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Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes

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Abstract

Cape porcupines (*Hystrix africaeaustralis*) appear to have an important influence on landscapes through both biotic (foraging) and abiotic (soil turnover) impacts. Porcupine abundance and abiotic effects across the landscape were investigated in Nieuwoudtville, South Africa, a semi-arid area characterized by an extraordinary diversity and abundance of geophytes. Porcupine numbers were measured in 50 burrows, and the number of burrow entrances was a good predictor of the number of porcupines it contained ($r^2 = 0.76$). Occupied burrow density was estimated to be 2.6 burrows km^{-2} and porcupine density on the study farm was estimated to be 8 animals km^{-2}, which is high relative to other *Hystrix* populations in semi-arid environments. This can probably be attributed to the high abundance of geophytes in the region. Annually, porcupines disturb 0.34% of the soil surface and 1.6 $m^3 ha^{-1} yr^{-1}$ of soil is displaced across the landscape, through the excavation of 160–3463 diggings per hectare. Up to 2.2 m^3 of soil is displaced per hectare per year in the natural Dolerite Plains vegetation, but very little foraging activity occurs in previously or currently ploughed lands. The extent of disturbance in Nieuwoudtville is on a par with or higher than that recorded for other porcupine populations in arid or semi-arid regions. Other studies have shown that porcupine diggings disturb plant community structure and create fertile sites for plant germination and recruitment. Porcupine diggings in Nieuwoudtville contained significantly more seedlings than adjacent areas. Thus, through widespread foraging pits, soil turnover, and numerous burrows, porcupines modulate the availability of resources to

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other organisms. Therefore, Cape porcupines are likely to act as ecosystem engineers in this landscape. Porcupines should be included in any conservation actions involving the unique geophyte flora of Nieuwoudtville.
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Keywords: *Hystrix africaeaustralis*; Disturbance; Foraging diggings; Porcupine density; Ecosystem engineers; Geophytes; Burrows

1. Introduction

Cape porcupines (*Hystrix africaeaustralis*) are moderately large herbivores (12–24 kg) that are widely distributed throughout southern Africa. They consume a variety of subterranean and above-ground plant parts, including geophytes (perennial plants which resprout from underground storage organs), rootstocks and the stem tissue of trees (Skinner and Smithers, 1990), and have been shown to have important trophic effects in savannah woodland (Yeaton, 1988).

Porcupines may have differential effects on the mortality, dispersal, and recruitment of plants in their environment. Foraging can disperse vegetative propagules of plants such as geophytes (Gutterman, 1982; Lovegrove and Jarvis, 1986). Their diggings also create pits that capture water, organic matter and seeds (Gutterman and Herr, 1981; Dean and Milton, 1991), and provide sites for recruitment (Gutterman and Herr, 1981). The potential role that porcupines play in physically modifying ecosystems has been recognized in the Negev Desert of Israel, where Wilby et al. (2001) classified Indian crested porcupines (*Hystrix indica*) as ecosystem engineers. Ecosystem engineers are defined as ''organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain and/or create habitats'' (Jones et al., 1994, p. 373).

Evidence of foraging by porcupines is very conspicuous in parts of the Bokkeveld Plateau in the Northern Cape province of South Africa. The region has an exceptional diversity of geophytic plant species (309 species in a flora of ca. 1350 species) with high levels of endemism (23%) and threat (19% are listed on the IUCN Red List; Hilton-Taylor, 1996). Despite the obvious disturbance by porcupines, and their potential impact on geophyte diversity, the relationship between porcupines and plant diversity has not been studied. The area has also been substantially transformed by agricultural land use and it is not clear how different forms of land use have affected porcupine abundance and activity.

In this study, we investigated the abundance of Cape porcupines, and their effects on soil turnover on a farm near Nieuwoudtville on the Bokkeveld Plateau, which included a variety of land uses. The study was set up to test whether porcupine activity is higher than would be expected for a semi-arid region and to determine the level of disturbance associated with porcupine foraging in different parts of the landscape.

