



## Biopedturbation by mammals in deserts: a review

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Disturbance-caused patchiness is important for development and maintenance of spatial and temporal heterogeneity in ecosystems. Mammals are important agents of biopedturbation (soil disturbance by organisms) which is a major source of patchiness in arid ecosystems. The contribution of soil disturbance by mammals to heterogeneity is a function of the size and longevity of the soil disturbance. Foraging pits produced by a variety of mammals are relatively short-lived features that trap plant litter and seeds that are rapidly buried. These form nutrient-rich germination sites. High water infiltration rates, a low bulk density rooting environment, and frequently increased soil nutrient content (especially mounds of central-place foragers and larder-hoarders) characterize warren complexes. Productivity tends to be higher on these mounds and the vegetation tends to differ in composition and richness from the surrounding areas. Soil ejected from fossorial mammal burrow systems is generally of low bulk density, erodes readily, and varies greatly with respect to concentration of nutrients and organic matter depending upon the species and landscape in which the species lives. The variability in soil properties of fossorial burrow system ejecta mounds precludes generalizations about the effects of these disturbances on vegetation. Long-lived features such as Mima-like mounds and heuweltjies are nutrient-rich features that support high productivity and a distinct floral assemblage. There is a significant relationship between longevity of mammal soil disturbance and size of the disturbance: longevity in years =  $9.33 \text{ Area}^{0.735}$ . The data suggest that pedturbation by mammals can be an important force in pedogenesis, in structuring landscapes, and in maintaining heterogeneity in ecosystems. Data on mammalian pedturbation is based on scattered autecological studies. There is a need for long-term studies that focus on biopedturbation (soil disturbance by invertebrates and vertebrates) as a process at scales from the patch to the landscape.

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## Introduction

Temporal and spatial heterogeneity are important variables affecting the functioning of ecosystems of a landscape. Understanding the origin of and the processes producing this heterogeneity is essential for sustainable management of ecosystems. Temporal and spatial heterogeneity characterize patterns of plant and animal species distributions and levels of productivity. The heterogeneity of terrestrial systems originates with soil patchiness with respect to water infiltration and storage and to concentrations of nutrients within the soil profile. Biopedturbation (soil disturbance by animals) plays a major role in establishing the temporal and spatial characteristics of soil patches. The diversity of biopedturbation should vary with the diversity of animals in the ecosystems. Because biopedturbation affects ecosystem processes such as productivity and nutrient cycling, it is a process that must be considered in analysis of ecosystem function. In addition to a process viewed at the ecosystem scale, biopedturbation affects landscape scale processes such as sediment transport and soil erosion, hence must be examined from the patch to landscape scale.

In arid regions soil heterogeneity may have an even greater impact on ecosystem properties and processes than those recorded for mesic environments. In deserts, small mammals may be the most important mechanism in the system for 'pumping' soluble nutrients from deep soil layers (10–200 cm) on the surface and may be the only mechanism for bringing insoluble materials to the surface for weathering (Abaturon, 1972). Here we review the literature to address several questions concerning the role of pedturbations by small and intermediate size mammals on the properties and processes of arid ecosystems. We address questions of convergence of properties and processes of mammal pedturbations in the arid and semi-arid zones of the world, and of the temporal and spatial relationships of small-scale and large-scale perturbations by mammals.

Scientific interest in biopedturbation (the effects of living organisms on the soil) has a long history. Darwin (1881) showed that earthworms are important in mixing and aerating soils and that their activities changed the composition of soil. Recent reviews have examined the effects of ants and termites and a variety of burrowing animals on soil properties and processes (Lobry de Bruyn & Conacher, 1990; Meadows & Meadows, 1991; Reichman & Smith, 1991). Contreras *et al.* (1993) recently summarized information on the effects of pocket gophers (Geomyidae), mole-rats (Bathyergidae), and colonial cururos (Octodontidae) on the ecology of semi-arid areas. In this review we examine the characteristics of pedturbation by mammals and their effects on hydrological properties of soils, soil nutrients, pedogenesis, soil erosion and deposition, and on plant communities.

### *Size of disturbance and pedogenesis*

The characteristics of pedturbation by mammals vary in predictable patterns that are dependent upon the behavior of the animals. Some soil disturbance is the result of one-time digging, i.e. excavation of roots, bulbs, and tubers, excavation of insect larvae, excavation of food caches, and construction of temporary shelter burrows. These pedturbations are relatively short-lived features of the landscape (Table 1) and the resulting pits trap debris and seeds that are transported by wind or water. The small quantity of material ejected by such digging is generally of lower bulk density and is hypothesized to have a smaller fractional volume of stable soil aggregates. These characteristics of the ejecta contribute to the susceptibility of the material to wind and water erosion. In arid and semi-arid regions the quantities of material ejected from foraging digs, caches, and temporary shelter burrows may cover up to 15–20% of the

Table 1. *Characteristics of biopedturbation by mammals in semi-arid and arid regions*

Species	Area (cm <sup>2</sup> )	Volume (m <sup>3</sup> )	Density (No. ha <sup>-1</sup> )	Time (years)	Reference
<b>Foraging digs</b>					
Heteromyids	15.2	2.3 × 10 <sup>-6</sup>	37,200	0.3	Steinberger & Whitford (1983), Chihuahuan Desert, U.S.A.
<i>Hystrix indica</i> Indian porcupine	267.7	0.07		1-20	Boeken <i>et al.</i> (1995), Israel
<i>Hystrix indica</i> Indian porcupine			100-1000	2.5-6	Alkon & Olsvig-Whittaker (1989), Israel
<i>Hystrix indica</i> Indian porcupine	22.7		100-1700 ( <i>M</i> = 500)		Yair & Rutin (1981), Israel
<i>Hystrix africaeustralis</i> Cape porcupine			19-52.7		DeVilliers & Van Aarde (1994), South Africa
<i>Cyanomys ludovicianus</i> Prairie dog	28.2	2.5 × 10 <sup>-4</sup>	37,000-64,000		Koford (1958), Day & Detling (1994), short-grass prairie, U.S.A.
<i>Otocyon megalotis</i> Bat-eared fox and <i>Oryzteropus afer</i> Aardvark	21-290	1.3 × 10 <sup>-5</sup> -1.7 × 10 <sup>-3</sup>	94		Dean & Milton (1991 a), South Africa
<b>Fossorial mounds</b>					
<i>Heterocephalus glaber</i> Naked mole-rat		0.11	400-500 per colony		Brett (1991)
<i>Ctenomys azarae</i> Tuco-tuco	28.6-150.0	0.31-1393.0	316-507	> 16	Roig <i>et al.</i> (1988), Argentina
<i>Myopalax cansus</i> Cansu mole rat	1.84	0.55	200-800		Hongo <i>et al.</i> (1993), China
<i>Spalacopus cyanus</i>	287	7.5	3.0		Contreras <i>et al.</i> (1993), Chile
<i>Splax ehrenbergi</i> Mole rat *total ha <sup>-1</sup>	706	4wc22.9-142.8 142.8		1-3	Heth (1989), Israel
<b>Burrows</b>					
<i>Dipodomys ingens</i> Giant kangaroo rat	50.2 13,000 (a)		42.0		Grinnell (1932), California, U.S.A.
<i>Tetera robusta</i> Gerbil (b)— colonial burrow system	211.1 2041.8 (b)	0.13 0.7 (b)	5925-6775 ( <i>M</i> = 64,332) 1000 (b)		Senzota (1984), Tanzania

surface area per year in habitats where mammals concentrate their foraging activity (Table 1).

Surface foraging by small and medium-sized mammals results in excavations of a

Table 1—Continued

Species	Area (cm <sup>2</sup> )	Volume (m <sup>3</sup> )	Density (No. ha <sup>-1</sup> )	Time (years)	Reference
<i>Pseudomys chapmani</i> Pebble mound mouse	2000	0.03	1800		Anstee <i>et al.</i> (1997), Anstee (1996), Western Australia
Burrow systems					
<i>Tympanocymys barrerae</i> Red vizchaca rat	390.4	147.9	7.3		Ojeda <i>et al.</i> (1996), Argentina
<i>-Lasiorhinus latifrons</i> Hairy-nosed wombat	314–706.5	214.5–918.5	0.1–0.3	> 50	Löffler & Margules (1980), South Australia
<i>Dipodomys spectabilis</i> Banner-tail kangaroo rat	12.8 14.3	5.1 6.8	7–10 8.2	> 35	Reichman <i>et al.</i> (1985), Moroka <i>et al.</i> (1982), southern Arizona and New Mexico
<i>Cynomys ludovicianus</i> Black-tail prairie dog	0.28 18.0 (c)	0.023 1.4 (c)	47.9–89.7		White & Carlson (1984), Arizona U.S.A.
Colonial					
<i>Rhombomys opimus</i> Great gerbil	113–907.5 (d)	135.6–1905 (d)		0.5 > 10 > 100	Prakash & Ghosh (1975), Kazakhstan
Mima-type mounds					
Heuweltjies (mole rats and termites)	615.4–803.8	1230.8–1607.7	2.3–3.9; 3.7–5.0	> 100	Lovegrove (1991), Moore & Picker (1991), South Africa
Mima mounds (pocket gophers <i>Geomys</i> spp. and <i>Thamomys</i> spp.)	50.2–149.5	15.0–74.8	20–50 > 100	> 100	Cox (1990 <i>a</i> ), Cox & Sheffer (1991), Western U.S.
Mima-like mounds	35–227	11.0–363.0	2–126	> 100	Cox <i>et al.</i> (1989)

(a) = burrow soil heaps; (b) = burrow system; (c) = soil disturbance per ha; (d) = burrow system depressions.

variety of sizes and densities (Table 1). Shallow pits are dug by rodents (primarily kangaroo rats, *Dipodomys* spp.) seeking or caching seeds (Table 1) but similar pits may be dug by small carnivores excavating grubs, other invertebrates, or small vertebrates. One such example is the foraging pits produced by echidnas in semi-arid Western Australia (Apensperg-Traun *et al.*, 1991). Prairie dog surface foraging activities (digging for roots and rhizomes) produce changes in soil structure that result in increased soil moisture and evapo-transpiration (Koford, 1958; Day & Detling, 1994). Depressions produced by badgers digging-out honey-pot ant (*Myremecosystus* spp.) nests slowly in-fill with silt and litter (Chew, 1979), presumably adding to soil nutrients as the buried litter decomposes. Indian porcupine digs disturb up to 3.5 m<sup>3</sup> soil ha<sup>-1</sup> and remain as identifiable depressions for 1–6.5 years (Alkon & Olsvig-Whittaker, 1989).

