or be thrown out onto the surface when it becomes moldy (Reichman *et al.*, 1985). (2) Nitrogen is deposited in the mound by generations of rodents in urine and faeces. (3) Mun and Whitford (1989) found that in some years the peak biomass of herbaceous plants per unit area can be 2- to 4-fold larger on mounds than between mounds. When legumes are a main part of the increase on mounds (Moorhead *et al.*, 1988), this is potentially a larger source of nitrogen input by fixation than in intermound areas. (4) The modification of soil by its turnover by rodents may enhance bacterial activity so that more of total nitrogen is made available to plants in mound soil than in intermound soil (Brooks *et al.*, 1985). (5) If shrubs are larger on and around mounds (as in present study), simply their larger size, and consequent greater litter production, may help sustain and perpetuate a nitrogen-rich microsite (Burke, 1989; Virginia & Jarrell, 1983).

*Mounds as potentially moister microsites:* Soil of mounds has a lower bulk density than intermound soil; this permits better infiltration of precipitation, but soil down to 30 cm can have a lower water potential because of easier evaporation, infiltration to lower depths, and/or greater plant transpiration (because of higher herb cover on mound) (Mun & Whitford, 1989). However, because of the depth of loosened soil within a mound, particularly when the mound is a basin in calcium-impregnated surrounding soil, as in the present study (Table 2), mound soil can achieve more water storage during rainy seasons than intermound soil.

There may be an interactive effect when creosotebushes are growing adjacent to mounds. When rainfall is sufficiently intense, water will run off the mound to its periphery, where it may be held by plant litter. Also, the stems of creosotebushes act as 'funnels' in intercepting rainfall and directing it down to the root crown. As much as 25% of rain onto a bush may be thus 'funneled down' (Whitford, unpubl.). Such water could go into the basin formed by the underground parts of the mound. The limited data of Table 2 are consistent with this speculation, but a thorough study of the soil water conditions of mounds through time is needed.

*Creosotebushes, nitrogen and water:* It has become obvious through 32 years of observation, that the creosotebushes in the study plot are, in general, declining in size, increasing in their percentage of dead stems, and with increasing frequency, completely dying. This is occurring not only within the study enclosure, but within the local watershed as a whole (Chew, unpubl. data). The exception to this general condition, the growing, flowering creosotebushes around old banner-tail mounds, and those in areas where there is soil deposition, suggests these are nutrient and/or water rich microsites, and that the watershed in general is nutrient and/or water deficient.



Nitrogen and water enhance the growth of creosotebushes, but interact in a complex way. Growth is significantly influenced by the seasonal timing and pattern of rainfall (Cunningham *et al.*, 1979). Small frequent rains are more effective in producing growth than an equal amount in large infrequent rains (Ludwig & Flavill, 1979). Wet weather may decrease N availability in the soil, by enhancing bacterial uptake of N, whereas drought can increase N availability to shrubs by inhibiting prior microbial uptake (Fisher *et al.*, 1987a). When N and water were artificially added: +N produced increased reproductive and vegetative growth in irrigated and nonirrigated creosotebushes; with irrigation without +N there was increased vegetative growth but decreased reproductive growth; 6 mm per week added water was more effective than 25 mm once a month (Fisher *et al.*, 1988). Sharifi *et al.* (1988) found that +N and irrigation increased leaf production in Sonoran Desert creosotebushes in 1 year, but not in another. In the laboratory, +N produced 2-month old seedlings with more root growth, shoot growth and biomass, than controls, if there was adequate P (Lajtha & Klein, 1988).

If banner-tail mounds are N-rich water reservoirs, they may act to even out vagaries of growth response of creosotebushes that result from specific patterns of rainfall and bacterial growth.

*Creosotebushes and soil depth:* Particularly for water, soil functions as a reservoir. It must have a sufficient volume to be able to hold the amount of water necessary for plant growth. The necessary volume, as dependent on depth, will vary depending on physical factors that affect retention of water. The shallow soil of the study site is limited by the underlying caliche layer. This layer is not necessarily a handicap, it can hold water from percolating beyond the root zone of shallow-rooted plants (Chew, 1982; Herbel *et al.*, 1972). On the other hand, it can hold water nearer the evaporative surface, thus hastening its loss to the atmosphere.

