Journal of Arid Environments (2001) **47:** 325–337
doi:10.1006/jare.2000.0685, available online at http://www.idealibrary.com on IDEAL®

The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland

David J. Eldridge*†‡ & Chris A. Myers†

**Centre for Natural Resources, Department of Land and Water Conservation, School of Geography, University of NSW, Sydney, 2052, Australia*
†School of Geography, University of NSW, Sydney, 2052, Australia

(Received 25 February 2000, accepted 13 July 2000)

We examined the impact of the European rabbit (*Oryctolagus cuniculus* L.) on vegetation and soils of three microsites associated with rabbit warren complexes: the elevated mounds, the non-mound control areas, and an intermediate disturbed area. Mound surfaces supported significantly fewer plant species ($n = 6{\cdot}4$) compared with control surfaces ($n = 14{\cdot}2$). Mounds were typically raised structures with a local microrelief of 20 cm, and characterized by significantly more bare ground, and less litter and cryptogam cover, compared with the control surfaces. The flat micro-surfaces on the warrens were dominated by bare soils and lag gravel, whilst those on the control surfaces were dominated by cryptogams. Levels of dry and water-stable aggregation indicated that warren surfaces were significantly less stable than adjacent control surfaces. The results indicate that rabbit warrens are inherently unstable and erodible, and support a plant community of substantially reduced diversity and richness. Mechanical destruction of the warren, combined with destruction of the resident rabbit population is probably necessary to restabilize the area associated with the warrens.

Keywords: rabbit warrens; European rabbit; burrowing; soil processes; patchiness; bioturbation; biopedturbation; semi-arid woodland

Introduction

Much has been written about the damage inflicted by the European rabbit (*Oryctolagus cuniculus*) on Australia's vegetation (Wood, 1988; Leigh *et al.*, 1989; Myers *et al.*, 1994). Rabbits generally live in large, communal, subterranean burrows (warrens) which are conspicuous landscape features due to the distinctive vegetation communities they often support around their perimeter (Wood, 1988). Warrens form the centre of a circumferential grazing gradient, with grazing intensity decreasing with distance away from the warrens (Lange & Graham, 1983). Anecdotal evidence suggests that warrens are unfavourable sites for colonization of native plants, and abandoned warrens often support similar plant species to those which are occupied by rabbits.

‡Corresponding author. E-mail: D.Eldridge@unsw.edu.au

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Warrens comprise a complex of underground burrows, with entrance holes on the surface of the mounds (Butler, 1995). Rabbits regularly excavate soil from the warrens, opening up new burrows and channels, particularly when the soil is damp, and depositing freshly excavated soil at the surface (Parer *et al.*, 1987; Myers *et al.*, 1994). In many areas warrens occur at high densities, and a single warren may cover a few hundred square metres. The boundaries of warrens are generally well-defined due to differences in slope and disturbance between the elevated, disturbed section of the warren, and the adjacent undisturbed areas (Eldridge & Myers, 1999).

Together with badgers (Platt, 1975), kangaroo rats (Guo, 1996; Hawkins, 1996; Anderson & Kay, 1999), porcupines (Gutterman *et al.*, 1990; Alkon, 1999), ibex (Gutterman, 1997) and feral pigs (Kotaman, 1995), rabbits are known to move considerable volumes of soil during excavation of their warrens (Volslamber & Veen, 1985; Rutin, 1992). Surprisingly however, apart from a few references, there is little mention of this in the literature (Rutin, 1992). Previous reviews of the role of animals in soil processes, and a recent review of fossorial (digging) mammals in particular (Mitchell, 1988; Whitford & Kay, 1999), reinforce the fact that little is known about how rabbits influence soil processes.

Over the past decade, individual land managers and land management agencies such as the Department of Land and Water Conservation and New South Wales National Parks and Wildlife Service (NPWS) have invested large amounts of money in the destruction of rabbit warrens on properties which they manage. At Yathong Nature Reserve the NSW NPWS has undertaken a regular program of mechanical ripping of rabbit warrens in order to reduce rabbit numbers. Unfortunately, some warrens cannot be ripped because they are in steep country, or close to trees or rock outcrops. These warrens then become refuge warrens for recovery of rabbit populations and often support weedy plant species. In order to seek answers to some of the problems of managing rabbit- and warren-infested landscapes, agencies such as NPWS seek information on the distribution and abundance of plants on the warrens, the nature of warren soils and the likely impact of abandoned, intact warrens on the persistence or demise of weeds, given the extirpation of rabbits.