The ejecta mounds from porcupine digs erode readily and contribute significantly to sediment transport on hillslopes in the Negev (Yair & Rutin, 1981). The life-span of Cape porcupine diggings is greatest on rock outcrops possibly because overland flow during storms is reduced on the outcrops (de Villiers & van Aarde, 1994).

Foraging holes dug by a variety of small and medium-sized carnivores, including bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), armadillo (*Orycteropus afer*), and North American badgers (*Taxidea taxus*) are similarly variable. Fox and armadillo digs move large volumes of material from moderate depths in the profile to the surface (Table 1). This results in translocation of subsoil to the surface where it is exposed to weathering and the influences of plants and soil microflora and mesofauna. This is one way that soluble nutrients are 'pumped' to the surface, *sensu* Abatorov (1972). The abundance of digs by foraging small and medium-sized mammals is sufficient to have an important effect on the development of soils (Table 1).

In the Chihuahuan Desert of North America, badgers (*Taxidea taxus*) produce large pits with accompanying ejecta piles when they excavate honey-pot ant (*Myrmecocystus* spp.) nests (Table 1). The abundance and frequency of badger digs are considerably lower than reported for African medium size carnivores. However these digs may make important contributions to soil development over several centuries which is a brief span in a geological time reference. A small mammalian carnivore that produces large numbers of excavations is the echidna (*Tachyglossus aculeatus*). The excavations of termites and ants made by echidnas are classified as shallow (< 4 cm in depth) which result from digging with the forelimbs, and deep excavations (> 4 cm) which are up to 20 cm in diameter (Abensperg-Traun *et al.*, 1991). Unfortunately these authors provided no estimates of rates of pit digging nor of size range and volume of soil ejected from the digs which could be used to evaluate their contribution to pedogenesis and ecosystem processes.

The best studied mammalian pedturbations result from burrowing (Meadows & Meadows, 1991). Open burrows that are occupied by an animal during its lifetime, and open burrows that are occupied by successive generations of the same species or of different species result in two distinct, but related forms of pedturbation, burrow tunnels and piles of soil mined from the burrows. Mounds of soil ejected from burrows vary with the size of the burrow. Mammals that construct multiple entrance burrow systems may produce large accumulations of soil ejecta. Deep burrow systems dug by mammals such as armadillos and large kangaroo rats produce soil piles that differ markedly in chemistry and texture from surrounding soil. In areas where soils are underlain by calcrete, burrowing may transport small to medium-size (2–6 cm diameter) chunks of calcrete to the surface of the ejecta mound. Calcrete ejecta has been reported on hairy-nose wombat mounds in South Australia (Johnson, 1990) and observed on banner-tail kangaroo rat mounds in the Jornada Basin in New Mexico. Excavations by animals such as wombats, kangaroo rats, and pocket gophers have been hypothesized to be important in biomantle evolution and redistribution of materials in soil profiles (Johnson, 1990). The mound and burrow system may be intimately related with burrows occurring within the soil mounds, or the mounds may be discrete entities found at intervals within an otherwise hidden burrow system.

Burrow construction by fossorial mammals does not produce ejecta mounds of large size or of great longevity. However, the cumulative volume of soil moved to the surface by fossorial mammals can cover a large proportion of the area inhabited by these mammals over time. For example, colonial cururos (*Spalacopus cyanus*) in Fray Jorge National Park, Chile produced a mined soil mass of about 3.2 tons which covered up to 92.4 m<sup>2</sup> year<sup>-1</sup> of soil surface (Contreras *et al.*, 1993; Cox *et al.*, 1995) (Table 1). Over decades this level of soil disturbance results in the turnover of the entire soil surface.

Soil mounds of the dune mole-rat (*Bathyergus suillus*), hottentot mole-rat (*Cryptomys*

*hottentotus*), cape mole-rat (*Georhynchus capensis*), and naked mole-rat (*Heterocephalus glaber*) combined occupied up to 28.2% of an area (Reichman & Jarvis, 1989). *Bathyergus suillus*, the largest species, produced the most mounds (1852 ha<sup>-1</sup>) followed by *G. capensis* (435 ha<sup>-1</sup>) and *C. hottentotus* (277 ha<sup>-1</sup>). Jarvis & Bennett (1991) calculated that an individual *B. suillus*, or a colony of 87 *H. glaber*, produced up to 500 kg of soil mounds per month. A naked mole-rat (*H. glaber*) colony in Tsavo National Park, Kenya, produced 400–500 molehills (mounds) per year moving 3.6–4.5 tons of soil and producing 2.3–2.9 km of burrows annually (Brett, 1991).

The soil ejecta mounds of the Cansu mole-rats (*Myospalax cansus*, Muridae) can occupy up to 40% of the surface in shrub steppe vegetation of north-western China when the mole rats are at high population densities (Hongo *et al.*, 1993). The Palestine mole rat (*Spalax ehrenbergi*, Muridae) burrows result in high densities of soil ejecta mounds in the semi-arid region of Israel (Heth, 1989, 1991) (Table 1). Mounds may cover as much as 25% of an area and new mounds account for about 0.8% of the total each year. Burrowing activity of mole rats follows soil moisture gradients where those exist (Zuri & Terkel, 1997). Quantities of soil mined by Palestine mole rats depend on soil type. One mole rat was estimated to mine about 790 kg of rendzina soil and 664 kg of terra-rossa soil each year. Heth (1991) estimated that 1.4 million tons of soil are turned over annually in all of Israel by these mole rats. This is another example of large quantities of subsoil transported to the surface by a fossorial mammal.

Burrow systems may persist as landscape features for several decades because such systems tend to be occupied by successive generations of animals. For example, the burrow systems of banner-tail kangaroo rats in Chihuahuan Desert grasslands in North America contain a complex labyrinth of burrows (Vorhies & Taylor, 1922; Best, 1972; Schroder & Geluso, 1975; Kay & Whitford, 1978). Once constructed the soil ejecta mound weathers and erodes. Burrow system maintenance may add small amounts of materials to the mounds but the mound system tends to remain at essentially the same size over long periods of time. There are no published estimates of the quantities of soil moved by banner-tail kangaroo rats. However these are long-lived features of desert grasslands, and at only 40 m<sup>2</sup> ha<sup>-1</sup> represent far less soil turnover than that estimated for mole rats in the Afro-Asian region.

Black-tailed prairie dogs (*Cynomys ludovicianus*) burrow extensively and develop substantial mounds around their burrow entrances (Hoogland, 1996). Black-tailed prairie dogs occur on disturbed areas of relatively low slope with deep (> 1 m), well-drained clay-loam and loamy soils (Reading & Matchett, 1997). Prairie dog towns vary considerably in size (Table 1). These rodents dig numerous burrows during the vegetation growing season, many of which are abandoned by the end of the growing season. Koford (1958) reported that more than half of 100 holes produced during the early summer were abandoned by autumn. Each burrow entrance has a pile of mined soil around the perimeter. The mined soil around abandoned burrow entrances of prairie dogs contributes to soil mixing and the abandoned burrows serve as litter and seed traps. The rate of soil mixing on prairie dog colonies exceeded the normal rate of soil formation in non-colony areas (Munn, 1993). White & Carlson (1984) cautioned that the time required for complete mixing of the soil profile by prairie dogs has been overestimated and they concluded that these rodents are not important agents of soil mixing over extensive areas.

Colonial burrowing mammals produce perturbations that are extensive and persist for long time periods (Table 1). Colonies of great gerbils (*Rhombomys opimus*) in arid areas of central Asia occur in depressions. These depressions may have resulted from erosion of soil ejecta mounds over centuries of time (Naumov & Lobachev, 1975). Indian desert gerbil colonies may move as much as  $1.04 \times 10^6$  kg km<sup>-2</sup> of soil each day (Fitzwater & Prakash, 1969). On the arid shortgrass Serengeti Plain, colonies of the gerbil *Tatera robusta* produce burrow soil piles 0.68 kg m<sup>-2</sup> at a density of 0.1 piles per m<sup>2</sup> on the midslopes of rocky hills (kopjes) (Senzota, 1984).

Mounds and burrow systems often remain intact, or increase in area, remaining as significant structures in the landscape for long time periods. The largest of the mound and burrow systems may cover several hundred square meters. For example, warrens of the hairy-nosed wombat (*Lasiorhinus latifrons*) are visible in LANDSAT satellite imagery of Australia (Löffler & Margules, 1980). Other types of mounds may not be visible from space, but are important features of local or regional landscapes such as the large mounds associated with the extinct burrowing bettong (*Bettongia lesueur*) in Australia (Noble, 1993), Mima mounds in North America, Mima-like mounds in Kenya and Argentina, and heuweltjies in South Africa.

