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# Effects of pocket gophers on desert soils and vegetation

Graham I.H. Kerley\*, Walter G. Whitford, Fenton R. Kay

USDA Jornada Experimental Range, MSC 3 JER, New Mexico State University, Las Cruces, N M 88003, USA

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#### Abstract

The effects of pocket gophers (Geomyidae) on soils and vegetation were studied on Chihuahuan Desert and Sonoran Desert catenas for comparison with the effects of pocket gophers on soils and vegetation in mesic environments. Two species of gophers, *Thomomys bottae* and *T. umbrinus*, ejecta mounds were located on upper slopes of piedmonts where runoff from mountains increase soil moisture. *Geomys arenarius* ejecta mounds were restricted to small valley bottoms on ridge and valley mesa topography. Soil bulk density of ejecta mounds soils was lower than undisturbed soil at the Chihuahuan Desert sites but not at the Sonoran Desert site. Significantly higher annual plant cover were recorded only for ejecta mounds of the Chihuahuan Desert piedmont. The effects of pocket gopher burrowing differed between the species, with *G. arenarius* sites showing greater extent of soil disturbance at a local scale, but effects of these disturbances on desert soils vegetation are dependent upon the properties of the undisturbed soil. These findings of limited impacts of burrowing on soil chemistry contrast with the situation in more mesic areas. © 2003 Elsevier Ltd. All rights reserved.

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## 1. Introduction

Small mammals are important agents as "bioengineers" especially those species that affect soil structure and soil processes by their burrowing activity (Jones et al., 1994). Fossorial mammals can produce large areas of soil disturbance that have a

<sup>\*</sup>Corresponding author. Address: Department of Zoology, Terrestrial Ecology Research Unit, University of Port Elizabeth, P O Box 1600, Port Elizabeth 6013, South Africa. Tel.: +27-41-504-2946. *E-mail address:* zlagik@zoo.upe.ac.za (G.I.H. Kerley).

variety of effects on ecosystem properties and processes (Whitford and Kay, 1999). Pocket gophers (Geomyidae) are widely distributed in North America and occur at high densities in local areas. They are fossorial herbivores that feed on roots or entire plants near burrow openings (Anderson and McMahon, 1987). Pocket gophers change soil and vegetation heterogeneity by their burrows and soil ejecta mounds. The physical and chemical differences of soils around burrows and ejecta mounds have an effect on processes such as wind and water erosion, infiltration, and soil fertility (Reichman and Smith, 1985).

Burrowing activities of small mammals affect a number of soil properties and soil processes (Whitford and Kay, 1999). Studies of pocket gophers in mesic and xeric alpine meadows have documented homogenization of soil particle sizes within mounds (Mielke, 1977), reduction in concentration of total C, N, exchangeable Ca and K plus increased  $NO_3^-$  and nitrogen fluxes (Litaor et al., 1996). Subsequent studies of gopher mounds in this environment found that increased nitrate pools decreased to pre-disturbance levels after 1 year (Sherrod and Seastedt, 2001). Pocket gophers have been shown to affect microtopography (Foster and Stubbendeick, 1980; Inouye et al., 1997) and to decrease erosion and runoff (Hakonson, 1999). Lower bulk density of pocket gopher mounds probably contributes to increased water infiltration rates in comparison with undisturbed soils (Laundre, 1993).

Changes in the physical and chemical properties of soil and changes in soil processes such as decomposition and nutrient cycling (Cortinas and Seastedt, 1996) can affect the revegetation rates and biomass production on pocket gopher mounds (Tilman, 1983; Stromberg and Griffin, 1996). However, pocket gopher burrowing had no effect on plant biomass or plant community structure in a floristically diverse coastal prairie in Texas (Rezsutek and Cameron, 2000). In some studies, pocket gophers have been reported to affect plant species composition on ejecta mounds (Hobbs and Mooney, 1985; Reichman and Smith, 1985; Spencer et al., 1985, Martinsen et al., 1990; Cortinas and Seastedt, 1996) while other studies have reported little or no effect on plant species richness and species composition (Rezsutek & Cameron, 2000; Rogers et al., 2001). In arid ecosystems, where infrequent rainfall has dramatic effects on decomposition, nutrient mineralization, and plant germination (Whitford, 2002), the effects of pocket gophers on soils and vegetation cannot be predicted from the literature. In order to evaluate the ecosystem effects of pocket gophers in arid environments, we designed studies to examine physical and chemical characteristics of pocket gopher mounds and the vegetation patterns on gopher mounds in Chihuahuan Desert and Sonoran Desert ecosystems.

