Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains

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Small mammals were sampled along altitudinal gradients in two mountain localities, the Swartberg and Baviaanskloof, in the southern Cape in summer 1977 – 1978. Species composition varied according to altitude and aspect with a total catch of six rodent and two shrew species. Correlations were found between abundance of rodent species and habitat variables, particularly vegetation structure and the cover of rock and bare soil. Rodent species diversity was negatively correlated with the proportion of total foliage at low to mid heights (40 – 80 cm). Factors controlling apparent habitat preferences are discussed together with modes of rodent niche separation. Extrapolation of the results is limited by the single season and restricted geographical coverage of the survey.

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Klein soogdiere is gedurende die somer van 1977 – 1978 langs 'n hoogtegradient in die Swart- en Baviaanskloofberge van die Suidkaap versamel. 'n Totaal van ses knaagdiere en twee skeerbekspesies is gevind. Hoogte en aspek het 'n beduidende invloed op die soortesamestelling gehaal. Korrelasies is tussen knaagdiergetalle en habitatveranderlikes gevind, veral met plantegroeistruktuur en die hoeveelheid bedekking van rotse en kaal grond. Daar was ook 'n verband tussen knaagdierverskeidenheid en die persentasie van die totale blaarmassa op lae tot medium hoogtes (40 – 80 cm). Die faktore wat oënskynlike habitatvoorkeure beheer, sowel as wyses van nisskeiding, word bespreek. Omdat die opname net oor een seisoen strek en 'n beperkte geografiese gebied dek, is veralgemening en die wyer toepassing van die resultate egter beperk.

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Very little published information is available on the ecology of the small mammal fauna of the mountains of the southern Cape. Recent developments in the multiple use planning and management of mountain catchments (Wicht 1971) have focussed attention on the flora and fauna of the area and their ecological relationships.

An understanding of small mammal distribution and dynamics would be of value in conservation management of mountain ecosystems. Conservation for maximum species diversity, for example, requires knowledge of factors controlling diversity. Habitat structure and diversity have been correlated with species diversity of birds (MacArthur & MacArthur 1961; Terborgh 1977) and of small mammals (Rosenzweig & Winakur 1969). Structural diversity of fynbos is rather low and has been cited as one cause of low bird species diversity (Bigalke 1980). Since most mammal and bird species are widely distributed within the fynbos (crossing phytogeographical boundaries) habitat features are probably of greater significance in niche partitioning than is floristic composition. Due to marked plant structural convergence, floristic diversity or plant species lists will probably be of less value in predicting small mammal diversity or population size, than plant life-form composition or variables describing habitat structure.

We conducted a survey of small mammals along altitudinal gradients in two of the inland ranges of the southern Cape showing distinct gradients in vegetation structure. The aim was to determine the numbers of small mammal species present, their location along the altitudinal gradient, and the ways in which available habitat was divided between species. We were interested in exploring the relationships (if any) between small mammal diversity, relative abundance of species, and population size with habitat structure, with a view to predicting community composition from easily measured habitat variables.

Study areas

Two study areas were sampled over a single summer season by trap sites located at intervals along an altitudinal gradient. One area, of eight trap sites, was located along the Swartberg Pass between Oudtshoorn and Prince Albert (33°23′ – 33°16′S, 22°02′ – 22°06′E) and the other, of seven trap sites, across the Baviaanskloof mountains near the confluence of the Kouga and Baviaanskloof Rivers (33°39′ – 33°35′, 24°22′ – 24°27′). A habitat description of each trapping site is shown in Table 2.

The sites were placed on north and south slopes in transects across steep, east-west trending mountains. Gently sloping areas, of relatively minor extent, occur at mid altitudes. The underlying rocks are sandstone and quartzite, with minor shale elements, of the Table Mountain Group of the Cape System. These rest on pre-Cape argillaceous rocks in the lower part of the Baviaanskloof and at the southern foot of the Swartberg Pass. Soils are shallow, acid, infertile and sandy in the Swartberg. Finer textured sandy loams and sandy clay loams occur in the Baviaanskloof. Soil consistence of the top-soil is mostly very friable becoming hard on the lower slopes. Soil surface is mostly stony or rocky.

Climate

There are no weather stations in the mountains in the southern Cape though some information is available on rainfall in the Swartberg Pass area (Weather Bureau 1965; Table 1). Rainfall is distributed throughout the year, increasing with altitude and decreasing north of the watershed. The same pattern probably obtains in the Baviaanskloof.

Temperature data are not available but temperatures probably decrease with altitude and are lower on south and east in contrast to northern and western aspects. Snow falls 5 — 6 times a year on the higher elevations of Swartberg Pass but is less frequent and lasts for shorter periods in the Baviaanskloof. Climatic data for the Cango Caves, on the southern Swartberg foothills, are shown in Fig. 1.

Table 1 Rainfall along an altitudinal/aspect gradient in the Swartberg Pass area (*ex* Weather Bureau 1965)

	Low	Mid	High
Southern aspect			
Altitude (m)	640^1	732^2	914^3
Rainfall (mm)	381,7	428,8	745,0
Ratio (Winter: Summer)	55:45	53:47	54 46
Northern aspect			
Altitude (m)	686^4	1 370^5	1 600^6
Rainfall (mm)	181,9	451,3	536,1
Ratio (Winter: Summer)	53:47	43:57	49:51

^{1}Cango Caves.
^{2}Matjies River.
^{3}Swartberg Pass.
^{4}Prince Albert.
^{5}Kliphuisvlei.
^{6}Swartberg.

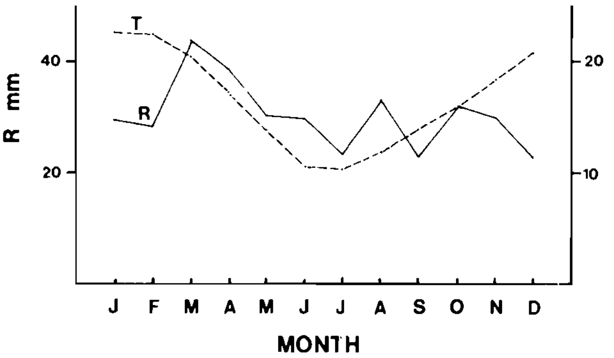

Fig. 1 Climodiagram for Cango Caves (640 m) near the foot of the Swartberg Pass. The solid line is rainfall (mm) and the broken line is temperature (°C). Mean annual temperature is 16,5 °C and mean annual rainfall is 363,1 mm (21 years).

Vegetation

The vegetation of the high mountains is fynbos (False Macchia according to Acocks 1975) with succulent Karroid veld types on lower north slopes of the Swartberg (site SW8) and Baviaanskloof (north, site B7, and south, site B1).

Swartberg

Most of the southern slopes and upper northern slopes are covered with Protea fynbos. Sample areas were selected in ± 20 year-old stands. These typically have two to three layers with an upper layer of Proteaceae 1,5 — 2,5 m high, a mid layer of narrow sclerophyllous shrubs mixed with Restionaceae, grasses, Cyperaceae and geophytes and a rather irregular ground layer of small sedges, grasses, shrubs, herbs and rosette plants.