This paper examines some basic information on warren vegetation and soils in an area where rabbits are a major vertebrate pest. In particular we wished to test the popularly held belief that warrens are floristically poorer than non-warren sites, and that warrens are a refuge for environmental weeds. Further, we wished to test whether warren surfaces were inherently more unstable than non-warren surfaces, in order to make some predictions about the likely impact of further disturbance created by warren destruction. We did this by comparing soil surface morphology, soil physical processes, and cover and composition of vascular plants on rabbit warrens with adjacent warren-free surfaces. A subsequent paper examines spatial distribution of soil nutrients within and between individual warrens.

Materials and methods

The study area

The study was carried out at Yathong Nature Reserve (32°35′S; 145°35′E, altitude 200–425 m), which is located 130 km south of Cobar, New South Wales, Australia. Sheep and cattle were removed from the reserve, which comprises three former grazing leases, totalling 107, 110 ha in 1977. Average annual rainfall for the site is approximately 350 mm (Leigh *et al.*, 1989), with an even distribution of rainfall in the six cooler months (March–August) compared with the six warmer months (September–February). Annual rainfall is highly variable, and evaporation (approx. 1950 mm annum^{-1}) is high.

Maximum and minimum diurnal temperatures range from 35·0 and 19·6°C in summer, to 16·0 and 3·6°C in winter (Eldridge & Greene, 1994).

The soils are classified as massive red earths (Gn2·13; Northcote, 1979) or Typic Haplargids (Soil Survey Staff, 1975). The soil profile consists of a loam-clay loam A horizon up to 80 cm thick overlying a light-medium clay B horizon. Detailed profile descriptions are given in Eldridge & Greene (1994). Slopes in the area are typically $< 1\%$.

The vegetation in the study area is classified as a semi-arid woodland, and is dominated by red box (*Eucalyptus intertexta*), bimble box (*E. populnea*) and white cypress pine (*Callitris glaucophylla*). The herbaceous vegetation in the general area is dominated by perennial grasses such as white-top grass (*Notodanthonia caespitosa*) and No. 9 wiregrass (*Aristida jerichoensis*), and biennial grasses such as speargrasses (*Stipa* spp.). Together with low-growing annual forbs such as cut-leaf medic (*Medicago laciniata*) and common white sunray (*Rhodanthe floribunda*), the herbaceous vegetation occupies approximately 30–40% of the soil surface, with a similar proportion of the soil surface occupied by biological soil crusts (Eldridge & Greene, 1994).

Selection of the warrens

Five warrens were selected for detailed measurements of soil physical and chemical properties, as well as vegetation cover and biomass. All warrens were located within a 50-ha section of *Eucalyptus intertexta–E. populnea* woodland near Wagga Tank, on the eastern boundary of Yathong Nature Reserve. Warrens were selected on the basis of three criteria. First, they needed to be more than 150 m from the nearest adjacent warren in order to ensure that warren-free surfaces were not unduly influenced by nearby warrens. Second, only warrens present in open woodland sites were chosen for study. Since *Eucalyptus* trees are known to influence soil physical and chemical properties (Tongway & Smith, 1989; Chilcott *et al.*, 1997), warrens under trees were avoided. Third, only warrens of comparable size were selected in order to avoid possible confounding effects of warren size (and therefore rabbit population) on plants and soils.

Each warren complex comprises three distinct microsites; the mound, the disturbed area, and the control area. The mound is the elevated section of the warren system where rabbits tend to congregate and hence is generally extensively disturbed. The area away from the influence of the warren where no soil disturbance is evident is referred to as the control. In areas where rabbits are extremely active, their effect on the vegetation may extend up to 100 m from the mounds (Leigh *et al.*, 1989). In our study area however, the rabbit population had been dramatically reduced by rabbit calicivirus disease (RCD) about 12 months prior to field work, and control sites with little evidence of disturbance by rabbits were found within 10 m of the mounds. Despite the use of RCD, the warrens were still active, i.e. occupied by rabbits. An intermediate area occurs between the mound and control microsites that is termed the ‘disturbed’ area. This exhibits characteristics of both microsites, and is characterized by scratchings dung piles, small mounds of disturbed soil and undisturbed biological soil crust (Wood, 1988; Eldridge & Myers, 1999).