The study site and its watershed is generally an eroding surface. It may be that soil depth, and soil water capacity, has now decreased to the point where in drier years, creosotebushes are susceptible to die back. Shreve & Mallery (1933), commented that they found they could predict soil depth from the size and density of creosotebushes in a site. Our accumulated data support a relationship of shrub volume to soil depth. When shrub volumes along 30-m transects (measured in 1986, Chew, unpubl.), were regressed against soil depth in the 17 transects measured for soil depth in this study, there was a significant relationship: canopy volume ( $\text{cm}^3 \times 10^{-3}$ ) =  $-835.4 + 76.97$  (mean soil depth, cm),  $r^2 = 0.33$ , where canopy volume is the total volume for all creosotebushes intercepted by the 30-m transect.

Therefore, the greater soil depth under the old banner-tail mounds, within each zone of influence, may be a factor in the enhanced vigor of the creosotebushes within the zone. It is unknown whether banner-tailed kangaroo rats created the greater soil depth at old mound sites, by digging into and disrupting the caliche, or whether the mounds were located where there were pockets of deeper soil within the general calcified layer. Limited observations suggest both are possible. Banner-tailed kangaroo rats have been observed to throw out calcified soil fragments on mounds at the New Mexico State University Ranch and other areas in south-western New Mexico (Whitford, unpubl. observation), so they have some ability in this regard. In the present study there was one instance of a group of large, flowering creosotebushes, without an apparent remnant mound, associated with deeper than average soil.

These cumulated observations suggest the following scenario: (1) the study site was originally grassland occupied at a low density by banner-tailed kangaroo rats. The mounds became nitrogen-rich microsites in the general habitat; (2) degradation of the grassland due to overgrazing and drought, was followed by invasion of shrubs, principally creosotebushes, which led to avoidance dispersal of *D. spectabilis* from the area; (3) mounds vacated by kangaroo rats persisted as nutrient-rich patches, and as soil erosion progressed, the deeper soil under the mounds became important as soil moisture reservoirs; (4) creosotebushes in the zone of influence of these patches were able to

continue their vegetative and reproductive growth, to some degree free of nutrient and water limitations, whereas the general population declined.

The final outcome of the scenario for creosotebushes in the study site is uncertain, but the mounds are unlikely to be able to sustain the population long term, in the face of continuing soil erosion. The old mounds are few ( $2.87 \text{ ha}^{-1}$ ) and the above ground parts of some have completely disappeared. Within the protection of the cattle enclosure, the study site seems to be trending to an increase in small woody shrubs (*Parthenium incanum* H.B.K. and *Zinnia pumila* Gray) and grasses, especially *Bouteloua eriopoda* Torr., which was probably dominant in the grassland predating the creosotebush vegetation. If grazing protection were extended to the entire watershed, it is possible that a return to grassland could occur, in the long term (decades).

Regardless of the true scenario to the present time, the observed positive effect of old banner-tailed kangaroo rat mounds on creosotebushes is an unusual, if not unique, relationship. In terms of the classification of relationships by Odum (1971: page 211), this is 'predation' a '+ - relationship'. The positive effect for the larger species (creosotebushes), is delayed in time, after it (and other shrub species) has caused the demise of the 'prey' (banner-tailed kangaroo rats) in the system.

It is unusual for a small vertebrate to have an impact on woody perennial vegetation. Cantor (1989) observed that gopher digging and feeding kept aspen out of the deep soils of meadows, where aspen grows best, in the absence of gophers. Even for herbs the effects of small mammals is largely negative except for those species that can opportunistically occupy disturbed soil (Reichman & Jarvis, 1989). The present case for banner-tailed kangaroo rats is the only instance to our knowledge of a positive effect of a small vertebrate on the physiological ecology of a woody perennial plant by modification of the environment of the plant. Of course, there are instances in which small vertebrates are of positive importance in the pollination and seed dispersal of woody perennials.

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