SMALL MAMMAL RESPONSES TO ENVIRONMENTAL GRADIENTS IN THE GROOT SWARTBERG OF THE SOUTHERN CAPE

by

GIDEON JOHANNES BREYTENBACH

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by G.J. BREYTENBACH

Supervisor: Prof. J.A.J. Nel
Department of Zoology
University of Pretoria
Pretoria
Co-Supervisor: Dr. N. Fairall
Mammal Research Institute
University of Pretoria
Pretoria

ABSTRACT

Small mammal communities were sampled at eight sites along an altitudinal gradient in the Groot Swartberg mountains of the southern Cape. The plant communities sampled at each of these sites represented different altitudinal zones and rainfall regimes. Vegetation cover (as expressed by a point cover survey and foliage profiles) increased with increasing altitude and rainfall. Foliage cover was however compressed into the lower layers of the foliage profile at high altitudes. Rock and plant cover were inversely related.

The small mammal communities reached higher density and alpha diversity in fynbos heathlands than in either fynbos shrublands or succulent karoo shrublands. Population densities of some species e.g. Acomys subspinosus and Otomys irroratus increased during the 15 month trapping period while those of Rhabdomys pumilio and Aethomys namaquensis decreased. Breeding of all species occured throughout the year and the diet of the various species differed.

The population density of some species, e.g. A. subspinosus, O. irroratus and R. pumilio increased with increasing altitude. Alpha diversity increased with increasing altitude and hence probably with increasing rainfall and productivity. Alpha diversity in fynbos communities were similar to those recorded in other biomes. Beta diversity or species turnover was greatest between sites on the arid end of the moisture gradient.

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INTRODUCTION

Small mammals (here defined as terrestrial mammals with a mass smaller than 200 g) have been studied extensively as sizeable natural populations occur almost everywhere, they have a great impact on agricultural and other crops (Myllymäki 1979), act as vectors of human diseases (Davis 1963, Coetzee 1965, Arata 1975) and are usually easy to keep in captivity (Davis 1963). Small mammal studies were given greater impetus when the IBP's Terrestrial Productivity Section decided to concentrate on small mammals in various ecosystems e.g. (Batzli 1975, Flemming 1975, Golley, Ryszkowski & Sokur 1975 and Naumov 1975).

Various aspects of the biology and ecology of the southern African small mammal fauna have been studied, such as bio-geography (e.g. Davis 1962, Meester 1965, Davis 1974, Rautenbach 1978a) and life histories and general biology (e.g. Measroch 1954, Choate 1972, Christian 1976, Haim & Fourie 1980, Perrin 1981). Studies of community structure and diversity are, however, less common (e.g. De Witt 1972, Swanepoel 1972, Nel 1978, Withers 1979, Bond, Ferguson & Forsythe 1980, Jooste 1980).

Almost nothing is known of community dynamics and the effect of habitat manipulation, Swanepoel (1972) has, investigated the effect of spraying dieldrin broadcast on a small mammal community and Christian (1977) and Kern (1977) for example have described the effect of fire on small mammals.

For the last two decades the Cape mountains and their flora have elicited increasing public interest (Wicht 1971, Hall 1978). The Directorate of Forestry of the Department of Environment Affairs, the organisation responsible for the management of the mountain catchment areas, has also been faced with increasing criticism of its management policies (e.g. Moll, McKenzie & McLachlan 1980). Management, planning and research programmes with the maintenance of existing water and biotic resources as goal (Ackerman 1976) have, however, been developed and executed over many years.

The present study arose from the need to identify faunal distribution patterns, their influence and dependence on existing plant communities and the influence of management practices on these interacting physical and biotic systems in the Southern Cape mountains. Small mammal studies in the fynbos biome have really only been undertaken during the last decade (Toes 1974, Willan 1979 a & b, Rautenbach & Nel 1980, Nel, Rautenbach & Breytenbach 1980, and Bond _et_ _al_ 1980).