At each warren we selected an area of approximately 16×16 m, centring on the point of highest elevation on the mound. For the smaller warrens, the area selected was reduced to 14×16 m. A detailed stadia survey was made of the elevation of the surface to the nearest 1 mm, on a 1×1 m grid. This grid formed the basis for soil and vegetation measurements. Each grid square was defined as either mound, disturbed or control, based on the relevant percentage of attributes used to define these microsites. The size and location of entrance burrows were mapped on two warrens.

Vegetation and soil surface measurements

Ground cover was assessed systematically, using a square, 25-point quadrat frame of area 0·5 m^2, at every 5th grid square using a predetermined protocol. Because of the differing sizes of the warren complexes, sampling was adjusted so that a total of 45 quadrats was sampled on each warren. Cover was determined by species, and cover of bare ground, litter and cryptogamic crust was also assessed. Biomass of the same 45 squares was assessed using the comparative yield technique (Friedel & Bastin, 1988), supported by a series of photostandards developed for the site.

The proportion of the soil surface comprising various microtopographical cover classes was assessed using the line intercept method on two replicate mound and control surfaces of each warren. A 1-m tape measure was positioned at two randomly determined locations on the surface of each warren, and the total length of scarps, depressions and flats was calculated to the nearest millimetre. Scarps are micro-erosion features showing evidence of water erosion; depressions are localized micro-hollows and sinks; and flats are areas where the local surface roughness is less than 1 mm in amplitude. Flats and scarps were each further subdivided into bare soil, litter, cryptogam, lag material (deposits of coarse sand) and dung (generally rabbit, but sometimes kangaroo). Together these features can be used as an indication of the degree to which the surface has resisted or undergone change through erosion processes (Eldridge, 1998).

Soil physical and chemical analyses

Dry aggregate structure, determined by hand sieving (Leys *et al.*, 2000), was used as a measure of the capacity of the soil to resist erosion by wind. A British standard sieve No. 18 (0·85 mm), as specified in the Australian Standard (No. AS 1289.C6.2-1977), was used in this study, with five replicates of each of the three microsites for all five warrens. Bulk density was assessed using a core of 50-mm diameter by 25-mm depth, from three locations on each of the three microsites by five warrens. The locations of these were randomly determined.

Laboratory assessments of electrical conductivity, pH, aggregate stability and particle size distribution were carried out on a bulked sample collected from a depth of 0–25 mm. Samples were collected from five random sites in each of the three microsites, bulked and sub-sampled prior to analyses. The following methods were used:

(1) Aggregate stability: 2 to 6 mm size-fraction using a modified method after Greene (1992). This wet-sieving technique involved the rapid immersion of the 2–6 mm fraction of the soil in water, followed by wet-sieving for 10 min (300 oscillations). Four sieve sizes (2·0 mm, 1·0 mm, 0·5 mm and 0·25 mm) were used, and the results are expressed as the percentage $>$ 0·25 mm.
(2) Particle size analysis of the $<$ 2·0 mm fraction according to Loveday (1974) using dispersed samples.
(3) pH and electrical conductivity (EC): 1:5 soil-water suspension shaken for 1 h.

Statistical Analyses

Differences in the measured soil and vegetation variables between the three microsite locations were tested using one-way analysis of variance (Minitab, 1994) on data transformed, where necessary, to satisfy assumptions of ANOVA, and after testing for normality and homogeneity of variance (Bartlett's test). *Post-hoc* tests of differences between means were carried out using Least Significant Difference testing.

Three diversity measures were used to compare differences between the three microsites, pooled over the five warrens. The Shannon-Weiner diversity index incorporates components of species richness, i.e. the number of different species within the samples, and equitability, or how evenly the individuals are distributed among the different species. Margalef's Richness index is the number of species for a given number of individuals, and Pielou's Evenness index expresses how evenly the individuals are distributed between the different species and is termed equitability (Clarke & Warwick, 1994). These indices, along with the total number of species found within the samples, were calculated for all species pooled together using the PRIMER (Version 4) statistical package (Clarke, 1993).

To examine whether microsites supported a unique species assemblage, a species matrix comprising the cover-abundance of each species within each microsite was converted to a similarity matrix using the Bray-Curtis similarity coefficients contained within the PRIMER statistical package. This similarity matrix was subjected to Hierarchical Agglomerative Clustering and Multidimensional Scaling (MDS) using one of the PRIMER (Version 4) routines. Hypothesis tests of differences between groups of species, defined *a priori* according to warren microsite, were performed using ANOSIM, which is comparable to a distribution-free two-way ANOVA (Clarke, 1993). Using a number of random permutations on the similarity matrix, ANOSIM produces a test statistic (Global R) with a significance level.