Mima mounds are thought to result from centripetal soil movement by pocket gopher (Geomyidae) burrowing over long time-spans (Cox & Allen, 1987; Cox, 1990*b*; Cox & Scheffer, 1991). Pocket gophers push soil from burrows toward a focal point resulting in soil accumulation in the mound. Mima mounds in North America (both historic and current) are often associated with grasslands on shallow, poorly drained soils (Cox, 1984, 1990*a*; Reifner & Pryor, 1996). Individual pocket gophers (*Thomomys bottae*) may mine and push as much as 105,000 kg ha<sup>-1</sup> of soil to the surface each year and leave 2.5 times that much mined soil in their below-ground tunnels (Cox, 1990*b*; Cox *et al.*, 1995). This represents a turnover of up to 1% of the soil in the top 20 cm each year.

Heuweltjies are large soil mounds in the semi-arid regions of Southern Africa. Mima-like mounds have been also been described in the semi-arid highlands of Kenya (Table 1). Heuweltjies and Mima-like mounds have been hypothesized to result from fossorial mole-rat (Bathyergidae and Rhizomyinae) burrowing in a manner analogous to Mima mounds, from termites, or from termites and mole-rats (Lovegrove & Siegfried, 1986, 1989; Cox *et al.*, 1987; Milton & Dean, 1990; Lovegrove 1991; Moore & Picker, 1991). While the origin of heuweltjies and Mima-like mounds may not be resolved, there is no doubt that these are important features of the landscapes in which they occur.

Soil mixing by burrowing mammals is an important pedogenic process. Johnson (1990) reviewed the evolution of biomantles (a mantle of material sorted and brought to the surface by animals). When freshly excavated material is exposed to the beating action of rain, soil fines may be carried away in runoff. Pocket gophers were shown to alter stone zones and mantle layers in semi-arid California (Johnson, 1989). Wombat burrow systems were also implicated as sources of biomantles (Johnson, 1990). Selective size sorting of materials brought to the surface by burrowing mammals may be a widespread consequence of burrowing activity, or it may be a local phenomenon that occurs only in certain kinds of soils.

### Longevity and size of mammalian biopedturbations

We hypothesized that there is a relationship between size (area) of mammalian pedturbations and the longevity of those patches in the landscape. We tested this hypothesis with data from the literature in this review and from discussions with experts. Longevity of mammal pedturbations scaled significantly with area of soil disturbances (Fig. 1). The regression is significant ( $F = 54.6$ ;  $df = 1, 11$ ;  $p < 0.001$ ) as are the slope ( $t = 7.4$ ,  $p < 0.001$ ) and the intercept ( $t = 5.8$ ,  $p < 0.001$ ). The regression has an  $r^2$  of 0.845. The exponent of the regression equation (0.735) is very close to 0.75, an important allometric scaling factor for many mammalian processes related to body size. Included in the data are two classes of pedturbations, those resulting from feeding activities and those resulting from mammal burrow systems. We have included heuweltjies and Kenyan Mima-like mounds (dotted symbols) in the data because, even though the primary source of the mounds in both cases appears to be termites, they are

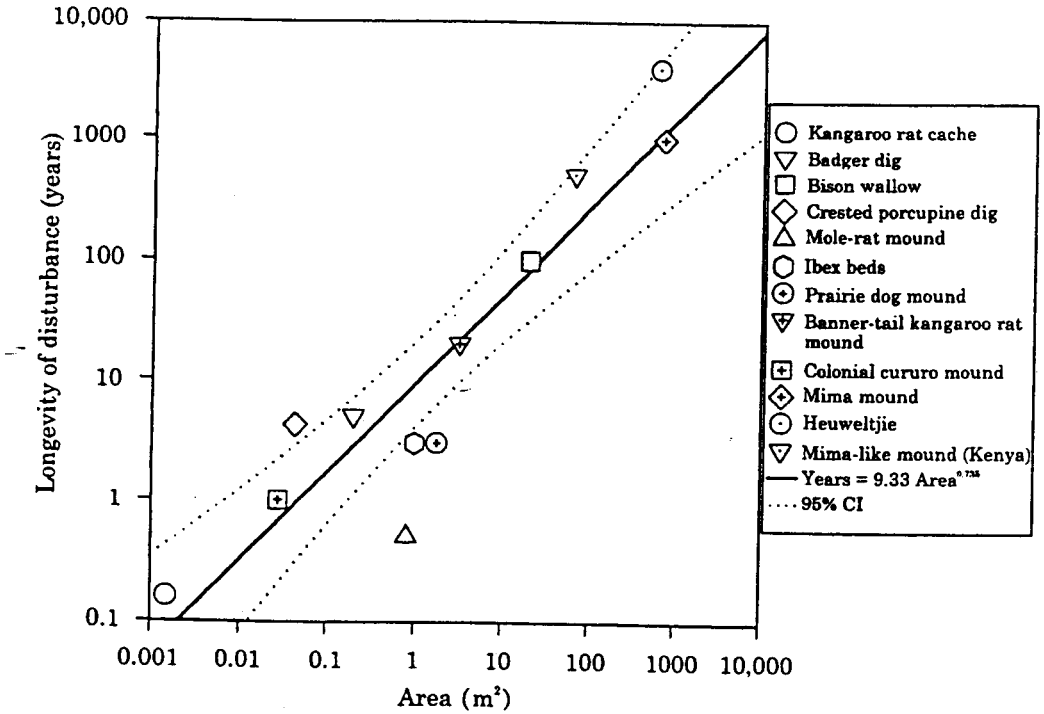


Figure 1. Relationship between area of disturbance and longevity of biopedturbations of a variety of mammals.

important to and partially maintained by both feeding and living quarters of mammals. The former are represented by the activities of aardvarks (Milton & Dean, 1990; Dean & Milton, 1991a) and the latter by mole-rats and whistling rats (*Parotomys brantsii*) (Lovegrove & Siegfried, 1986, 1989; Cox & Gakahu, 1987; Martin, 1988; Cox *et al.*, 1989; Midgley & Musil, 1990; Milton & Dean, 1990; Du Plessis & Kerley, 1991; Moore & Picker, 1991). Very large, very old pedturbations are maintained by the chronic disturbance of long-term occupation (prairie dog and banner-tail kangaroo rat mounds, heuweltjies, Mima mounds). Small and short-lived disturbances result from feeding activity (kangaroo rat caches, badger and porcupine digs, mole-rat mounds) or periodically renewed living or bedding sites (colonial cururo mound, ibex beds).

#### Distribution of disturbances on a desert watershed

Most studies of pedturbation by mammals focus on a single species. In order to gain an appreciation for the combined effects of mammals on soils of a desert landscape unit, we enumerated soil surface disturbances by various animals along a 30 m by 1100 m transect encompassing the length of a small Chihuahuan Desert watershed. Pedturbation by mammals was common along the entire transect. Kangaroo rats (*Dipodomys ordii*, *D. merriami*, and *D. spectabilis*) produced most of the surface disturbance (burrows, burrow systems, and foraging pits) ( $M = 101.8 \text{ m}^2 \text{ ha}^{-1}$ ; Fig. 2). The next most common disturbance was by unidentified rodents and consisted mostly of burrows ( $M = 36.1 \text{ m}^2 \text{ ha}^{-1}$ ; Fig. 2). Pocket gopher (*Thomomys bottae*) soil piles were found only in the black grama (*Bouteloua eriopoda*) grassland community on the upper slope of the watershed and averaged  $68.5 \text{ m}^2 \text{ ha}^{-1}$ . Badger diggings, although present in



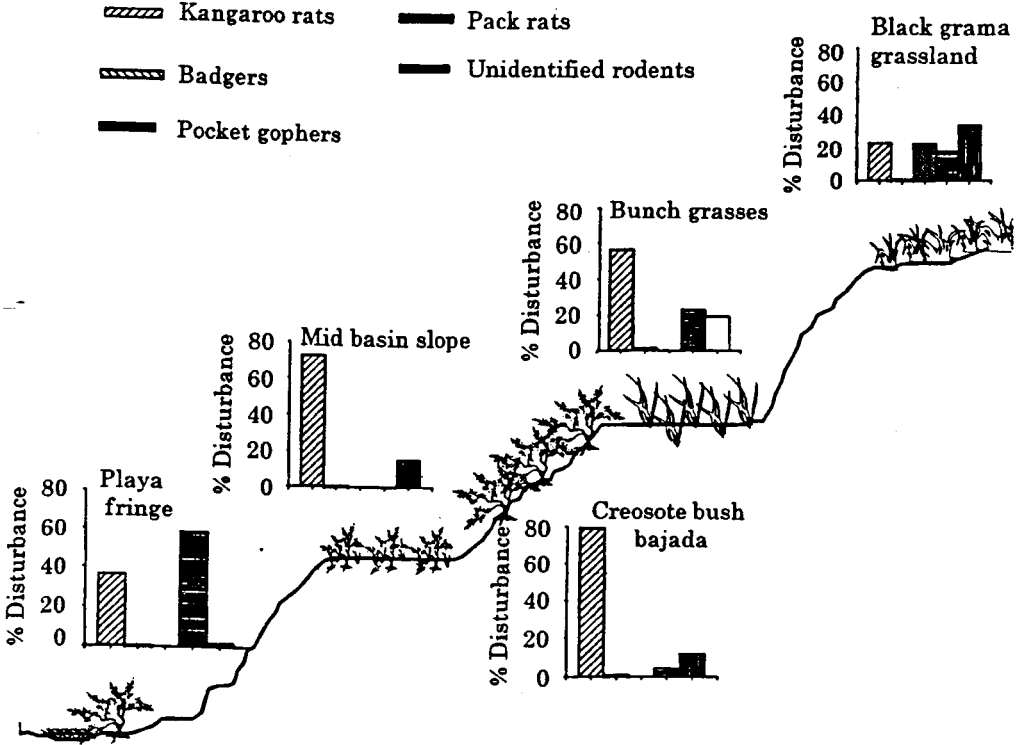


Figure 2. Frequency of soil disturbance by small mammals along an elevational and plant community gradient in the Chihuahuan Desert of New Mexico, U.S.A.