In Chihuahuan Desert grasslands, the burrow-mounds of bannertail kangaroo rats (*Dipodomys spectabilis*) have higher soil nitrogen, higher N mineralization rates, higher infiltration rates, higher plant biomass and different plant species composition than surrounding soils (Moorhead et al., 1988; Mun and Whitford, 1990). Pocket gopher mounds are short-lived soil disturbances (1–3 years) compared with bannertail kangaroo rat mounds (several decades) (Whitford and Kay, 1999). Short-lived soil disturbances have little or no effect on soil physical and chemical properties and on vegetation (Whitford and Kay, 1999). Therefore, we predicted that pocket gophers would have little or no effect on physical and chemical properties mound soils or on mound vegetation.

Pocket gophers are patchily distributed in the hot desert regions of North America. We selected areas with known populations of pocket gophers for these studies. We examined the distribution of pocket gopher mounds on catenas (connected series of landscape units) associated with mountain piedmonts and ridge and valley topography in a desert basin in an attempt to understand the spatial patterns of pocket gophers in arid landscapes.

### 2. Study sites

# 2.1. Chihuahuan desert

Piedmont catenas were on the south-, east- and north-facing bajadas of Mt Summerford (T20–21S, R1E) on the Chihuahuan Desert Rangeland Research Center, 40 km NNE of Las Cruces, NM, USA. Soils vary from gravelly loams on the toe slopes to sandy soils mid-slope and sandy loams on the lower slopes of the catenas. Toe slope vegetation is desert grassland dominated by black grama grass (*Bouteloua eriopoda*) with scattered soaptree yucca (*Yucca elata*), mormon tea (*Ephedra trifurca*) and prickly pear cacti (*Opuntia* spp.). Upper slope vegetation is a mesquite (*Prosopis glandulosa*)–grass (*Beriopoda, Aristida* spp., *Sporobolus* spp.) mosaic.

Mesa catenas were located on sloping ridge and valley topography on Apache Flats (T22S, R2W) on the Corralitos Ranch approximately 50 km west of Las Cruces, NM. Ridges are gravelly sands to sands grading into sandy loams on the lower slopes. Valley bottom soils are silty loams. Ridges and slopes are dominated by creosotebush (*L. tridentata*) and the valley bottoms or swales are dominated by tabosa grass (*Pleuraphis* (*Hilaria*) *mutica*). The swale tabosa grass distribution is a banded-mosaic vegetation pattern (Montana, 1992).

# 2.2. Sonoran desert

These catenas are located on the Santa Rita Experimental Range approximately 60 km south of Tucson, AZ on a north-facing piedmont slope originating in Florida Canyon in the Santa Rita Mountains. The soils are sandy loams. The vegetation is a mesquite (*P. velutina*) savanna. The dominant grass is an alien species from Africa, Lehmann's lovegrass, *Eragrostis lehmanniana*. Other grasses in the savanna are scattered tussocks of native grasses (*Bouteloua* spp., *Heteropogon* spp., and *Aristida* spp.).

# 3. Methods

# 3.1. Species identity

Pocket gophers were identified from distribution records (Findley et al., 1975; Hoffmeister, 1986) and inspection of the mammal collection of the New Mexico State Biology Department. According to Hoffmeister (1986) only *Thomomys umbrinus* has been reported from the Santa Rita Mountains in Arizona. The extensive trapping records represented by the New Mexico State University (NMSU) mammal collection record only *T. bottae* in the vicinity of Mt Summerford and *Geomys arenarius* in the vicinity of Apache Flats. These distributions also agree with the published distributions and habitats of these species (Findley et al., 1975).

## 3.2. Catenary distribution

The distribution of pocket gopher activity across the landscape was estimated from transects down the catena. At least four transects were walked downslope at each sampling location and evidence of pocket gopher activity within 5 m each side of the transect was recorded in relation to the distance from the top of the transect. Transects were continued until there had been no records of pocket gopher activity for 500 m or the bottom of the catena (a drainage system) was reached. We further surveyed the landscape from a vehicle along roads at the three sites to confirm the validity of this approach. The frequency distribution of pocket gopher activity was plotted in relation to the position on the catena.