None of the studies in fynbos and other areas in southern Africa so far have investigated the ecological determinants of diversity and of population densities in any great detail. Nel (1978) investigated diversity and population size to some extent, but the present study and that of Bond _et_ _al_ (1980) were the first to tackle the problem systematically by using the direct gradient analysis approach (MacArthur & MacArthur 1961, McIntosh 1967, Collier, Cox, Johnson & Miller 1973, Whittaker 1975, Cody 1975, 1980 and Kessell 1979). It was decided to use gradient analysis as basic research strategy, since it was impossible to sample all the various plant communities that exist within the mountains controlled by the Department of Environment Affairs. The individualistic concept of species distributions (Gleason 1926) was accepted and sampling was therefore not aimed at sampling distinct "plant communities" identified *a priori*. Also gradient analysis is the more direct approach used to identify the "ecological determinants of species distributions and community responses" (Collier *et al* 1973). There are many environmental gradients that could be measured, but the best results are achieved if resource gradients along which niche overlap is minimised can be used (Whittaker 1975, Kessell 1979). Resources are here seen as those requirements needed by an organism to exist and reproduce (Hutchinson 1957). Resource gradients explaining the trends in community diversity have already been identified for many taxa, the implication being that the species concerned are partitioning that resource in some way to reduce niche overlap (Pianka 1978). Such resources may be measured directly and small mammal abundance and community diversity trends can be assessed directly against such gradients.

Some such environmental resource gradients have already been identified for rodent communities, i.e. foliage height diversity (Rosenzweig & Winakur 1969), various foliage profile parameters (Bond *et al* 1980), rainfall and concomitant primary production (Brown & Lieberman 1973), habitat diversity (Hafner 1977, Fox 1981), seed size (Brown & Lieberman 1973, Brown & Davidson 1977, and Munger & Brown 1981).

This study tested the importance of some of the above identified resource gradients on small mammal communities in the southern Cape mountains, i.e. habitat diversity and various foliage profile parameters. Small mammal, bird and insect communities were surveyed in the Swartberg, Outeniqua and Baviaanskloof mountains, areas selected to represent the major climatic extremes that occur in the southern Cape. The humid coastal Outeniqua and subhumid to semi-arid interior Swartberg ranges fall within the predominantly year-round rainfall climatic regime. The Baviaanskloof mountain is representative of the drier inland mountains of the predominantly summer rainfall area of the south-eastern Cape. Only the results of the small mammal survey of the Swartberg mountain will be presented here.

STUDY AREA

The study area is in the vicinity of the Swartberg pass on the Groot Swartberg range and is bounded by lat. 33° 23'S and 33° 17'S and long. 22° E and 22° 6'E. The general location of the study area in relation to the whole of the Fynbos Biome is shown in Fig. 1. Sites where intensive surveys were conducted within the general area were selected so that:

1. They were free of obvious disturbances such as too frequent fires, fires in the wrong seasons, invasion by exotics and erosion.
2. They were in close proximity of the Swartberg pass to allow easy access in the difficult terrain.
3. They were fairly evenly spaced along the sampled altitudinal gradient with four sites (1-4) on the south facing slopes and four sites (5-8) on the north facing slopes.
4. They represented the prevailing plant communities of each vegetation zone within the dominant landscape (i.e. ravines, water courses, rocky outcrops and scree slopes were avoided) at that altitude.
5. They supported vegetation of between 15 and 20 years post fire age. (The post fire age of the communities were standardised to exclude the potential complication of succession, senescence and phenology). Site 8, the Spekboom succulent site did not meet this last requirement since it is in a fire free vegetation type.

CLIMATE

The Swartberg is situated in the transitional area between the winter and summer rainfall areas. Rain occurs throughout

