

Hip holes: kangaroo (*Macropus* spp.) resting sites modify the physical and chemical environment of woodland soils

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Abstract Hip holes are shallow, reniform-shaped depressions found next to the trunks of many trees and shrubs in arid and semi-arid Australia. They are constructed by kangaroos (*Macropus* spp.), who use them as diurnal resting sites, particularly during hot weather. Physical and chemical properties of soils in hip holes were compared with non-hole microsites adjacent to the trunk ('trunk'), microsites below the canopy ('canopy') and microsites out in the open ('open') under two trees (*Eucalyptus intertexta*, *Alectryon oleifolius*) and one shrub (*Dodonaea viscosa*) in a semi-arid woodland in eastern Australia. Overall, there were few effects under *D. viscosa* apart from a greater (10-fold) mass of litter in the hip holes compared with the trunk microsite. Hip holes under *E. intertexta* and *A. oleifolius*, however, contained six times more dung compared with the trunk microsite. For the two tree species, soils in the hip holes were significantly more erodible, as measured by aggregation levels, compared with the other microsites, but there were no significant differences in bulk density nor pH. Steady-state infiltration rates at the hip hole and trunk microsites were significantly greater than those in the open, but there was no significant hip hole effect. Soils in the hip holes contained greater levels of exchangeable calcium and magnesium (*E. intertexta*) and greater exchangeable sodium (*A. oleifolius*) compared with trunk microsites. Hip holes under *E. intertexta* contained approximately 68% more organic carbon, total carbon and nitrogen, and 86% more sulfur compared with trunk microsites. Similarly, hip holes under *A. oleifolius* contained on average 38% more organic and total carbon, and 47% more nitrogen than trunk microsites. Given the density of hip holes and their impact on soil chemistry, kangaroos are considered to be important elements in the maintenance of heterogeneity in these woodlands.

Key words: biopedturbation, burrowing, hip hole, kangaroo, landscape patchiness, pedoturbation, woodlands.

INTRODUCTION

Soil disturbance by animals, or biopedturbation, is important for the development of patchiness in arid and semi-arid landscapes. Animals that affect soil properties vary in size from microscopic fauna, to mesofauna and larger animals such as porcupines, rodents, herbivores and even humans (Meadows & Meadows 1991). This patchiness manifests itself in microsites with favourable physical and chemical soil properties that influence germination and survival of vascular plants, and the structure and function of their resident animal communities.

Burrowing by vertebrates often profoundly affects soil physical and chemical properties such as soil texture, structure, fertility, bulk density, water and nutrient flows (Huntly & Inouye 1988; Whicker & Detling 1988; Reichman & Smith 1990; Butler 1995; Kinlaw 1999; Whitford & Kay 1999). Seeds, soil, organic matter, insect frass and animal faeces are often

trapped within depressions excavated by mammals seeking or caching food (Gutterman & Herr 1981; Steinberger & Whitford 1983; Gutterman 1987; Dean & Milton 1991b; Boeken *et al.* 1995; Yair 1995; Tardiff & Stanford 1998) or depressions used as bedding sites (Gutterman 1997a,b; Dean *et al.* 1999). In Australia, pits created by Gould's sand goanna (*Varanus gouldii*) are reported to play an important role in the maintenance of patterning in mulga woodlands (Whitford 1998), while woylie (*Bettongia penicillata*) diggings enhance the development of water absorbent patches in hydrophobic sandy soils (Garkaklis *et al.* 1998).

In Australia, kangaroos excavate pits termed 'hip holes' as resting sites. These pits are generally constructed within 30 cm of the trunks of trees and large shrubs. Pits are thought to be used for cooling, as diurnal soil surface temperatures are lower in the depressions (Gutterman 1987) and a bedded animal loses most of its heat to the ground by conduction (Mysterud & Ostbye 1995). Scraping a depression can also be interpreted as comfort behaviour, as creating a soil depression accommodates the kangaroo's hip bone, which is very large (hence the term 'hip hole'). Similar

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behaviour has been recorded in the European roe deer (*Capreolus capreolus*) in southern Norway (Mysterud & Ostbye 1995). Field observations and anecdotal accounts suggest that hip holes accumulate water, organic matter and seeds, and often support a vegetation community distinctively different from that of the surrounding landscape. Despite this, and the high densities of hip holes in many wooded landscapes, there are no empirical data on these structures and their physical and chemical characteristics.

The aim of this paper was to document some basic attributes of hip holes produced by western grey (*Macropus giganteus*) and eastern grey (*Macropus fuliginosus*) kangaroos, and to describe the physical and chemical properties of the soils associated with these structures. We did this by comparing the physical and chemical properties of the soil within hip holes with comparable control sites, under three different tree species, in an area where hip holes are a common feature of the landscape.