Results

Floristics, ground cover and biomass of vascular plants

Thirty-five vascular plant species were recorded on the rabbit warrens (Table 1). The total number of species (α-diversity) decreased markedly with the level of disturbance ($F_{2,12} = 11{\cdot}95$, $p = 0{\cdot}001$), and there were more than twice as many species on the control microsites (14·2) compared with the mound microsites (6·4; Table 2). Richness and Shannon-Weiner indices were also significantly greater on the control microsites compared with either the disturbed or mound microsites ($F_{2,12} = 23{\cdot}65$, $p < 0{\cdot}001$ and $F_{2,12} = 7{\cdot}76$, $p = 0{\cdot}007$, respectively). There were no significant differences in evenness between the three microsites.

Total cover of vegetation ranged from 27% on the control and disturbed microsites to 37% on the mounds (Table 3). The large amount of variability between plots within a microsite, however, meant that there was no significant microsite effect on total cover. Nine of the 35 vascular plant species (*Centaurea melitensis, Erodium crinitum, Hyalospermum semipapposum, Medicago laciniata, Marrubium vulgare, Rhodanthe floribunda, Sisymbrium irio, Sclerolaena diacantha* and *Stipa* spp.) had cover values greater than 2% in one or more of the warren microsites (Table 1).

Analysis of the plant species data using Cluster Analysis and Multi-Dimensional Scaling revealed a poor separation of microsites based on species cover (Fig. 1). Similarity analyses (ANOSIM) revealed an insignificant dissimilarity between the three microsites (Global *R*: 0.076 for $p = 0{\cdot}20$). The cover of *Centaurea melitensis*, *Nicotiana* sp., *Hordeum leporinum, Marrubium vulgare, Medicago laciniata, Salsola kali* and *Sisymbrium irio*, all exotic species, was greater on mounds compared with control or disturbed microsites, although differences were significant only for *Centaurea melitensis* ($F_{2,12} = 3{\cdot}94$, $p = 0{\cdot}048$; Table 1). Only six species, all endemic (*Chloris truncata, Panicum* sp., *Goodenia pusiflora, Enteropogon acicularis, Malva parviflora* and *Omphalolappula concava*) were restricted to control microsites, and two species (*Hordeum leporinum*, *Marrubium vulgare*) were found only on mounds (Table 1).

Table 1. *Ground cover (%) of all vascular plants associated with the three warren microsites in order of relative cover on the mound*

Species	Warren microsite		
	Mound	Disturbed	Control
*Centaurea melitensis**	9·4[a]	1·5[b]	1·5[b]
*Sisymbrium irio**	8·9	3·2	1·5
*Marrubium vulgare**	5·9	0	0
*Medicago laciniata**	4·5	3·9	2·9
Rhodanthe floribunda	2·8	8·2	4·9
Stipa sp.	2·1	2·8	2·8
Sclerolaena diacantha	1·7	0·5	3·0
*Schismus barbatus**	1·4	1·6	0·1
*Salsola kali**	1·2	0·2	0·6
Erodium crinitum	0·7	2·3	1·1
Nicotiana sp.*	0·3	0·1	0
Monachather paradoxa	0·2	1·0	0·2
*Hordeum leporinum**	0·2	0	0
Aristida jerichoensis	0·1	0·4	1·5
*Hedypnois rhagodioides**	0·1	0	1·5
Hypochaeris radicata	0·1	0	0·5
Vulpia myuros	0·1	0	0·1
Hyalospermum semipapposum	0	1·6	2·9
Ptilotus sp.	0	1·0	0·3
Actinobole uliginosum	0	0·8	0·3
Sida corrugata	0	0·7	0·4
Vittadinia triloba	0	0·7	1·0
Notodanthonia caespitosa	0	0·3	0·3
Calotis sp.	0	0·2	0·2
Harmsiodoxa blennodioides	0	0·2	0
Euphorbia drummondii	0	0·1	0
Daucus glauchidiatus	0	0·1	0
Chenopodium curvispicatum	0	0·1	0·4
Boerhavia dominii	0	0·1	0
Chloris truncata	0	0	0·3
Panicum sp.	0	0	0·3
Goodenia pusiflora	0	0	0·2
Enteropogon acicularis	0	0	0·1
Malva parviflora	0	0	0·1
Omphalolappula concava	0	0	0
Total cover	39·7	31·3	28·9

*Denotes exotic species; different letters within a row indicate a significant difference in cover at $p < 0{\cdot}05$.