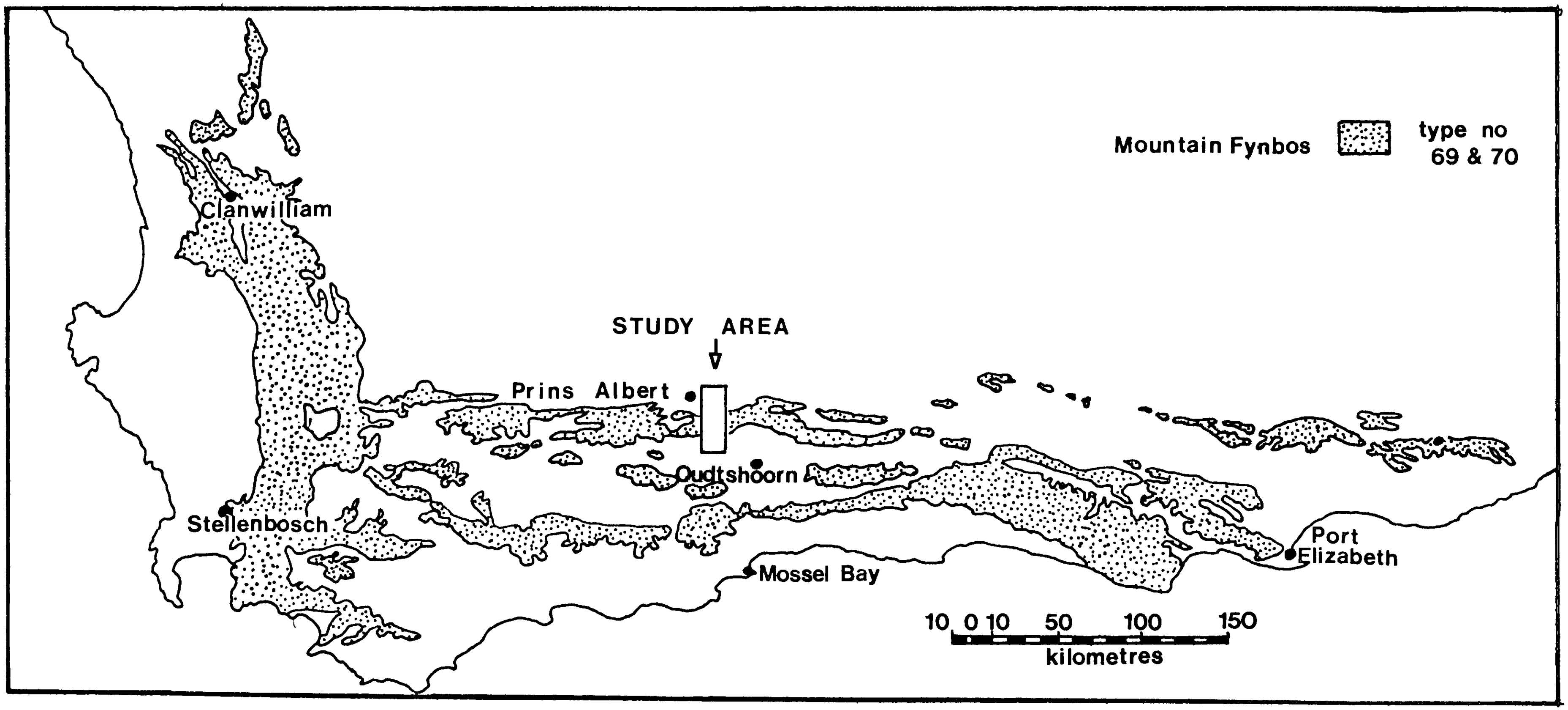


Fig. 1. Distribution of Mountain Fynbos in the southern Cape (from Acocks 1953) and the location of the study area.

the year.

The areas adjacent to the Swartberg, the Little and Great Karoo, receive less than 250 mm per annum while the Swartberg peaks probably receive between 800 and 900 mm per annum.

Rain in the Swartberg is of a cyclonic-orographic nature. Rainfall is therefore highest on the south slopes that face into the rain-bearing south-westerly winds with a distinct rain shadow on the lower north facing slopes.

Mean monthly rainfall for five rainfall stations are given in Table 1. Although precipitation is nearly always of a cyclonic-orographic nature, thunderstorms occur 10 to 20 times per year. Snowfalls occur five to six times a year at higher altitudes and snow may remain _in situ_ for as long as two weeks (Schulze 1965).

Mist precipitation is probably only significant at elevations above 1400 m. For Table Mountain in the western Cape mist precipitation was estimated to be in the region of 2500 mm yr^{-1} (Marloth 1904, 1907). Fuggle and Ashton (1979) estimate that mist precipitation is at least 500 mm yr^{-1} at high altitudes in the south-west Cape. There were no data available for the southern Cape mountains.

Long term temperature data were available only from the weather station at Kango Grotte 48/383 some 10 km to the east-south-east and 100 m lower than the lowest study site on the south facing slope. Using dry adiabatic temperature lapse rates

TABLE 1. Mean monthly rainfall and mean annual total rainfall (in mm) for the Swartberg and immediate environs.*

Station	Altitude (m.a.s.l.)	Period (y)	J	F	M	A	M	J	J	A	S	O	N	D	Year
South facing slopes															
Kango Grotte	640	21	29,3	28,1	43,9	39,5	30,0	29,6	23,1	32,9	22,7	31,7	29,9	22,4	363,1
Albertberg	1067	10	58,6	76,7	82,6	51,6	73,8	48	56,6	66,2	49,4	66,2	48,9	50,3	727,9
North facing slopes															
De Wetsvlei BOS **	1525	10	73,9	82,6	80,3	65,2	82,2	54,8	59,6	73,4	71,2	90,7	64,4	67,7	866,0
Kliphuisvlei BOS **	1370	10	28,9	36,4	38,1	29,9	50,3	41,3	45,9	46,1	42,5	40,4	24,3	27,2	451,3
Prince Albert TNK	686	83	11,5	18,5	26,6	19,2	21,2	13,4	9,6	10,2	12,5	13,3	14,0	11,7	181,9

* Data from Schulze 1965 and Weather Bureau unpublished data.