METHODS

Study site

The study was conducted at Yathong Nature Reserve, approximately 140 km south-west of Cobar near Mount Hope (145°35'E, 32°35'S, 200–425 m a.s.l.), in western New South Wales, Australia. Yathong was formerly a sheep grazing property before being declared a 'Man in the Biosphere' reserve in 1977. Eastern grey kangaroos (*M. giganteus*) and western grey kangaroos (*M. fuliginosus*) are present in high numbers within the reserve, up to 40 kangaroos per km² (D. Freudenberger pers. comm. 2000), having benefited from past clearing, establishment of watering points (mainly dams) and frequent burning.

Most of the reserve lies between the 325 and 350 mm rainfall isohyets, but rainfall is highly variable from year to year. Maximum and minimum diurnal temperatures range from 35.0°C and 19.6°C in January to 16.0 and 3.6°C in July (Eldridge & Greene 1994). Evaporation is high, particularly in the non-winter months, with an annual mean of 1952 mm (Leigh *et al.* 1989).

The soils at the study site are classified as massive red earths (Gn 2.13, Northcote 1979). They are generally infertile, with a low phosphorus content (Harrington *et al.* 1984). Red earth soils support an open woodland dominated by inland red box (*Eucalyptus intertexta*), white cypress pine (*Callitris glaucophylla*) and wilga (*Geigeria parviflora*). The groundstorey vegetation at the time of the present study comprised mainly grasses such as speargrasses (*Stipa* spp.), wiregrasses (*Aristida* spp.) and white-top grass (*Austrodanthonia caespitosa*). Low-growing ephemeral and annual species such as burr medic (*Medicago polymorpha*) and common white

sunray (*Rhodanthe floribunda*) were also present in the grassy interspaces.

Field measurements

All measurements were made within an area of approximately 25 ha on the eastern boundary of the reserve. The specific site was chosen because it represented open, semi-arid, wooded rangeland frequented by eastern and western grey kangaroos, and hip holes were common under trees and shrubs taller than 1 m approximately. The study consisted of two phases: (i) a general survey was undertaken to document the physical characteristics of the hip holes; and (ii) a detailed study focused on the physical and chemical characteristics of hip hole soils.

General survey: Morphology of hip holes

For the general survey, we selected hip holes at random by walking to the nearest *Eucalyptus intertexta*, *Alectryon oleifolius* or *Dodonaea viscosa* plant on a given compass bearing, and recording length, width, depth and litter and plant cover. We then walked to the next closest tree and repeated the measurements until we had obtained data for approximately 220 hip holes. More than one hip hole was present under some trees, and some holes were active, that is, had evidence of recent use by kangaroos, while others were relatively inactive, in a partial state of stabilization or regeneration, or were partially excavated by rabbits. Measurements were restricted to hip holes showing evidence of use during the past 12 months. These were distinguished by their morphology, and had evidence of kangaroo scratching or digging and/or fresh kangaroo dung. Some hip holes, which were close to active rabbit warrens and had been excavated by rabbits, were disregarded. Consequently, the survey underestimates the true density of hip holes found at this site. After these anomalous hip holes were eliminated, the data set consisted of 177 hip holes: 119 from under *E. intertexta*, 15 from under *A. oleifolius* and 43 from under *D. viscosa*. These numbers reflect the relative abundance of these three woody species in the woodland at Yathong.

For each of the 177 hip holes we measured five attributes: (i) the size of the longest axis (length); (ii) the width through the centre of the hip hole perpendicular to the longest axis; (iii) depth at three locations along the width (in the centre, and approximately 0.1 m in from both edges); (iv) percentage of plant cover; and (v) percentage of cover of dung and litter in the hole. Length, width and depth were measured to the nearest 10 mm, and percentage plant and dung/litter cover assigned to cover classes of 0–10, 11–25, 26–50, 51–75 and >75%. Cover was estimated using a set of photographic standards. Data for the first two

categories were amalgamated for analyses. A cross-sectional profile of one hip hole under each of the three species was measured using the following procedure. A solid steel bar was supported approximately 50 cm above the hip hole and normal to the direction of the longest axis parallel to the ground surface, and the distance to the ground surface or hip hole measured at 10 mm intervals using a 1-m rule. Sufficient measurements were made to include a substantial area of natural ground surface on either side of the hip hole.

Defining the microsites

Given the typically strong gradients in soil, physical and chemical properties radiating out from trees and shrubs in many woodlands (Ryan & McGarity 1983; Belsky *et al.* 1989; Vetaas 1992; Belsky *et al.* 1993), the effect of hip holes could be confounded with distance from the trunk. To avoid this we collected soil and vegetation data at four microsites in relation to each tree: a non-hip hole site adjacent to the trunk ('trunk'), a site adjacent to the trunk but within a hip hole ('hip hole'), a site at mid-canopy ('canopy') and a site 10 m outside the edge of the canopy ('open'). Although we focused on the differences in properties between hip hole and trunk microsites, which were both located at a similar distance from the trunk, we also examined the two other microsites in order to obtain a better understanding of the magnitude of the differences between hip hole sites under trees and non-hip hole sites in the open.