The relative importance of these layers and of component life forms varies with altitude: the proteoid layer disappears at high, cool elevations and low, hot, dry elevations; the cover of mid layer shrubs and ground layer plants increases towards cooler, moister altitudes (e.g. site SW4), while grass cover decreases. Succulent plants are common only in arid, lower elevations (site SW8). Scattered clumps of vegetation are typical of arid low elevations (e.g. sites SW7 & SW8) thickening to a compact, continuous, more or less closed canopy at high elevation (e.g. sites SW3 & SW4).

Baviaanskloof

The Baviaanskloof area has affinities with subtropical vegetation of the eastern Cape. A thicket vegetation, resembling Acocks' Valley Bushveld but mapped by him as Succulent Mountain Scrub (Spekboomveld, Veld Type 25) with spiny and succulent evergreen trees and shrubs predominating, occurs on steep lower south slopes (site B1). On silcretes and Table Mountain sandstone at mid and upper elevations (sites B2, B5 & B6), fynbos similar to that in the Swartberg occurs but with additional communities quite unlike any on the Swartberg. These include shrub communities with a very grassy substratum at mid elevations (site B3), and tall, dense Proteoid-*Berzelia* fynbos (site B4), typical of the coastal Outeniqua/Tsitsikamma ranges, at high elevations.

Materials and Methods

All trapping was undertaken between 24 November 1977 and 20 January 1978 to minimize temporal variation of small mammal populations and facilitate comparisons. The majority of trapping grids (three each on south and north sides of each area) were of identical design. The traps in these 12 sites were placed in a rectangular grid of five lines spaced at 10 m (measured) intervals with 10 traps placed at 5 m (paced) intervals along each line.

In addition and because of a shortage of traps, the highest site on the southern side of Baviaanskloof (B4) consisted of 20 traps on a grid of four trap lines at 10 m intervals with five traps placed 5 m apart on each line. Traps were set for 10 days (200 trap days).

Two additional sites in the Swartberg, the southern lower-mid (SW2) and northern, upper-mid (SW6) were used to compare three bait types. Seventy-five traps were set in a grid of five trap lines, 10 m apart, with trap stations spaced

Table 2 General habitat features of trap sites in the Swartberg and Baviaanskloof

Trap site	Altitude (m)	Aspect	Topography	Vegetation
Swartberg				
SW1	940	South	Sloping, rocky foothill	*Protea repens, P. lorifolia P. eximia* fynbos with moderate *Restio* cover
SW2	1 150	South	Gently sloping, somewhat rocky mid-slopes	*Protea repens, P. lorifolia, P. eximia, P. punctata* fynbos with moderate *Restio* cover
SW3	1 220	South south-east	Steep, rocky mid-slope	*Protea punctata, P. lorifolia* fynbos with *Erica* spp. understory and moderate *Restio* cover
SW4	1 600	South south-east	Very steep, rocky, upper slopes with boulders	*Protea punctata, Erica* spp., high altitude fynbos with moderate *Restio* and grass/sedge cover
SW5	1 460	North	Steep, rocky upper mid-slopes	*Protea punctata, Leucadendron album* fynbos with ericoid understory and moderate *Restio* cover
SW6	1 400	North north-west	Level, mid-slope plain on shale band, no rocks	*Protea eximia* fynbos with high *Restio* and moderate grass cover
SW7	1 280	North north-west	Steep, very rocky slope below small ridge	*Protea lorifolia, Leucospermum calligerum, P. repens* fynbos with high *Restio* cover
SW8	900	North north-east	Very steep, very rocky, lower mountain slopes	*Portulacaria afra, Crassula* spp., *Eriocephalus* succulent, Karoo vegetation with moderate grass cover
Baviaanskloof				
B1	330	South	Sloping, stony scarp on shales	*Portulacaria afra, Aloe* spp., *Putterlickia,* succulent and spiny evergreen thicket
B2	515	South	Gently sloping, somewhat stony, plateau edge	*Diosma prama, Erica pectinifolia, Passerina* arid fynbos with low to moderate *Restio* and grass cover
B3	770	South	Steep, somewhat rocky mid-slope	*Protea arborea, Leucadendron salignum, Rhus, Helichrysum* spp. fynbos/bush with high grass cover
B4	1 040	South	Steep, rocky, upper slopes with rare boulders	*Leucadendron* spp., *Protea mundii, Berzelia mesic* fynbos with high *Restio* cover
B5	1 070	North north-east	Steep, rocky, upper slopes with boulders	*Leucadendron uliginosum, Erica* spp. fynbos with moderate grass and *Restio* cover
B6	870	North	Steep, stony and rocky mid-slopes	*Phylica, Cliffortia apiculata* arid fynbos with low *Restio* and moderately high grass cover
B7	680	North	Steep, stony and rocky lower mountain slopes	*Dodonea, Eriocephalus, Elytropappus, Aloe* Karroid shrubland with succulents, low to moderate grass cover

at 10 m intervals along each line. Three traps were set at each station baited with normal bait (see below), whole wheat bread and fresh apple respectively. Traps were set for three days (225 trap days per stand). No significant differences could be detected between the baits for the small numbers caught and the two plots will be treated homogeneously henceforth.

Aluminium Sherman traps (23 × 8 × 9 cm) were used throughout the study baited with a mixture of peanut butter, oats and candle wax mixed to a fudge-like consistence.

Traps were prebaited for one day, set for four days (i.e. 200 trap days per site) and checked every morning. Captured animals were weighed, measured and marked by clipping the coat to expose the darker undercoat.

Site factors

Altitude, aspect and slope were recorded for each trapping site (Table 2). Samples of 100 points (effectively a small quadrat $< \pm 10\ \text{cm}^2$) were used to characterize conditions at ground level in each site. Points were at intervals of five paces on a line following the contour. There were 10 lines, at 5 m intervals down the slope, in each stand.

The state of the ground surface at each point (i.e. in the vicinity of the boot tip) was recorded as rock (with diameters centring on 3, 6, 5, 13, 25, 50, 100, 200, 400 cm, or bedrock), grass (defined as narrow leaved or stemmed monocots and including Cyperaceae and most Restionaceae), litter (dead plant material less than 10 mm above soil surfaces), bare soil, or undifferentiated (mostly shrubs). These measures are referred to as ground cover to distinguish them from subjective estimates of the relative above ground cover of different plant life forms made using a Braun Blanquet scale for four height classes (0 – 0,25; 0,25 – 1,0; 1,0 – 2,25; 2,25 – 5,0 m). Life forms included graminoid herbs, restinoid herbs, geophytes, other herbs and shrubs (Moll, Campbell & Probyn 1976). Shrubs were further classified by Raunkiaerian leaf size categories. A list of visually prominent species and their relative abundances was compiled for each plot.