** Rainfall stations situated within the study area.

(Smith & Geller 1979) temperature data were calculated for use with the Swartberg 45/51 rainfall station data and a climograph was compiled (See Fig. 2). Moisture deficit or excess was estimated using a Thornthwaite estimate of potential evapotranspiration (Fig. 3 and 4). These show that the lower slopes are subject to considerable and prolonged drought stress during the hot summer months, i.e. from September to April. These sites are therefore subjected to prolonged summer moisture stress, similar to the winter rainfall areas of the western Cape in spite of occuring in the all year rainfall zone.

At Oudtshoorn the ratio of actual to potential sunshine is 0,71 (Bond 1981). No data are available for Swartberg. Radiation inputs and losses are probably high, and daily temperature fluctuations of up to 28 °C have been recorded by Schulze (1965).

No wind data were available for Swartberg. Over the subcontinent, the wind direction in the upper layers of the atmosphere are westerly to south-westerly throughout the year. Surface winds, however, show great variability, with easterly winds more common in summer, as opposed to south-westerly in winter (Anon 1942). Wind speeds generally increase with altitude over Port Elizabeth, Mossel Bay and Beaufort West (Anon 1942), and similar trends were observed along the sampled altitudinal gradient on the Swartberg within this triangle.

GEOLOGY AND TOPOGRAPHY

The Swartberg, part of the Cape folded mountain belt, separates the Little and Great Karoo. The study area (Fig. 5) is

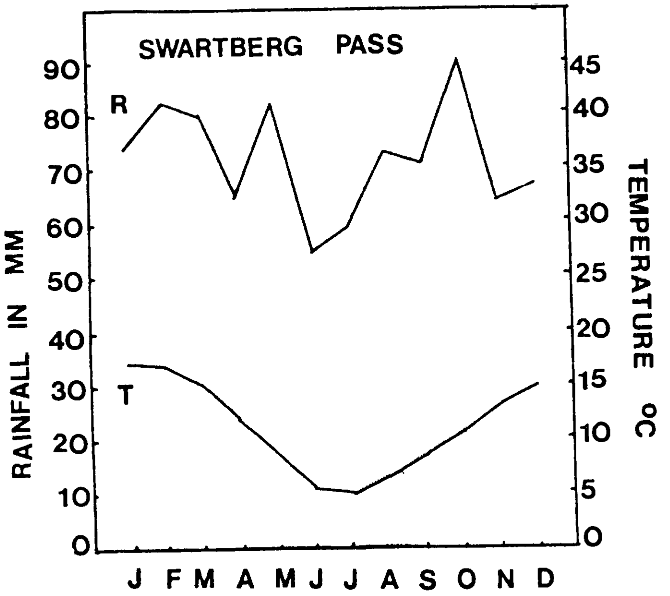


Fig. 2. Climograph for Swartberg Pass Rainfall Station.

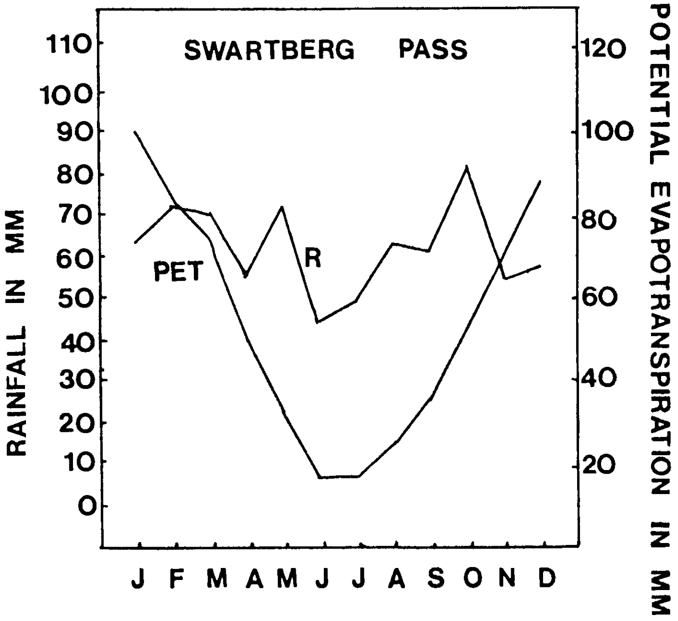


Fig. 3. Rainfall and estimated potential evapotranspiration for Swartberg Pass Rainfall Station