## 3.3. Mounds

Within the area of pocket gopher activity identified above, mound systems were identified as groups of mounds separated by less than 1.5m. The abundance of mound systems on the landscape was estimated using the point quarter method (Bonham, 1989). Seven and 22 point quarter samples were collected for the Santa Rita and Mt Summerford sites, respectively. The number of mounds were counted within 36 and 110 mound systems for the Santa Rita and Mt Summerford sites, respectively. Mound density was then estimated from the density of mound systems per hectare and the mean number of mounds per system. For the Apache Flats site, individual mound systems could not be differentiated and mound density was estimated using a nearest neighbour approach (Bonham, 1989), with 87 measurements between mounds.

Mound area and volume was estimated from two diameters and a height measurement for a sample of 30 mounds each from the Summerford and Apache Flats sites, and 20 mounds from the Santa Rita site. For area, mounds were assumed to be circular with a mean diameter estimated from the two diameter measurements, and volume was approximated as that of a rectangular prism.

Soil samples were collected on mounds and from adjacent apparently undisturbed areas using a 47 mm diameter core that was inserted to a depth of 10 cm. Soil samples were dried, weighed and bulk density estimated. The soil samples were analysed for the silt and clay faction smaller than 250 µm by sieving. Chemical analyses for pH, electrical conductivity, Mg, Ca, Na adsorption ratio, organic C, nitrate N, P, and K were conducted by the NMSU Soil, Water and Air Testing Laboratory using standard techniques (Page et al., 1982).

Plant communities were sampled using  $0.5 \text{ m}^2$  quadrats, divided into  $10 \times 10 \text{ cm}^2$  blocks. Quadrats were placed over randomly chosen mound systems (on-mound) and then on adjacent unmounded areas (off-mound). Percentage perennial and annual plant species cover was estimated and the number of annuals counted. At least 11 paired quadrats per site were recorded during March and April 1998, while the spring growth of annuals was present. We compared perennial plant cover (%) and species richness (S), and annual plant cover (%) and species richness (S) as well as the number of annuals on- and off-mound. We did not use statistical indices of diversity due to the low diversity within our samples (Zar, 1984).

## 3.4. Data analysis

Sites were compared using ANOVA, except where data failed normality tests, in which case the Kruskal–Wallis ANOVA on ranks was used. In view of the paired on-mound/off-mound sampling strategy, we used a paired *t*-test for these comparisons, except where data were not normally distributed, in which case the Wilcoxon Signed Rank Test was applied. Proportional data were arcsin transformed for statistical analyses (Zar, 1984) but are reported as proportions for ease of interpretation. All analyses were conducted with SigmaStat<sup>TM</sup> for Windows version 2.03.

## 4. Results

### 4.1. Distribution across the landscape

Pocket gopher distribution was not uniform across the landscape, showing clear clumping across the catena. At the Mt Summerford site in the Chihuahuan Desert, *T. bottae* activity was clumped towards the top of the catena, as was the activity of *T. umbrinus* at the Santa Rita Experimental Range in the Sonoran Desert (Fig. 1a & b). Neither of these species produced mounds in the mid-slope and lower slope portions of the catenas. In contrast, *G. arenarius* showed distinct preferences for the lower portions of the landscape, with no activity towards the top of the catena of Apache Flats (Fig. 1c).

#### 4.2. Mounds

Pocket gopher activity varied extensively across the landscape (Fig. 1a–c). Within the areas of maximum pocket gopher activity, densities of 0.9, 1.4 and 4.8 mounds m<sup>-2</sup> were estimated for the Mt Summerford, Santa Rita and Apache Flats sites, respectively. The size (area and volume) of mounds differed significantly between sites (Kruskal–Wallis H = 19.7 and 24.4 for area and volume, respectively, df. = 2, p < 0.0001), being larger at the Apache Flats (mean area =  $1225 \pm 621.6$  cm<sup>2</sup>, mean volume =  $10995 \pm 7149.8$  cm<sup>3</sup>) than the Mt Summerford (mean area =  $725 \pm 413.7$  cm<sup>2</sup>, mean volume =  $4541 \pm 3722$  cm<sup>3</sup>) and Santa Rita sites (mean