Foliage profiles

Foliage profiles were constructed from the amount of vegetation (measured as area of plant matter per unit volume of space) at different heights. They are thus an approximation of the vertical distribution of biomass. Rosenzweig and Winakur (1969) found that both species diversity and the species composition of desert rodent communities could be predicted from foliage profile parameters.

Boards (2 m high and 10 cm wide divided, like a surveyor's pole, into height classes of 20 cm) were used to determine foliage density profiles (MacArthur & MacArthur 1961). Four points were selected by random coordinates in each trap site and the distance from the point at which 50% of each height class was obscured on the density board was measured.

The reciprocal of this distance is directly proportional to foliage density. Measurements were repeated in the four cardinal directions from each point. A number of canopy variables were derived from the foliage profiles.

These included:

— Fi,j — the relative amount of foliage between heights i and j. This is calculated as the average of the reciprocals of board distance at these heights (and intermediate height classes) multiplied by the distance in metres between the heights,

e.g. For F20,40 where board distance at 20 cm is 1,0 m and at 40 cm is 2,0 m $F = ((\frac{1}{1} + \frac{1}{2})/2)\,(0,4 - 0,2) = 0,15$.

Fi,j was calculated at F20,60; F40,60; F20,80; F60,200; and F0,200 (Total foliage).

— Proportions of foliage above 60 cm, between 20 and 60 cm, and between 40 and 60 cm, e.g. F20,60/F0,200.

— The number of readings at which the distance of the board is greater than 50 cm at the 20 cm height level. This is a measure of horizontal diversity. For example, one out of 16 readings greater than 50 cm implies very dense foliage with low horizontal diversity whereas eight out of 16 has a high diversity.

A horizontal diversity index was calculated for the two categories greater or less than 50 cm using the Shannon–Wiener function and a vertical foliage diversity index (V) was calculated as

$$V = (p_2 + p_3)^3/(p_2{}^2 + p_3{}^2)$$

following Rosenzweig and Winakur (1969) where p_2 = F20,60/F0,200 and p_3 = F60,200/F0,200.

Results

Five rodent and two shrew species (107 individuals) were caught in the Swartberg with a total capture of 149 in 1 650 trap days, i.e. 9,0% capture rate. In the Baviaanskloof five rodent and one shrew species (125 individuals) were caught with a total capture of 228 in 1 400 trap days, i.e. 16,3% capture rate. Numbers caught appeared proportional to true population densities except perhaps for *Otomys*. Prebaiting seems necessary in this species (Table 3) as it appeared reluctant to enter traps until familiar with them. Trapping success was substantially higher than in the western Cape (Bigalke 1980) suggesting densities at least two or three times greater in the Swartberg and Baviaanskloof respectively. However, a prolonged trapping programme would be needed to confirm that this was neither a seasonal artefact nor due to longer term population fluctuations.

Species distribution and numbers of individuals are shown in Figs. 2A and 2B. *Rhabdomys pumilio* was the most widespread and abundant species, occurring in 12 out of 15 stands and most abundant in seven of these. *Aethomys namaquensis* was confined to mid and lower elevations in relatively arid vegetation where it dominated the catch. *Otomys* cf. *irroratus* occurred in all stands on the southern slopes of the Swartberg, none of which was near water. Toes (1974) also reports this species occurring high up on the mountain slopes. It seems probable that more than one species of *Otomys* is present on the southern (and in Toes's study, western) Cape mountains including *O. saundersiae* and/or *O. laminatus* in addition to *O. irroratus* (G.J. Breytenbach *pers. comm.*). These species could not be distinguished as live specimens in the field so that, although voucher specimens were identified as *O. irroratus*, species complex is designated *Otomys* spp. throughout.

The Shannon–Wiener function (Krebs 1972) was used to calculate a diversity index where

$$H = -\sum (p_i)(\log_2 p_i)$$

H = diversity index (information content of sample in bits/individual)

p_i = proportion of total sample belonging to the i species.

This index is a measure both of the number of species and equality of representation of the individuals of each species.

Species diversity (H) and species richness (= No. of species) are indicated in Fig. 2.

Species – Habitat relationships

Correlation coefficients between species numbers and habitat variables were calculated. Unless otherwise stated, only correlations applicable to both Swartberg and Baviaanskloof are discussed. Correlations common to both areas are considered to be of greater value and generality in understanding habitat relationships.

Rhabdomys pumilio (Sparrmann 1784)

Numbers of *Rhabdomys* were positively correlated with grass ground cover measured in the point survey ($r = 0,8235$, $n = 14$, $p < 0,01$). Site B3 had an exceptionally high grass cover and *Rhabdomys* catch. The correlation coefficient without this plot is $r = 0,6059$, $p < 0,05$. SW6

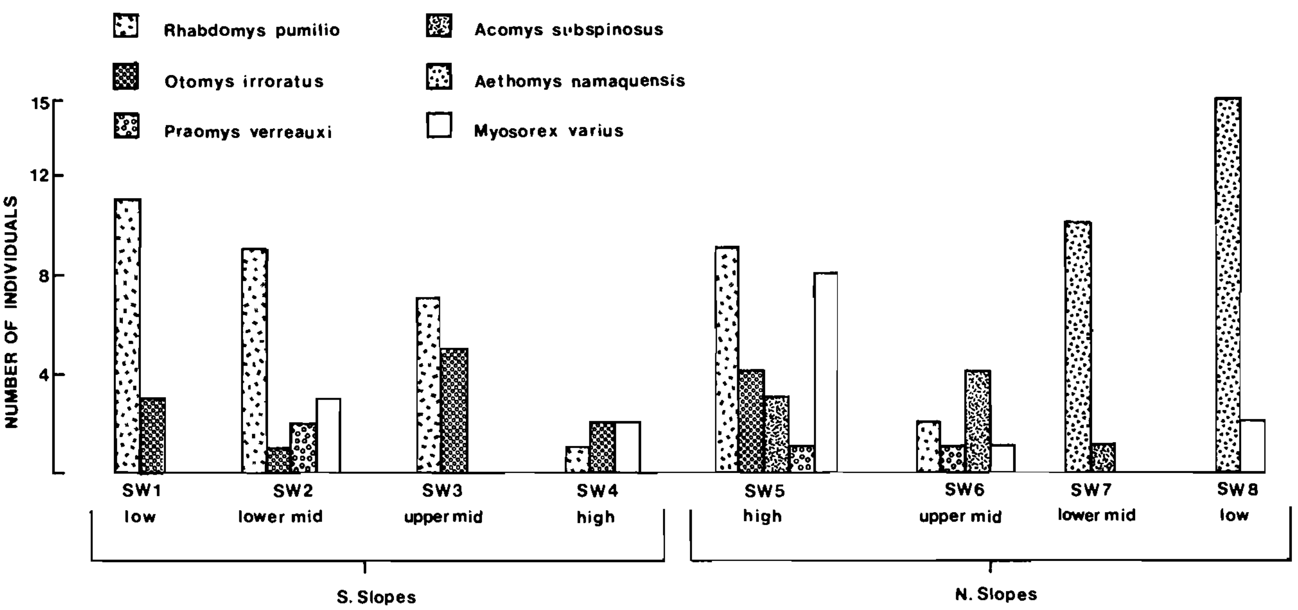

Fig. 2A Small mammal distribution along an altitudinal and aspect gradient in the Swartberg mountains, December 1977. The vertical axis represents the number of individuals of each species caught in 200 trap days except for SW3 and SW6 which represent 225 trap days.