every community, are also most abundant in the black grama grassland where they averaged  $3.5 \text{ m}^2 \text{ ha}^{-1}$ . Total badger excavations averaged  $1.9 \text{ m}^2 \text{ ha}^{-1}$  along the entire watershed. Pack rat (*Neotoma* spp.) nests were most common in the large mesquite (*Prosopis glandulosa*) clumps at the margins of the ephemeral lake at the base of the watershed (Fig. 2). Pack rat nests averaged  $180.5 \text{ m}^2 \text{ ha}^{-1}$  on the playa fringe and  $23.2 \text{ m}^2 \text{ ha}^{-1}$  over the rest of the watershed. Taken together, soil disturbance attributable to the activities of mammals affected between 1.4% and 3.0% of the soil surface on this watershed. Since most of this pedturbation has a short half-life, the entire soil surface would be affected by mammals within a century.

### Characteristics of other pedturbations

Resting forms, night beds, and trails produced by mammals represent relatively unstudied, but potentially important sources of biopedturbation. Nubian ibex beds are depressions  $0.5$  to  $1.5 \text{ m}^2$  in area and 7 to 15 cm deep (Gutterman, 1998), and occur at densities of up to  $770 \text{ ha}^{-1}$  in the Negev Desert. The beds are used for varying periods and when abandoned, fill in with silt and litter over several years (Gutterman, 1997a, 1998).

We have observed that jackrabbit (*Lepus californicus*) forms in western North America and Mexico result in shallow depressions under the edges of shrubs and large grass tussocks. Other hares (Leporidae) probably produce similar resting forms. Kangaroos in Australia produce hip pits associated with their resting locations

(Whitford, pers. obs). There are no published measurements of size or densities of such forms or hip pits.

Many small mammals use regular travel routes, e.g. elephant shrews (*Macroscelides proboscideus* and *Elephantulus* spp.) in South Africa and banner-tailed kangaroo rats (*Dipodomys spectabilis*) in the Chihuahuan Desert of North America. Several *M. proboscideus* individuals move in-line, hopping on paths of a linear series of bare patches where each animal, in turn, lands (Sauer & Sauer, 1972). *Elephantulus* spp. develop paths from their burrows to their feeding grounds (Walker, 1964) and banner-tail kangaroo rats develop a complex of trails linking individual burrows, escape holes, and foraging areas (Vorhies & Taylor, 1922). The areal extent and density of these various trails has not been reported in the literature.

Nests of the white-throated woodrat (*Neotoma albigula*) are common throughout the Sonoran and Chihuahuan Deserts of Arizona, New Mexico, and Texas, U.S.A., and Mexico (Vorhies & Taylor, 1940; Vaughn, 1990) where they are found under shrubs, cactus, and yucca plants, and in rock crevices. The nests consist of masses of small branches and twigs of local shrubs, yucca leaves, cattle and horse droppings, segments of cholla cactus (*Opuntia* spp.), and other materials piled over shallow burrows (Vorhies & Taylor, 1940; Vaughn, 1990). In some cases where woodrat nests are built in *Yucca* spp. or *Opuntia* spp. cactus clumps, soil disturbance is very evident (pers. obs.). There are no quantitative data on soil movement or turnover by woodrats.

### Effects of pedurbation on soil properties and processes

Small mammal pedurbation has a variety of impacts on soil properties and processes. Generally, porosity is increased resulting in increased water infiltration and evaporation in soil piles or on surface-disturbed soil. Soil nutrients, rates of litter decomposition, mineral concentration, and rates of mineralization tend to increase in small mammal pedurbed soils. Rates of erosion may also increase, but may be offset by increased capture of wind transported soil and suspended soil in overland flow in surface pits and holes produced by mammals.

The temporal characteristics of the pits, burrows, burrow systems, and Mima-type mounds largely determine how these features affect soil properties and processes. Water infiltration is higher on short-lived, low bulk density soil ejecta mounds and in areas with numerous small burrows than on long-lived mounds. However, most pedurbation mounds have higher water infiltration rates than surrounding soils. Burrow systems occupied by successive generations of central-place foragers that are larder-hoarders (store foods in the burrow system) are characterized by higher organic matter content than the surrounding undisturbed soil. Fossorial mammal burrow systems that include storage and defecation chambers also provide patches of various size that are rich in organic matter. Concentrations of organic matter support a diverse soil microflora and micro-mesofauna that interact to affect rates of decomposition and mineralization. Most of the evidence reviewed here supports these generalizations.

In the Chihuahuan Desert, foraging pits and food cache pits result in nutrient-rich, seed-rich patches. Litter and seeds transported by wind or water become trapped in these small pits and are covered by transported soil (Table 2). Kangaroo rats (*D. merriami*) and pocket mice (*Chaetodipus* [*Perognathus*] *penicillatus*) dig for buried seeds and to recover seed caches. The litter trapped in these pits as they in-fill decompose at a higher rate than litter on the soil surface (Steinberger & Whitford, 1983). This decomposing material produces nutrient-rich microsites which support the germination and establishment of annual plant species that have relatively high nitrogen requirements. Foraging pit turnover and quantities of litter buried in pits was highest during the season of highest leaf litter input from the evergreen creosotebush (*Larrea*

Table 2. *Effects of mammalian perturbation on soil properties and processes, and on vegetation in the area of disturbance and / or on the mounds of soil ejected from burrows and digs*

Property/ Process	Disturbance type	Vegetation response	Reference
Litter accumulation	Cache and foraging pits	> annual plants	Steinberger & Whitford (1983), McAadoo <i>et al.</i> (1983)
Litter accumulation	Nubian ibex bedding sites	> density annual plants	Gutterman (1997a, 1998)
Litter and seeds trapped	Crested porcupine foraging digs	> density geophytes	Alkon & Olsvig-Whittaker (1989), Boeken <i>et al.</i> (1995, 1998), Gutterman & Herr (1981)
Fecal pellet accumulation	Gemsbok resting form	> density annuals	Dean & Milton (1991b)
Subsoil to surface	Aardvark, bat-eared fox, Cape porcupine foraging digs	> density geophytes < perennial grasses > annual forbs	Dean & Milton (1991a, b)
< bulk density	Burrow system, <i>Dipodomys spectabilis</i>	> biomass annuals < perennials $\Delta$ species annuals	Geene & Reynard (1932), Greene & Murphy (1932), Moorhead <i>et al.</i> (1988), Mun & Whitford (1990), Guo (1996)
< bulk density	Burrows, <i>Spermophilus elegans</i>		Laundre & Reynolds (1993)
< bulk density	Burrows, <i>Spermophilus townsendii</i>	> grass biomass > <i>Artemisia tridentata</i> biomass	Laundre (1993, 1998)
< bulk density	Fossorial system ejecta piles		Heth (1991)
< soil moisture	Burrow system		Mun & Whitford (1990)
< soil moisture	Burrow system, desert gerbils		Sharma & Joshi (1975)
> infiltration	Rodent burrows	< native annual grass > biomass two shrubs	Soholt <i>et al.</i> (1975), Soholt & Irwin (1976)
> infiltration	Fossorial system, Cansu mole rats		Hongo <i>et al.</i> (1993)
> infiltration	Abandoned <i>Gerbillus</i> colonies	> grass production	Cox (1987)
> pH, < N, > P	Burrow system, prairie dog ejecta mounds		Carlson & White (1988)
> total soluble salts, > CaCO <sub>3</sub>	Burrow ejecta mounds, <i>Citellus</i>		Abaturov (1972)
> K, > P, > SOM	Fossorial system ejecta mounds, pocket gophers ( <i>Geomysidae</i> )	> biomass production $\Delta$ species composition	Mielke (1977), Martinsen <i>et al.</i> (1990), Reichman & Smith (1991)
< SOM, < N	Fossorial systems ejecta mounds, mole rats	$\Delta$ species diversity	Hongo <i>et al.</i> (1993)

Table 2—*Continued*

Property/ Process	Disturbance type	Vegetation response	Reference
> N, > SOM	Fossorial system ejecta mounds, mole rats	establishment of geophytes	Heth (1989, 1991)
No change pH, total N, P, SOM	Fossorial system ejecta mounds	> pioneer species > exotic <i>Mesembryanthemum</i>	Contreras <i>et al.</i> (1993), Contreras & Gutierrez (1991), Cox <i>et al.</i> (1995)
> SOM, > N	Burrow system, <i>Dipodomys</i> spp.		Mun & Whitford (1990)
> SOM, > N, > Fe, > Mg	Burrow mounds, Cottontail rabbit		Dhillion <i>et al.</i> (1994)
> N, K, Ca, Mg, Zn, Mn, B, Fe, Al	Heuweltjies	$\Delta$ species composition > productivity	Midgley & Musil, (1990), Lovegrove (1991), Moore & Picker (1991)
	Giant kangaroo rat burrow system	> exotic annuals	Schiffman (1994)
	Fossorial system, <i>Ctenomys australis</i>	> plant biomass > species richness	Zenuto & Busch (1995)
	Mima mounds, Colorado, U.S.A.	endemic flora	Reifner & Pryor (1996)
	Mima-like mounds, Argentina	> exotic tree <i>Tamarix gallica</i>	Roig <i>et al.</i> (1988)
	Gerbil colonies	< grass production	Sentoza (1984)
	Red viscacha rat mounds	support succulent halophytes	Ojeda <i>et al.</i> (1996)
	Batherygid mole rats	< plant biomass, $\Delta$ community structure	Reichman & Jarvis (1989)
> fertility	heuweltjies	$\Delta$ community structure	Knight <i>et al.</i> (1989) Lovegrove (1991), Midgley & Musil (1990), Esler & Cowling (1995)

SOM = soil organic matter.

