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We investigated the relations between environmental features (biotic and abiotic) and small mammal communities in the Groendal Wilderness Area, South Africa. Habitat architecture (expressed as both horizontal and vertical foliage density) and total plant canopy cover (especially shrub canopy cover) are the most important correlates of small mammal community structure at this site. The mechanisms for these relationships are complex, probably involving physiological, social and anti-predator effects as well as reflecting nutritional resources. Furthermore, man and fire influence small mammal community structure. These effects are as a result of altered plant community composition and structure by plantation and pasture establishment and burning. In order to maintain a diversity of small mammal communities, management should ensure a mosaic of diverse vegetation communities.

Keywords: rodents, shrews, community structure, fire, management.

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Introduction

Small mammals are generally overlooked in both the planning and management of conservation areas, largely due to the difficulty in censusing this group. A number of studies have demonstrated that small mammal community structure is a function of plant architecture (Rosenzweig & Winakur 1969; Bond, Ferguson & Forsyth 1980; Kerley 1992). An understanding of how these small mammals relate to environmental features should therefore be of use to managers who could manage small mammal communities indirectly through the management of habitat features. The False Sclerophyllous vegetation type (fynbos or macchia - Acocks 1975) is subject to regular perturbations in the form of frequent natural and anthropogenic fires (Manry & Knight 1986) as well as other

anthropogenic disturbances in the form of establishment of pastures and plantation. Fynbos vegetation is therefore highly dynamic in terms of plant species composition and architecture, with similar variability in terms of the small mammal community in this biome (e.g. Willan & Bigalke 1982).

This study examines the relationships between abiotic and biotic habitat variables and small mammal community structure in the Fynbos vegetation of the Groendal Wilderness Area in the Eastern Cape, South Africa. Based on the above studies we hypothesised that small mammal diversity would be related to both horizontal and vertical foliage density at intermediate heights above the ground. We also tested the hypothesis that man and fire, in changing the habit