2. Methods and materials

2.1. Study site

The study was carried out on the farm Glenlyon (1623 ha), south of Nieuwoudtville (31°23′S and 19°07′E) in the Northern Cape Province of South Africa. The town is situated on the Bokkeveld Plateau, which straddles the boundary between the Cape Floristic Region and the Succulent Karoo Biome, both recognized centres of plant diversity (van Wyk and Smith, 2001). The Bokkeveld Plateau itself has a high plant diversity (ca. 1350 species) and high levels of endemism (6.5%) (van Wyk and Smith, 2001). Nieuwoudtville lies on the western margin of the plateau and is characterized by cold, wet winters and dry summers, with a mean annual rainfall of 350 mm and a CV of 33%. Plant biomass and flowering peaks in late winter and early spring (August–October), and many plant species become dormant during the dry season (November–March).

The Nieuwoudtville region is of special interest because of the marked variation in edaphic substrata. Table Mountain Sandstone (TMS) strata are exposed along the Bokkeveld escarpment in the west, but to the east dwyka sediments (tillite) and shales overlie the TMS. In the vicinity of Nieuwoudtville, a dolerite sill intrudes into the tillite sediments. The sill is visible as a rocky dolerite ridge, but the weathered dolerite has formed deep self-mulching vertisols on the moist east slopes of the ridge. This has resulted in parallel bands of TMS, dwyka tillite and dolerite substrata, which support characteristic vegetation and floras (Snijman and Perry, 1987). The dwyka tillite forms relatively hard, grey, clay soils that naturally support Renosterveld vegetation (with the attendant geophyte species) (Snijman and Perry, 1987). Renosterveld vegetation is a threatened vegetation type, with less than 2% remaining in South Africa (Kemper et al., 1999) and ca. 30% of the Renosterveld vegetation remains in the Nieuwoudtville region. Dolerite forms heavy, red, self-mulching clay soils, which, within the study area, have been less affected by cultivation.

There are five distinct landscape units of interest in the Nieuwoudtville region: Renosterveld fragments on tillite soils; Dolerite Plains (vertisol soils); the rocky Dolerite Ridge; Old Lands (fallow pastures) on tillite soil which were ploughed a minimum of 10 years ago and are now used as pasture for livestock; and Active Lands (tillite soil), which are currently cultivated.

2.2. Study animal

The Cape porcupine is a nocturnal, hystricomorph rodent, which occupies a broad range of natural, urbanized and agricultural ecosystems (Skinner and Smithers, 1990). Porcupines inhabit burrows, rock crevices or caves. They often excavate their own burrows but also modify aardvark (*Orycteropus afer*) burrows (Skinner and Smithers, 1990). Their burrows consist of prominent mounds and may have one to several entrances with distinct paths leading to them. Porcupines cause extensive damage to agricultural crops like maize and potatoes (de Graaff, 1981; Skinner and

Smithers, 1990) and are also considered pests due to the damage they cause to fences and plastic water pipes. Porcupines are also hunted for their meat but this study was conducted on a farm where no porcupine hunting is allowed.

2.3. Materials and methods

2.3.1. Porcupine abundance and burrow distribution

Porcupine burrows on the farm Glenlyon were located opportunistically during September 2000–September 2001, and systematically by traversing each paddock from October 2001–January 2002. The position of each burrow was recorded using handheld GPS and the number of entrances recorded. During January 2002, the number of porcupines was recorded for 50 burrows in order to estimate porcupine density. A 25 cm wide strip of white paper was pegged down at all the entrances of each burrow, and a band of coloured non-toxic powder paint was sprinkled in front of the paper (called the "paint-and-paper method" hereafter). Trial experiments showed that porcupines walking through the paint left clearly distinguishable pawprints making it possible to differentiate between pawprints left by porcupines and those of other animals, as well as between exit and entry pawprints. Pawprints from returning animals were ignored (entry as opposed to exit prints), so that individual porcupines were not counted twice. Claw-marks in the paper also made it easy to distinguish between exit and entry sets of prints even if the paint had worn off. If there was any uncertainty in estimating the number of resident porcupines, a video camera with a motion sensor and an infrared light was used to film the occupants overnight in conjunction with the paint-and-paper method.

Paper was set out during the late afternoon before the porcupines started foraging, and was collected at midnight, before the return of the porcupines from foraging. If no prints were evident the first night, the paper was left out for a further night in case porcupine activity had been curtailed due to disturbance to their burrows.