We sampled under two tree and one shrub species. *Eucalyptus intertexta* had a large canopy, up to 15 m in diameter, and trunks up to 900 mm diameter at breast height (d.b.h.). *Alectryon oleifolius* was a medium-sized tree with a smaller canopy (~5 m diameter), d.b.h. of 120–350 mm, that densely shaded the soil surface. *Dodonaea viscosa* is a small shrub less than 3 m tall with a canopy less than 3 m in diameter. Mean (\pm standard error of the mean) d.b.h. dimensions for the three tree species recorded during the general survey were 650 (\pm 37.6) mm for *E. intertexta* ($n = 119$), 150 (\pm 13.1) mm for *A. oleifolius* ($n = 15$), and 54 (\pm 3.3) mm for *D. viscosa* ($n = 43$).

Five replicate trees of each species were randomly selected. When a tree had more than one hip hole beneath it, the southern-most hip hole was chosen. At each microsite associated with each tree we collected all dung and litter present within two 260 mm \times 250 mm quadrats. Faecal pellets were separated into kangaroo and rabbit dung, and their oven-dried mass expressed in g m⁻².

Soil physical properties

Dry aggregate stability was measured using the method described by Leys *et al.* (in press). The upper 25 mm

of the soil surface from each of the three microsites was gently scalped with a flat, square-faced trowel, and passed through a 0.85-mm sieve. Dry aggregation was calculated as the proportion of the soil >0.84 mm in diameter (Leys *et al.* in press). For each tree, three subsamples were taken (and averaged) for each microsite, resulting in a data set of $n = 60$ (five replicates for each of three tree species \times four microsites).

Bulk density was measured using a soil corer, 47 mm in diameter and 75 mm in depth, at each of the four microsites. Soil samples were oven dried at 105°C for 24 h. Two subsamples were taken from each tree (and averaged) for each microsite by tree species combination.

Soil chemical properties

Soils for nutrient and chemical analysis were assayed for total nitrogen, carbon and sulfur using a high temperature combustion method (LECO 2000 CNS system). Exchangeable calcium, potassium and magnesium were determined using inductively coupled plasma spectroscopy (Perkin Elmer Optima 3000 DV ICP-OES). Electrical conductivity and pH were determined on a 1:5 soil to water extract. The organic carbon content was determined using the Walkley–Black method (Colwell 1969). Three subsamples from the same tree were bulked for each microsite by tree species combination.

Infiltration

Water flow through the hip holes was assessed by measuring steady-state infiltration (mm h⁻¹) with a disc permeameter under ponded (+ 10 mm water) conditions (Perroux & White 1988). The permeameter was placed on a steel ring of 220 mm internal diameter, which was gently pressed into the soil to a depth of about 7–10 mm, and sealed with reworked moist clay along the outside edge to prevent leakage of water. The permeameters were run for 30 min by which time steady-state infiltration had been achieved. Steady-state infiltration was calculated according to the method of White (1988). Infiltration was measured adjacent to the trunk, within the hip holes, and in the open sites only under 10 *E. intertexta* trees.

Statistical analyses

For the general survey, differences in hip hole size (length, width) among plant species were assessed using one-way ANOVA, after checking for normality and homogeneity of variance (Bartlett's test). Hip hole depth data, which could not be stabilized or normalized by transformation, were analysed using the

non-parametric Kruskal–Wallis test. Categorical data (plant cover, dung and litter cover) were analysed using χ^2 tests, to determine if there were differences in characteristics of hip holes under different plant species.

For the detailed study we used a split-plot model, with replicates of tree species as the whole plots, and microsites within trees as the subplots, and analysed data averaged over subsamples at a microsite. Because the tree species varied widely in the size of their canopies, we considered the usual partitioning of microsite effects into ‘microsites’ and ‘microsite by tree species’ interaction to be potentially misleading. The average effect of, say, hip holes, would be confounded with tree species effects because, conceivably, one hip hole could occupy the entire area under a small *D. viscosa* shrub, and could therefore trap a greater proportion of the litterfall compared with a similar sized hole under a much larger *E. intertexta* canopy. Accordingly, we partitioned the subplot stratum source of variation into three more meaningful lines: (i) variation due to microsites within *E. intertexta*; (ii) variation due to microsites within *A. oleifolius*; and (iii) variation due to microsites within *D. viscosa*.

All analyses were performed using MINITAB (1997) after checking for normality and homogeneity of variance (Bartlett’s test). Differences between microsites within a tree species were compared using least significant difference (LSD) testing.

RESULTS

Density and morphology of hip holes

Hip holes were present under more than 80% of shrubs and trees over 2 m tall. For those *E. intertexta*, *A. oleifolius* and *D. viscosa* trees with hip holes, 58% had only one hole, 34% had two to four holes, and 8% had five or more hip holes below their canopies. Generally, larger trees had more hip holes ($P < 0.05$) although these holes were not significantly deeper than those under smaller trees ($P > 0.05$).

Hip holes were typically reniform to subcircular shaped, and located within 0.5 m of the tree trunk. The outer edge (further from the trunk) tended to be more sharply angled than the inner edge, which sloped toward the original ground level. This characteristic

was however, less pronounced under *D. viscosa* (Fig. 1).