*tridentata*) (Fig. 3). Since buried litter contributes to soil nutrient stores as it is decomposed, and decomposing surface litter contributes little to the soil organic matter (Mun & Whitford, 1998), the foraging and cache pits produced by these small mammals contribute directly to the productivity and spatial heterogeneity of the ecosystems in which they occur.

Scatter hoarding in seed cache pits may be a perturbation that is only common in regions inhabited by heteromyid rodents. The external cheek pouches of these rodents makes seed collection and scatter hoarding feasible. Rodents of the African, Asian, and Australian deserts may dig pits to locate rich accumulations of buried seeds but probably do not dig many caches. The absence of cached seeds probably reduces the densities of foraging pits and consequently the impact of such pits on the patchiness of soil properties and vegetation. Studies on foraging pits in deserts other than North America are needed to resolve this question.

In the Negev Desert, depressions formed on hillslopes by Indian porcupine digging

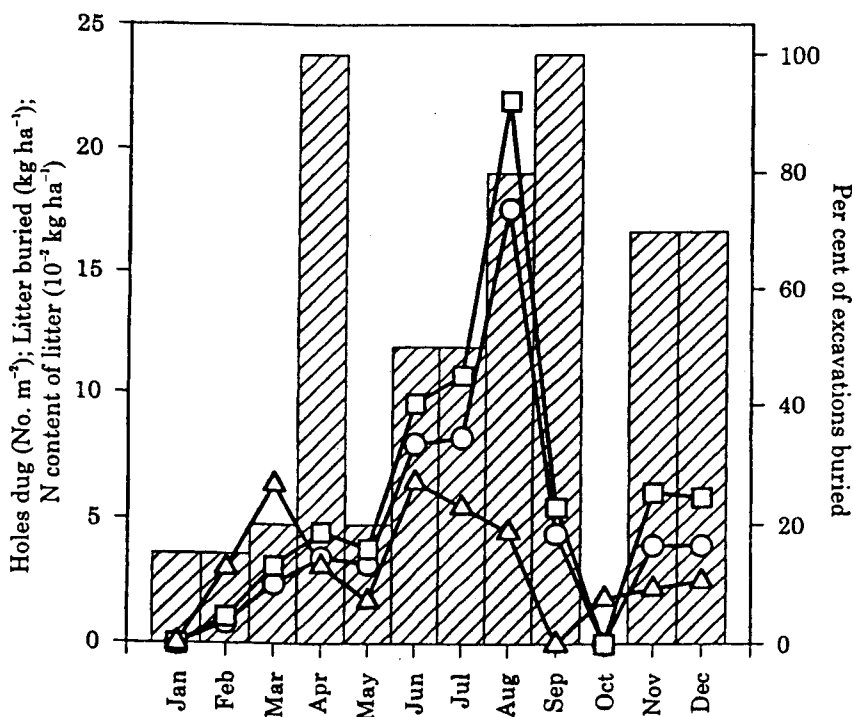


Figure 3. Number of holes dug ( $\square$ ), per cent of holes buried ( $\Delta$ ), litter buried ( $\circ$ ), and N content of litter ( $\square$ ) along a Chihuahuan Desert watershed in New Mexico, U.S.A. Data from Steinberger & Whitford (1983).

modify the soil by trapping sediment, litter, seeds, and water (Table 2), resulting in reduced soil surface temperature. The soil surface at the bottom of 10-cm deep depressions was cooler than the south side of the depressions and was similar to soil temperature at 10 cm depth (Gutterman, 1997b). Density of porcupine diggings influences interception of windblown litter and seeds, and runoff of low intensity rainfall events. Porcupine foraging contributes to soil erosion and sedimentation on limestone ridges in the Negev Desert where from 40 to 100% of the available sediment on small watersheds is attributable to porcupines (Yair & Rutin, 1981).

There is a limited literature on the effects of bedding sites. Bedding sites of large herbivores such as the Nubian ibex (*Capra ibex*), springbok (*Antidorcas marsupialis*), and gemsbok (*Oryx gazella*) are collection sites for fecal pellets and plant debris (Dean & Milton, 1991b; Gutterman, 1997a, 1998).

There are feedbacks between soil structural characteristics, soil moisture, and mammal burrowing. Soil type can influence water penetration both by soil structural characteristics and by influencing the structure and depth of rodent burrows. Kangaroo rat (*Dipodomys ordii*) burrows are deeper, larger, and more complex in soils higher in silt and clay (Laundre & Reynolds, 1993). Ground squirrel (*Spermophilus elegans*) burrows are deeper, longer, and more complex in soils with lower bulk density and increased silt and clay fractions. However burrows of *Spermophilus townsendii* are not influenced by soil properties (Laundre & Reynolds, 1993). Banner-tail kangaroo mound soils (Fig. 4) have higher concentrations of soil nutrients, lower bulk density, and lower soil moisture than intermound areas (Table 2). Significantly greater amounts of water

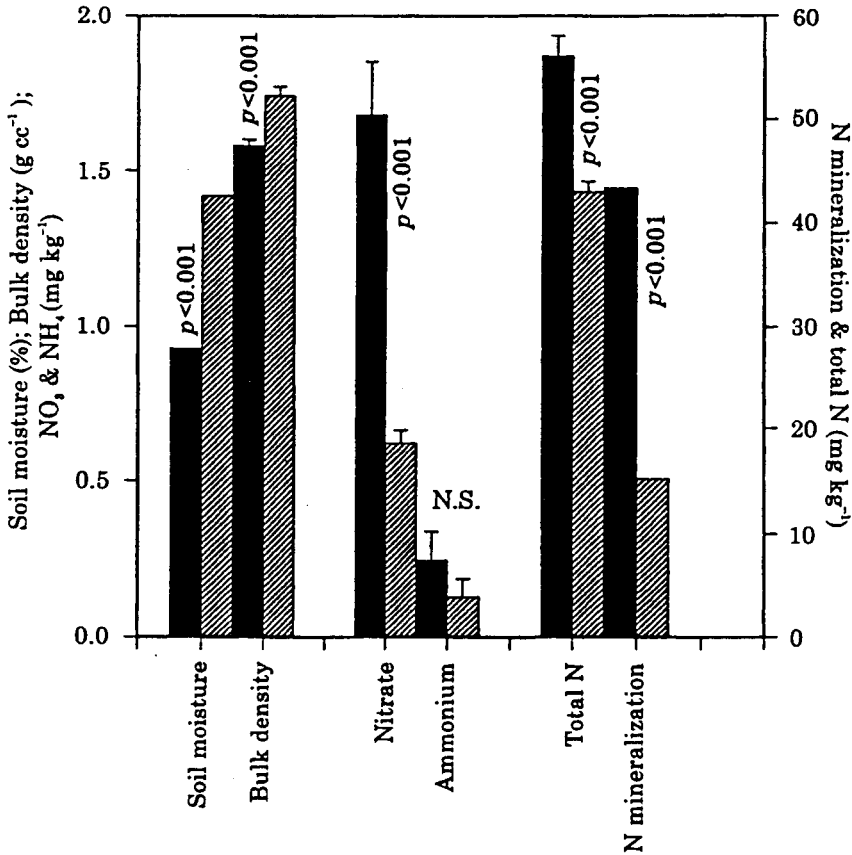


Figure 4. Comparison of bulk density, soil moisture, and soil N of *Dipodomys spectabilis* burrow mounds (■) and intermound areas (▨) in the Chihuahuan Desert of New Mexico, U.S.A. Data from Moorehead *et al.* (1985) and Mun & Whitford (1990).

(up to 34%) and increased depth of water penetration occurs in areas with ground squirrel burrows. Soil moisture is positively correlated with burrow densities in areas with ground squirrel (*Spermophilus townsendii* and *S. elegans*) burrows in the northern Great Basin Desert of North America (Laundre, 1993). Rodent burrowing disturbs as much as 4–5% of the surface of northern Mojave Desert bajadas and leads to increased water infiltration and decreased bulk density (Fig. 5), but the effect is significant only at depths greater than 5 cm. The effect of burrows on water infiltration is greatest under shrubs (Soholt *et al.*, 1975; Soholt & Irwin, 1976).

