

Soil disturbance by native animals along grazing gradients in an arid grassland

D.J. Eldridge^{a,*}, W.G. Whitford^b

^a Department of Environment and Climate Change, c/- Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of NSW, Sydney 2052, Australia

^b USDA-ARS Jornada Experimental Range, MSC 3JER, New Mexico State University, Las Cruces, NM 88003, USA

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ABSTRACT

Domestic grazing animals that congregate around watering points in arid rangelands create clearly-defined trampling-induced grazing gradients. Grazing and trampling alter soil and vegetation condition, often leading to substantial reductions in ecological function. We measured foraging pits and mounds created by native soil foraging animals over 12 months at three watering points in a Chihuahuan Desert grassland, and hypothesized that the density and cover of their disturbances would increase with increasing distance from water. We recorded an average of 3756 disturbances ha⁻¹ and cover of 34.18 m² ha⁻¹ across the grazing gradients, which comprised mainly pits (43%) and mounds (25%) of heteromyid rodents, ants and spiders. Soil turnover was estimated at 1.43 m³ ha⁻¹. We detected no differences in density, cover, soil volume or composition of disturbances in relation to distance from water, but there were significant, though ill-defined, differences across the five sampling periods, with generally more activity in the warm-wet months. Small animal-created mounds and pits are important sources of soil and sinks for litter within grazing gradients, and may represent the only sites where plants can establish given a relaxation in grazing pressure.

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1. Introduction

Watering points are focal points of grazing by domestic and some native animals in rangelands. Concentrations of relatively large numbers of domestic grazers such as sheep and cattle around watering points, particularly over summer, create gradients of degradation across the landscape, with the magnitude of trampling and its associated degrading effects such as removal of some plant species decreasing exponentially out from the watering point (Fusco et al., 1995; Lange, 1969). Changes across grazing gradients include soil compaction, removal of the cryptogamic crust, reductions in surface roughness, increases in soil particle mobilization, loss of fine material through wind and water erosion, alterations to the normal flow of surface water, reduction in vegetation cover and complexity, and reductions in cover and survivorship of perennial plants (Nash et al., 2003; Tabeni and Ojeba, 2003; Thrash, 1998; Whitford et al., 1999). Many of these changes are irreversible, and lead to substantial reductions in ecosystem functions such as soil nutrient cycling and infiltration (Andrew, 1988). An increase in the number and size of stock watering points across the world's

rangelands during the past century has resulted in dramatic, and often irreversible, changes in landscape condition over increasingly larger areas of rangelands.

Trampling-induced degradation in areas close to watering points (i.e. within 500 m) invariably leads to flow-on effects to a range of ecosystem properties such as habitat quality for native animals (James et al., 1999). A worldwide review of the effects of cattle grazing on small- and medium-sized mammals (Tabeni and Ojeba, 2003) reveals a range of responses, from decreases in density and richness of small mammals in sagebrush steppe (Eccar et al., 2000), to increased diversity and abundance in grazed (desertified) grassland (Whitford, 1997). Less well-known, however, are the effects of trampling-induced degradation around watering points on reptiles and invertebrates. Small reptiles and invertebrates would be differentially affected by water point-centered, trampling-induced disturbances because habitat alteration occurs at scales much smaller than that of piospheres, but at a scale that corresponds to the body size and therefore home range of these organisms (e.g. Jackson et al., 2002; Whitehouse et al., 2002). Changes in animal populations could arise from reductions in the cover of grasses, or reductions in soil surface roughness or litter depth, which are known to affect small reptile populations (James, 2003). It is likely that some small animals, other than some ants and various agamid lizards that are known to benefit from reduced

* Corresponding author. Tel.: +61 2 9385 2194; fax: +61 2 9385 1558.

E-mail addresses: d.eldridge@unsw.edu.au (D.J. Eldridge), wlawhit@zianet.com (W.G. Whitford).

vegetation cover (e.g. Read, 2002; Read and Andersen, 2000) would avoid foraging close to stock watering points where the trampled soil surface has lower levels of cover, and therefore less protection against predators, and reduced density of potential prey items.