was an outlier having high grass cover but low *Rhabdomys* numbers and was excluded from all the calculations. The 'grassy' component in this trap site was low and spreading unlike the other sites, where it was mostly erect and tussocky. There was an apparent preference for continuous 'grass' patches (grass including Poaceae, Cyperaceae and Restionaceae for the purposes of the survey) or, at least, of extensive grass patches. In the Karoo sites, grass cover was comparatively high but each grass clump was of small diameter and separated from its neighbour by bare soil or rock. The correlation between *Rhabdomys* numbers and the ratio of grass to bare soil and total rock ground cover (measured by the point survey) was used to assess this effect ($r = 0{,}9622$, $n = 14$, $p < 0{,}01$; without B3, $r = 0{,}8623$, $n = 13, p < 0{,}01$; see Fig. 3).

The lack of a significant correlation between *Rhabdomys*

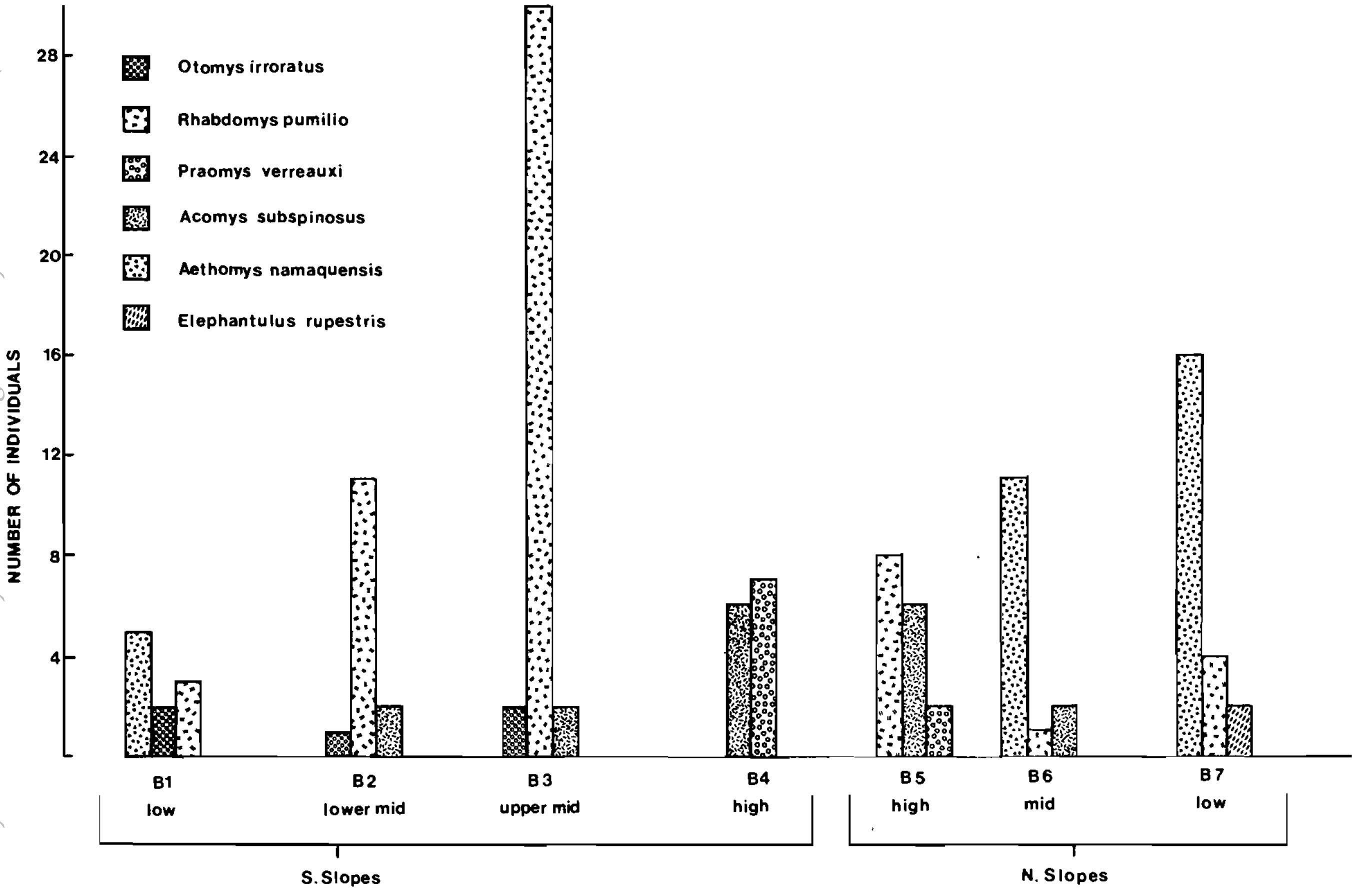

Fig. 2B Small mammal distribution along an altitudinal and aspect gradient in the Baviaanskloof mountains, January 1978. The vertical axis represents the number of indivuals of each species caught in 200 trap days. B4 was set for 10 days in contrast with the remaining sites (four days).

Table 3 Cumulative percentage of individuals caught, Day – 1

Species	Area	Trap Day 1	2	3	4	
Rhabdomys	Swartberg	39	75	93	100	(excluding SW2 & SW6)
Rhabdomys	Baviaanskloof	36	56	81	100	
Aethomys	Swartberg	40	60	88	100	
Aethomys	Baviaanskloof	49	73	91	100	
Acomys	Baviaanskloof	33	67	84	100	(excluding BM4)
Otomys	Swartberg	13	33	53	100	