In the Thar Desert of India, desert gerbil burrowing is a major contributor to soil water loss, erosion, and dune formation because the moist soil brought to the surface desiccates and is easily moved by the wind (Sharma & Joshi, 1975). *Spalax ehrenbergi* soil piles have lower soil density, and higher dehydration rate and lower water content than adjacent undisturbed soil (Heth, 1991). The low bulk density soil ejected from mammal burrows is probably moved easily by wind and water in most locations. In order to evaluate the relative importance of this material in pedogenesis and as a landscape process, data on rates of loss with various wind velocities and rainfall intensities are needed. Ejected soil mounds do not differ from non-burrow soils in all respects. For example, water-holding capacity of soil from the shallow burrows of

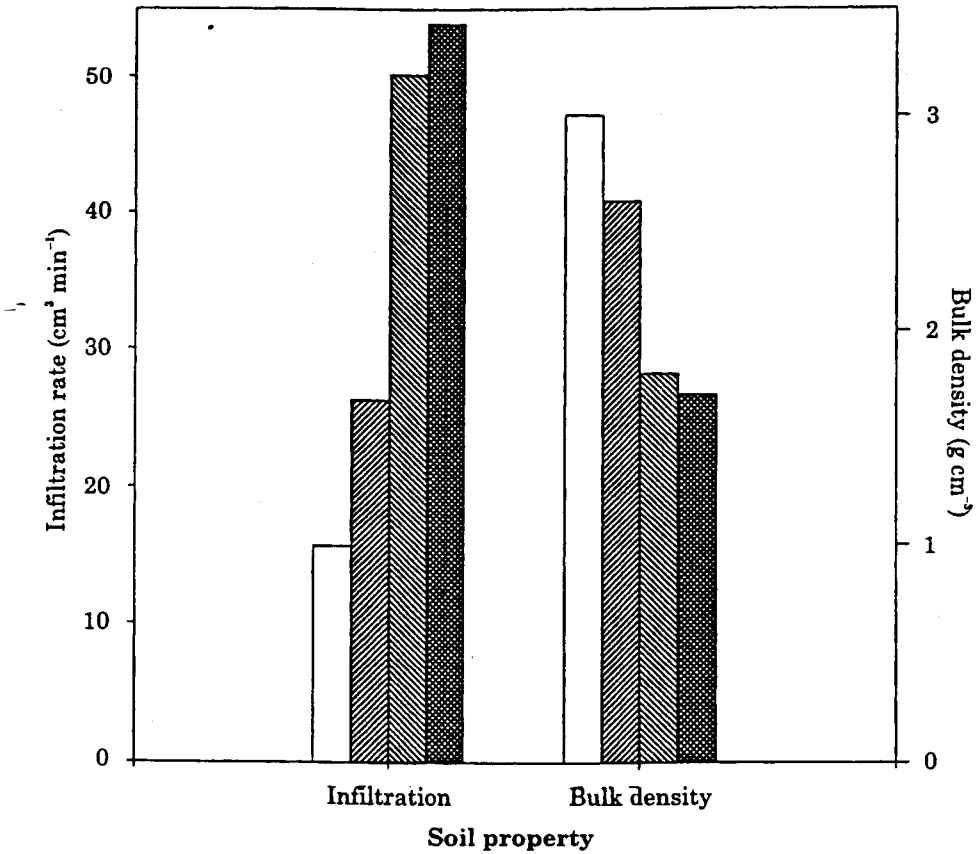


Figure 5. Comparison of bulk density and moisture infiltration rate associated with small mammal burrows and shrubs on a northern Mojave Desert site in Nevada, U.S.A. Data from Soholt *et al.* (1975) and Soholt & Irwin (1976). (□) = open, no burrow; (▨) = open, burrow; (▧) = shrub, no burrow; (▩) = shrub, burrow.

woodrats (*Neotoma* spp.) did not differ from non-burrow soil (Greene & Murphy, 1932).

Soil minerals, C, N, and organic materials tend to be elevated and pH modified in soils associated with small mammal burrows and burrow mounds. Elevated mineral concentrations may result from decomposition of animal bones and urine or minerals mined from depth in the soil and brought to the surface. Carbon, N, and organic materials tend to result from decomposition of animal feces and tissue, nest material, and stored food. The latter may be in underground chambers, mixed into the mound soil, or both, or mixed into the soil under surface-stored material.

Carlson & White (1987, 1988) described differences in soil properties, including pH, N, and P content associated with black-tailed prairie dogs. The pH of mound soils was generally higher than off-mound soils, apparently as a result of the rodents bringing calcareous soils to the surface. Mound-soil N was reduced and P elevated compared to off-mound soils (Table 2). They attributed increased mound-soil P to accumulation of subsurface soil, prairie dog skeletal material, and feces. Nitrogen was lower than P, but more uniformly distributed on mounds than off because of soil mixing in the mound.

Burrow mounds of small suslik (*Citellus pygmaeus*) in the semi-desert Caspian

lowland contain 97% more total soluble salts than nearby non-mound soils (Abaturov, 1972). Small suslik bring as much as  $1500 \text{ kg ha}^{-1}$  of soil, rich in  $\text{CaCO}_3$ , to the surface from 40–200 cm depth which reduces the salinity of the 0–10 cm soil layer. In this region and in other arid regions, mammal burrowing is frequently more important than capillary infiltration from the subsoil or leaching of litter for mineral transport to the soil surface (Abaturov, 1972; Chew, 1978).

In the arid Central Valley and the Sierra Nevada Mountains of California, pocket gophers (*Thomomys* spp.) turn over large volumes of soil, an important process that loosens soils compacted by livestock in heavily grazed areas (Grinnell, 1923). In Colorado grasslands, K, P, soil organic matter, water-holding capacity, and soil granularity are elevated on gopher mounds (Mielke, 1977). Pocket gopher mounds in arid regions probably lose water faster than surrounding soils thereby creating rapidly drying patches in the landscape (Cortinas & Seastedt, 1996).

In north-west China,  $\text{CaCO}_3$  accumulated in surface soils on west- and north-west-facing slopes, but not north-facing slopes, irrespective of the presence of Cansu mole-rats. Water percolated deeper on slopes with mole-rats than on slopes with no mole rats. Organic matter and total N were lower in the top 10 cm of soil on an old Cansu mole-rat mound than off, and the same in both soils below 20 cm depth (Hongo *et al.*, 1993). Soil pH was similar in the top 10 cm on- and off-mound and increased with depth off-mound (Hongo *et al.*, 1993).

*Spalax ehrenbergi* feeding burrow soil piles have elevated N and organic matter, and abandoned nest chambers contain decomposing plant material (Heth, 1989, 1991). Many bathyergid mole rats store rhizomes and tubers and defecate in chambers underground providing potential sources of nutrients in nutrient-poor Mediterranean soils (Davies & Jarvis, 1986; Reichman & Jarvis, 1989; Jarvis & Bennett, 1991). Similarly, tuco-tucos (*Ctenomys* spp.) store food in their burrows (Walker, 1964) which, if not utilized, decays and enriches the soil. Contreras *et al.* (1993) feel that burrow systems contribute to soil nutrients by acting as litter traps and accumulating plant material from food and nests even though they find no difference in pH, N, P, or organic matter in soils from cururo mounds. Cururo (*Spalacopus cyanus*) colonies occupy large areas for long time-spans (Contreras *et al.*, 1993). It is possible that the periodic reworking of the soil in an area occupied by cururos results in homogenization of nutrients which masks the influence of the burrows. Total organic matter, total N,  $\text{NH}_3^-$ ,  $\text{NO}_3^-$ , Fe, and Mg were all significantly higher on cottontail rabbit (*Sylvilagus auduboni*) burrow mounds than off-mounds in a sand shinnery oak (*Quercus havardii*) community in Texas, U.S.A. (Dhillion *et al.*, 1994).

Greene & Reynard (1932) and Greene & Murphy (1932) reported that total soluble salts were higher in the shallow burrows under woodrat nests than in adjacent, non-burrow soil in the Sonoran Desert of Arizona, U.S.A. Calcium,  $\text{HCO}_3^+$ , and  $\text{NO}_3^-$  were the major ions represented (Greene & Reynard, 1932) and each was higher in the burrows than outside. The high levels of soluble salts associated with woodrat nests may be attributed to decomposition of urine and feces in the rats' middens (Greene & Murphy, 1932; Greene & Reynard, 1932; Finley, 1990). When wood rat nests are abandoned, the breakdown of the nest structure over time also contributes to the soil nutrient pool (Vorhies & Taylor, 1940).

The long-term, cumulative effects of biopedturbation also lead to modified soil properties. Heuweltjies in South Africa have elevated water content, and N, K, Ca, Mg, Zn, Mn, B, Fe, and Al concentrations that are similar to termite mounds (Midgley & Musil, 1990; Lovegrove, 1991; Moore & Picker, 1991). Heuweltjies, and Mima-like mounds in other areas of Africa, invariably are underlain by a calcrete ( $\text{CaCO}_3$ ) layer that appears to be formed by the interaction of  $\text{CaHCO}_3$ -bearing ground-water and low pH soil of the mound (Moore & Picker, 1991). This also resembles termite mounds. Mima mounds are generally found over depressions in a hardpan or bedrock substrate, often with shallow ground-water present (Cox, 1984; Cox & Scheffer, 1991). The small



stone and gravel component of the soil of heuweltjies, Mima-like mounds, and Mima mounds are similar and are generally distinct from non-mound soils (Cox, 1984; Lovegrove & Siegfried, 1986; Cox *et al.*, 1989; Cox & Scheffer, 1991; Moore & Picker, 1991).