In the Chihuahuan Desert of the southwestern United States, a large number of small vertebrate and invertebrate taxa have demonstrated engineering effects on ecosystem properties and processes, largely through their soil-disturbing behaviour. Soil disturbance by these animals contributes to soil formation (pedogenesis) when subsoil is mixed with surface materials as the animals excavate soil to construct shelter or forage for food (Whitford and Kay, 1999). Animal-induced soil disturbances contribute to variations in water infiltration, spatial heterogeneity in soil seed banks, soil organic matter and therefore soil nutrients, and to variation in soil erosion due to changes in the stability of excavated soil (Whitford and Kay, 1999). Thus the loss of these animals from areas within the grazing gradient of watering points is likely to have substantial flow-on effects on ecosystem function. Unlike the widespread mobilization of soil brought about by live-stock trampling and overgrazing, soil movement by native animals is generally of a lower magnitude, discontinuous, and temporally variable. Effects of changes in native animal activity across watering points in relation to infiltration, soil nutrients and soil deposition are likely to be substantial across landscape scales when one considers that few areas of the world's productive rangelands are outside the watering range of domestic livestock (e.g. Australia's rangelands; James et al., 1999).

We hypothesized that the conspicuous changes in soil surface characteristics, and plant cover and composition close to watering points would induce marked effects in soil disturbance by animals, and specifically, that the area of soil surface and the volume of soil moved by animals would increase with increasing distance from stock watering points. This is based on the view that areas distant from water, and with greater cover and diversity of vegetation, would provide a greater variety of habitat for animals, many of which forage or burrow in the soil. We also hypothesized that the spectrum of soil disturbance types would change between sites close to, and sites distant from, watering points given that some animals differ in the preference for sites. For example, some ants may prefer bare sites close to water (Read and Andersen, 2000) while rodents and seed harvesting ants may only forage at a distance from water where seed-bearing grasses are present. Similarly, different disturbance structures (e.g. nests, mounds, burrows) are likely to have differential resistance to surface disturbance by live-stock. Thus their relative distribution within the grazing gradient would likely be a reflection of this resistance to disturbance.

2. Methods

The study was conducted at the Chihuahuan Desert Rangeland Research Center and the USDA Jornada Experimental Range located approximately 40 km north of Las Cruces, New Mexico. Soil disturbance by animals was measured on grazing gradients centered on three livestock watering points; West, Mayfield and Camp wells. Each watering point was located in a different paddock and the watering points were approximately 2 km apart. There are few reliable records of long-term stocking rates for the three wells. However, during the period of the study, West and Camp Wells were generally grazed during the winter–spring period whereas Mayfield Well was continuously grazed (Whitford et al., 1999). Stocking rates varied with range condition, and the rotation grazing treatment could be as little as 30 days or as long as a full year. Thus for example, West Well has been used sparingly over the past decade, with only 20–30 head of cattle for 30–60 days. In the 1980s and 1990s however, stocking rates were much greater. Therefore in

terms of the development of grazing gradients, the piospheres in our study are relatively old, as they were installed more than 75 years ago and have undoubtedly changed substantially over that time. The three wells were chosen because they are oriented in an east–west direction across the Jornada Basin and because the vegetation more than 1 km from the water points was high condition black grama (*Bouteloua eriopoda*) dominant (Whitford et al., 1999). Although we did not measure dung directly, areas close to water were typically covered in fresh dung, but it was very sparse at the largest distances.

The dominant vegetation on the grazing gradients is black grama grass with scattered honey-mesquite shrubs (*Prosopis glandulosa*). The grazing gradients at each watering point were on the same soil series. The soil is an aridisol (coarse-loamy, mixed, thermic Typic Petrocalcid) with an indurated calcareous layer at depths ranging from 40 to 100 cm. The mean grass and perennial forb cover was 0.85% at 50 m, 3.3% at 250 m, 6.4% at 450 m and 24.0% at 1050 m from the watering points (Nash et al., 1999). Mesquite shrubs accounted for an average of 9.5% cover at the three areas nearest the water point, and 5.4% cover in the least disturbed grassland at the greatest distance from water (Whitford et al., 1999).