2.3.2. Disturbance by porcupines

In January 2001, 30 transects of 2 m × 50 m were laid out randomly in each of the five habitat types: Renosterveld, Old Lands, Active Lands, Dolerite Plains, and Dolerite Ridges. All porcupine diggings within these transects were identified. Porcupine diggings were distinguishable by their narrow ellipsoid shape and a mound of excavated soil on one side of the hole. Excavations made by all other species were ignored. Other animals within this landscape that make excavations are the aardvark (*Orycteropus afer*) and yellow mongoose (*Cynictis penicillata*). Aardvarks produce a differently shaped excavation with clear, large claw marks. Yellow mongooses make very small holes (less than 3 cm wide).

Diggings were classified as one of two states: "recent" (since the last rains), or "old" (prior to the last rains and highly eroded but still a clearly defined digging), depending on the 'freshness' and conglomeration extent of the soil excavated by the porcupine. If the soil was hard and coagulated, the digging was classified as "old". If the soil was fine and the particles relatively separated, it was classified as "recent". It

is reasonably easy to distinguish between diggings created before and after the major rains, but to be precise, only freshly made diggings were classified as "recent".

Diggings were counted, and the depth, shortest width and longest width measured to determine the volume of earth removed. The formula for half of an ellipsoid cylinder, (i.e. $v = \frac{2}{3}\pi abc$, where $a =$ longest width/2; $b =$ shortest width/2; and $c =$ depth), was used to approximate the natural shape of a porcupine digging. Within the Dolerite Ridges there were areas of churned over soil, which were not measurable using the above formula. Instead a grid was laid over these areas and the average depth per $0.04\,m^2$ quadrat measured and multiplied by the length and breadth. These churned over areas were not used in the digging statistics involving density estimates.

Habitat utilization by porcupines was estimated by comparing the number of diggings between different parts of the landscape. It was first necessary to compare the rate at which diggings fill up within each habitat type. Thirty artificial diggings were made in each habitat type and the rate of filling by soil and organic litter was measured at irregular intervals over a year. A final measurement was done almost 2 years after the diggings had been made. The artificial diggings were excavated to approximate the shape of natural porcupine diggings. The excavated soil was left next to the digging, as occurs naturally. The volume of artificial diggings was calculated in the same way as for the natural diggings (see above). Regression analysis was used to determine the best-fit relationship between volume and time. Life-spans for the artificial diggings in each habitat type were estimated from the 95% asymptote of the equations describing the change in proportion filled of diggings over time. Artificial diggings were assumed to be filled in, or inconspicuous in the landscape, at 95% of their original volume.

There was a significant logarithmic relationship between the filling-in rate for artificial diggings and the time since the digging was made. This meant that the life-span of a porcupine digging could not be calculated by multiplying the initial volume of a digging by the average filling rate. As the filling rates change over time and the holes fill in slower as they become smaller, using the average filling in rate would yield unrealistically truncated life-spans. Filling-in rates were therefore calculated independently for intervals between monitoring sessions (change in volume over the interval period). The initial (measured) volume of each digging was multiplied by the first monitoring session's filling-in rate, for the duration of that monitoring session, whereupon the second monitoring session's rate was used, and so forth until it filled up completely. This method resulted in a distribution of life-spans for each habitat type, which could be compared using non-parametric Kruskal–Wallis ANOVA and multiple comparisons tests (Zar, 1984).

Because life-spans differed significantly between habitat types, digging densities were adjusted for differences in longevity. Comparisons were based on numbers of recent diggings per hectare per day (DHD) for each habitat type, calculated as the density of all recent diggings per hectare divided by the average life-span. Mean DHDs were calculated for each transect within a habitat type and compared across habitat types (using Kruskal–Wallis ANOVA and multiple comparisons tests). The overall extent of each habitat type on the farm was calculated in ArcView GIS v. 3.1

(Environmental Research Institute, Inc.) from a scanned and geo-registered aerial photograph of the Nieuwoudtville region (obtained from the South African Department of Land Affairs). Indications of habitat use are only relevant to Glenlyon within one season and do not necessarily apply universally to these substrata.

Measuring the volume of diggings and the total area that was disturbed also serves as a surrogate measure for a possible ecological service provided by porcupines—soil turnover. The annual rate of soil displacement by porcupines was calculated for each habitat type as the number of diggings made per hectare per day (DHD) multiplied by the mean volume of recent diggings per habitat type. This figure was extrapolated to obtain an estimate of disturbance levels for the entire area of habitat type. The annual soil turnover rate is based on the assumption that the numbers of diggings made per habitat type per day remains constant throughout the year, i.e. that there are no seasonal effects. Surface area of diggings was estimated for the surface area of an ellipse, πab (where a and b are half the shortest width and longest width, respectively). Disturbance within each habitat type was calculated as the DHD multiplied by the mean of surface area of all the recent diggings.