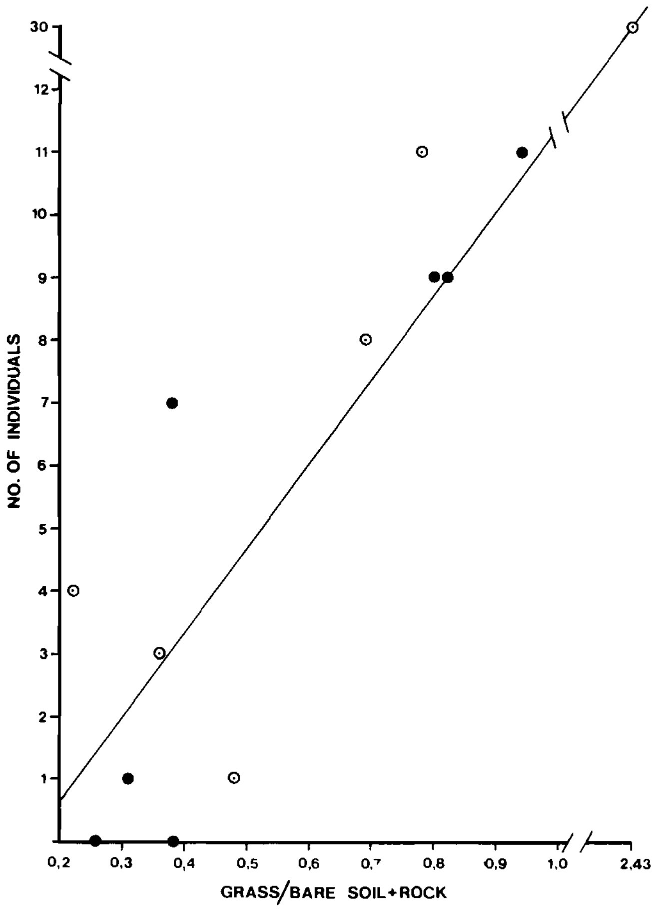

Fig. 3 The relationship between numbers of *Rhabdomys pumilio* individuals caught and the ratio of grass to bare soil plus rock cover measured in point samples. 'Grasses' included all narrow-leaved or stemmed plants belonging to Poaceae, Cyperaceae and Restionaceae. Regressions are, for Swartberg (●): $y = -3{,}07 + 15{,}05x$ ($r^2 = 0{,}8031$) and for Baviaanskloof (o): $y = -2{,}49 + 14{,}98x$ ($r^2 = 0{,}6615$) (or $y = -1{,}67 + 13{,}13x$ ($r^2 = 0{,}9517$) if the extreme value B3, is included.)

and shrub cover points to the selection of the 'grass' life form type as habitat for this species.

Rhabdomys was not significantly correlated with above ground cover-abundance of any single plant life form (including grasses) indicating lack of sensitivity of this measure to habitat structure as it effects this species.

The affinity of *Rhabdomys* for grassy areas has also been recorded in the mountain grasslands of the Golden Gate Highlands National Park (Rautenbach 1976).

Acomys subspinosus (Waterhouse 1838)

In the Baviaanskloof range *Acomys* numbers were positively correlated with increasing altitude (Spearman's rank correlation, $r = 0{,}830$, $p < 0{,}05$) and with percentage ground cover of 1,0 m diameter rock (Spearman's $r = 0{,}821, p < 0{,}05$).

Acomys was also strongly positively correlated with foliage density between 20 and 60 cm (Fig. 4) (Spearman's $r = 0{,}955$, $p < 0{,}01$) and with total foliage (Spearman's $r = 0{,}848$, $n = 7$, $p < 0{,}05$) in Baviaanskloof. Since both of these variables are correlated with altitude, with which amount of medium-sized rocks is correlated, no single factor controlling *Acomys* distribution can be identified. In general, for Baviaanskloof, optimal conditions were dense phytomass particularly below 60 cm, high elevation, and rocky areas.

Acomys was caught only at three sites on the northern slopes of the Swartberg at mid and upper altitudes but one site (SW6) was virtually devoid of rock or stones, suggesting that, although boulders and rocks may be optimal habitat, the species is not restricted to this environment. The species overlaps in distribution with *R. pumilio* but was never found to dominate the latter in any site. It is nocturnal thus, presumably, avoiding competition with *Rhabdomys* by temporal partitioning of resources.

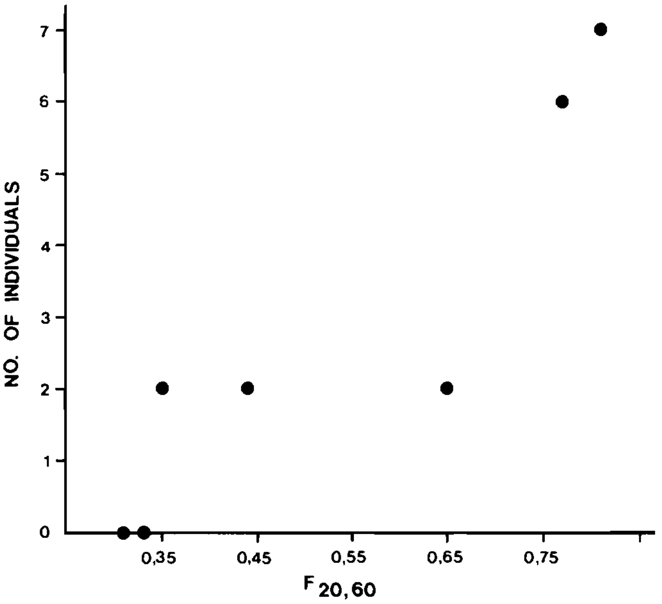

Fig. 4 The relationship between *Acomys subspinosus* and foliage density betwen 20 and 60 cm in the Baviaanskloof range.

Otomys spp.

Otomys spp. were caught mostly in the Swartberg study area, and principally on southern aspects. *Otomys irroratus* was caught in the Valley Bushveld in the Baviaanskloof and at higher elevation in grassy bush (B3). Only Swartberg results are discussed.

Otomys ranked second in abundance after *Rhabdomys* on the south slopes. It was found in habitats ranging from relatively arid *Protea repens* fynbos on dry foothills to high altitude heathland vegetation on upper mountain ridges.

Although a more extensive survey is needed for reliable population estimates of the vlei rat, our results show a significant positive correlation of *Otomys* numbers with shrub ground cover estimated by the point survey, and with shrub and litter ground cover (Spearman's $r = 0{,}952$, $n = 8$, $p < 0{,}01$) Fig. 5.

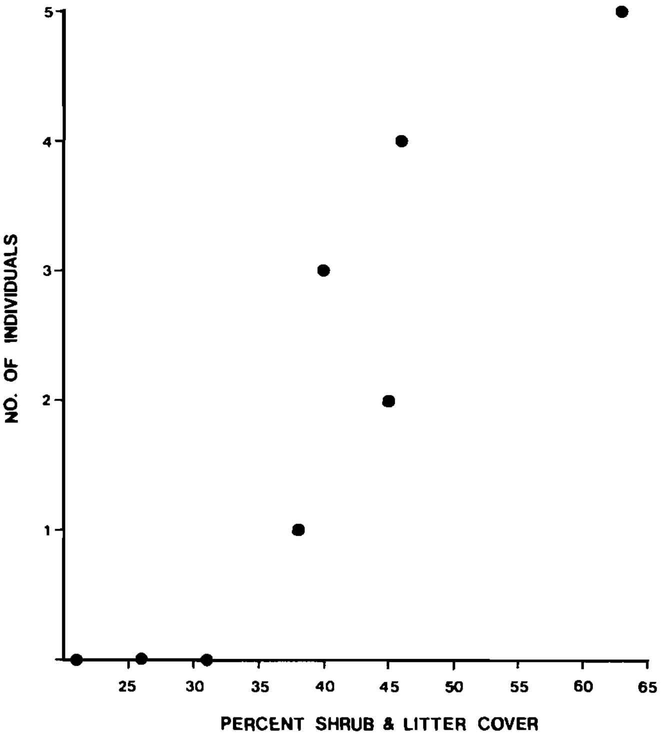

Fig. 5 The relationship between *Otomys irroratus* abundance, and percentage shrub cover measured by point samples, Swartberg mountains.