Across all tree species, mean (\pm standard error of the mean) hip hole dimensions were 0.818 ± 0.21 m long by 0.579 ± 0.14 m wide by 0.090 ± 0.26 m deep. Although neither length nor width differed among tree species ($P > 0.05$), holes under *E. intertexta* were significantly deeper than those under either *A. oleifolius* or *D. viscosa* ($H_2 = 16.62$, $P < 0.001$; Table 1).

There were no significant differences in plant cover in the hip holes under the three plant species ($P > 0.05$). However, there was a significantly greater cover of dung and litter ($\chi^2 = 19.32$, d.f. = 6, $P < 0.004$) under *D. viscosa* (median = 50–75% cover) compared with *E. intertexta* and *A. oleifolius* (median = 25–50%; Fig. 2).

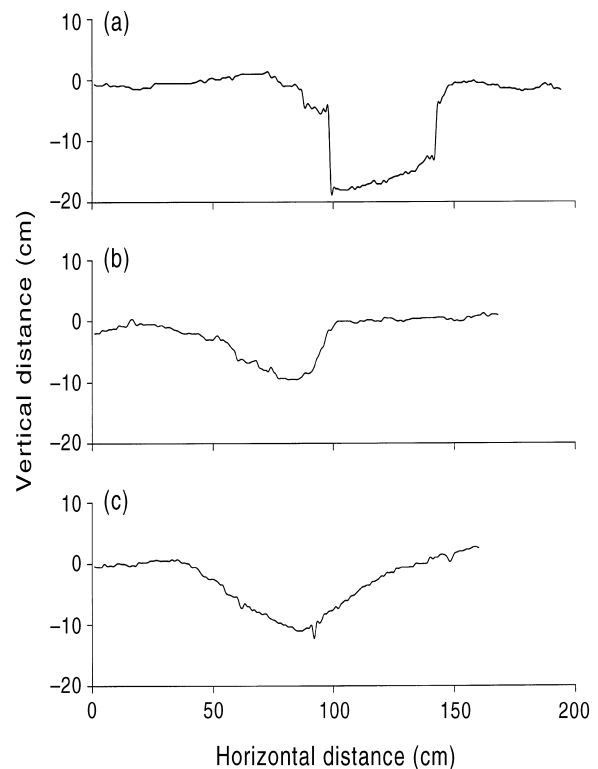


Fig. 1. Cross-sectional profile of a typical hip hole beneath the tree and shrub species (a) *Eucalyptus intertexta*, (b) *Alectryon oleifolius* and (c) *Dodonaea viscosa*. The cross-section was measured at 10 mm intervals in the direction away from the tree or shrub normal to the longest axis. The vertical distance of zero indicates ground level.

Table 1. Mean (and standard error of the mean) of size dimensions of hip holes under three tree species

Variable	<i>Eucalyptus intertexta</i> (n = 119)	<i>Alectryon oleifolius</i> (n = 15)	<i>Dodonaea viscosa</i> (n = 43)
Length (mm)	838 ^a (27.1)	763 ^a (70.8)	782 ^a (36.4)
Width (mm)	595 ^a (17.5)	587 ^a (37.4)	532 ^a (28.0)
Depth (mm)	94 ^a (2.61)	71 ^b (4.7)	86 ^b (7.6)

Different letters within a row indicate a significant difference at $P < 0.05$.

Effects of hip holes on mass of dung and litter

Hip holes under *D. viscosa* contained a significantly greater mass of litter compared with the other microsites ($F_{3,36} = 3.91$, $P < 0.01$). Under *A. oleifolius* and *E. intertexta* substantial litter was found close to the tree trunk, both inside and outside the hip holes. This was approximately an order of magnitude greater than the mass found away from the trunk (canopy and open microsites; $P < 0.01$; Table 2). Hip holes under *E. intertexta* and *A. oleifolius* trees contained significantly more dung compared with the adjacent trunk microsite ($F_{3,36} = 3.8$ – 6.7 , respectively, $P < 0.05$). The litter category comprised mainly bark, small twigs, leaves and decomposing organic matter, whereas the dung category comprised mainly kangaroo (79%) and rabbit (21%) faeces.

Hip holes and soil physical properties

Dry aggregation of soils in the hip holes was, on average, 45% less than mean values adjacent to the trunk for both *E. intertexta* ($F_{3,36} = 27.31$, $P < 0.01$)