### *Effects on biota*

The effects of pedturbation by mammals on bulk density, water infiltration and storage, and soil nutrient stores result in soil patches that support a different plant community with qualitative and quantitative differences in patterns of primary productivity from the matrix landscape in which the patches are imbedded. In addition to effects on the plant communities, mammal burrows provide habitat and/or refugia for a variety of animals, some of which are obligate commensals (see Kinlaw, this volume).

Seed handling and caching by *Dipodomys* spp. are important to successful recruitment of Indian rice grass (*Oryzopsis hymenoides*) in the Great Basin Desert of North America. Many clumps of rice grass emerge from lost or 'forgotten' seed caches (Table 2) (Longland, 1995). In a South African arid grassland, burrowing by rodents (*Tatera brandtsii*) and surface foraging by Cape porcupines, aardvarks, and foxes reduce perennial grasses and provide patches suitable for invasion by annual forbs (Dean & Milton, 1991 *a, b*). Indian porcupine foraging is important for germination and renewal of the geophytes on which they feed (Table 2). Porcupine foraging digs may get covered with the next rain, remain visible for > 20 years, or remain uncovered for 5–10 years. Those that remain open for 5–10 years support the geophytes favored by porcupines (Guterman, 1987).

Litter, seeds, and moisture trapped by abandoned beds of Nubian ibex (Guterman, 1997 *a*, 1998) improve soil nutrients and aid in seed dispersal and germination of annual plants. Deposition of feces and trampling associated with resting forms of springbok and gemsbok also improve soil nutrients and aid in establishment of annual plants (Dean & Milton, 1991 *b*).

Banner-tailed kangaroo rats substantially reduce the standing crop of perennial plants on their burrow mounds (Vorhies & Taylor, 1922; Monson, 1943; Wood, 1969; Moroka *et al.*, 1982). However, abandoned banner-tail mounds provide nitrogen-rich, high water storage sites on which perennial shrubs such as creosotebush *Larrea tridentata* may have higher productivity than shrubs growing on undisturbed soils. The residual effects of banner-tail mounds were measureable as long as 50 years after the kangaroo rats abandoned the mounds (Chew & Whitford, 1992). Active banner-tail kangaroo rat mounds support a distinct annual plant assemblage (Guo, 1996) and greater above- and below-ground biomass than intermound areas (Fig. 6; Mun & Whitford, 1990). Annual plant diversity is lowest on banner-tail mounds, greater at intermediate distances, and decreases again with increasing distance from the mound (Guo, 1996). Giant kangaroo rats' (*Dipodomys ingens*) burrowing and foraging promote introduced Mediterranean weeds at the expense of native annuals on the Carrizo Plain Natural Area of California (Schiffman, 1994). The lack of disturbance resulting from exclosure of kangaroo rats (primarily *D. merriami* and *D. spectabilis*) from plots in a Chihuahuan Desert grassland favored development of Lehman lovegrass (*Eragrostis lehmanniana*), an introduced perennial (Heske *et al.*, 1993). The impact of mammal pedturbation on the establishment and spread of exotic plants must be considered in restoration of degraded ecosystems and in management strategies designed to control spread of exotics.

As the density and number of distinct types of soil disturbances by small mammals increased in a Texas sand shinnery oak (*Quercus havardii*) community, density of

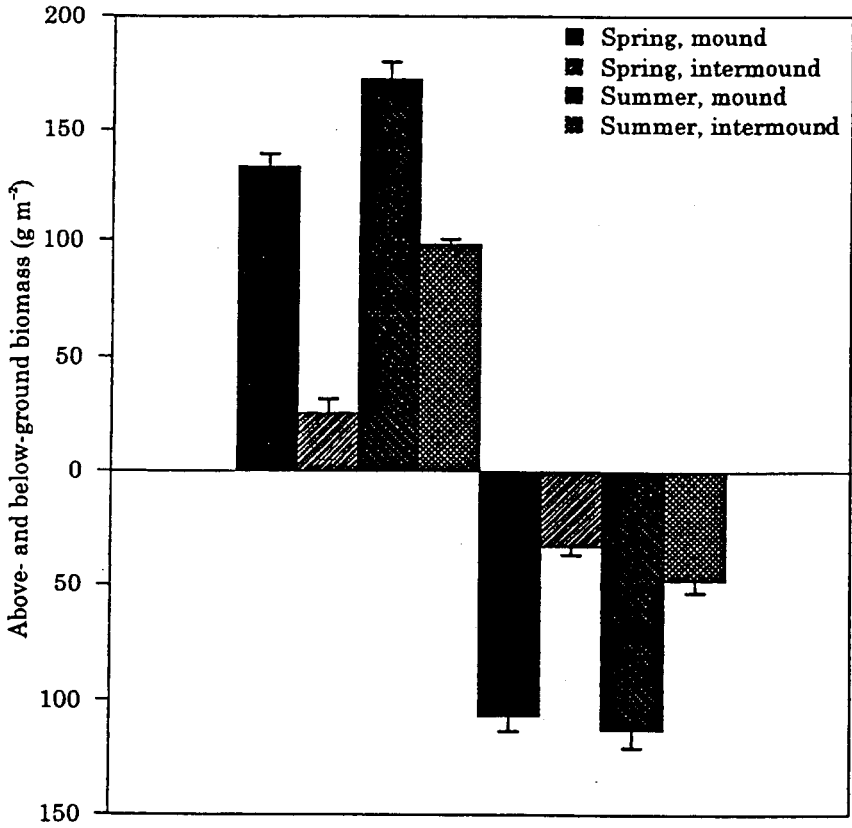


Figure 6. Peak annual plant above- and below-ground biomass on *Dipodomys spectabilis* burrow mounds and intermound areas in the Chihuahuan Desert of New Mexico, U.S.A. Data from Mun & Whitford (1990).

herbaceous plants increased (Dhillon *et al.*, 1994). On a site in the northern Mojave Desert of North America, a native annual grass, *Festuca octoflora*, suffered reduced density on small mammal burrowing plots (Soholt & Irwin, 1976) (Table 2). However, an introduced grass (an exotic), *Bromus rubens*, was not affected. Growth of two Mojave Desert shrubs, *Larrea tridentata* and *Grayia spinosa*, showed only a slight positive response on soils with antelope ground squirrel (*Ammospermophilus leucurus*) burrows (Soholt & Irwin, 1976).

Soil water infiltration increased on abandoned rodent (probably *Gerbillus vullinus*) colonies in the Namib of southern Africa, and abundant grasses on the periphery of these colonies resulted in circles of vegetation (Cox, 1987). Gerbil colonies on the Serengeti of Africa inhibited grass production and encouraged secondary succession (Senzota, 1984). Gutiérrez *et al.* (1997) conjectured that increased annual plant diversity and production was a result of foraging and soil perturbation by degus (*Octodon degus*) which reduced shrub cover, changed soil structure and nutrients, and favored germination of annual plants. Mounds of red viscacha rats (*Tympanoctomys barrarae*) in Argentina maintain communities of succulent halophytes on the sandy margins of salt flats (Ojeda *et al.*, 1996).

Prairie dog grazing and burrowing influences water relations of grasses, community evapo-transpiration (Day & Detling, 1994), nutrient dynamics, and biomass of plants growing on the colonies (Coppock *et al.*, 1983a). Elimination of prairie dogs does not

result in immediate changes to the vegetation (Uresk, 1985), suggesting the importance of pedturbation in maintaining the prairie community. Prairie dog colonies represent patches of modified diversity, plant production, and soil in what would otherwise be relatively uniform grasslands (Whicker & Detling, 1988, 1993).

Soil disturbance by fossorial rodents results in a variety of responses by vegetation. Some studies found that the ejecta soil mounds benefits pioneer or 'weedy species' while killing the perennial vegetation under the mound. Other studies document negative effects on the productivity of perennials and some annuals (Table 2). In some heavily grazed areas in the arid Central Valley of California the only forage abundantly available may be on pocket gopher mounds (Grinnell, 1923). There is a negative correlation between pocket gopher (*Thomomys bottae*) burrowing and frequency of perennial short grasses, and a positive correlation with perennial dicots. Plant species diversity in the short-grass prairie responded to increasing gopher disturbance in a manner compatible with the intermediate disturbance hypothesis (Martinsen *et al.*, 1990). On the Konza Prairie, Kansas, pocket gopher (*Geomys bursarius*) burrows resulted in reduction in biomass of overlying vegetation that differed between grasses and forbs (Reichman & Smith, 1985). This caused distinct edge effects that propagated as a wave into the surrounding vegetation (Reichman *et al.*, 1993). Pocket gopher activity tended to move vegetative composition away from tap-rooted species, but biomass production on mounds was greater than on intermound areas (Mielke, 1977) (Table 2).

Pocket gopher (*Thomomys bottae*) presence in alfalfa fields in California resulted in local damage to the plants, but overall yields were improved. Alfalfa yield and soil moisture at 60–80 cm depth were negatively correlated with increasing distance from the nearest gopher mound in a field (Smallwood & Geng, 1997). On serpentine soils in California, gopher mound soil had a negative effect on the growth of some annual plants. Elevated concentrations of Mn, Co, and Ni occurred in the shoots of *Plantago erecta* and *Bromus mollis*, and both species had reduced growth when grown in pots of mound soil (Koide *et al.*, 1987). Soil chemistry of pocket gopher soil mounds seems to be slowing the rate of invasion of serpentine soils by non-native grasses. Pocket gopher burrowing is the primary factor affecting the soil chemistry (Koide *et al.*, 1987).