Plots were established at 50 m, 250 m, 450 m, and 1050 m from each of three livestock watering points. A centre post was located at the selected distance on a randomly selected compass heading between 1 and 180° oriented to keep the plots along the gradient within the paddock assigned to a grazing treatment (Whitford et al., 1999). At each sampling date a circular plot 10 m in radius was established by flagging the perimeter of the plot centered at the selected distance from the watering point. All soil disturbances by animals within each circular plot (rodent foraging pits and mounds, invertebrate burrows, ant mounds, termite galleries, etc) were measured to obtain estimates of the area of disturbance and the volume of disturbed soil. Mounds consisted as accumulations of soil excavated to construct a pit or burrow. We measured two diameters through the centre of the disturbance and the depth for each soil excavation and each identifiable pile of soil ejected from an excavation. Volume was calculated using the formula for a half-prolate spheroid. Average diameters (estimated from long axis and short axis) were measured for ant colony discs and for soil spread from the circular entrances of wolf spider (*Geolycosid* spp.) burrows. The volume and area of termite galleries were estimated from length and diameter measurements and calculated as a volume of a cylinder. Termite constructed foraging gallery sheeting was estimated as an area only. We assessed soil disturbances at each site and distance at five dates: September 2000, January 2001, April 2001, July 2001 and September 2001. Data were missing for the 1050 m distance for Camp Well and West Well in April 2001 because the plots could not be located. We therefore had 58 measurements in total. Mayfield Well was measured five times over four distances ($n = 20$), and both West and Camp Wells were missing one site \times time observation ($n = 19$ each).

2.1. Statistical analyses

We used a mixed-models General Linear Models (GLM) approach with two strata to examine differences in the density (disturbances ha^{-1}), cover (%) and volume ($\text{m}^3 \text{ha}^{-1}$) of animal disturbances. The first stratum examined differences between the four distances across the piosphere (distance), and the second stratum the effects over time ($n = 5$) and its interaction with distance. In all cases, data were checked for homogeneity of variance (Levene's test) and normality using diagnostic tests in the Minitab (2007) statistical program, and transformed (square root, \log_{10}) where appropriate. For all analyses, significant differences

between means were examined using Fisher's Protected Least Significant Difference (LSD) test where the effect was significant.

We used permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008) to test whether the composition of the various disturbances varied in relation to time and distance from water, and their interactions. PERMANOVA allowed us to partition the multivariate variation using more complicated experimental designs of the same structure as the univariate analyses described above. Each of six separate matrices of animal disturbances (invertebrates or vertebrates, based on cover, density and volume), was converted to a similarity matrix using the Bray Curtis similarity coefficients contained within the PRIMER-E (PERMANOVA) statistical package (Anderson et al., 2008). Pair-wise *a posteriori* comparisons were made, where necessary, using a multivariate analogue of the *t* statistic, the probability levels being obtained by permutations. Thus it was unnecessary to correct for a large number of multiple comparisons.

3. Results

3.1. General trends

We recorded a total of 6844 disturbances by vertebrates and invertebrates over the 12 months of the study, which represented an average of 3756 disturbances ha^{-1} , or about one disturbance for every 3 m^2 . The density of disturbances ranged from 289 (920 ha^{-1}) in April 2001 to 3401 (9021 ha^{-1}) in September 2001. Three types of structures (pits 43%, mounds 25%, termite galleries 25%) made up 93% of all disturbances. Burrows accounted for a further 5.6% (Table 1). The distribution of disturbance types differed markedly among the three watering points, with very few termite galleries at West Well, but abundant galleries at Mayfield Well, a greater proportion of mounds at Camp Well, and many more pits at West Well (Table 1).