The area of bare ground increased significantly with the degree of disturbance ($F_{2,12} = 9{\cdot}89$, $p = 0{\cdot}003$), and litter cover was significantly higher on control plots, compared with mounds ($F_{2,12} = 7{\cdot}01$, $p = 0{\cdot}010$; Table 3). As expected, cryptogam cover was significantly greater on control surfaces, compared with mound surfaces ($F_{2,12} = 4{\cdot}87$, $p = 0{\cdot}028$, Table 3). There were no significant differences in biomass between the three microsites (Table 3).

Table 2. *Measures of diversity of vascular plant species on the three warren microsites*

	Control		Disturbed		Mound	
	mean	(S.E.M.)	mean	(S.E.M.)	mean	(S.E.M.)
Total number of species	14·2[a]	(1·46)	9·8[b]	(0·37)	6·4[c]	(1·25)
Shannon-Weiner index	2·08[a]	(0·16)	1·67[ac]	(0·15)	1·28[bc]	(0·12)
Richness	4·03[a]	(0·19)	2·74[b]	(0·20)	1·53[c]	(0·25)
Evenness	0·79[a]	(0·06)	0·73[a]	(0·06)	0·74[a]	(0·05)

Different superscripts within a row indicate a significant difference at $p < 0{\cdot}05$.
S.E.M. = standard error of the mean.

Soil and landscape attributes

Soil physical properties

Although we expected excavated mound soils to have lower bulk densities compared with the control soils (Whitford & Kay, 1999), no significant differences were detected between the three microsites (Table 4). However, mound soils contained significantly higher levels of clay ($F_{2,12} = 10{\cdot}68$, $p = 0{\cdot}002$), higher electrical conductivity ($F_{2,12} = 8{\cdot}28$, $p = 0{\cdot}005$) and higher pH levels ($F_{2,12} = 13{\cdot}10$, $p = 0{\cdot}001$), compared with either disturbed or control soils.

Soil aggregation

Pooled across the five warrens, there were significant differences in dry aggregation between the three microsites ($F_{2,12} = 21{\cdot}46$, $p < 0{\cdot}001$), with values ranging from 79·8% on the controls to 59·3% on the disturbed sites (Table 4). When sites were analysed separately, there was no significant difference in dry aggregation between the control and disturbed sites. Water-stable aggregation of soil aggregates from the mound surfaces was significantly less than that from the control soils ($F_{2,12} = 4{\cdot}69$, $p = 0{\cdot}031$).

Table 3. *Ground cover (%) of various components of the mound, disturbed and control microsites*

	Control		Disturbed		Mound	
	mean	(S.E.M.)	mean	(S.E.M.)	mean	(S.E.M.)
Bare ground cover (%)	10·9	(2·00)[a]	29·9	(5·88)[b]	46·2	(7·50)[c]
Litter cover (%)	29·8	(6·13)[a]	22·9	(2·18)[ab]	9·3	(1·98)[b]
Cryptogam cover (%)	32·4	(8·31)[a]	19·8	(4·69)[ab]	7·8	(1·53)[b]
Vegetation cover (%)	26·9	(5·10)[a]	27·4	(7·07)[a]	36·7	(6·14)[a]
Biomass ($g\,m^{-2}$)	26·1	(1·47)[a]	23·6	(2·30)[a]	35·5	(4·38)[a]
Replicates	5		5		5	

Different superscripts within a row indicate a significant difference at $p < 0{\cdot}05$.
S.E.M. = standard error of the mean.

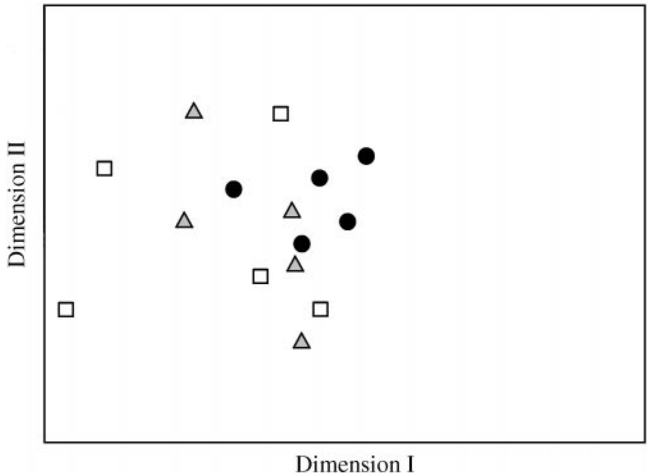

Figure 1. Multi-dimensional scaling biplot showing the distribution of control (●), mound (□) and disturbed (△) microsites based on the cover of vascular plants. Stress = 0·17.