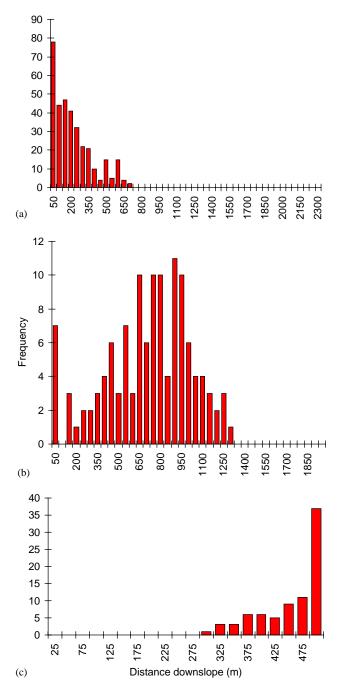


Fig. 1. Distribution of pocket gopher mounds down the landscape catena for (a) Mt Summerford, Chihuahuan Desert (b) Santa Rita Experimental Range, Sonoran Desert and (c) Corralitos Ranch, Chihuahuan Desert.

area =  $585.5 \pm 356.3 \text{ cm}^2$ , mean volume =  $3965 \pm 2871 \text{ cm}^3$ ), with the Mt Summerford and Santa Rita sites not differing (Dunn's multiple comparison).

The volumes and densities of mounds and soil bulk densities (Table 1) were used to estimate the mass of material deposited on the surface. Soil eject mounds averaged 5.76, 7.16 and  $45.39 \text{ kg m}^{-2}$  for the Summerford, Santa Rita and Apache Flats sites, respectively, reflecting the larger size and higher density of mounds at the Apache Flats site (see above).

Soil bulk density tended to be lower for the mounded soils (Table 1); this was significant for the Summerford and Apache Flats sites, but not for the Santa Rita site. The silt and clay fraction did not differ between the mound soils and reference soils for any of the sites. There were few statistically significant differences in the chemistry of pocket gopher mound soils and undisturbed soils adjacent to the mounds (Table 1). If p < 0.1 is considered significant (the high variability in concentrations of minerals in both mound soils and undisturbed soils suggests that accepting a probability level of 0.1 may be justified), the pocket gopher mound soils at the Mt Summerford site had higher concentrations of Mg, Ca, K, and NO<sub>3</sub>-N. Soil pH was also elevated at the Mt Summerford site. Except for elevated K in mound soils at all of the sites, there were no differences in mineral nutrients of mound soils and undisturbed soils at the Apache Flats and Santa Rita sites.

Although perennial cover was consistently lower in the on-mound quadrats than off-mounds for the three sites (Table 2), this difference was only marginally significant at the Santa Rita Experimental Range site (paired-t = 1.82, df. = 11, p = 0.096). Conversely, while annual cover was consistently higher in the on-mound quadrats than the off-mound quadrats (Table 2), this was only significant at the Mt Summerford site (paired-t = 4.46, df. = 16, p < 0.001). Perennial and annual species richness and the number of annuals did not differ between the on- and off-mound quadrats for any of the sites (Table 2, paired-t < 2.57, p > 0.05). There were also no significant differences in perennial or annual plant community composition on the ejecta mounds and undisturbed soils at any of the study sites.

#### 5. Discussion

Pocket gopher distribution is very patchy on catenas of desert mountain ranges and on mesa catenas. There was no evidence of pocket gophers on the upper slopes of catenas of adjacent mountains in the Dona Ana mountain range. Mt Summerford is the northernmost peak in the Dona Ana range and is lithologically different (monzonite granite) from the rest of the range (rhyolytic granites) (Gile et al., 1981). However, there are similar catenary sequences of soil and vegetation on these mountains. Pocket gophers are absent from the Jornada Basin grasslands but do occur in some restricted localities in desert grasslands approximately 120 km north of the Jornada Experimental Range (W.G.W., unpublished data). Gophers were also absent from several of the valleys in the Apache Flats areas where *G. arenarius* 

Table 1

Summarized soil data (mean  $\pm$  S.D., n = 5) for on and off pocket gopher mounded areas for the three study sites, with results of the within-site paired *t*-tests (or Wilcoxon Signed Rank Test for non-normal data)