The cover of animal disturbances totaled 62.28 m^2 over the 12 months, amounting to $34.18 \text{ m}^2 \text{ ha}^{-1}$ (0.34% cover). Eighty-four percent of the total cover of disturbances was contributed by three structures; mounds (40.1%, mainly unidentified), burrows (26.5%, mainly rodents) and pits (16.9%, unidentified). A total of 2.60 m^3 of soil was removed from pits, burrows, scrapes and dust baths over the study, which represented about $1.43 \text{ m}^3 \text{ ha}^{-1}$. This does not represent a turnover rate however, as we were likely recording an unknown number of structures at more than one sampling.

3.2. Effects of time and distance from water

We detected no differences in cover or volume of all disturbances in relation to either distance from water ($P=0.66$ and $P=0.63$ respectively) or time ($P=0.48$ and $P=0.33$ respectively). However, there were significant differences in density of all disturbances over time ($F_{4,30}=11.25$, $P<0.001$ on \log_{10} -transformed data), with the largest densities in September 2000 and

2001 (9021 ± 1671 disturbances ha^{-1} ; mean \pm SEM), and the smallest in April 2001 (704 ± 147 disturbances ha^{-1}).

We detected significant differences in disturbance densities when we pooled disturbances into those constructed by vertebrates ($F_{4,30}=3.14$, $P=0.029$ on \log_{10} -transformed data) or invertebrates ($F_{4,30}=17.15$, $P<0.001$ on \log_{10} -transformed data). Density of vertebrate structures ranged from about 1000 ha^{-1} in April 2001 to 3000 ha^{-1} in January 2001 (Fig. 1). Density of invertebrate disturbances was about 6000 ha^{-1} in September 2001 (Fig. 1), mainly due to large amounts of termite gallery material. We also detected a significant difference in the volume of material moved by invertebrates between sampling times ($F_{4,30}=6.95$, $P<0.001$ on $\sqrt{}$ -transformed data). The volume was greatest in September 2001 ($0.34 \text{ m}^3 \text{ ha}^{-1}$), intermediate in September 2000 ($0.104 \text{ m}^3 \text{ ha}^{-1}$) and very low at the other times ($0.002\text{--}0.006 \text{ m}^3 \text{ ha}^{-1}$).

3.3. Cover, density and volume of specific animal disturbances

There were strong temporal trends in the total cover of disturbances by ants (disks, mounds, holes), with a tendency towards very sparse cover in the cool months ($4.7 \text{ m}^2 \text{ ha}^{-1}$, January, April) and moderate to extensive cover ($16\text{--}23 \text{ m}^2 \text{ ha}^{-1}$) in the warm-wet months (July–September, $F_{4,30}=10.27$, $P<0.001$). This was reflected in the cover of termite sheeting, which also differed significantly over time ($F_{4,30}=7.13$, $P<0.001$). Thus we recorded substantially greater cover in the warm-wet season ($1.82\text{--}2.66 \text{ m}^2 \text{ ha}^{-1}$) compared with the cool-dry season ($1.2\text{--}1.5 \text{ m}^2 \text{ ha}^{-1}$). The significant difference in the cover of pits excavated by rodents over time ($F_{4,30}=3.06$, $P=0.032$) did not correspond with any clearly-defined seasonal pattern, with about twice the cover of disturbances in September 2000 ($9.3 \text{ m}^2 \text{ ha}^{-1}$) compared with the other sampling times ($5.1\text{--}5.4 \text{ m}^2 \text{ ha}^{-1}$).

We found slight temporal differences in the density of rodent pits ($F_{4,30}=2.94$, $P=0.037$), which again did not correspond with any seasonal effect. Densities were greatest in January and September 2001 ($2064\text{--}2180 \text{ ha}^{-1}$) and lowest in April, the cool season (803 ha^{-1}). Density of ant mounds was greatest in the warm-wet season in September 2001 (1111 mounds ha^{-1}) but also low in September 2000 and the other periods ($5\text{--}111$ mounds ha^{-1} ; $F_{4,30}=7.56$, $P<0.001$).