Otomys abundance was also positively correlated with cover above ground of the microphyll layer between 1,0 and 2,5 m (Spearman's $r = 0,75$, $n = 7$, $p < 0,05$) and the total microphyll layer (Spearman's $r = 0,812$, $n = 7$, $p < 0,05$). The microphyll layer mostly corresponds with the Proteaceae canopy on the Swartberg.

Otomys numbers were compared with total above-ground shrub cover estimates. *Otomys* was always caught in areas with more than, but never in areas with less than, 75% shrub cover.

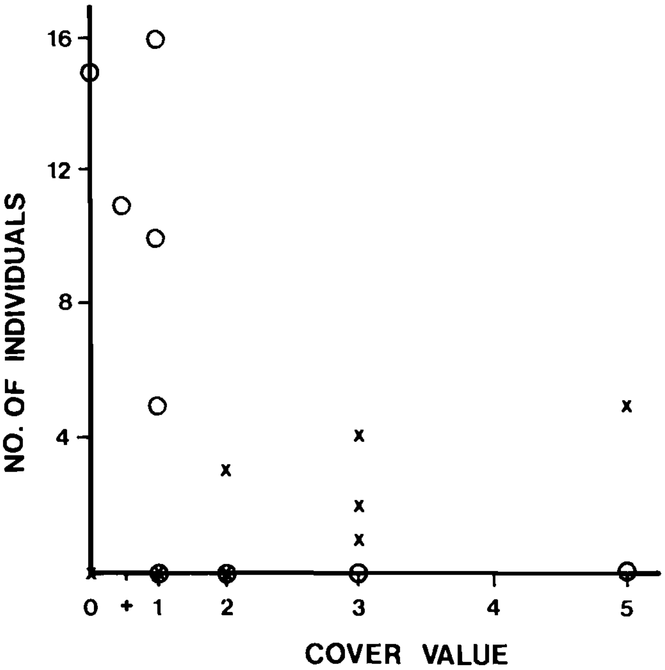

Fig. 6 The distribution of *Otomys irroratus* in the Swartberg (x) and *Aethomys namaquensis* (⊙) in the Swartberg and the Baviaanskloof in relation to microphyllous shrub cover (microphyll = leaf area of 225 – 2 025 mm^2). Cover value refers to cover estimates on a cover-abundance scale (+ = present; 1 = 10%; 2 = 10 – 25%; 3 = 25 – 50%; 4 = 50 – 75%; and 5 = 75 – 100%).

The general preference of *Otomys* for dense shrubby vegetation may be partially related to protection from predators together with the need for adequate material and sufficiently dense vegetation for runway establishment. It is separated from direct competition with *Rhabdomys*, its most common associate, by being primarily crepuscular (Davis 1972) whereas *Rhabdomys* is diurnal (Brooks 1974), preferring shrubby rather than grassy cover and, living on green plant material rather than seed. It appears to be more tolerant of cool temperatures with no losses from exposure in traps, whereas *Rhabdomys* mortality was high in the traps at temperature extremes.

Aethomys namaquensis (Smith 1834)

Aethomys namaquensis was confined to lower, mostly northern slopes supporting arid fynbos or Karroid shrubs and succulents usually forming vegetation clumps in a matrix of bare soil or quartzite stones.

Numbers of *Aethomys* were strongly correlated (Spearman's $r = 0,752$, $n = 14$, $p < 0,01$) with rock ground cover less than or equal to 13 cm in diameter (point survey; see Fig. 7) and with total ground cover of rocks and bare soil (Spearman's $r = 0,846$, $n = 14$, $p < 0,01$). This species thus occupies a ground layer niche widely separated from that of *Rhabdomys pumilio*, which requires a high ratio of grass cover to bare soil and rock, and, predictably, there was very little overlap between the two species. *Aethomys* is nocturnal (Choate 1972), an essential behavioural adaptation in an exposed habitat and one in which *Rhabdomys* would be at a disadvantage.

Small stones may be merely an incidental indicator of preferred *Aethomys* habitat, in both Swartberg and Baviaanskloof, as these are characteristic of lower, arid, foothills of the southern Cape mountains.

Aethomys numbers were also correlated with above ground vegetation features. It was never found in areas with more than 75% total shrub cover in direct contrast to *Otomys*, and was restricted to areas with less than 10% cover of microphyllous shrubs — virtually synonymous

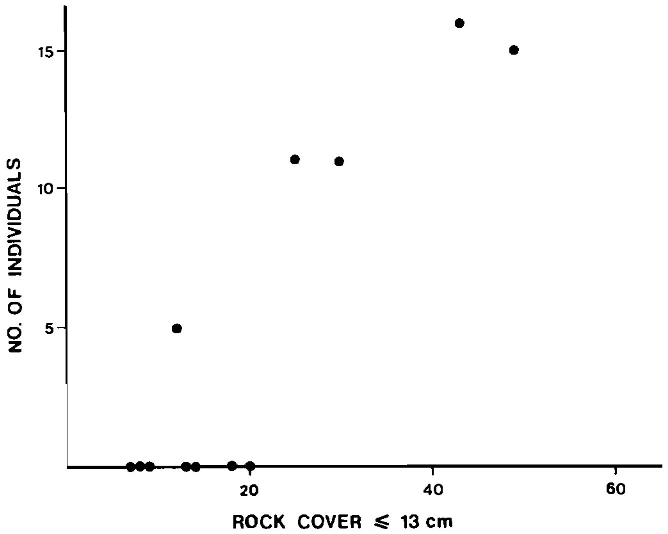

Fig. 7 The relationship between *Aethomys namaquensis* and cover or rocks less than, or approximately equal to, 13 cm in diameter, measured by point samples in the Swartberg and Baviaanskloof.

with the Proteaceae canopy layer — also in direct contrast to *Otomys irroratus* (Fig. 6).

Aethomys numbers were positivelycorrelated with succulent cover percentages (Spearman's $r = 0{,}740$, $n = 14$, $p < 0{,}01$) though (as in the lower mid site at Swartberg) not necessarily confined to areas with succulents.

Total foliage, measured from foliage profiles, was negatively correlated with *Aethomys* numbers ($r = 0{,}5663$, $n = 14$, $p < 0{,}05$), this being related to the low biomass in arid portions of the altitudinal gradients.

Praomys verreauxi (Smith 1934)

Insufficient *Praomys* were collected for analysis of habitat preferences. In the Baviaanskloof the species was restricted to the highest elevations in the gradient. In the Swartberg the species was most frequently captured on high, northern slopes, but also at mid elevations on southern slopes.