Soil surface condition

The soil surfaces on the mound and control were similar in their relative composition of flat surfaces (75–80%), depressions (12–20%) and microscarps (6%; Table 5). Within the depression and flat categories however, there were marked differences between the mounds and control surfaces. On the mounds, about half of the depressions contained coarse sand (lag material) whilst on the control, the depressions were occupied by cryptogams. Similarly, on the control sites, 93% of the flat surfaces were occupied by cryptogams compared with only 3% on the mounds, which comprised mainly bare surfaces (81%). Overall, the control sites were characterized by stable surfaces with little lag material whilst mound sites were bare, unstable surfaces.

Geomorphology of the warrens

Rabbit warrens were typically elliptical in shape, and had a local elevation of 10–20 cm (Fig. 2). Entrances to the extensive network of subterranean chambers and tunnels were

Table 4. *Soil physical properties of the control, disturbed and mound microsites*

	Control		Disturbed		Mound	
	mean	(S.E.M.)	mean	(S.E.M.)	mean	(S.E.M.)
pH (water)	6·3	$(0{\cdot}11)^a$	6·5	$(0{\cdot}12)^a$	7·3	$(0{\cdot}11)^b$
Bulk density ($Mg\,m^{-3}$)	1·34	$(0{\cdot}04)^a$	1·35	$(0{\cdot}03)^a$	1·38	$(0{\cdot}08)^a$
EC ($dS\,m^{-1}$)	0·024	$(0{\cdot}004)^a$	0·034	$(0{\cdot}004)^a$	0·070	$(0{\cdot}01)^b$
Silt content (%)	7·8	$(0{\cdot}58)^a$	6·0	$(0{\cdot}54)^a$	6·6	$(1{\cdot}17)^a$
Clay content (%)	20·4	$(0{\cdot}25)^a$	21·6	$(0{\cdot}93)^a$	24·2	$(0{\cdot}37)^b$
Water-stable aggregation (% > 0·25 mm diameter)	84·5	$(3{\cdot}28)^a$	70	$(4{\cdot}57)^{ac}$	64·9	$(5{\cdot}88)^{bc}$
Dry aggregation (%)	79·9	$(2{\cdot}15)^a$	65·8	$(2{\cdot}94)^b$	59·3	$(3{\cdot}78)^c$

Different superscripts within a row indicate a significant difference at $p < 0{\cdot}05$.
S.E.M. = standard error of the mean.

Table 5. *Micro-surface features of the control and mound surfaces*

	Control	Mound
Scarp	6·2[a]	6·6[a]
Depression		
bare	8·1[a]	6·0[a]
litter[c]	0	0
cryptogam[c]	10·5	0
lag	1·3[a]	5·6[a]
dung[c]	0	0·5
	19·9[a]	12·1[a]
Flat		
bare	5·2[a]	65·7[b]
litter	0·3[a]	0·9[a]
cryptogam	68·4[a]	2·1[b]
lag[c]	0	12·6
dung[c]	0	0
	73·9[a]	81·3[a]

Different letters within a row indicate a significant difference at $p < 0{\cdot}05$.
[c]unable to test for differences due to presence of zeros.
The sum of scarp, depression and flat equals 100%.

concentrated in the elevated sections of the warren (the mound) which also had the highest slopes. Mound microsites were also characterized by large internal depressions resulting from the collapsing of individual entrance burrows.

Discussion and conclusions

Despite the widespread distribution of the European rabbit (*Oryctolagus cuniculus*) in Australia (Myers *et al.*, 1994), there is still little known about how it influences soil and ecological processes though construction of warrens (Wood, 1988). The present work, undertaken in an area where rabbits have historically been very active (Leigh *et al.*, 1989), indicates that rabbits have a major impact on the soil surface in and around their warrens. Despite the large degree of overlap in the vegetation communities on the various warren microsites, warren surfaces supported significantly fewer species and were characterized by surfaces with markedly different surface morphology and physical characteristics compared with warren-free surfaces (Tables 3–5).