There was a weakly statistical difference in the volume of rodent foraging pits among times and distances from water (distance by time interaction: $F_{12,30}=2.16$, $P=0.045$; Fig. 2). For example, in January and July 2001 the maximum volume of foraging pit soil removed was at intermediate distances from water, in April 2001 it

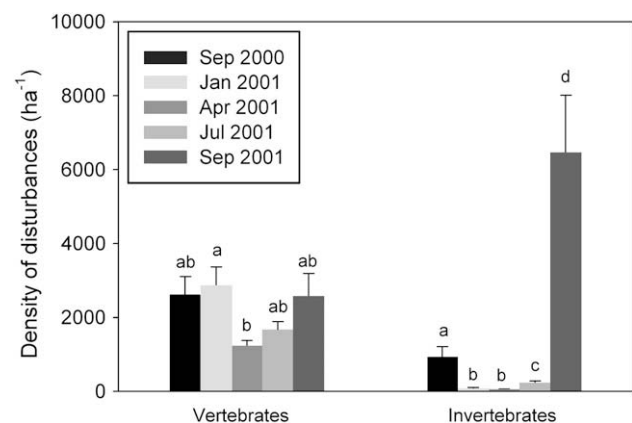


Fig. 1. Density of vertebrate and invertebrate disturbances (ha^{-1}) averaged over distances and watering points. Different letters within separate (vertebrate or invertebrate) groups indicate a significant difference in density at $P<0.05$.

Table 1

Percent occurrence of the various disturbance types by well and the principal animal creating the disturbance.

Disturbance type	Organism	Well location			Mean
		Camp	Mayfield	West	
Pit	Rodent	34.4	24.4	78.4	45.7
Gallery	Termite	16.5	50.9	0.1	22.5
Mound	Spider, rodent, ant	40.9	20.6	12.9	24.8
Burrow	Rodent, spider	6.9	3.2	7.5	5.9
Sheeting	Termite	1.3	0.4	0.0	0.6
Scrape	Rabbit	0.1	0.4	0.8	0.4
Dust bath	Rabbit	0.0	0.0	0.2	0.1

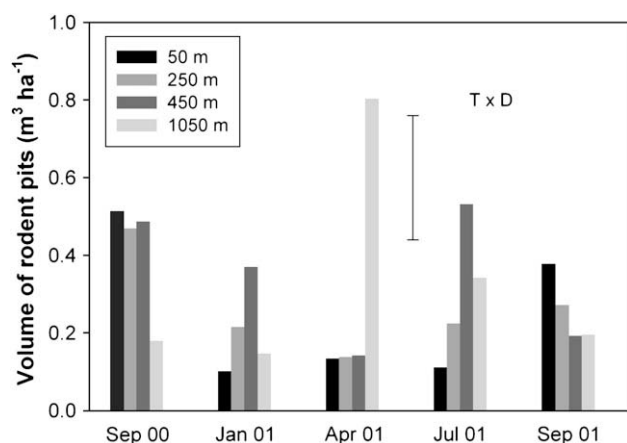


Fig. 2. Volume ($\text{m}^3 \text{ha}^{-1}$) of rodent foraging pits in relation to sampling date and distance from water. The 5% LSD bar for the time \times distance interaction is shown.

was greatest furthest from water, and in September 2000 greatest close to water (Fig. 2). The volume of termite gallery material was greatest in September 2001 ($0.35 \text{ m}^3 \text{ha}^{-1}$) compared with other sampling dates ($0.005\text{--}0.10 \text{ m}^3 \text{ha}^{-1}$; $F_{4,30} = 3.78$, $P = 0.013$).

3.4. Community structure of animal disturbances

Permutational multivariate ANOVA indicated that there were significant differences in the composition of animal-created structures among the five sampling times using data based on density ($F_{4,30} = 6.25$, $P(\text{perm}) = 0.001$) or percentage cover ($F_{4,30} = 2.82$, $P(\text{perm}) = 0.001$). There were no differences in composition across the grazing gradient however. We detected significant differences in composition between January 2001, and September 2000 and 2001 ($F_{4,30} = 2.04$, $P(\text{perm}) = 0.005$; based on volume data). Examining these trends in more detail, it was apparent that the composition of disturbance types constructed by invertebrates (e.g. ant nests, cicada burrows, ant mounds) differed markedly among all sampling times ($F_{4,30} = 4.85$, $P(\text{perm}) = 0.001$; based on density data). There was a suggestion of a weak difference in the composition of rodent disturbance types (foraging pits, ejecta mounds) in the cool season (April 2001) compared with any other sampling ($F_{4,30} = 1.90$, $P(\text{perm}) = 0.045$; based on density data).