Insectivores

Myosorex varius was common in the Swartberg over a surprisingly diverse habitat range but absent in the Baviaanskloof. *Elephantulus rupestris* occurred in the Karroid vegetation on the north slopes of the Baviaanskloof (B7). Neither species was incorporated in species diversity indices because they are clearly separated from rodents by dietary preferences.

Rodent species diversity and foliage profiles

No significant correlations were detected between rodent species diversity and foliage diversity measured by the Shannon–Wiener function. The latter proved insensitive to variations in the proportions of foliage so Rosenzweig Winakur's index, V, was used. Species diversity was negatively correlated with this index for the vegetation layers below and above 60 cm. The index is a composite one combining a diversity measure of two foliage layers (excluding one immediately above the ground) and the relative importance of these layers. Since no relationship was found for foliage diversity alone, relationships between the relative importance of the foliage layers were investigated.

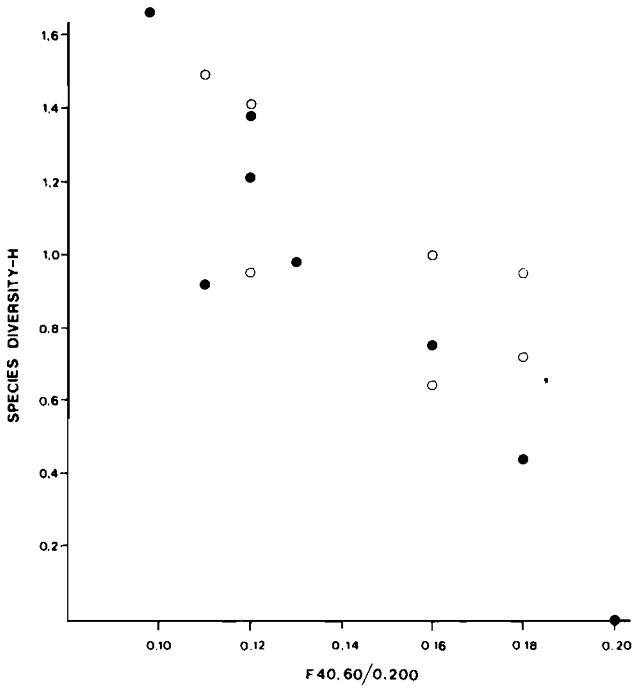

Fig. 8 The relationship betwen rodent species diversity, H, and the relative importance of low to mid-height foliage, F40,60/F0,200 in the Swartberg (●) and Baviaanskloof (○). See text for calculation of diversity indices. The layer between 40 and 60 cm is selected from the low to mid-height layers since it gave the best correlation with diversity (r — 0,9467, S = Swartberg; r — 0,7569, B = Baviaanskloof). Foliage layers up to 80 cm were correlated with diversity (F40,80/F0,200 r — 0,6733S, r — 0,6947B, F60,80/F0,200 r — 0,5567S, r — 0,7517B) but without statistical significance. Layers starting below 40 cm were not correlated with rodent species diversity.

Eighty-eight per cent of the variablility in rodent species diversity in the Swartberg was explained by the proportion of total foliage between 40 and 60 cm ($p < 0{,}01$) and 57% in Baviaanskloof ($p < 0{,}05$) (Fig. 8). Only the foliage proportion in the lower layer and not the diversity of foliage layer, is thus significant. Comparisons with Rosenzweig and Winakur's (1969) results with desert rodents is extremely difficult because of their use of a composite habitat index. However, they found a positive correlation with species diversity and habitat diversity whereas in both Swartberg and Baviaanskloof rodent diversity declined with increase in the proportion of vegetation in the lower layer.

No consistent relationship was found between horizontal or 'pattern' diversity and species diversity. These were negatively correlated in the Swartberg ($r = -0{,}7643$, $n = 8$, $p < 0{,}05$) but positively correlated in the Baviaanskloof ($r = 0{,}44$, $n = 7$), no significance. The difference in response suggests that horizontal diversity, as defined in the study, does not directly affect species diversity.

Discussion

Distinct gradients in the relative abundance of rodent species were detected and were correlated with structural variation in vegetation along the altitudinal gradients. Habitat preferences and correlations are summarized in Table 4. Floristic differences were of little significance in differentiating rodent niches except in so far as they reflect vegetation structure. Our results provide evidence for the possibility of prediction of relative abundance of some rodent species and of community diversity using structural variables.

Rodent species were habitat specific for the season and areas sampled. A general habitat description (Moll *et al.* 1976) would not suffice in specifying species location and relative abundance in the gradient. *Rhabdomys,* for example, occupied a confusingly broad range of plant communities of widely differing floristic and structural composition, yet its abundance could largely be explained by a single variable, the grass component, of the habitat. Floristic descriptions are, perhaps, the least useful in describing or locating rodent habitat. *Aethomys,* for example, was indifferent to major floristic changes (proteoid fynbos to succulent Karoo) but could be located, with confidence, by small surface stones!

Selection of meaningful variables for habitat description and the measurement of those variables is a major difficulty. The human's scale of perception is obviously different from a rodent's, so that a priori selection is difficult. Variables most useful in this study are summarized in Table 4. The point survey results were more useful than subjective cover estimates. With suitably defined structural criteria, point surveys are rapid and results are reasonably repeatable. Foliage profiles are the most time consuming

Table 4 Significant habitat variables and habitat preferences of rodents in mid-summer 1977 – 1978

Sampling technique	Habitat variable	*Rhabdomys*	*Otomys*	*Acomys*	*Aethomys*	*Praomys*	Species div.
Foliage profiles	F20,60			*p* 0,01			
	F0,200			*p* 0,05	Negative correlations		
	F40,60/F0,200						*p* 0,01
Point survey. Cover at or near groundlevel	'Grass' }	*p* 0,01					
	Bare soil }						
	Rock: 13 cm				*p* 0,01		
	Rock: 25 – 50 cm	Ratios or combinations of bracketed variables			Ratios or combinations of bracketed variables		
	Rock: 100 cm			*p* 0,05			
	Shrub }		*p* 0,05 Ratios or combinations of bracketed variables				
	Litter }						
Subjective estimates. Above ground vegetative cover	Total shrub		*p* 0,05		Negative correlations		
	% Microphylls		*p* 0,05		Negative correlations		
	% Succulents				*p* 0,05		
Site variables	Altitude			*p* 0,05		Not tested, insufficient numbers	

measure, and are the least susceptible to subjective error, but (cf. Rosenzweig & Winakur 1969) were of little value in predicting species abundance. Cover estimates of plant life forms are most useful as general habitat indicators, particularly where plant species are numerous and change in response to geographical rather than environmental gradients (Moll *et al.* 1976).