2.3.3. *Seedling germination within and outside porcupine diggings*

To assess whether porcupine diggings act as germination and recruitment sites, a preliminary comparison was made of seedling numbers within pits and in undisturbed soil in Renosterveld vegetation. Porcupine diggings were randomly selected, but freshly made diggings were excluded as not enough time had passed for seeds and organic matter to accumulate in the pits. All plant seedlings were counted in the digging and in a nearby, undisturbed area in the soil matrix of similar size and shape.

Statistical analysis was done using UNISTAT v. 5 (UNISTAT Ltd.) and $p<0.05$ was the designated level of significance. Data are presented as mean ± 1 SE, unless otherwise indicated.

3. Results

3.1. *Porcupine abundance and burrow distribution*

There were 64 potentially active burrows on Glenlyon at the time of the study. Of these, 33 were occupied, 17 unoccupied, and 14 were not evaluated using the paint-and-paper method. Assuming the same proportion of occupied burrows (66%) in the untested sample gives a total of 42 occupied burrows on the entire farm (1623 ha) or 2.6 burrows km^{-2}. There were at least 30 additional collapsed burrows, but these were not included in the study. Most burrows occurred in Dolerite Plains (69%), with 20% in Dolerite Ridges and 9% in Renosterveld on tillite soil (Table 1). Only one burrow occurred in Old Lands and no burrows were found in the small area of Active Lands (42 ha).

Occupied burrows supported 102 porcupines, at an average of 3 ± 2.3 porcupines per burrow ($n = 33$) (Table 1). The numbers of porcupines in the 14 burrows that were not evaluated using the paint-and-paper method were estimated from the number of burrow entrances. However, as the number of entrances differed between habitat types (Bragg et al., unpublished data), the regression for entrances and number of porcupines was calculated for each habitat type separately. There were eight untested burrows within the Dolerite Plains, and these were estimated to contain 17 porcupines, (95% CI: 16–24), using the regression equation (Fig. 1).

Table 1
Number and distribution of porcupine burrows, and mean number of porcupines per burrow on Glenlyon farm

Habitat	Number of burrows					Mean ± SD number of porcupines per burrow (*n*)
	Area (ha)	Occupied	Unoccupied	Of unknown occupancy	Total	
Dolerite Plains	1011	24	12	8	44	3.5 ± 2.5 (24)
Dolerite Ridges	88	5	3	5	13	2 ± 1.2 (5)
Renosterveld (tillite)	206	3	2	1	6	1 ± 0 (3)
Old Lands (tillite)	276	1	0	0	1	5 (1)
Active Lands (tillite)	42	0	0	0	0	0
Total	1623	33	17	14	64	3 ± 2.3 (33)

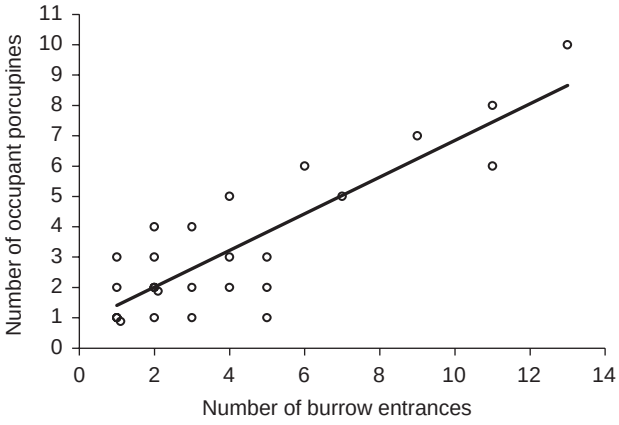


Fig. 1. Regression of porcupine numbers against number of burrow entrances on Dolerite Plains habitat type on Glenlyon farm ($y = 0.604x + 0.807$; $r^2 = 0.72$; $n = 24$; $p < 0.001$). Unoccupied burrows were excluded. Clustered circles represent more than one data point.