4. Discussion

Many studies have identified marked biotic and abiotic changes along grazing gradients, with sites close to water characterized by increased intensity of livestock trampling and therefore greater dung density (Dougill and Cox, 1995), altered plant chemistry and soil nutrient concentrations, increased soil erosion, a breakdown in soil surface integrity, and declines in ecosystem function and stability (Andrew and Lange, 1986; Dougill and Cox, 1995; Landsberg et al., 2003; Thrash, 2000; Tolsma et al., 1987; Turner, 1998; Whitford et al., 1999). Contrary to our hypotheses we detected no significant differences in either the density or cover of animal disturbances, nor their composition, for distances up to 1050 m from water, despite marked differences in the cover and composition of the perennial vegetation, and the general increase in surface microtopography with increasing distances from the watering points (Nash et al., 2003). Some differences were evident between water points, however, such as a greater proportion of mounds at Camp Well, and substantially more pits at West Well. These differences probably reflect local changes in soils and vegetation which might favour different suites of animals, or alter the

longevity of structures through differences in soil texture or structure, for example, at a site.

4.1. Temporal changes in animal disturbances

Temporal changes in soil disturbance by vertebrates and invertebrates were more pronounced than spatial changes, and probably reflect the activity pattern of many of these soil-disturbing taxa (Fig. 1). Thus, for example, disturbances by ants were generally less in the cooler months and greatest in the warm-wet period. This is consistent with the marked variation in diel and seasonal activity of ants observed in the Chihuahuan Desert, which results from differences in precipitation and productivity between different years (Whitford, 1978).

Despite the lack of quantitative differences in plant cover and soil, there were some differences in average depth of foraging pits. Average pit depth was about 2.5 cm over most time periods, but pits were about twice as deep in April 2001. This is probably related to the seasonal patterns of scatter hoarding by heteromyid rodents and excavation of grubs and other insect larvae by ground squirrels (*Spermophilus spilosoma*) and skunks (*Mephitis* spp.). The deepest pits (60–65 cm) were probably produced by small mammals searching for grubs and other insect larvae, far deeper than the cache pits excavated by heteromyid rodents (mean 2.5 cm). Larger, deeper pits are known to collect more litter and seed (James and Eldridge, 2007; James et al., in press) and may be more effective microsites for plant germination and establishment. The total area of termite gallery and sheeting also changed over time, with generally sparse cover in the cool months and extensive cover (up to $13.4 \text{ m}^2 \text{ha}^{-1}$) in the warm-wet months. Termites contribute substantially to decomposition processes, and in the Chihuahuan Desert consume more than half of potential inputs to soil organic matter (Nash and Whitford, 1995). They also affect soil hydrological processes, which are thought to have watershed-wide implications for organic matter distribution (Whitford, 2002). Termites are therefore likely to be functionally important in degraded sites close to the watering point for the decomposition of livestock dung.

4.2. The functional importance of animal disturbances

Many forms of soil disturbance by animals result in the translocation of materials from subsurface horizons to the soil surface. Translocated soil has a reduced aggregate stability, which results from the physical act of disturbance combined with high surface temperatures and exposure to wind, raindrops and ultraviolet light. Soil disturbance by digging animals destroys the biological crust or raindrop impact crust (Whitford, 2002), leaving it more susceptible to removal by wind erosion or entrainment in overland flow. Any effects of animal disturbance are likely to be more pronounced in arid areas where primary production is highly resource-limited and will be exacerbated in areas where domestic stock are concentrated (Dougill and Cox, 1995), i.e. close to watering points.