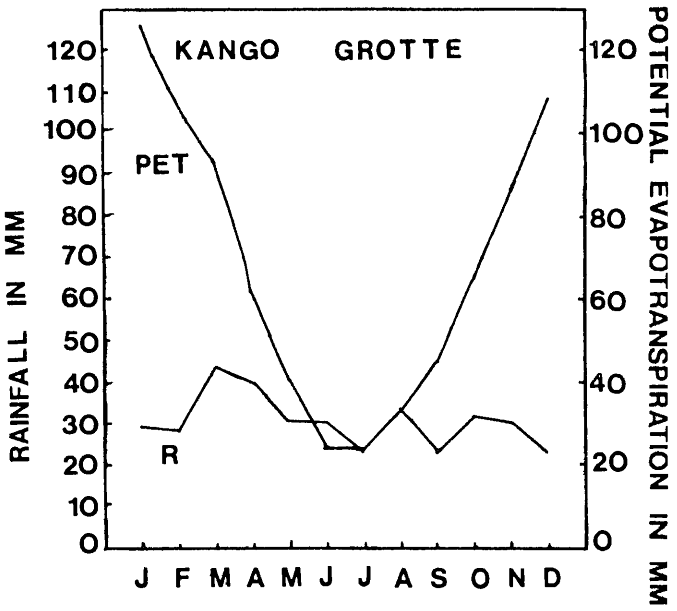


Fig. 4. Rainfall and estimated potential evapotranspiration for Kango Grotte Rainfall Station.