There were too few burrows to establish a significant correlation between entrance numbers and porcupines in Dolerite Ridges and Renosterveld so the average number of porcupines per burrow was used instead. The untested Renosterveld burrow was estimated to contain one porcupine, and the Dolerite Ridges burrows, 10 porcupines. This results in a conservative total of 130 porcupines in the area (1623 ha), at a density of 0.08 porcupines ha^{-1} (8 porcupines km^{-2}) or 12.5 ha per porcupine.

3.2. Disturbance by porcupines

3.2.1. Artificial diggings

After 663 days of monitoring, 58% of artificial diggings had filled up and 19% of the diggings were less than 3 cm deep. The filling up rate slowed down as the holes became shallower, possibly due to less erosion as the sides of the hole became worn down or a lower likelihood of trapping organic matter. A logarithmic relationship best described the relationship between volume and time, (Table 2), and depth and time, in all habitat types. Diggings in tillite (Renosterveld and Active Lands) filled up more slowly than those in the Dolerite Plains and Dolerite Ridges (Table 2). Diggings in Old Lands filled in relatively quickly (Table 2), which was unexpected as the soil is hard tillite. However, these lands were generally clear of all shrubs or other vegetation that might trap litter and windblown matter, making it likely that litter quickly fills up these holes. The soil of the Dolerite Plains is very soft and self-mulching and it is expected that it would fill up more quickly than the hard tillite clay soil. Dolerite Ridges have a sandy dolerite soil of intermediate hardness, and diggings filled in more slowly than those on Dolerite Plains, but faster than those on tillite soils.

3.2.2. Porcupine diggings

There were no significant differences between the mean volume and depth of diggings between habitat types, but there was wide variation within habitats (Table 3). There was also a large amount of spatial variation in the number of

Table 2
Regression parameters relating volume of the artificial diggings to time, per habitat type

Habitat type	Regression parameters		r^2	p	Life-span in days (upper and lower 95% CI)
	a	b			
Dolerite Ridges	−476.7	2908.7	0.69	<0.001	350 (198–667)
Renosterveld (tillite)	−329	2441.1	0.68	<0.001	1140 (562–2551)
Old Lands (tillite)	−523.6	3441.6	0.71	<0.001	512 (295–945)
Active Lands (tillite)	−451.3	3135.8	0.79	<0.001	766 (414–1529)
Dolerite Plains	−547.3	3261.8	0.67	<0.001	306 (155–668)

Each regression is expressed in the form: $y = a\ln(x) + b$, where x is time in days and y is volume in cm^3. Life-span is calculated as the time to reach the 95% full asymptote from the relationship between time and proportion filled for all the artificial diggings.

Table 3
Mean digging volume, projected life-span, digging density and digging numbers $day^{-1} ha^{-1}$ (DHD) for four different habitat types on Glenlyon farm, Nieuwoudtville

Habitat type	Mean volume ± SE (cm^3) (*n*)	Mean life-span ± SE (days) (*n*)	Mean digging density ± SD (no. ha^{-1})(*n*)	Mean digging no. $ha^{-1} day^{-1}$ (DHD) ± SE (*n*)
Renosterveld	491 ± 56 (28)a	854 ± 61 (28)a	1453 ± 339 (30)a	1.6 ± 0.3 (30)a
Dolerite Plains	428 ± 62 (30)a	319 ± 67 (30)b	2110 ± 392 (30)a	14 ± 3 (30)b
Dolerite Ridges	352 ± 43 (26)a	519 ± 99 (26)c	3463 ± 917 (30)a	16 ± 5 (30)c
Old Lands (Tillite)	645 ± 221 (9)a	794 ± 272 (9)ac	160 ± 61 (30)b	0.7 ± 0.4 (30)d

The sample size for the Active Lands habitat type was too small for inclusion in the analysis. "*n*" refers to the number of transects per habitat. Different letters in italics indicate significant differences between habitat types from Kruskal–Wallis ANOVA.

digging within and between habitat types. Within 30 transects on Dolerite Ridges, for example, recent diggings ranged from 0 to 220 per transect, or 0 to 2.2 diggings m^{-2} (mean of 34.6 ± 9.2 diggings $100 m^{-2}$, $n = 30$). If old and churned diggings were included, accumulated digging densities averaged 42.4 ± 10.2 $100 m^{-2}$ ($n = 30$). Active Lands, on the other hand, had only 2 diggings in a total of 30 transects, indicating very little porcupine activity.