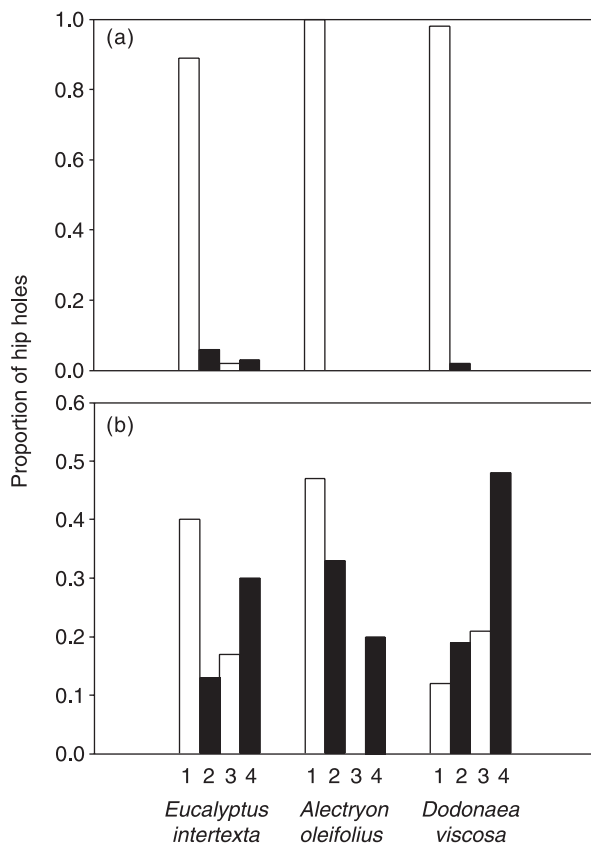


Fig. 2. Distribution of cover classes for (a) plant cover and (b) litter and dung cover within hip holes under the three species. 1 = <25% cover, 2 = 26–50%, 3 = 51–75%, 4 = >75%.

and *A. oleifolius* ($F_{3,36} = 21.84$, $P < 0.001$), but there were no differences under *D. viscosa* (Table 2). Bulk density of the soil was significantly greater in hip holes beneath *E. intertexta* ($F_{3,36} = 27.68$, $P < 0.01$) indicating possible soil compaction, but not under the other tree species (Table 2). There was no effect of hip holes on steady-state infiltration ($P > 0.05$), which was significantly less in the open (20.9 mm h^{-1}) microsites compared with hip hole (45.0 mm h^{-1}) and canopy (59.8 mm h^{-1}) microsites ($F_{2,27} = 10.94$, $P < 0.001$, Table 3).

Hip holes and soil chemical properties

There were no significant differences in soil pH between the various microsites ($P > 0.05$). Under both *E. intertexta* and *A. oleifolius* there was a clear and significant trend of decreasing electrical conductivity with distance from the hip hole ($F_{3,36} = 23.93$, $P < 0.001$ and $F_{3,36} = 9.34$, $P < 0.05$ for *E. intertexta* and *A. oleifolius*, respectively). Differences in electrical conductivity under *D. viscosa* were not significant ($P > 0.05$). Compared with the trunk microsite, there was significantly more organic carbon in the hip holes under both *A. oleifolius* ($F_{3,36} = 10.5$, $P < 0.01$) and *E. intertexta* ($F_{3,36} = 13.88$, $P < 0.01$). This was mirrored by changes in total carbon in *E. intertexta* and *A. oleifolius*, with a strong gradient of decreasing total carbon with distance from the hip hole microsite ($F_{3,36} = 15.17$, $P < 0.05$ and $F_{3,36} = 8.68$, $P < 0.05$, respectively). Similarly, there were strong gradients in total soil nitrogen from hip hole to open microsites for *E. intertexta* and *A. oleifolius* ($F_{3,36} = 10.7$ and $F_{3,36} = 12.8$, $P < 0.01$, respectively). On average, hip holes contained approximately 37% more total nitrogen compared with adjacent trunk sites (Table 2). Levels of total sulfur were significantly greater in hip holes compared with the other microsites but only for *E. intertexta* ($F_{3,36} = 10.67$, $P < 0.01$).

In general, there was a gradient in exchangeable cations from low levels in the open to highest levels in the hip holes. Levels of exchangeable magnesium and calcium were significantly greater in the hip holes compared with trunk sites for *E. intertexta* only ($F_{3,36} = 12.49$ and $F_{3,36} = 21.06$, $P < 0.01$, respectively).

DISCUSSION

Hip holes are a common feature of woodlands and shrublands in arid and semi-arid eastern Australia. Like rodents and other small digging animals, kangaroos create pits that are physically and chemically different from the surrounding soils (Andersen 1987; Huntly & Inouye 1988; Whitford & Kay 1999; Sherrod & Seastedt 2001), thus leading to a redistribution of

Table 2. Mean values of soil physical and chemical properties for the four microsites between the three tree species