Soil variable	On-/off- mound	Mt Summerford	Apache Flats	Santa Rita Experimental Range
Bulk density	On	$1.41 \pm 0.0.10^*$	$0.86 \pm 0.05^{**}$	1.29±0.19
	Off	$1.58 \pm 0.07 \\ t = 3.04,  p = 0.04$	$1.21 \pm 0.08 t = 9.90, p = 0.0006$	$\begin{array}{l} 1.42 \pm 0.08 \\ t = 1.19,  p = 0.30 \end{array}$
Silt and clay (%)	On	$30.7 \pm 8.6$	73.5±2.4	$25.25 \pm 7.83$
	Off	$28.0 \pm 10.6 \\ t = 1.40, p = 0.24$	$71.3 \pm 4.4 t = 1.85, p = 0.14$	$20.08 \pm 3.61 W = 5.00, p = 0.59$
Soil pH	On	$7.1 \pm 0.55$	$7.4 \pm 0.21$	$6.0 \pm 0.62$
	Off	$6.8 \pm 0.33$ t = 1.98, p = 0.12	$7.3 \pm 0.39 \\ t = 0.60, p = 0.58$	$6.1 \pm 0.29 t = 0.08, p = 0.94$
Electrical conductivity	On	$1.40 \pm 0.73^*$	$0.97 \pm 0.27$	$0.49 \pm 0.27$
(mʊ/cm)	Off	$0.52 \pm 0.09$ t = 2.89, p = 0.04	$1.17 \pm 0.73$ t = 0.49, p = 0.65	$0.42 \pm 0.06$ t = 0.52, p = 0.63
Mg (mEq $l^{-1}$ )	On	$2.35 \pm 2.03$	$1.34 \pm 0.34$	$0.84 \pm 0.47$
Mg (mEq1 )	Off	$0.81 \pm 0.18$	$1.48 \pm 1.00$	$0.57 \pm 0.07$
		t = 1.83, p = 0.14	t = 0.26, p = 0.81	t = 1.41, p = 0.23
Ca $(mEq l^{-1})$	On Off	$\frac{10.59 \pm 9.89}{2.77 \pm 1.07}$	$5.71 \pm 1.58$ $6.15 \pm 3.54$	$2.42 \pm 1.22$ $1.85 \pm 0.30$
		t = 1.96, p = 0.12	t = 0.20, p = 0.85	t = 0.92, p = 0.41
Na adsorption ratio	On Off	$0.14 \pm 0.02$ $0.16 \pm 0.02$	$0.16 \pm 0.03$ $0.19 \pm 0.12$	$\begin{array}{c} 0.17 \pm 0.05 \\ 0.16 \pm 0.05 \end{array}$
	Oli	t = 1.32, p = 0.26	t = 0.63, p = 0.57	t = 0.73, p = 0.51
Organic matter (%)	On	$0.77 \pm 0.37$	$1.07 \pm 0.43$	$1.62 \pm 0.98$
	Off	$\begin{array}{l} 0.57 \pm 0.10 \\ t = 1.03,  p = 0.36 \end{array}$	$\begin{array}{l} 0.91 \pm 0.37 \\ t = 1.10,  p = 0.33 \end{array}$	$\begin{array}{l} 1.79 \pm 0.68 \\ t = 0.91,  p = 0.41 \end{array}$
NO <sub>3</sub> -N (p.p.m)	On	$4.74 \pm 3.53$	$13.8 \pm 8.53$	$5.32 \pm 3.83$
	Off	$1.86 \pm 0.40$ t = 2.02, p = 0.11	$17.7 \pm 18.5$ t = 0.34, p = 0.75	$2.32 \pm 0.56$ t = 1.76, p = 0.15
P (p.p.m.)	On	$14.14 \pm 6.40$	$8.28 \pm 6.56$	$14.12 \pm 4.03$
r (p.p.m.)	Off	$13.28 \pm 4.59$	$9.4 \pm 8.03$	$15.65 \pm 2.65$
		t = 0.23, p = 0.83	t = 1.02, p = 0.37	t = 1.29, p = 0.27
K	On Off	$30.4 \pm 7.60^{*}$ $18.4 \pm 1.67$	$21.8 \pm 5.68$ $37.2 \pm 17.18$	$15.2 \pm 6.14$ $19.2 \pm 8.26$
		t = 3.16, p = 0.03	t = 2.49, p = 0.07	t = 2.43, p = 0.07

df. =4 for all tests, \*\* = p < 0.01, \* = p < 0.05.