Impact of warrens on the soil

Compared with the control sites, mounds comprised significantly more bare ground, less cryptogam cover and less litter cover (Table 3), consistent with results from a study of vegetation on warrens in the same area (Simpson, 1999). Gross differences in plant cover between mound and control microsites are reflected in the finer-scale differences in soil surface micromorphology, with flat surfaces on the mounds being dominated by bare soil or lag gravel, whilst flat surfaces on the control surfaces are dominated by cryptogams (Table 5). Moreover, levels of both dry aggregation and water-stable aggregation were about 25% lower on the mound surfaces, compared with

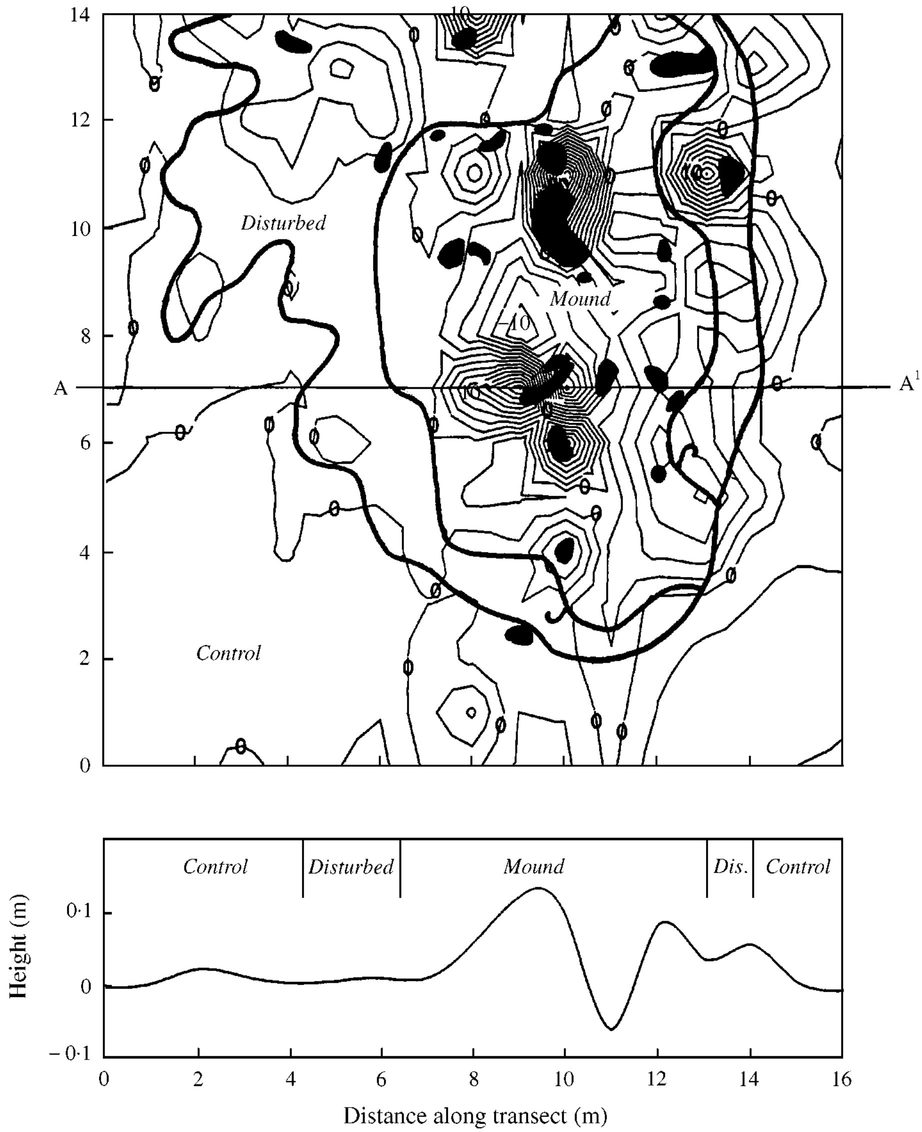

Figure 2. Plan view and cross-section A–A[1] through rabbit warren no. 5. Distances along both axes are in metres. The dark areas indicate warren entrances and the contour intervals are in centimetres.

the control surfaces (Table 4). Together these highlight the degraded nature of the warren surfaces compared with the adjacent non-mound control sites.