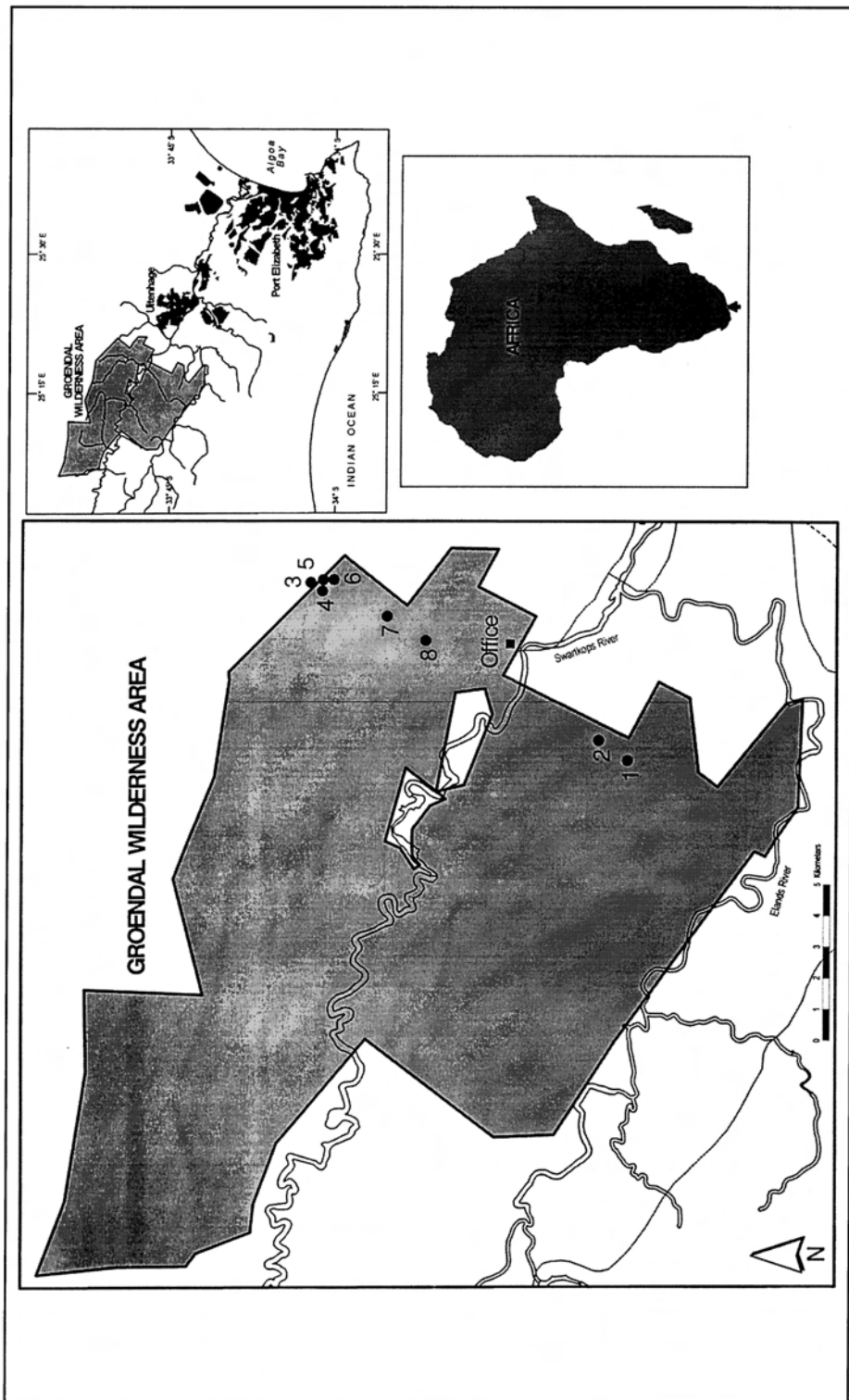


Fig. 1: The Groendal Wilderness Area in the Eastern Cape, South Africa, with the location of the specific study sites within the Groendal Wilderness Area (see Table 1 for the characteristics of the sites).

structure through disturbance, alter small mammal community structure.

Study area

The Groendal Wilderness Area (21 793 ha), managed by Eastern Cape Nature Conservation, is situated between 33°37'S–33°49'S and 25°08'E–25°22'E, approximately 13 km northwest of Uitenhage in the Eastern Cape, South Africa (Fig. 1).

The climate is temperate and typically continental thermal conditions prevail, with marked diurnal and seasonal extremes. Precipitation (mean = 750 mm p.a.) occurs throughout the year, although there is a tendency towards wetter spring and autumn months. Precipitation generally increases with altitude, whilst due to the rain-shadow effect, north-facing slopes receive substantially less rain than south-facing slopes. Rare snowfalls are limited to the higher peaks (> 1 000 m a.s.l.).

The rugged topography drops from the Groot Winterhoek Mountains (1180 m a.s.l.) in the north, to the valley of the Kwa-Zungha/Swartkops River. Soils, derived from the quartzitic rocks of the Cape Fold Belt, tend to be poor in bases and nutrients.

The False Sclerophyllous Bush vegetation type predominates on the nutrient-poor soils and is characterised by the presence of a restionoid element (Restionaceae), low evergreen ericoid shrubs and taller broad sclerophyllous proteoid shrubs. The Karroid vegetation type (Acocks 1975) is found on the more arid north slopes, with Coastal Tropical Forest (Acocks 1975) restricted to the valleys.

The fynbos in the Groendal Wilderness Area is largely made up of one of the fynbos sub-groups termed Short Fynbos (Campbell 1985). This is characterised by the presence of *Leucospermum cuneiforme* and

Leucadendron salignum, and to a lesser degree, *Protea foliosa*. Basal cover tends to be dominated by grasses (largely *Themeda triandra*) rather than restios. Campbell (1985) subdivides this fynbos type into Dry Grassy Fynbos (annual rainfall < 700 mm) and Mesic Grassy Fynbos (annual rainfall 700–900 mm).

Methods

Small mammal communities were sampled between 18 December 1989 and 6 January 1990 to minimise temporal variation of small mammal populations and facilitate comparisons. The habitat variables (biotic and abiotic) were measured during the same period.

Study sites

Eight sites were sampled for small mammal communities (Table 1).