Table 2

Summarized vegetation data (mean  $\pm$  S.E.) for on and off pocket gopher mounded areas for the three study sites, with results of the within-site paired *t*-tests: \*\*=p < 0.01, \*=p < 0.05

Vegetation variable	On-/off- mound	Mt Summerford $(n = 17)$	Apache Flats $(n = 11)$	Santa Rita Experimental Range $(n = 12)$
Perennial cover (%)	On Off	$10.6 \pm 9.43 \\ 13.5 \pm 10.71 \\ t = 1.19, p = 0.25$	$5.3 \pm 4.1 6.7 \pm 10.5 t = 0.12, p = 0.91$	$5.1 \pm 3.4^*$ 10.6 ± 7.8 t = 1.82, p = 0.09
Annual cover (%)	On Off	$10.4 \pm 2.3^{**}$ $4.4 \pm 1.0$ t = 4.46, p < 0.001	$0.3 \pm 0.8$ $0.2 \pm 0.4$ W = 3.0, p = 0.84	$13.6 \pm 6.1 \\ 13.1 \pm 12.1 \\ t = 0.46, p = 0.65$
Perennial species richness S	On Off	$2.0 \pm 1.8$ $1.8 \pm 1.7$ t = 0.45, p = 0.66	$2.4 \pm 1.6 2.5 \pm 2.0 t = 0.43, p = 0.68$	$1.4 \pm 0.8$ $1.4 \pm 0.8$ t = 0.0, p = 1.0
Annual species richness S	On Off	$4.1 \pm 2.06 3.9 \pm 2.00 t = 0.62, p = 0.54$	$0.4 \pm 0.5$ $0.7 \pm 0.8$ W = 10.0, p = 0.19	$4.7 \pm 0.9 \\ 3.7 \pm 1.4^* \\ t = 2.57, p = 0.03$
Annual numbers	On Off	$19.7 \pm 18.07 14.7 \pm 14.14 t = 1.26, p = 0.23$	$0.3 \pm 0.5$ $0.8 \pm 1.4$ W = 11.0, p = 0.31	$21.5 \pm 11.2 30.0 \pm 25.5 t = 1.02, p = 0.33$

occupied neighbouring valleys. Pocket gophers were limited to a small portion of the upper catena of Florida Canyon in the Santa Rita Range and were not detected in the remaining > 20 km of toe slope bajada examined.

Chihuahuan and Sonoran Desert grassland and savanna landscapes have changed considerably during the past 150 years (Buffington and Herbel, 1965; Hastings and Turner, 1965; Bahre and Shelton, 1993). Changes in vegetation and soils may have affected the distribution of pocket gophers in the Chihuahuan and Sonoran Desert landscapes and may have reduced the geographic area of distribution of pocket gophers to remnant patches of suitable habitat in these deserts. The suitable habitats appear to be areas with enhanced soil moisture from runoff from surrounding watersheds with poor infiltration capacity.

The data on physical and chemical characteristics of gopher disturbed soils partially support the prediction that short-term soil disturbances do not change the physical and chemical properties of disturbed soils (Whitford and Kay, 1999). The high variability in chemical and physical properties of mound soils probably results from the variable and indeterminate age of the gopher mounds. Freshly excavated soil mounds were virtually absent from all sites. Most of the mounds had intact surface crusts that form from raindrop impact (Moore and Singer, 1990). Surface crusts could have formed in any rain event preceding our study. Studies of pocket gopher activity in alpine areas have documented age-dependent changes in plant available nutrients in gopher mound soils and soils below mounds. Plant available P

and  $NO_3^-$  initially increased then decreased to pre-disturbance levels by 1 year after disturbance (Sherrod and Seastedt, 2001).