Contrary to our expectations, mound soils were not clay-depleted (Table 4). We attribute the significantly higher clay percentage on the mounds to the transport of clay-rich subsoil (Eldridge & Greene, 1994) to the surface by the rabbits. Significantly higher pH levels in the mound soils compared with control and disturbed soils (Table 4) are consistent with studies by Carlson & White (1988) who attributed increased surface pH to bioturbation of calcareous subsoils. Based on the water-stable aggregation and dry aggregation figures, our results also indicate a greater erodibility of the mound surfaces, compared with the relatively resistant control soils. Erosion on the mound also results in litter and nutrient transport off the mounds, creating depleted mound litter levels (Table 3) and an accumulation of litter in the annular zone surrounding the warren.

Much of the resistance of the control soils to erosion is due to cryptogams, which are a dominant feature of these surfaces (Eldridge & Greene, 1994). Cryptogamic crusts and their constituent organisms stabilize the soil surface against water and wind erosion (Eldridge & Kinnell, 1997; Leys & Eldridge, 1998), and influence water flow across the landscape. Organisms in the crust secrete gels and polysaccharides, turning erodible micro-aggregates into stable macro-aggregates, which resist erosion. Disturbance of the cryptogamic crust by scratching and digging, or smothering of the crust under piles of soil kills crust organisms and results in a breakdown of organic compounds holding the crust together. As the soil below the crust is inherently more unstable than the crust itself (Eldridge & Greene, 1994), erosion is likely to result.

In general, rabbits prefer loamy soils for ease of digging and burrow stability, and excavate their burrows when soil and moisture conditions are suitable (Voslamber & Veen, 1985). In some woodland areas, burrowing may be restricted by the presence of a hardpan layer (Parer *et al.*, 1987) which is often calcareous in origin. Calcareous material was present on the surface of some warrens at Yathong, having been transported to the surface through burrowing activity.

Field observations suggest that although warrens may become abandoned, usually through extirpation of the resident rabbit population (Wood, 1988), their influence on the environment is likely to be long-lived. Estimates based on the size of the above-ground (mound) structure of the warren are in the order of 300–500 years (Whitford & Kay, 1999). Whilst we know of no studies of the longevity of warrens in these landscapes, we believe that they will continue to act as a sediment source as long as they maintain their convex structure. The current practice of mechanically ripping rabbit warrens to prevent further rabbit infestation, probably halts or minimizes the potential for export of sediment away from the warren, by removal of the localized micro-relief associated with these soil mounds.

Impact of warrens on the vegetation

The major impact of rabbits on the vegetation around the warrens was to create a community of significantly lower diversity and richness (Table 2). Mean cover of many species was higher on the mounds, compared with the controls, but because of the considerable variability within a microsite, only one species, *Centaurea melitensis*, had a significantly higher cover on the mound compared with the control (Table 1). Rabbit grazing preferentially removes palatable plants in an area radiating out from the warrens. Previous studies at Yathong Nature Reserve have demonstrated large differences in plant composition at distances of 50–100 m from the warrens (Leigh *et al.*, 1989). Rabbits generally prefer grasses such as *Monochather paradoxa* and *Notodanthonia caespitosa* to other plants (Bhadresa, 1977; Leigh *et al.*, 1989), leading to a disappearance of these species from the vegetation as a result of prolonged rabbit grazing. In our study, unpalatable plants such as horehound (*Marrubium vulgare*) and maltese cockspur (*C. melitensis*) dominated the vegetation community on the mounds, both in cover and height, giving the mounds the characteristic appearance of being 'weedy'. Leigh *et al.* (1989) noted that when rabbit numbers were high, warrens were dominated by unpalatable *Urtica* spp. and *C. melitensis*, with only small amounts of the palatable *Schismus barbatus* and *Medicago laciniata*. The observed morphological and physical characteristics of the mounds and the reduced competition from perennial grasses (Leigh *et al.*, 1989) make warrens a likely site for weed proliferation. These weeds may proliferate due to reduced competition from palatable plants or they may have enhanced germination and/or survival rates on the degraded mound surfaces.

Soil inversion associated with older, generally abandoned, rabbit warrens may also explain the differences in vegetation communities between mounds and non-mounds. In many areas of southern Australia, rabbit activity may expose substantial amounts of surface gypsum, encouraging the growth of gypsophilous plants such as *Nicotiana glauca* (Noble & Tongway, 1986).

We thank Ms Lullo Bák-Olsson and Ms Dorothy Yu for field and laboratory assistance, respectively, and Dr Jim Noble and Dr Claudia Campos for comments on the manuscript. This work was undertaken with the generous financial assistance of the School of Geography, University of NSW. This research was undertaken under a permit from the NSW National Parks and Wildlife Service (Permit No. A2069). This is publication no CNR99.050 of the Centre for Natural Resources.

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