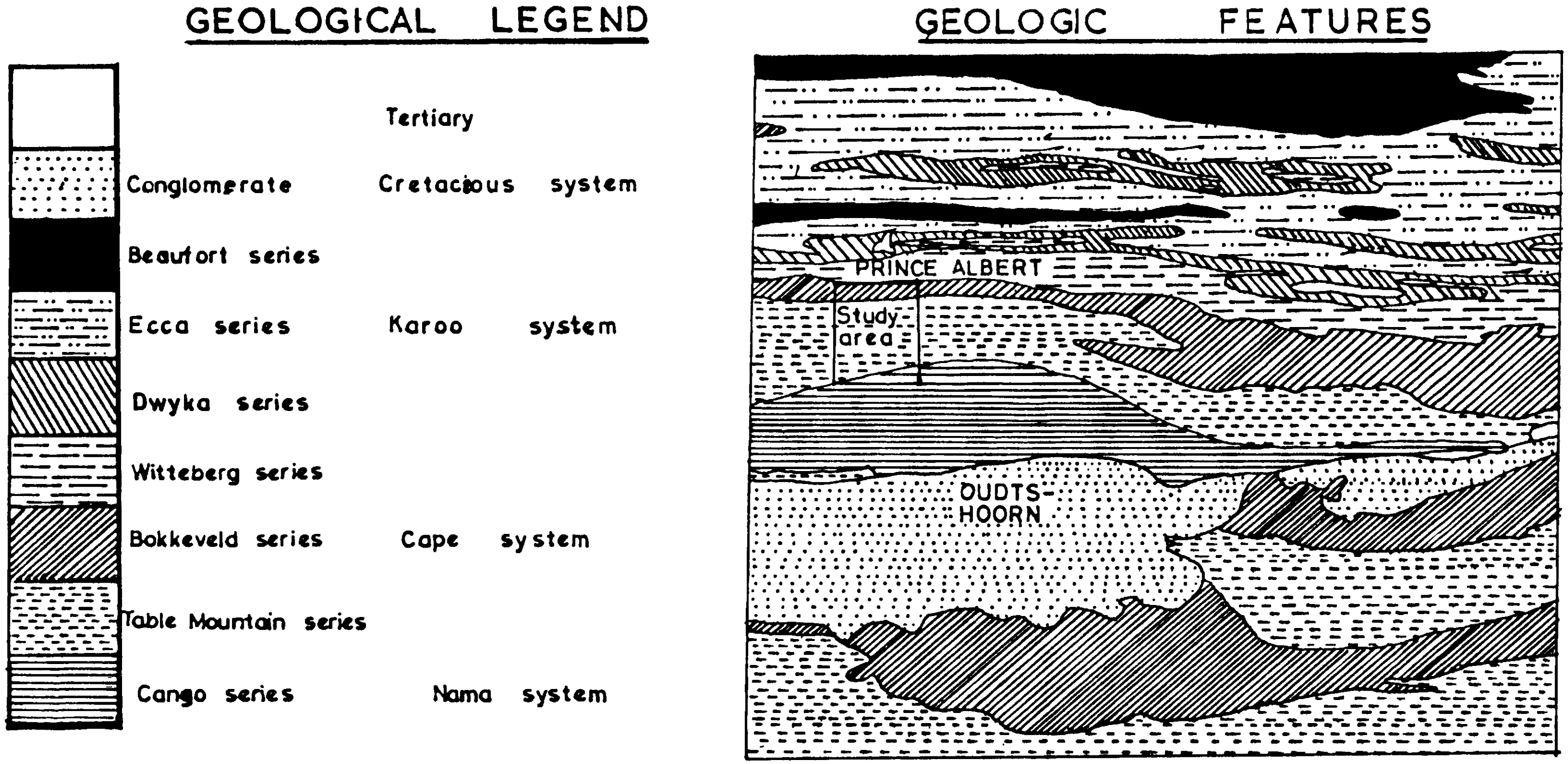


Fig. 5. Major geological features of the Swartberg and surrounds.

situated on the mountain massif which consists almost exclusively of quartzite, although narrow shale bands occur. The plains of the Great Karoo, consisting of sediments of the Karoo System, reach up to the northern foothills which are part of the Bokkeveld and Witteberg series. The mountain itself forms part of the Table Mountain Sandstone Series of the Cape system that dates back to lower Carboniferous and Ordovician times. To the south of the mountain the Cango Caves series adjoins the Bokkeveld series and the Enon conglomerates of Cretaceous origin (Truswell 1977).

Due to the northward directed folding, the southern slopes are very steep, rising from 850 m above sea level (a.s.l.) to 1900 m a.s.l. within 2 km. The northern slopes are also steep, and the whole mountain range is extremely rugged with high peaks and deep drainage lines. The Swartberg extends from east to west, and the major surface areas are therefore directed either to the north or the south. Within the study area the northern slopes are more rugged and eroded than the southern slopes.

SOILS

Studies of fynbos soils in the southern Cape are extremely limited, although Neethling (1970) has completed studies on the soils of the moist coastal plateau to the south of the Outeniqua mountains.

Soil conditions on the Swartberg were studied by Bond (1981). Soils on north facing slopes are mostly apedal loamy sands or sandy loams with pH from 4-6. There is minimal development of the B horizon and they are typically Mispah or Glenrosa forms. (Soils were classified according to the South African binomial system of MacVicar, De Villiers, Loxton, Verster, Lambrechts, Merryweather, Le Roux, Van Rooyen & Harmse 1977). Red soils occur on stable slopes and colluvial fans and are either Hutton or Oakleaf forms. Most of these soils had developed *in situ*.

A horizons of the soils on south facing slopes, however, normally have a stone line interface with B horizons which indicate a colluvial origin while B horizons developed *in situ*. These soils are deeper, darker and more acidic (pH3,5-5,5) than those on the north facing slopes. Soils are again loamy sand to sandy loam with red, yellow or dark brown subsoils. Bond (1981) recognised the following forms: Oakleaf, Hutton, Glenrosa and Clovelly.

VEGETATION

Acocks (1953) recorded four vegetation types in close proximity to the study area at Swartberg pass, viz. Succulent Mountain

Scrub (Spekboomveld), Karroid Broken veld, Succulent Karoo and False Macchia (Veldtypes 25,26,28 and 70). On the shales of the southern foothills Mountain Renosterveld occurs, but this was not mapped by Acocks (Veldtype 43).