There was a significant difference in the accumulated density of recent diggings per hectare between habitat types (Kruskal–Wallis ANOVA, $\chi^2 = 46.67$, d.f. = 3, $p < 0.001$), with Old Lands having the lowest densities and Dolerite Ridges the highest (Table 3). However, the mean life-span of diggings also varied between habitat types (Kruskal–Wallis ANOVA, $\chi^2 = 31.92$, d.f. = 3, $p < 0.001$, Table 3). As artificial diggings in tillite fill up more slowly than on dolerite, it is not surprising that diggings in Renosterveld had the longest mean life-span, which was significantly different from the shortest mean life-span recorded for diggings on Dolerite Plains.

Activity within a particular habitat type was based on the density of diggings per hectare integrated with data on the life-span of diggings, defined as the turnover of diggings per hectare per day (DHD). This implicitly takes into account the age of the diggings. There was a significant difference in DHD between habitat types (Kruskal–Wallis ANOVA, $\chi^2 = 58.96$, d.f. = 3, $p < 0.0001$, Table 3). Old Lands and Renosterveld had the lowest DHDs, whereas the porcupines were obviously more active in the Dolerite Ridges and Plains, which had DHD values of 14 and upwards.

3.2.3. Soil turnover

We estimated that porcupines annually displaced a total of $1.6 m^3$ of soil ha^{-1} (Table 4). The greatest disturbance took place in the Dolerite Plains ($2.2 m^3 ha^{-1} yr^{-1}$) and Dolerite Ridges ($2.1 m^3 ha^{-1} yr^{-1}$) (Table 4). The Old Lands had very few diggings but the volumes of the individual diggings on these lands

Table 4
Estimated volume of soil displaced from porcupine diggings and surface area disturbed per habitat type on Glenlyon Farm, Nieuwoudtville

Habitat type	Area (ha)	Mean volume turnover ± SE ($m^3 ha^{-1} yr^{-1}$)	Mean surface area disturbed ± SE ($m^2 ha^{-1} yr^{-1}$)	Percentage surface area disturbed (% yr^{-1})
Renosterveld (tillite)	206	0.3 ± 0.03 (28)	6 ± 0.5 (28)	0.06
Old Lands (tillite)	276	0.2 ± 0.05 (9)	3 ± 0.8 (9)	0.03
Dolerite Plains	1011	2.2 ± 0.3 (30)	47 ± 3 (30)	0.47
Dolerite Ridges	85	2.1 ± 0.3 (26)	52 ± 3 (26)	0.52
Landscape	1578	1.6	34	0.34

Sample size is in parentheses. Active Lands habitat type was excluded because of its small sample size.

were larger than those in other habitat types, so that total soil turnover was remarkably high.

We estimated that 0.34% of the total surface area of the study site is disturbed per year by porcupines (Table 4). Of all the habitats, Dolerite Ridges has the most disturbance ($52 \pm 3\ m^2 ha^{-1} yr^{-1}$) (Table 4), even though this estimate did not include the accumulated densities of churned over soil ($27.6 \pm 92.1\ m^2$ (mean ± 1 SD) per hectare, $n = 30$).

3.2.4. *Germination in porcupine diggings*

A Wilcoxon-matched pairs test showed that there were significantly more seedlings in porcupine diggings, (15.8 ± 14.9 (1 SD)), than in the soil matrix (10.3 ± 8.1 (1 SD); $z = 3.08$, $p < 0.002$, $n = 30$).

4. Discussion

Porcupine density on Glenlyon (2.6 occupied burrows km^{-2} and 8 individuals km^{-2}) is consistent with expectations of high abundance considering the high densities of diggings in the landscape and other circumstantial evidence of their presence (many quills, faeces and burrows). However, in the relatively few published accounts of porcupine densities, the general trend appears to be towards lower densities in arid/semi-arid areas and higher densities in more mesic environments. For example, in the Negev desert, Indian crested porcupines occurred at densities of 2.1 animals km^{-2} (Alkon, 1999) and 4 animals km^{-2} on the coastal plains of Israel (Server and Mendelssohn, 1991), whereas in a deciduous forest in western India with a relatively high mean annual rainfall of 650 mm, porcupines reached densities of 12 animals km^{-2} (Sharwa, 2001). Similarly, in areas with high food availability, there tend to be higher densities of porcupines (e.g. 7.5 animals km^{-2} estimated for Indian crested porcupines utilizing potato crops; Alkon, 1999). Given the relatively low annual rainfall at the Nieuwoudtville study site (350 mm p.a.), porcupine densities

would be expected to fall within the lower end of the spectrum. The higher than expected densities that were observed at Nieuwoudtville may therefore be due to the unusually high density of geophytes (up to 400 geophytes m^{-2}, S. Todd, unpublished data), which are one of the main sources of food for porcupines.