Table 1
Location and characteristics of the study sites and their respective vegetation types after (Campbell 1985)

Site	Location	Altitude (m)	Aspect	Vegetation type
1	33°45'10"S 25°16'4"E	430	NE	Dry Grassy Fynbos
2	33°44'40"S 25°17'05"E	480	N	Dry Grassy Fynbos burnt 10/89
3	33°39'50"S 25°20'15"E	580	SE	Pasture private farm
4	33°40'05"S 25°20'20"E	580	SW	Mesic Grassy Fynbos burnt 04/89
5	33°40'05"S 25°20'25"E	580	SW	Mesic Grassy Fynbos
6	33°40'10"S 25°20'25"E	580	S	Plantation - experimental
7	33°41'00"S 25°19'40"E	520	SW	Vaalvlei Mesic Grassy Fynbos
8	33°41'40"S 25°19'10"E	480	S	Mesotrophic Proteoid Fynbos

Sites 1–7 are representative of Short Fynbos, whilst site 8 is an example of High Fynbos (Campbell 1985). Sites 2 and 4 had been naturally burnt two

and eight months prior to the study, respectively. Sites 3 and 6 (both originally the same vegetation type as site 5) had been anthropogenically transformed to pasture and *Eucalyptus/Acacia* plantation, respectively.

Small mammal assemblages

Small mammals were trapped with Museum Special snap-traps, baited with peanut butter and rolled oats. For each sampling session at each locality 50 traps were set 10 m apart, on marked 5 x 10 grids. Two grids (100 m apart) were used per site, with the traps set for four consecutive nights for a total of 2 x 200 trapnights/site. Traps were checked at dawn and dusk, and rebaited if necessary. Captured animals were identified, measured, weighed and sexed according to De Graaff (1981) and Smithers (1983). Classification follows Meester *et al.* (1986). Small mammal species diversity was estimated as the Shannon-Wiener information theory index and the relative abundance or evenness of the component species was determined as the equitability index (Pielou 1975). Total biomass was used as the measure of the standing stock of small mammals at each site.

Environmental features

The following parameters were measured within the grids at each locality, sampling points being selected randomly.

- Horizontal foliage density was estimated following Bond *et al.* (1981), at heights of 10, 20, 40, 60, 100 and 150 cm using a marked board. For the height classes up to 200, 300, 500 and 1000 cm, the horizontal foliage density was visually estimated, except for site 6 (plantation) where it was measured. At each site horizontal foliage density was measured along the four cardinal directions at ten points. Vertical foliage diversity was calculated for the height classes between 20 and 200 cm (V1) and between 20 and 1000 cm (V2) following Rosenzweig & Winakur (1969).
- Canopy cover of plants intercepting a tape were recorded to the nearest cm, over five 30 m lines at each site (Mueller-Dombois & Ellenberg 1974). The cover for each plant growth form (tree, shrub, herb, grass and restio) encountered was calculated, as was the total plant cover.
- Basal cover (soil surface features) was estimated

using a descending point technique (Mueller-Dombois & Ellenberg 1974) with points at 10 cm intervals along two 30 m lines of tape per site. Features recorded were basal cover for each plant growth form (tree, shrub, herb, grass and restio), cover of plant litter and cover of rocks in different size classes (diameters of 1 cm, 2 cm, 3-5 cm, 5-10 cm, 10-25 cm, and bedrock). Total basal plant cover was calculated.

- Soil depth was determined by hammering a pointed steel rod, 1.6 cm in diameter, into the ground until it could penetrate no further (Rosenzweig & Winakur 1969). The mean of five readings per site was used. Soil characteristics were determined from a pooled sample of ten soil scrapes, 5 cm deep, from each site. Sieving as well as a sediment settling tube (Carver 1971) were used to obtain grain size parameters.

Small mammal communities - habitat relations

Correlation analyses were used to investigate relations between small mammal community characteristics and environmental features. The 95 % level ($P < 0.05$) was regarded as statistically significant for all tests (Zar 1984), whilst for all correlations $df = 6$.

Results

Relatively few small mammals were caught and trap success averaged 2.4 % (range 0 - 5.5 %, Table 2). Captures for the replicate trapping grids at each site were therefore pooled for analysis. Five rodent and two insectivore species were captured with rodents dominating the catch at all sites, except for Site 1, where shrews dominated the catch in terms of both numbers and biomass (Table 2). Biomass averaged 454.5 g (range 0 - 1438 g, Table 2). An average of 2.3 ± 1.2 species of small mammals were captured at each site.