In this study a total of $1.43 \text{ m}^3 \text{ha}^{-1}$ of soil was removed from pits across the three watering points. Although some deeper pits and some burrow systems may have been measured more than once during the study, we believe that these would have accounted for less than 10% of all disturbances measured. Thus an estimate of annual turnover rate of $1.29 \text{ m}^3 \text{soil ha}^{-1}$ is reasonable. Assuming a conservative value of soil bulk density of 0.80 mg m^{-3} for disaggregated soil, this amounts to about $1.0 \text{ t soil ha}^{-1} \text{yr}^{-1}$ across the watershed.

In the Chihuahuan Desert grasslands, areas within 0.5 km of a livestock water point are characterized by reduced soil surface microtopography and large gaps (fetches) between clumps of sparse, low stature perennial vegetation (Nash et al., 2003; Whitford et al., 1999). These conditions conspire to create a situation

characterized by reduced threshold velocities for wind erosion and reduced obstructions to water erosion. Given its greater erodibility, the animal-excavated material will likely be redistributed to other landscape positions, sometimes including old foraging pits themselves. However, in relatively untrampled, little-impacted grassland at distances >1 km from watering points, the high density and stature of the vegetation and narrow inter-tussock spaces virtually eliminate wind and water-transport of soil. High velocity winds, which are common over summer (Gillette and Monger, 2006), transport small soil particles short distances from the inter-tussock spaces (<50 cm length) into the canopies of the grass tussocks where this soil contributes to the tussock-depression microtopography of the grassland. Aeolian accretion of eroded soil can also have other positive effects such as increasing soil moisture in the vicinity of the grasses (Sarah, 2002).

Rodent foraging pits are important microsites in arid ecosystems, and abundant evidence worldwide suggests that they trap greater quantities of seed and litter, and support more plant species than non-pit surfaces (e.g. Whitford, 2002). Unlike litter that lies on the surface and is photo-oxidised by ultraviolet light, litter trapped in pits is broken down by microbes, and the nutrients returned to the soil (Whitford, 2002). Thus pits are important 'hot-spots' of biological activity, particularly at sites close to the watering points, where they may represent micro-catchments where plants can establish and from where restoration can commence given a cessation of grazing. Indeed the larger, longer-lived pits may be the only patch types where seedlings are able to establish close to water once the vegetation has been destroyed by grazing and trampling.

In conclusion, we detected no significant difference in the density, cover or volume of animal disturbances, nor differences in their composition across the grazing gradients. However, the lack of significant differences out from water should not be interpreted as the absence of an effect of soil-disturbing animals around watering points. While livestock trampling, which mobilises large amounts of sediment, often during droughts and produces disastrous effects on landscapes because of the large pulse of eroded sediment, we maintain that smaller, temporally- and spatially-variable sediment produced by rodents and ants would be functionally important. Smaller amounts of soil moved by native animals would also contribute sediment (and nutrients) to the areas surrounding perennial grass tussocks.

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References

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
 Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. *Trends in Ecology & Evolution* 3, 336–339.