It is likely that the density of porcupines is even higher than estimated, as the paint-and-paper method would underestimate the actual number of porcupines. This is because, firstly, suckling offspring might not exit the burrow; several burrows might have been missed in the survey; and the process of laying out the paint and paper could disrupt porcupine activity. An overestimate could possibly be obtained if porcupines used multiple burrows but during more than 2 months of radio-tracking exercises and 3 months of habituation attempts (involving close observations of a several porcupine family units in different burrows), no incidents of multi-burrow use were observed.

Burrows in arid regions alter biotic and abiotic elements of the ecosystem through causing major geomorphic changes to the landscape structure, affecting plant diversity and succession, and influencing soil nutrient cycles (Kinlaw, 1999). Burrows have also been shown to provide shelter not only for the builders but also for many other co-habiting species (Kinlaw, 1999). In Nieuwoudtville one of us (CJB) observed four other rodents (*Mystromys albicaudatus*, *Mus minutoides*, *Tatera afra*, and another unidentified gerbil species) occupying a multi-entrance porcupine burrow. Ant-eating chats (*Myrmecocichla formicivora*), spiders, bat-eared foxes (*Otocyon megalotis*), striped pole-cats (*Ictonyx striatus* Perry), and colonies of bees also inhabit new and collapsed Cape porcupine burrows at the study site (pers. obs.). Porcupine burrows therefore alter the landscape and provide a source of refuge for other species.

Comparisons with other disturbance studies show that the mean accumulated digging density on Glenlyon (160–3500 diggings ha^{-1}) far exceeds that made by the Cape porcupine in a savannah ecosystem (19–52.7 diggings ha^{-1}) (de Villiers and van Aarde, 1994), possibly because of the greater abundance of geophytes in the study area. In the Negev Desert, Indian crested porcupine accumulated digging densities ranged from 1300 to 10 300 diggings ha^{-1} on the Sede Zin plateau (Alkon and Olsvig-Whittaker, 1989), and 100–1700 diggings ha^{-1} in the northern Negev (Yair and Rutin, 1981). Accumulated digging densities in Nieuwoudtville reached up to 22 700 diggings ha^{-1} in transects in the Dolerite Ridges, including old and churned diggings. However, the mean digging density across all sites in Alkon and Olsvig-Whittaker's plots (1989) was higher (0.5 digs m^{-2}) than in this study (0.1 digs m^{-2}), probably because this study was not based on selected plots but used transects to assess levels of disturbance across the landscape. Additionally, this study was conducted in the dry summer season, and digging densities might be higher in the growing season (winter/spring) when food resources are more abundant. Gutterman (1982) described Indian crested porcupine digging densities of up to 3 diggings m^{-2} in some Negev highland areas, but in Nieuwoudtville, in patches of the geophyte *Sparaxis pillansii*, porcupines disturb areas of more than 7 m^2 in extent.

Digging dynamics differed considerably between habitat types. Active Lands had no burrows or foraging diggings, probably because of the lack of geophytes in the

ploughed soils, the high levels of human disturbance, and the lack of cover. Taking area and filling-in life-spans of diggings in the different substrata into account, porcupines are most active in Dolerite Ridges and Plains during summer. Dolerite Ridges are very rocky and hilly and probably provide cover when foraging. These are areas of high geophyte availability, but Renosterveld also offers abundant and diverse geophyte species (S. Todd, unpublished data). We propose that habitat preferences change seasonally: porcupines probably utilize the Renosterveld habitat type during the rainy season when the soil becomes soft and waterlogged, and less energy is required to dig out food plants. Jarvis et al. (1998) observed that mole-rats, (fossorial hystricomorphs that also feed on geophytes), mobilize a work force rapidly after rainfall, when the soil is moist and easy to work.