The most significant physical change in pocket gopher excavation mound soils is the lower bulk density of the mound soils. Lower bulk density of mound soils increases rates of water percolation into the soil. The volume of soil detached by the kinetic energy of rain drops varies inversely with the bulk density of soil (Poesen, 1985). Water and sediment washed from mounds accumulates in the immediate vicinity of mounds. This water-sediment accumulation is available for plant growth and probably is responsible for the higher cover and production of herbaceous annuals on mounds in comparison to adjacent undisturbed soils at the Mt Summerford sites. The higher species richness of herbaceous annuals on the ejecta mounds at the Santa Rita sites may result from increased soil water availability or may result from the relative absence of the alien grass, E. lehmanniana on the mounds. E. lehmanniana appears to compete with herbaceous annuals and areas dominated by this grass have fewer annuals than nearby native grass habitats (W.G.W., unpublished data). In arid ecosystems, hydrological effects on patchy distribution of soil water are the most important effect of pocket gopher activities.

Some of the differences between gopher mound soils and undisturbed soils at the Mt Summerford site reflect the nature of the soil profile on the upper catena inhabited by pocket gophers. The elevated pH and concentrations of divalent cations are related to the shallow depth of the soils (depth to indurated calcrete) and therefore the shallow depth of calcium carbonate deposition at this site. The pocket gopher ejecta mounds at the Mt Summerford site had numerous calcrete-covered pebbles on the surface. Tunnel excavation ejecta deposited at the surface by pocket gophers consists mostly of subsoil from varying depths (Huntley and Reichman, 1994). The calcium carbonate deposition layers are shallow on the south-facing aspect of the Mt Summerford catena. The transport of this material to the surface accounts for the higher electrical conductivity and higher pH of mound soils. The only cation that occurred in higher concentration on mound soils at all of the sample sites was K. Potassium is a very mobile monovalent cation and is easily carried to the average depth of wetting fronts.

The lack of significant differences in soil chemistry and in plant cover on gopher mounds and adjacent undisturbed soil on the mesa catenas and the Santa Rita catenas, suggests that different soils exhibit variability in the changes of physical properties resulting from pocket gopher burrowing. Whitford and DiMarco (1995) reported spatial variability in the effects of harvester ant nests on physical and chemical properties of disturbed soils with nutrient enrichment of nest disk soils in some areas and no enrichment of nest disk soils in other areas. Pocket gophers in tall grass prairie had no effect on plant community composition and species richness (Rogers et al., 2001) but were reported to effect vegetation in shortgrass prairie, alpine meadows, and California serpentine-soils grasslands (Hobbs and Mooney, 1985; Martinsen et al., 1990; Cortinas and Seastedt, 1996). Topography and grazing have been shown to affect the plant cover and composition on pocket gopher ejecta mounds in shortgrass prairie (Carlson and Crist, 1999). In desert areas, these effects or lack thereof are probably a function of the characteristics of the soil and the vegetation of the areas colonized by pocket gophers.

This study documented that some of the effects of pocket gopher burrowing reported from mesic habitats occur in Chihuahuan and Sonoran Desert ecosystems. Most of the literature dealing with the effects of pocket gophers on soils and vegetation are reports of studies at a single location (Mielke, 1977; Hobbs and Mooney, 1985; Reichman and Smith, 1985; Martinsen et al., 1990; Cortinas and Seastedt, 1996). The most consistent effect of pocket gophers on mesic and desert soils is the lower bulk density of ejecta mound soils. Other effects of pocket gopher burrowing on physical and chemical properties of desert soils appear to be dependent upon the nature of the undisturbed soil at that site.