Grasses were the dominant growth form, contributing the most to the plant canopy cover (Table 3), except for at site 6, the plantation, where trees dominated. Vegetation tended to be dense close to the ground,

Table 2
Community composition and characteristics for small mammal communities
sampled at each site

Species	Sites							
	1	2	3	4	5	6	7	8
Order Rodentia								
<i>Aethomys namaquensis</i>	0	0	1	0	0	0	0	0
<i>Otomys irroratus</i>	0	0	0	2	4	0	5	12
<i>Rhabdomys pumilio</i>	1	0	0	6	4	0	6	7
<i>Saccostomus campestris</i>	0	0	1	0	0	0	0	0
<i>Grammomys dolichurus</i>	0	0	0	0	0	1	0	0
Rodent captures	1	0	2	8	8	1	11	19
Rodent biomass (g)	65	0	70	370	641	27	694	1407
Order Insectivora								
<i>Crocidura flavescens</i>	2	0	0	0	1	0	0	1
<i>Myosorex varius</i>	11	0	0	0	0	0	11	1
Shrew captures	13	0	0	0	1	0	11	2
Shrew biomass (g)	187	0	0	0	25	0	119	31
Small mammal								
Captures	14	0	2	8	9	1	22	21
Biomass (g)	252	0	70	371	665	27	813	1438
Species richness S	3	0	2	2	3	1	3	4
Diversity H'	0.66	0	0.69	0.56	0.97	0	0.04	0.98
Evenness J'	0.6	0	1	0.81	0.88	0	0.95	0.7

becoming more open above about 40 cm (vide foliage profiles in Table 3).

Intercorrelations of environmental features

V1 and V2 were positively correlated ($r = 0.998$; $P < 0.05$). Total plant canopy cover was correlated with horizontal foliage density between 10-20 cm ($r = 0.811$; $P < 0.05$) and between 20-40 cm above the ground ($r = 0.860$; $P < 0.05$), whilst the horizontal foliage density between 40-60 cm above the ground, was correlated with basal rock ($r = 0.804$; $P < 0.05$) and the cover of small surface stones of 1 cm diameter ($r = 0.867$; $P < 0.05$).

Small mammal communities - Environmental features

Both measures of small mammal species diversity, H' and S, were positively correlated with plant canopy cover and horizontal foliage diversity between 20 - 40 cm (Table 4). The measure of evenness of the community, J', correlated with none of the environmental factors. Although there are a number of the small mammal community, habitat relations that were negatively correlated, none were statistically significant. There were also no significant relations found between small mammal community structure and soil parameters. Biomass of small

Table 3
Community and environmental features of the study sites. See text for details of measurements and analyses

Site attributes	Sites							
	1	2	3	4	5	6	7	8
Total Canopy Cover (%)	100	68.8	86.4	74	97.5	79.9	97.9	96.5
Tree (%)	0	0	0	0	0	99.9	0	0
Shrub (%)	18	5	0	29	15.1	0	41.3	70
Herb (%)	22.3	10	63.1	9	6.2	0.1	8.7	3.3
Grass (%)	57.3	85	36.9	60.9	76.8	0	46.3	23.6
Restio (%)	2	0	0	1.1	1.9	0	3.7	3.1
Total Basal Cover (%)	88.3	23.8	23.3	13.7	81.5	100	80.2	58.3
Plant Litter (%)	77.2	39.8	3.6	21.9	81.8	95.3	78	53.7
Rock, 1cm (%)	0	0	0	0	0	0	0	2
Rock, 2cm (%)	0	3.5	0	0	0.4	0	0.6	6.6
Rock, 3-5cm (%)	0	2.1	0	0	0	0	0.6	5.7
Rock, 5-10cm (%)	0	4.2	0	0	0	0	0	2.3
Rock, 10-25cm (%)	0	4.2	1.4	0	0	0	0.6	2.3
Foliage Profiles								
F0-10	5.63	0.42	1.16	0.61	1.98	2.54	1.61	1.07
F10-20	0.74	0.06	0.18	0.24	0.4	0.05	0.46	0.34
F20-40	0.28	0.1	0.04	0.09	0.18	0.06	0.23	0.32
F40-60	0.6	0	0	0.01	0.02	0.04	0.11	0.22
F60-100	0.02	0	0	0	0.01	0.07	0.29	0.24
F100-150	0.01	0.01	0.01	0.01	0.01	0.09	0.01	0.07
F150-200	0.01	0.01	0.01	0.01	0.01	0.09	0.01	0.01
F200-300	0.01	0.01	0.01	0.01	0.01	0.21	0.01	0.01
F300-500	0.02	0.02	0.02	0.02	0.02	0.48	0.02	0.02
F500-1000	0.05	0.05	0.05	0.05	0.05	1.35	0.05	0.05
V1	0.006	0.009	0.007	0.027	0.012	0.012	0.052	0.154
V2	0.004	0.004	0.004	0.012	0.005	0.01	0.026	0.079
Soil parameters								
Soil Depth (cm)	63.2	43.6	58.8	48.8	68	46	35	43.8
Very Coarse Sand (%)	0	2.7	0	1.3	1.2	0.4	0.4	0.7
Mud (%)	39	42	51	46	44	45	66	36