Only two of these veld types were included in the present study: False Macchia, hereafter called Mountain Fynbos (Kruger 1977) and Spekboomveld. Fynbos is a vegetation type with a limited distribution in South Africa and has many ecological peculiarities. It is characterised by the presence of members of the Restionaceae family. Also normally present in fynbos communities, but not always so, are members of the families Ericaceae and Proteaceae. "Trees" are also generally absent from the fynbos landscape (Taylor 1978, Kruger 1979a). This definition of fynbos therefore includes only Acock's (1953) macchia, false macchia and coastal macchia, Veldtypes 69,70 and 47 (Taylor 1978, Kruger 1979a, Kruger & Taylor 1979). The fynbos biome as defined by Kruger (1979 b) also includes Acocks (1953) Coastal Renosterbosveld and Strandveld Veldtypes 46 and 34). According to Davis (1962) and Meester (1965) the Southwest Cape Biotic Zone corresponds with the distribution of Macchia veldtypes (Acocks no. 69, 70 and 47). Their maps however enclose the fynbos biome veldtypes as defined above as well as some Valley Bushveld, Spekboomveld and Karroid Broken Veld (Acocks 1953 veldtypes 23, 25 and 26).

The fynbos biome cannot be characterised by a specific climatic type. Fuggle & Ashton (1979), for example, were able to recognise ten climatic zones using Köppen's and Thornthwaite's climatic classification. Fynbos therefore grows under various climatic conditions but normally occurs on sites that receive at least 250 mm precipitation per year and a significant amount of winter rainfall (Kruger 1979c).

The limiting factor for true fynbos is not climatic as one would assume from the structural convergence that exists between Mediterranean type ecosystems, but the occurrence of nutrient poor soils (Kruger 1979c, Lampbrechts 1979) as is the case with related heathlands all over the world (Specht 1979).

Spekboomveld, the only other veldtype sampled on the Swartberg, is characterised by the presence of Portulacaria afra, abundant other succulents, and Poaceae as well as the low number of geophytes. Annuals and ephemerals which are not common in fynbos communities, were present. Deciduosity also occurred, but was largely limited to shrubs growing on termitaria. These shrubs frequently harboured parasitic epiphytes.

FAUNA

The fynbos fauna is not as unique as the flora (Weimarck 1941, Bigalke 1979 b, Jarvis 1979). Of greatest significance in the fauna is the presence of Gondwana relics, such as certain Coleoptera (Endrödy-Younga 1978), Lepidoptera and Odonata (Pinhey 1978 a & b), amphibians (Bigalke 1978, Poynton & Broadley 1978) and reptiles (Poynton & Broadley 1978, Bigalke 1979 b, Jarvis 1979). The only group within which recent speciation is thought to have taken place are anthophillous

Diptera (Bowden 1978). Even within the Formicidae which play a major role in the seed dispersal of some 1500 myrmecochorous plants (Bond & Slingsby 1981) endemism is extremely low (Prins 1978, Giliomee pers. comm.).

This low degree of endemism and generally low gamma diversity can probably be attributed to certain unique features of fynbos. Because of sclerophylly and low soil nutrients the fynbos plant communities offer very little in the form of high quality grazing and browsing (Joubert, Stindt & Perold 1969, Joubert & Stindt 1979 a & b, Stindt & Joubert 1979). The low soil fertility and absence of structural anti-predator devices suggests that secondary compounds should feature prominently. This has been confirmed by the work of Puttick & Glyphis (1980). The presence of such compounds have been used to explain the low species diversity in various other biomes (Janzen 1974).

That poor quality grazing and browsing may have an influence on the community is suggested by the general absence of folivores. Even the endemic lycaenid Lepidoptera are myrmecophilous. Lycaenid larvae are fed ant larvae by ants, and complete the larval stages of their life cycle within the ant nest (Cottrell 1978).

Larger mammals occurring in the study area include klipspringer (*Oreotragus oreotragus*), vaal rhebuck (*Pelea capreolus*), grysbok (*Rhaphicerus melanotis*), leopard (*Panthera pardus*), caracal (*Felis caracal*), Cape wildcat (*Felis lybica*) and Cape grey mongoose (*Herpestes pulverulentus*).

The mammal fauna of the Fynbos veld types in South Africa has not been studied in any great detail and it harbours a somewhat depauperate mammal fauna (Davis 1962, Meester 1965, Rautenbach 1978, Bigalke 1979). Only four species of small terrestrial mammals were considered as being endemic to the southwest Cape Biotic Zone (Meester 1965, Bigalke 1979). A new *Myosorex* species was however described from the area (Meester and Dippenaar 1978) and the specific status of *Acomys subspinosus* has now also been confirmed (Rautenbach pers.comm.). There are six small mammals endemic to the area, two of which occur in the study area: *Praomys verreauxii* and *Acomys subspnosus*.