The interrelationships of small mammals and habitat structure, particularly vegetative cover, have been discussed by Birney, Grant and Baird (1976). They listed protection from predators, influence on micro-climate, and level of intraspecific confrontation and thus behavioural stress as some of the more important features. French *et al.* (1976 p.216) considered that habitat structure could be implicated in control of small mammal densities, probably through its effect on exposure of rodents to predators and other mortality factors. Vegetation structure is also an indicator of environment and may thus reflect indirect controls such as climate or primary productivity and thus food supply on mammal population. The strongest correlation between cover and rodent abundance is that between *Rhabdomys* and grass ground cover. This relationship would appear to be due to density dependent population control through behavioural stress.

G.J. Breytenbach (*pers. comm.* 1978) reported a catastrophic decline in *Rhabdomys* numbers on the same trap sites and using the same methods in the autumn following this survey. This suggests that *Rhabdomys* numbers had reached a peak in summer, 1977, when the linear relationship with grass cover was found.

Choate (1972) found that *Rhabdomys pumilio* males occupied well separated areas in the field and that most adult males would not tolerate other males in their cages in captivity. High cover values, resulting in diminished intraspecific confrontation, might thus allow higher population densities of this species because of reduction of behavioural stress. At lower population levels, cover would not be a limiting factor, at peak levels with frequent conspecific encounters, densities would be directly related to available cover. *Otomys irroratus* is antisocial and tends towards isolation (Davis 1972) so that it too would probably benefit from reduced conspecific conflict in high cover situations.

Birney *et al.* (1976) considered protection from predators, particularly diurnal predators relying on sight, to be the most important influence of cover on animal populations. *Rhabdomys* and *Otomys* are both diurnal animals, vulnerable to diurnal predators and had densities related to cover variables. Moreover, both species establish runways, which probably assist in predator evasion.

The functional significance of the relationship between stones and rocks, their abundance and size, is less clear. It could, for example, be related to nest site selection, thermal properties of rock, availability of shelter or refuge or merely an indirect relationship with rocks as general habitat indicators.

Habitat structure or vegetative cover also influences micro-climate (and reflects macro-climate) and consequently thermo-regulation. Micro-climate may dominate species distribution and population size at environmental extremes. In the Swartberg, SW4, a high exposed site had anomalously low species diversity (Fig. 8), perhaps because of the inability of rodents to adapt to the cold conditions.

Species diversity

Rodent species diversity was not correlated with any measured habitat variable, including altitude, except for foliage densities at low heights. The latter itself, however, was correlated with a number of variables, including altitude. This implies a direct influence of foliage profiles on diversity rather than as an indicator of other limiting factors.

The inverse relationship between species diversity and the proportion of foliage found in the 40 – 60 cm layer is not easily interpreted. More information from a larger sample is needed to test its generality. Nevertheless tentative hypotheses may be proposed:

- that the vertical distribution of plant material, irrespective of its form or nature, is significant in rodent niche partitioning
- that rodent species diversity can be predicted from foliage profiles.

(Foliage profiles, however, appear to have low value in predicting rodent population size and specific composition).

Fire

Fire in fynbos may effect rodent species diversity if these hypotheses are true. Low diversity, associated with a high proportion of total foliage below 60 cm, would be expected in young fynbos increasing as upper layers develop and perhaps decreasing with senescence of the plant community many years after the fire.

Burning may also effect relative species abundance. Correlations between population size of several species and woody cover or grass cover implies marked changes in species abundance after veld is burned. *Rhabdomys,* for example, ought not to appear in significant numbers until three or four years after a fire on the southern slopes of the Swartberg, where graminoid and restioid recovery is slow. In the Outeniquas, however, cover would be sufficient for high population levels only a year after a fire as the fynbos recovers rapidly. *Otomys* would recolonize more slowly since the development of appreciable shrub cover, particularly microphyll cover, lags behind hemicryptophytes.

Aethomys, adapted to low cover situations, may migrate upslope after a fire to occupy sparse seral vegetation. Studies on the impact of fire on rodent distribution along an altitudinal gradient could thus provide evidence for the significance of habitat structure on rodent population size and interspecific competition.

A cautionary note on the limitations of geography and time on results of the study is necessary. Seasonal fluctuations, in particular, may lead to local migrations or significant changes in relative abundance so the generality of the results, obtained from a single season only, are limited. Vegetation of the coastal Outeniqua — Tsitsikamma ranges is so different from the inland ranges that we hesitate to extend our results to this area without further observations.

Nevertheless, the survey is of value in indicating general species preference along an altitudinal gradient and apparent correlation of species number, diversity and population size with easily measured structural variables. It represents a first step in a study of faunal community composition and dynamics, which in turn will precede investigations of the effects of habitat management on these communities.

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References

ACOCKS, J.P.H. 1975. Veld types of South Africa. 2nd Edn. *Mem. bot. Surv. S. Afr.* No. 28 Government Printer, Pretoria, South Africa.

BIGALKE, R.C. 1980. Aspects of vertebrate life in Fynbos, South Africa. In: Heathlands and related shrublands (ed.) Specht, R.L. Elsevier, Amsterdam. In press.

BIRNEY, E.C., GRANT, W.C., & BAIRD, D.D. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology* 57: 1043–1051.

BROOKS, P.M. 1974. The ecology of the four-striped field mouse, *Rhabdomys pumilio* (Sparrman 1784). D.Sc. Thesis, University of Pretoria, Pretoria, South Africa.

CHOATE, T.S. 1972. Behavioural studies on some Rhodesian rodents. *Zool. Afr.* 7: 103–118.

DAVIS, R.M. 1972. Behaviour of the vlei rat, *Otomys irroratus* (Brant 1827). *Zool. Afr.* 7: 119–140.

FRENCH, N.R., GRANT W.E., GRODZINSKI, W. & SWIFT D.M. 1976. Small mammal energetics in grassland ecosystems. *Ecol. Monogr.* 46: 201–220.

KREBS, C.J. 1972. Ecology. pp.506–509. Harper & Row, New York.

MACARTHUR, R.H. & MACARTHUR, J.W. 1961. On bird species diversity. *Ecology* 42: 594–598.

MOLL, E.J., CAMPBELL, B.M. & PROBYN,T.A. 1976. A rapid statistical method of habitat classification using structural and physiognomic characteristics. *S. Afr. J. Wild. Res.* 6: 45–50.

RAUTENBACH, I.L. 1976. A survey of the mammals occurring in the Golden Gate Highlands National Park. *Koedoe* 19: 133–144.

ROSENZWEIG, M.L. & WINAKUR, J. 1969. Population ecology of desert communities: Habitats and environmental complexity. *Ecology* 50: 558–572.

TERBORGH, J. 1977. Bird species diversity on an Andean elevation gradient. *Ecology* 58: 1007–1019.

TOES, E. 1974. Vyftiende Jaarverslag van die Fakulteit van Bosbou, Universiteit van Stellenbosch, Stellenbosch, Suid-Afrika.

WEATHER BUREAU 1965. Climate of South Africa. Part 9. *W.B.* 29. Dept. of Transport, South Africa.

WICHT, C.L. 1971. The task of forestry in the Mountains of the western and southern Cape Province. *Proc. Grassld. Soc. Sth. Afr.* 6: 20–27.