mammals was positively correlated with the various measures of plant cover (Table 4).

Species - Environmental features relations

The only species that were caught in sufficient numbers for analysis of the relations of abundance with environmental features, were *Otomys irroratus*, *Rhabdomys pumilio*, *Myosorex varius* and *Crocidura flavescens*.

Otomys irroratus abundance correlated with shrub canopy cover, vertical foliage diversity (both V1 and V2), the cover of small rocks (1, 2 and 3 - 5 cm diameter) and horizontal foliage density at intermediate heights above the ground. *Rhabdomys pumilio* abundance correlated with shrub canopy cover and V1, while the abundance of the two shrew species correlated only with horizontal foliage density just above the ground (Table 5).

Table 4
Correlation coefficients for relationships between environmental features and small mammal community characteristics in the Groendal Wilderness Area. Note that only values where P < 0.05 are given (ns = not significant)

Environmental features	H'	S	Total biomass	Total number	Rodent biomass	Insectivore biomass
Plant canopy cover	0.809	0.877	ns	0.75	ns	ns
Shrub canopy cover	ns	0.741	0.94	0.875	0.919	ns
Rock 1 cm	ns	ns	0.801	ns	0.823	ns
F0-10						0.792
F10-20	ns	0.723	ns	ns	ns	0.909
F20-40	0.759	0.895	0.804	0.954	0.713	0.708
F40-60	ns	ns	0.865	0.809	0.834	ns
F60-100			0.751	0.798	0.721	ns
V1	ns	ns	0.896	ns	0.909	ns
V2	ns	ns	0.878	ns	0.891	ns

Discussion

The mean species richness recorded for the small mammal communities depicted in Table 3 is low (2.3), although it is comparable with that of 3.4 species recorded by N. J. Dippenaar (Unpubl.) at this locality. Nel *et al.* (1980) recorded a mean of 3.6 small mammal species in a variety of habitats in Fynbos in the Kammanassie Mountains, while Bond *et al.* (1980) recorded a mean of 3.1 and 2.8 small mammal species in Fynbos in the Swartberg and Baviaanskloof mountains, respectively. In contrast, Willan & Bigalke (1982) recorded a mean of five small mammal species in Fynbos, with up to 11 species in mesic microsites. These results indicate a relatively low alpha diversity of small mammals in Fynbos, although these values are comparable to the 3.8 species recorded in the semi-arid Karoo of southern Africa (Kerley 1992).

Bond *et al.* (1980) and MacCracken *et al.* (1985) maintain that microhabitat features such as vegetation structure, cover and

height, relative humidity, litter depth, and foliage height diversity are directly related to the life form and growth pattern of plant species within a plant community and these factors are important floristic variables affecting small mammal community structure. These types of relationships were also found in the present study, where sites differed in microhabitat features due to different plant growth forms. Furthermore, in the present study, small mammal diversity (H') correlated with horizontal foliage density for heights 20-40 cm above the ground, whilst species richness (S) and the total number of small mammals captured were correlated with horizontal foliage density for heights 10-40 cm and 20-100 cm above the ground, respectively. Total rodent biomass correlated with horizontal foliage density for heights 20-100 cm above the ground, and total insectivore biomass for heights 0-40 cm above the ground. The two most abundant rodent species, *R. pumilio* and *O. irroratus*, were also correlated with vertical foliage diversity. These results support our original hypothesis.