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# References

- Anderson, D.C., McMahon, J.A., 1987. Population dynamics and biogenetics of a fossorial herbivore, *Thomomys talpoides*, (Rodentia: Geomyidae) in a spruce-fir sere. Ecological Monographs 51, 179–202.
- Bahre, C.J., Shelton, M.L., 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. Journal of Biogeography 20, 489–504.
- Bonham, C.D., 1989. Measurements of Terrestrial Vegetation. Wiley, New York.
- Buffington, L.C., Herbel, C.H., 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35, 139–164.
- Carlson, J.M., Crist, T.O., 1999. Plant responses to pocket-gopher disturbances across pastures and topography. Journal of Range Management 52, 637–645.
- Cortinas, M.R., Seastedt, T.R., 1996. Short- and long-term effects of gophers (*Thomomys talpoides*) on soil organic matter dynamics in alpine tundra. Pedobiologia 40, 162–170.
- Findley, J.S., Harris, A.H., Wilson, D.E., Jones, C., 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque.
- Foster, M.A., Stubbendeick, J., 1980. Effects of the plains pocket gopher (*Geomys bursarius*) on rangeland. Journal of Range Management 33, 74–78.
- Gile, L.H., Hawley, J.W., Grossman, R.B., 1981. Soils and Geomorphology in the Basin and Range Area of Southern New Mexico—Guidebook to the Desert Project. Memoir 39. New Mexico Bureau of Mines and Mineral Resources, Socorro, NM.
- Hakonson, T.E., 1999. The effects of pocket gopher burrowing on water balance and erosion from landfill covers. Journal of Environmental Quality 28, 659–665.
- Hastings, J.R., Turner, R.M., 1965. The Changing Mile. The University of Arizona Press, Tucson.
- Hobbs, R.J., Mooney, H.A., 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia (Berlin) 67, 342–351.
- Hoffmeister, D.F., 1986. Mammals of Arizona. University of Arizona Press & Arizona Game and Fish Department, Tucson, AZ.

- Huntley, N., Reichman, O.J., 1994. Effects of subterranean mammalian herbivores on vegetation. Journal of Mammalogy 75, 852–859.
- Inouye, R.S., Huntley, N., Wasley, G.A., 1997. Effects of pocket gophers (*Geomys bursarius*) on microtopographic variation. Journal of Mammalogy 78, 1144–1148.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 73-386.
- Laundre, J.W., 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. Oecologia (Berlin) 94, 43–48.
- Litaor, M.I., Mancinelli, R., Halfpenny, J.C., 1996. The influence of pocket gophers on the status of nutrients in alpine soils. Geoderma 70, 37–48.
- Martinsen, G.D., Cushman, J.H., Whitham, T.G., 1990. Impact of pocket gopher disturbbance on plant species diversity in a shortgrass prairie community. Oecologia (Berlin) 83, 132–138.
- Mielke, H.D., 1977. Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. Journal of Biogeography 4, 171–180.
- Montana, C., 1992. The colonization of bare areas in two-phase mosaics of an arid ecosystem. Journal of Ecology 80, 315–327.
- Moore, D.C., Singer, M.J., 1990. Crust formation effects on soil erosion processes. Soil Science Society of America Journal 54, 1117–1123.
- 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. American Midland Naturalist 120, 443–447.
- Mun, H.T., Whitford, W.G., 1990. Factors affecting annual plant assemblages on banner-tailed kangaroo rat mounds. Journal of Arid Environments 18, 165–173.
- Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), 1982. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, 2nd Edition. American Society of Agronomy, Inc. & Soil Science Society of America, Inc., Madison, WI.
- Poesen, J., 1985. An improved splash transport model. Zeitschrift fur Geomorphologie 29, 193-211.
- Reichman, O.J., Smith, S.C., 1985. Impact of pocket gopher burrows on overlying vegetation. Journal of Mammalogy 66, 720–725.
- Rezsutek, M., Cameron, G.N., 2000. Vegetative edge effects and pocket gopher tunnels. Journal of Mammalogy 81, 1062–1070.
- Rogers, W.E., Hartnett, D.C., Elder, B., 2001. Effects of plains pocket gopher (*Geomys bursarius*) disturbances on tallgrass-prairie plant community structure. American Midland Naturalist 145, 344–357.
- Sherrod, S.K., Seastedt, T.R., 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55, 195–218.
- Spencer, S.R., Cameron, G.N., Eshelman, B.D., Cooper, L.C., Williams, L.R., 1985. Influence of pocket gopher mounds on a Texas coastal prairie. Oecologia (Berlin) 66, 111–115.
- Stromberg, M.R., Griffin, J.R., 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications 6, 1189–1211.
- Tilman, D., 1983. Plant succession and gopher disturbance along an experimental gradient. Oecologia (Berlin) 60, 285–292.
- Whitford, W.G., DiMarco, R., 1995. Variability in soils and vegetation associated with harvester ant (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. Biology and Fertility of Soils 20, 169–173.
- Whitford, W.G., Kay, F.R., 1999. Biopedturbation by mammals: a review. Journal of Arid Environments 41, 203–230.
- Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, London.
- Zar, J.H., 1984. Biostatistical Analysis 2nd Edition. Prentice-Hall, London.