The role of porcupines as biotic agents of disturbance is emphasized by the large volumes of soil displaced in digging activities (0.2–2.2 $m^3 ha^{-1} yr^{-1}$). The maximum volume displaced by Indian crested porcupines in the Negev was 3.5 $m^3 ha^{-1} yr^{-1}$ (Alkon and Olsvig-Whittaker, 1989), which is higher than that recorded in Nieuwoudtville, though a different equation was used to calculate soil displacement. Using their equation for half an ellipsoid gives greater volumes for the same sized diggings than the equation used in this study, (depth and shortest width were not assumed to be the same), and would result in extrapolated figures of 5.3 $m^3 ha^{-1} yr^{-1}$ of soil being displaced in the Dolerite Plains.

The widespread disturbance caused by porcupines is expected to have important ecological effects. Disturbance is not only important for soil processes but also plays a role in the dynamics of plant populations. Disturbance by gophers has been shown to kill existing vegetation at the foraging site and create sites for colonization by competitively inferior plant species (Martinsen et al., 1990). Disturbance also aids regeneration of geophytes with asexual reproductive features such as cormlets and bulbils (Lovegrove and Jarvis, 1986).

Other than aiding soil turnover and disturbance-adapted recruitment, porcupine diggings function as potential sites for plant germination (Gutterman and Herr, 1981; Dean and Milton, 1991). Diggings disrupt existing vegetation and/or soil structure and are richer in resources than the surrounding area (Boeken et al., 1995), as they collect water, organic matter, seeds and soil (Yair and Shachak, 1982; Dean and Milton, 1991). The rate of water infiltration in porcupine diggings in Nieuwoudtville was twice as high as on undisturbed areas (P. O'Farrell, unpublished data). Boeken et al. (1995) recorded higher density, biomass and species richness in porcupine diggings in the Negev than in the soil matrix. In Nieuwoudtville, there is evidence that seed germination is higher in the porcupine diggings. Porcupine diggings can therefore serve as an important resource for plant recruitment, productivity and diversity.

Our results show that porcupines are important biotic agents of disturbance in the Nieuwoudtville landscape. Porcupine-driven disturbance is pervasive and equals or exceeds levels of disturbance in other semi-arid regions where porcupines are considered to be ecosystem engineers (Jones et al., 1994; Wilby et al., 2001). Other organisms, which typically contribute to soil disturbance in South Africa, such as mole-rats (Bathyergidae species) and aardvark (*Orycteropus afer*), are scarce or

limited in distribution in the Nieuwoudtville area (pers. obs.). Porcupines are the main species that contribute significantly to soil turnover and landscape heterogeneity.

Jones et al. (1994) state that the biggest effects of ecosystem engineers are caused by those species living at high densities, over large areas for a long time, and which give rise to structures that persist for millennia and modulate resource flows. Porcupines come closest of all the species in the Nieuwoudtville region to fulfilling these conditions. In other semi-arid regions, pocket gophers, kangaroo rats and prairie dogs impact on ecosystem function and heterogeneity through their burrowing and foraging activities (Huntly and Inouye, 1988; Ceballos et al., 1999; Schooley et al., 2000). Banner-tailed kangaroo rats (*Dipodomys spectabilis*) and plateau zokors (*Myospalax fontanierii*) have been classified as ecosystem engineers through the effects of their widespread soil disturbance (Schooley et al., 2000; Zhang et al., 2003).

Considering the high density of porcupines, the wide distribution of their burrows and the extent of their diggings, porcupines appear to significantly alter the structure of the Nieuwoudtville environment. Although their impact on resource flows has not been studied in detail, it is difficult to avoid the conclusion that porcupines are the key engineers in this landscape. It is therefore important to consider porcupines in conservation actions aimed at maintaining the unique geophyte flora of the region. Porcupine disturbance promotes seedling recruitment, increases soil turnover and alters the disturbance regime. Bragg et al. (2003, unpublished data) have shown that porcupines also have important trophic effects on the geophyte flora in this region. Porcupines selectively feed on certain geophyte species, including endangered and endemic species, and change plant distribution and possibly abundance in the landscape (Bragg et al., 2003, unpublished data). Thus, although porcupines are considered agricultural pests and frequently hunted, conservationists need to be aware of their ecological importance in natural vegetation dynamics.

Research into the engineering and trophic impacts of the Cape porcupine in Nieuwoudtville is currently taking place through long-term exclusion experiments in order to assess how porcupine foraging activities affect plant community structure and to further quantify the impacts of this ubiquitous herbivore in the ecosystem.

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