Andrew, M.H., Lange, R.T., 1986. Development of a new piosphere in arid chenopod shrubland grazed by sheep. 2. Changes to the vegetation. *Australian Journal of Ecology* 11, 411–424.
 Dougill, A.J., Cox, J., 1995. Land Degradation and Grazing in the Kalahari: New Analysis and Alternative Perspectives. Pastoral Development Network, Network Paper 38c.
 Eccar, J.A., Walthers, R.B., Milton, S.J., 2000. How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments* 46, 103–106.
 Fusco, M.J., Holechek, J., Tembo, A., Daniel, A., Cardenas, M., 1995. Grazing influence on watering point vegetation in the Chihuahuan Desert. *Journal of Range Management* 48, 32–38.
 Gillette, D., Monger, H.C., 2006. Eolian processes in the Jornada Basin. In: Havstad, K.M., Huenneke, L.M., Schlesinger, W.S. (Eds.), *Structure and Function of a Chihuahuan Desert Ecosystem. The Jornada Basin Long-term Ecological Research Site*. Oxford University Press, Oxford, NY, pp. 189–210.
 Jackson, E.C., Krogh, S.N., Whitford, W.G., 2002. Desertification and biopedturbation in the northern Chihuahuan Desert. *Journal of Arid Environments* 53, 1–14.
 James, C.D., 2003. Response of vertebrates to fence-line contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecology* 28, 137–151.
 James, A.I., Eldridge, D.J., 2007. Reintroduction of fossorial native animals and the potential impact on ecosystem processes in a Central Australian desert landscape. *Biological Conservation* 138, 351–359.
 James, A.I., Eldridge, D.J., Hill, B. Animal foraging pits as sinks for litter and nutrients in an Australian desert shrubland. *Ecography*, in press.
 James, C.D., Landsberg, J., Morton, S.R., 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* 41, 87–121.
 Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., Stol, J.J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology* 40, 1008–1024.
 Lange, R.T., 1969. The piosphere: sheep track and dung patterns. *Journal of Range Management* 48, 396–400.
 Minitab, 2007. *References Manual*, Release 15. Minitab Inc., State College, Pennsylvania.
 Nash, M.S., Whitford, W.G., 1995. Subterranean termites: regulators of soil organic matter in the Chihuahuan Desert. *Biology and Fertility of Soils* 19, 15–18.
 Nash, M.S., Jackson, E., Whitford, W.G., 2003. Soil microtopography on grazing gradients in Chihuahuan Desert grasslands. *Journal of Arid Environments* 55, 181–192.
 Nash, M.S., Whitford, W.G., de Soyza, A.G., van Zee, J.W., Havstad, K.M., 1999. Livestock activity and Chihuahuan Desert annual-plant communities: boundary analysis of disturbance gradients. *Ecological Applications* 9, 814–823.
 Read, J.L., 2002. Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. *Austral Ecology* 27, 55–66.
 Read, J.L., Andersen, A.N., 2000. The value of ants as early warning bioindicators: responses to pulsed cattle grazing at an Australian arid zone locality. *Journal of Arid Environments* 45, 231–251.
 Sarah, P., 2002. Spatial patterns of soil moisture as affected by shrubs, in different climatic conditions. *Environmental Monitoring and Assessment* 73, 237–251.
 Tabeni, S., Ojeda, R.A., 2003. Assessing mammal responses to perturbations in temperate aridlands of Argentina. *Journal of Arid Environments* 55, 715–726.
 Thrash, I., 1998. Impact of large herbivores at artificial watering points compared to that at natural watering points in Kruger National Park, South Africa. *Journal of Arid Environments* 38, 315–324.
 Thrash, I., 2000. Determinants of the extent of indigenous large herbivore impact on herbaceous vegetation at watering points in the north-eastern lowveld, South Africa. *Journal of Arid Environments* 44, 61–71.
 Tolsma, D.J., Earnst, W.H.O., Verwey, R.A., 1987. Nutrients in soil and vegetation around two artificial water points in eastern Botswana. *Journal of Applied Ecology* 24, 991–1000.
 Turner, M.D., 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 2. Effects of a phosphorus gradient on spatial patterns of annual grassland production. *Journal of Biogeography* 25, 683–694.
 Whitehouse, M.E.A., Shochat, E., Shachak, M., Lubin, Y., 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. *Ecography* 25, 395–404.
 Whitford, W.G., 1978. Structure and seasonal activity of Chihuahuan desert ant communities. *Insectes Sociaux* 25, 79–88.
 Whitford, W.G., 1997. Desertification and animal biodiversity in the desert grasslands of North America. *Journal of Arid Environments* 37, 709–720.
 Whitford, W.G., 2002. *Ecology of Desert Ecosystems*. Academic Press, NY and London, 343 pp.
 Whitford, W.G., Kay, F.R., 1999. Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* 41, 203–230.
 Whitford, W.G., Rapport, D.J., DeSoyza, A.G., 1999. Using resistance and resilience measurements for 'fitness' tests in ecosystem health. *Journal of Environmental Management* 57, 21–29.