	<i>Dodonaea viscosa</i>			<i>Alecryon oleifolius</i>			<i>Eucalyptus intertexta</i>		
	Trunk	Hip hole	Open	Trunk	Hip hole	Open	Trunk	Hip hole	Open
Litter mass (g m ⁻²)	450.0 ^b	4237.9 ^a	732.5 ^b	4229.4 ^a	4237.9 ^a	883.1 ^b	5667.6 ^a	4566.1 ^a	513.7 ^b
Dung mass (g m ⁻²)	345.9 ^a	190.2 ^a	12.1 ^a	75.1 ^b	496.8 ^a	4.4 ^b	49.5 ^b	342.1 ^a	4.1 ^b
Bulk density (mg m ⁻³)	1.33 ^a	1.22 ^a	1.27 ^a	1.10 ^a	1.10 ^a	1.09 ^a	0.97 ^c	1.16 ^a	1.15 ^a
Dry aggregation (% >0.84 mm)	86.2 ^a	80.7 ^{ab}	75.9 ^b	80.1 ^b	45.8 ^a	72.0 ^c	77.7 ^b	42.1 ^a	74.4 ^b
pH (water)	6.35 ^a	6.26 ^a	6.28 ^a	6.20 ^a	6.23 ^a	6.14 ^a	6.89 ^a	6.85 ^a	6.68 ^{ab}
Electrical conductivity (dS m ⁻¹)	2.09 ^a	2.11 ^a	1.18 ^a	2.76 ^b	3.67 ^a	2.45 ^b	3.33 ^b	5.01 ^a	2.03 ^c
Exchangeable Ca (p.p.m.)	32.72 ^a	32.65 ^a	24.33 ^a	47.10 ^a	65.27 ^a	42.32 ^a	138.80 ^b	200.92 ^a	49.99 ^c
Exchangeable K (p.p.m.)	156.17 ^a	147.66 ^a	52.06 ^a	188.34 ^a	236.02 ^a	139.71 ^a	254.98 ^a	220.46 ^{ac}	115.12 ^{bc}
Exchangeable Mg (p.p.m.)	25.96 ^a	26.68 ^a	22.79 ^a	26.75 ^a	40.24 ^a	30.36 ^a	59.76 ^b	97.42 ^a	29.19 ^c
Exchangeable Na (p.p.m.)	12.82 ^a	11.79 ^a	8.07 ^a	19.14 ^b	9.21 ^a	8.86 ^a	11.63 ^a	14.35 ^a	9.13 ^{ab}
Organic carbon percentage	1.71 ^a	2.11 ^a	1.49 ^a	2.33 ^b	3.1 ^a	2.4 ^b	2.09 ^b	3.50 ^a	2.16 ^b
Total C (kg kg ⁻¹)	2.188 ^a	2.505 ^a	1.782 ^a	3.036 ^{bc}	4.323 ^a	3.478 ^{ac}	3.123 ^b	5.184 ^a	2.771 ^c
Total N (kg kg ⁻¹)	0.147 ^a	0.183 ^a	0.134 ^a	0.210 ^c	0.310 ^a	0.256 ^b	0.177 ^c	0.298 ^a	0.195 ^b
Total S (kg kg ⁻¹)	0.0100 ^a	0.0118 ^a	0.0094 ^a	0.0138 ^a	0.0170 ^a	0.0144 ^a	0.0083 ^b	0.0175 ^a	0.0126 ^b

For each species, different letters within a row indicate a significant difference at $P < 0.05$.

nutrients and the potential to affect plants and other animals.

The direct effect of kangaroo digging is to convert the soil surface into a depression, destroying the extant vegetation and reducing mean cover from 73% on the open microsites to 8% within the hip holes. Reduced vegetation cover associated with mammalian activity is widely reported in the literature. Grizzly bears (*Ursus arctos horribilis*) clear vegetation while excavating soil in search of glacier lilies (*Erythronium grandiflorum*; Tardiff & Stanford 1998), and springbok (*Antidorcus marsupialis*) and gemsbok (*Oryx gazella*) destroy perennial grasses while excavating bedding sites under *Parkinsonia africana* trees (Dean & Milton 1991b). The denuded areas beneath *Parkinsonia africana* trees are similar to hip holes created by kangaroos in eastern Australian woodlands.

The presence of deeper hip holes under *E. intertexta* canopies is probably a reflection of the ease with which soil beneath *E. intertexta* trees is excavated by kangaroos. Compared with open areas, the soil beneath the canopies of woodland trees generally has greater levels of favourable soil properties (Chilcott *et al.* 1997; Facelli & Brock 2000) and, conceivably, being easier to excavate, cooler subsoil is easier to reach under larger trees that produce an abundance of litter. Burrow systems of the kangaroo rat (*Dipodomys ordii*) are known to be deeper and larger in soils with greater silt and clay contents (Laundre & Reynolds 1993).

Hip holes as sinks for organic material

The phenomenon of depressions as resource traps has been noted extensively in the literature for a range of continents. In a desert landscape in New Mexico, excavations made by rodents (*Dipodomys merriami*, *Perognathus penicillatus*) and badgers trap large quantities of litter, silt and seeds (Chew 1979; Steinberger & Whitford 1983). In the Karoo shrublands and grasslands in South Africa, scrapings and holes excavated by baboons (*Papio ursinus*), aardvarks (*Orycteropus afer*), bat-eared foxes (*Otocyon megalotis*) and cape foxes (*Vulpes chama*) trap seeds, faeces and other organic detritus (Dean & Milton 1991b). In Australia, pits dug by Gould's sand goanna (*Varamus gouldii*) trap leaf,

Table 3. Steady-state infiltration (mm h⁻¹) within three microsites

Microsite	Mean	SEM	n
Trunk	55.0 ^a	4.1	10
Hip hole	59.8 ^a	7.0	10
Open	20.9 ^b	18.2	10

Different letters within a column indicate a significant difference at $P < 0.05$; SEM = standard error of the mean.

wood, faeces and grass fragments (Whitford 1998), and scrapings of the small kangaroo-like wylie (*Bettongia penicillata*) trap litter and other organic fragments (Garkaklis *et al.* 1998).