In China plant species diversity on a north-facing slope in an overgrazed pasture was highest on an old Cansu mole-rat mound, lowest on a new mound, and intermediate on a non-mound area (Hongo *et al.*, 1993). Plant abundance tended to be lower on *Spalax ehrenbergi* mounds, and 16 of 19 fugitive or ruderal species did not germinate when planted on mounds (Heth, 1991). Palestine mole rats feed on bulbs and corms of geophytes and store them in their burrows where some of them may germinate, suggesting that mole rats are important in dispersion and reproduction of their food plants (Heth, 1991). There was a significant impact of burrowing by three species of bathyergid mole-rats, *Bathyergus suillus*, *Cryptomys hottentotus*, and *Georchys capensis*, on overlying vegetation (Reichman & Jarvis, 1989). Overall plant biomass was reduced by 97% of what it would have been without mole rats. Bathyergid mole rats not only affected productivity, they affected the structure of the entire plant community (Reichman & Jarvis, 1989).

Sand-dune grasslands with tuco-tucos (*Ctenomys australis*) in Argentina had higher total plant biomass, made up largely of one grass (*Panicum racemosum*), a pioneer geophyte, but lower species richness and total diversity than areas without tuco-tucos (Table 2). At a microspatial scale, total biomass and above- and below-ground biomass were significantly reduced in areas of tuco-tuco mounds. At the scale of mounds, species richness was only slightly greater in intermound areas, and total diversity was not different between mound and non-mound areas. Burrowing by tuco-tucos in a sand-dune grassland leads to soil instability due to reduction in the vegetative cover that traps and holds blowing sand (Zenuto & Busch, 1995). Colonial cururo feeding

and burrowing promotes recruitment of native pioneer plant species and the introduced annual succulent *Mesembryanthemum crystallinum* (Table 2).

Heuweltjies are sources of elevated fertility and plant community diversity (Table 2). Vegetation on heuweltjies differs from several other plant communities with only a 15% species similarity to surrounding non-mound dry mountain fynbos and karroid broken veld communities. Heuweltjie vegetation is co-dominated by deciduous and evergreen species, while intermound areas are evergreen dominated (Midgley & Musil, 1990). No members of the Mesembryanthema subfamily Ruschoideae occur on mounds. Off-mound Mesembryanthema all tend to be long-lived woody shrubs with low seed germinability and high seed retention (Esler & Cowling, 1995). Domestic crop production is higher on mound soils than off (Lovegrove, 1991). Mima mounds in southern California, U.S.A. are associated with vernal pools, sites of highly endemic floras (Table 2). Mima mounds also serve as foci for establishment of upland plant species into coastal salt marshes (Cox *et al.*, 1995). Mima mounds in Colorado, when seeded, produce 2–5 times more grass than intermound soils (Chew, 1978). Mima-like mounds in Argentina are a preferred habitat of the introduced tree *Tamarix gallica* (Roig *et al.*, 1988).

#### Effects on other biota

Caches of larder-hoarded vegetative material in banner-tail kangaroo rat burrows tend to be rich in fungi (Vorhies & Taylor, 1922; Monson, 1943; Reichman *et al.*, 1985; Hawkins, 1996). The rats manipulate the level of fungal infection in the stores (Reichman & Rebar, 1985; Reichman *et al.*, 1986). At least one saprophytic fungus has co-evolved with banner-tail kangaroo rats (Frisvad *et al.*, 1987). The presence of saprophytic fungi in the mounds and cheek pouches of banner-tails and vesicular arbuscular mycorrhizal (VAM) fungi in plant roots in the vicinity of mounds (M. Walton, unpubl. data) suggest an important role for mounds as a foci for mutualistic endophytic fungi in desert grassland (Barrow *et al.*, 1997a, b).

Banner-tail kangaroo rat mounds contribute to the community structure of a variety of animals, including microarthropods and nematodes (Seastedt *et al.*, 1986), rodents (Bowers & Brown, 1992), invertebrates, and lizards (Hawkins & Nicoletto, 1992). Fully 3% of the known 4500 insect species of the Repetek District in the Karakum Desert of Turkmenistan are bothriobonts, i.e. species found exclusively within animal burrows. Thirteen species of non-insect arthropods are also reported as bothriobonts (Krivokhatsky, 1994). Several scarabeid beetles are found exclusively in rodent burrows in Mexico (Anduaga & Halfiter, 1991). A solifuge arachnid of the genus *Blossia* is known primarily from heuweltjies at Tierberg in the southern Karoo, South Africa (Dean & Griffin, 1993). Native ungulate grazers such as bison (*Bison bison*) and pronghorn (*Antilocapra americana*) preferentially select prairie dog colonies as feeding sites (Coppock *et al.*, 1983b). Prairie dog colonies function as local centers of animal biodiversity (Sharps & Uresk, 1990; Mulhern & Knowles, 1996). Sheep forage preferentially on heuweltjies (Armstrong & Siegfried, 1990).

#### Synthesis and conclusions

Most of the literature on perturbation by mammals is from North America, semi-arid South America, and southern Africa. Much of the perturbation research reports on relatively few species, primarily fossorial rodents in the Muridae, Bathyergidae, and Geomyidae. Mole-voles (*Ellobius* spp.) and numerous gerbils and jerboas are known to produce extensive burrow systems throughout arid areas of Eurasia (Naumov &

Lobachev, 1975; Stogova, 1986). We know of no quantitative data on pedturbation by any of those species.

Resting forms and beds of intermediate size mammals may represent important biopedturbation features. Studies of resting forms and beds produced by jackrabbits (*Lepus* spp.) in North American deserts, and of rabbit-size mammals in other deserts are needed to address this question. Small mammal foraging trails represent linear features with compacted soil that may affect hydrology and soil nutrient distribution. These linear micro-patches could also serve as areas of increased water flow and erosion.

Hyrax (*Procavia capensis*) in Africa and the Middle East, dassie rats (*Petromus typicus*) in Africa, and stick-nest rats (*Leporillus conditor*) in Australia all produce middens of feces and urine similar to those of woodrats (Fall *et al.*, 1990; Nelson *et al.*, 1990; Scott, 1990). Stick-nest rats produce nests very similar in structure to wood rat nests (Aslin, 1972; Robinson, 1975; Nelson *et al.*, 1990). Although we know of no studies that describe soil effects, the potential for those species' middens and nests to contribute to local soil conditions is apparent. The pebble-mound mouse (*Pseudomys chapmani*) of Western Australia builds mounds of pebbles over its burrow system (Dunlop & Pound, 1981; Anstee, 1996) (Table 1). Pebble-mound mice occur in areas of limited topsoil on rocky ridges (Dunlop & Pound, 1981) and appear to build the pebble mounds to help accommodate the lack of soil for burrowing. The effects of these mounds on soil properties and vegetation have not been investigated, however they probably affect soil moisture and possibly nutrient status of soils under the mounds. These mounds could also contribute to pedogenesis.

We note, as have previous reviews of animal burrowing (Meadows, 1991; Meadows & Meadows, 1991; Reichman & Smith, 1991), that there is a remarkable similarity in biopedturbation effects across taxa and habitats. For example, Whitford (1998) found that foraging pits produced by a varanid lizard trapped litter and seeds and may contribute to the sustainability of banded landscapes in semi-arid Australia. African and Australian deserts tend to have areas of large disturbances resulting from the activity of large herbivores such as elephants and kangaroos. Pedturbation by large herbivores (other than by trampling) is generally lacking in North and South America which no longer have native megafauna in the deserts and semi-deserts.

Pedturbations produced by mammals occur in most if not all arid and semi-arid landscapes. Factors that affect densities of mammals and the species composition of the mammal community determine the relative importance of the pedturbations produced by these animals. This review has shown that relatively shallow foraging pits and digs affect ecosystem properties and processes via the materials that accumulate in the pits and not from the soil removed during excavation. When in-filled, these become nutrient-rich germination sites for certain plant species. The effects of open burrows and burrow systems depends upon the depth and length of the burrows. These are the variables that determine the physical and chemical nature of the soil ejecta. Duration of occupancy is another variable that affects how burrows and burrow systems modify ecosystem properties and processes. Burrows that serve as short-term residences may have little effect on the surrounding ecosystem other than providing a pile of readily erodable soil. Burrows and burrow systems occupied by several generations of central-place foragers and larder-hoarders become nutrient-enriched 'hot spots' in the landscape as a result of accumulation of unconsumed food and deposition of feces. Because of the continuous disturbance and nutrient enrichment, such burrow systems may support relatively rare plant species or some exotic plant species.

Mounds of soil resulting from burrowing by fossorial rodents are generally short-lived features (with the exception of Mima mounds and Mima-like mounds). Long-term occupation of an area by fossorial rodents may result in small nutrient-rich patches at the locations of abandoned storage chambers and defecation sites. The high rates of soil turnover by fossorial rodents may have significant pedogenic effects. The maximum

pedogenic effect is the production of Mima mounds and Mima-like mounds (heuweltjies) in some landscapes.

This review has documented the large variety of mammalian perturbations that have many effects on ecosystems and landscapes. Some temporal and spatial scale problems have been identified in attempting to synthesize the information on mammalian perturbation. In order to understand bioperturbation as a process that contributes to ecosystem and landscape function, it will be necessary to design long-term studies of all types of bioperturbations. Such studies will have to focus on rates and types of disturbance, turnover of soils moved, and physical and chemical composition of ejecta soils. The available literature suggests that perturbation plays an important role in landscape-scale processes. Research is needed on 'source'-'sink' relationships at the landscape scale that are modified by bioperturbations.

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