Table 5
Correlation coefficients for relationships between environmental features and small mammal species abundance in the Groendal Wilderness Area.
Note that only values where $P < 0.05$ are given (ns = not significant)

Environmental features	<i>Otomys irroratus</i>	<i>Rhabdomys pumilio</i>	<i>Myosorex varius</i>	<i>Crocidura flavescens</i>
Shrub Canopy cover	0.923	0.881	ns	ns
Rock, 1 cm	0.88	ns	ns	ns
2 cm	0.732	ns	ns	ns
3-5 cm	0.799	ns	ns	ns
F0-10	ns	ns	0.801	0.771
F10-20	ns	ns	ns	0.812
F40-60	0.879	ns	ns	ns
F60-100	0.744	ns	ns	ns
V1	0.95	0.708	ns	ns
V2	0.937	ns	ns	ns

The mechanism of these relationships are complex and may reflect the physiological, nutritional, social and anti-predator requirements of the small mammals in question. Thus habitat structure or vegetative cover influences micro-climate (and reflects macro-climate) and consequently has an effect on the physiology of small mammals (Bond *et al.* 1980). Plant cover also reflects the forage availability of herbivores, as well as the resource base for prey for insectivores and carnivores.

Although *O. irroratus* numbers were positively correlated with the cover of 1-5 cm diameter surface rocks, the mechanism for this relationship is not immediately apparent. The presence of small surface stones (1 cm diameter) was shown to be correlated with horizontal foliage density at heights between 40-60 cm above the ground. This foliage density would presumably reflect both physiological and anti-predator protection, as well as being a measure of forage availability for this diurnal, herbivorous species. The correlation of *Otomys* numbers with small surface stones should therefore be consid-

ered an artifact of the relationship between stone cover and foliage density.

The structure of the substrate may influence the ability of small mammals to construct refuges (De Graaff 1981; Du Plessis & Kerley 1991), but no evidence was found to support this hypothesis in the present study, due to the lack of any significant correlation between small mammal communities and soil parameters.

Effects of disturbances

Transformation of natural Fynbos (site 5 – used as control in this study) into pastures (site 3) and plantations (site 6), changes the floristic and structural diversity of the habitat, with a concomitant decrease in small mammal species diversity, as the present study has shown. Site 3, when compared to site 5, represents a decrease in both total canopy cover and total basal cover, and an increase in the percentage of herbs present (Table 3). This has also resulted in a shift in small mammal species composition from

that of site 5 (Table 2). Furthermore, site 6, when compared to site 5, represents a decrease in total canopy cover, an increase in total basal cover (due to increased plant litter present), and an increase in the percentage of trees present (Table 3). Again, this has resulted in a different small mammal species community than that of site 5 (Table 2). At both these transformed sites, the major changes in small mammal community structure can be attributed to the disappearance of the diurnal *Otomys* and *Rhabdomys*, both species apparently relying on ground cover for specific resources.

Fire, both controlled and natural, can have a profound effect on the floral and faunal composition of a region (Edwards 1984). The Fynbos biome is adapted to regular and frequent natural or man-induced burning (Kruger & Bigalke 1984), and has many plant species whose evolutionary development accords with behavioural responses to fire (Manders & Cunliffe 1987). It can thus be expected that the fauna occurring in these fire-prone environments will similarly be well adapted to the periodic occurrence of fire.

No small mammals were captured at site 2, approximately two months after a fire. Fire apparently kills few animals (Breytenbach 1987) but alters the physical environment and vegetation structure. The major impacts are changes in the horizontal and vertical foliage densities (see Table 3), as well as the quantity and quality of available food in the post-burn environment (Willan & Bigalke 1982; Bigalke & Willan 1984; Kerley & Erasmus 1992). Diurnal rodent species, which are vulnerable to predation without the protection of plant cover, disappear from burns within days (Breytenbach 1987). Vegetation recovery is largely dependent on the prevalent fire regime (Bond 1980) and small mammal communities in the post-burn habitat undergo a successional sequence cor-

related with the seral stages of the vegetation secondary succession (Swanepoel 1981; Fox 1982; Willan & Bigalke 1982).

For a fire-prone conservation area like Groendal Wilderness Area, the management of small mammal communities should be based on the relationships of these communities with the regenerating vegetation. There is thus a need to maintain a mosaic of vegetation regeneration ages (same vegetation types, but of differing ages) for management and maintenance of diverse small mammal communities. This mosaic should consist of areas of sufficient size which can act as refugia and recolonisation sources (Willan & Bigalke 1982).

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