While the majority of dung in the hip holes is excreted by kangaroos during periods of resting, other litter and dung (e.g. rabbit faeces) are probably transported into the holes by water and wind erosion. Rainwater and canopy drip are likely to wash litter into the hip holes by rainsplash, and other surface organic material may be entrained by overland flow and deposited on the hip-hole surface. Raindrop action is likely to cover organic material in the holes, initiating the process of decomposition, and preventing it from being blown out of the hole. Further, because holes act as wind shadows, reducing wind velocity (Reichman 1984), capture of organic material is likely to be enhanced, particularly in deeper holes. During our study, substantial amounts of litter (predominantly leaves and small pieces of bark) were found adjacent to the *E. intertexta* and *A. oleifolius* trees, both inside the holes and on the soil surface. Our observations indicate that this litter is likely to remain in the hip holes for longer than it would in adjacent non-hole sites, increasing the chances of breakdown.

Hip holes under the smaller *D. viscosa* contained significantly greater amounts of litter compared with non-hole areas adjacent to the trunk (Table 2). The tendency for smaller trees (and shrubs) to have canopies closer to the soil surface, means that hip holes under *D. viscosa* are likely to catch more litter as the canopy reaches within 0.30 m of the ground. Other differences in litter capture may relate to variation in leaf fall between the three tree types, or differences in the transportability of the leaves by wind or water; a consequence of different leaf mass and architecture. Leaves of *D. viscosa* are linear-lanceolate and less than 10 mm across compared with the larger lanceolate-shaped leaves of *E. intertexta*, which are typically 20–30 mm across and may not as easily be transported by wind. Also *D. viscosa* leaves may have lesser decomposition rates compared with the other species. This would explain the lack of differences in carbon, nitrogen and exchangeable cations between hip holes and the other microsites under *D. viscosa* (Table 2).

Hip holes and soil physical properties

A major effect of kangaroos was to destroy soil structure and therefore aggregate stability through digging and scratching. Digging destroys the thin microphytic crust made up of lichens, bryophytes and bacteria (Eldridge & Greene 1994) that binds the soil and prevents soil erosion. Although crusts were more common in the open microsites, they also occurred in the ungrazed patches below trees, and contributed

substantially to soil stability. Given the gradational nature of the soils in the study area (Eldridge & Greene 1994), any substantial soil disturbance is likely to expose material that is both finer (clay-enriched; Abaturon 1972; Whitford & Kay 1999) and less dense (Sharma & Joshi 1975; Heth 1991) compared with soils at the surface. Indeed, many of the physical and chemical changes we observed in the hip holes can be attributed to a transport of finer material to the surface.

Digging and scratching also convert non-erodible macro-aggregates (>0.84 mm diameter) into micro-aggregates that are susceptible to erosion. Apedal or massive soil conditions may result, whereby fine soil particles with loose aggregates remain on the excavated soil surface (Hole 1981). In the Negev Desert, apedal conditions created by porcupines (*Hystrix indica*) while digging for bulbs (Yair & Rutin 1981; Yair 1995) result in reduced infiltration (Boeken *et al.* 1995). In our study, infiltration in the hip holes was always less than that at the non-hole control sites, though the data were not significantly different. Slaking, the breakdown in structure of the surface soil, is likely to result in further reductions in infiltration and some ponding of water entering the hip holes. The physical impact of resting kangaroos could conceivably lead to soil compaction and thus reduced stability. Although we found no differences in bulk density, compaction could result when the soils are wet. Pack (1928) demonstrated increased soil compaction caused by mountain goats (*Oreamnos americanos*).

Hip holes and soil chemical properties

The significantly greater levels of electrical conductivity in the hip holes compared with the trunk microsites for *E. intertexta* and *A. oleifolius* (~45% greater) can be attributed to the exposure of finer, clayey subsoils (which inherently contain more soluble salts) at the soil surface. Abaturon (1972) showed that burrow mounds of the suslik (*Citellus pygmaeus*) in the Caspian lowlands (Russia) contained almost twice the total soluble salt content of non-mound soils. Greater levels of electrical conductivity could result from the decomposition of faeces and urine, such as that observed in woodrat (*Neotoma albigula albigula*) middens (Greene & Murphy 1932).

Greater amounts of nitrogen, carbon, sulfur and some exchangeable cations in the hip holes under *A. oleifolius* and *E. intertexta* compared with the trunk soils were probably found because of the decomposition of a greater amount of faeces found in the holes, and presumably also urine and urea (Steinberger & Whitford 1983; Gessaman & MacMahon 1984; McNaughton *et al.* 1988; Dean & Milton 1991a; Ashton & Basset 1997; Dean *et al.* 1999; Whitford & Kay 1999). Kangaroos appeared to prefer the larger *E. intertexta* trees, probably because their larger crowns

provided more shade and therefore better bedding sites (Huot 1974). The greater use of *E. intertexta* trees as bedding sites would account for the greater mass of dung beneath these trees. Faecal pellets and urine are known to stimulate nitrogen mineralization in latrines and bedding sites (Huntly & Inouye 1988; Pastor *et al.* 1993), often enhancing the germination and survival of trapped seeds (Gutterman 1997a,b).

There are various explanations for the trend of greater nutrient levels in hip holes compared with non-hole sites. Evidence from other biopedturbational studies suggests that finer soils, brought to the surface by mammalian digging, may naturally contain greater amounts of nutrients and cations (Whitford & Kay 1999). For example, some soils associated with small mammal burrows and burrow mounds have elevated concentrations of carbon and nitrogen that may be attributable to minerals mined from depth being brought to the surface. This phenomenon has been observed in black-tailed prairie-dogs (Carlson & White 1987) and mima-like mounds in Africa, which have elevated concentrations of nitrogen, potassium, calcium and magnesium (Meadows & Meadows 1991). However, this mechanism seems at odds with the large body of literature demonstrating that nutrients in arid landscapes are concentrated at the surface and attenuate with depth (Nishita & Haug 1973; West & Klemmedson 1978; Rostagno *et al.* 1991; Schlesinger & Pilmanis 1998). Further, it is doubtful whether these mammals are preferentially selecting finer soil material of a greater nutrient content when they excavate.

Differences probably result from increased dung accumulation in the holes, as observed in our study under the two larger trees, and within bedding sites of the Nubian ibex (*Capra ibex*), springbok (*Antidorcas marsulialis*) and gemsbok (*Oryx gazella*) (Dean & Milton 1991a; Whitford & Kay 1999; Gutterman 2001). Although increased amounts of NH_4^+ and NO_3^- have been detected in grizzly bear digs, Tardiff and Stanford (1998) rule out the role of bear excretion in raising mineral nitrogen levels, as anthropogenically simulated digs had similar trends of increased mineral nitrogen. We believe that hip holes contain greater levels of nutrients because of a combination of increased capture of organic material, water and soil, and increased disturbance, which stimulates microbial processes (Johnson *et al.* 1995) and increases overall levels of mineralization. This is likely to be complemented by a reduced uptake of mineralized nitrogen in active holes because of the absence of plants under a regime of continuous surface disturbance.

Kangaroos as agents of landscape heterogeneity

In deserts and semi-deserts the spatial distribution of nutrients is markedly patchy (Schlesinger & Pilmanis

1998). Disturbance by kangaroos plays a major role in establishing and maintaining the spatial and temporal characteristics of soil patches (Whitford & Kay 1999) through accumulation of material in the pits, as well as removal of excavated soil. This patchiness is likely to influence the distribution of other organisms such as nematodes and microarthropods, which are strongly tied to the distribution of soil moisture and nutrients (Whitford 1996).

The present study has shown that hip holes are efficient resource traps. Ponding of water may explain our observations of enhanced germination of ephemeral plants (particularly members of the family Brassicaceae) in the hip holes after rainfall (*sensu* Gutterman 2001), analogous to high plant densities in porcupine digs in the Negev Desert (Gutterman & Herr 1981). Hip holes could conceivably affect the community structure of organisms such as microarthropods, nematodes, invertebrates, lizards and rodents, by creating favourable abiotic and biotic conditions (Whitford & Kay 1999; Gutterman 2001). Digging-induced patches of high fertility may also be preferred sites for shrub establishment (Chew & Whitford 1992), particularly for those plants that require highly fertile soils. Further, hip holes under shrubs are likely to enhance their status as 'islands of fertility' (Garner & Steinberger 1989) by positive feedback on microbial activity and infiltration processes.

Hip holes are likely to influence spatial heterogeneity by functioning as fertile patches during dry periods, providing a refuge for small animals requiring resource-rich environments. For example, the skink *Ctenotus leonhardii* is associated with fertile mounds of decomposing logs (mulga log mounds; Tongway *et al.* 1989) in the semi-arid woodlands, and large numbers of tenebrionid beetles normally found in litter and vegetation have been recorded from wombat burrows at Brookfield Conservation Reserve in arid South Australia (T. Weir, pers. comm. 2002). Hip holes could conceivably support a distinct microbial or invertebrate community in these landscapes.

Finally, given the high density of active hip holes in many woodland systems, densities far exceeding those recorded at Yathong Nature Reserve (~63 per ha), the volume of soil removed is considerable. Conservative estimates for Yathong are of the order of $2.7 \text{ t ha}^{-1} \text{ y}^{-1}$. Kangaroos should therefore be recognized as significant controllers of ecosystem processes.

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