Several small mammals that occur in the southern Cape were not collected during this study ie.

- *Saccostomus campestris*
- *Graphiurus ocularis*
- *Desmodillus auricularis*
- *Otomys laminatus*
- *Mus minutoides*
- *Graphiurus murinus*
- *Gerbillurus paeba*
- *Otomys irroratus*
- *Otomys saundersae*
- *Elephantulus rupestris*

Only 11 out of the known 25 species that occur in the southern Cape were collected during this study.

METHODS

HABITAT SURVEY

At each of the eight study sites trapping grids were placed out in homogenous habitats as set out in the introduction. The vegetation at each study site was named after the two dominant plants occurring in the plant community. Detailed structural and floristic classification of the plant communities was done by Bond (1981). The success of selecting homogenous habitats was tested by examining the distribution of captured small mammals on the trapping grids and determining whether irregular patterns (micro-habitat selection) in distribution existed.

Foliage density and diversity

Vegetation cover of a habitat was measured in terms of foliage profiles according to the technique of MacArthur and MacArthur (1961). The density of foliage cover in each 20 cm vertical layer of vegetation was estimated by means of cover density boards for the whole foliage profile. Cover density was estimated at 16 sample points per site. An assistant moved the board along a straight line away from the oberver until a given 20 cm sector was 50% obscured. The observer watched from a level at the midpoint of that sector, at the sample point (Fig. 6).

Sample points were located on the ground by using a set of random figures taken from a random figure table (x and y <20), each point being located on the grid as follows:

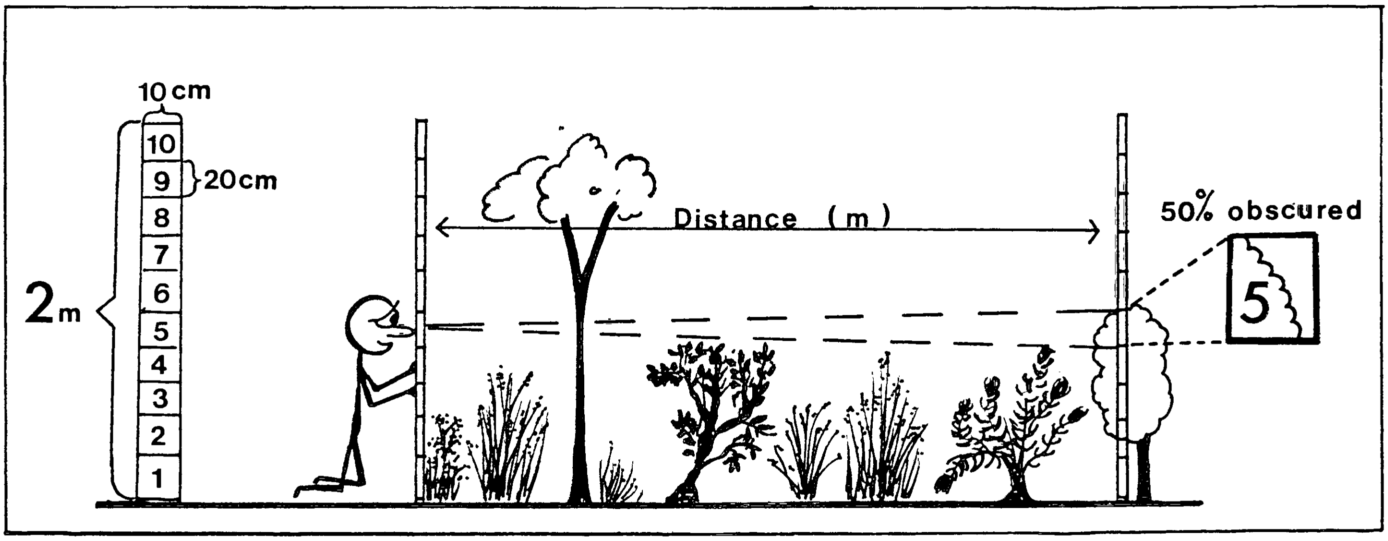


Fig. 6 Density board application in the field.

1. The observer would start at any corner of the grid.

2. The first point is then placed x metres along the long axis and y metres along the short axis of the oblong grids.

3. Consecutive points are then placed at x and y metres from the previous point. When the edge of the grid is reached the observer moves to an adjacent corner and the procedure is repeated.

To compensate for the possible effect of slope, observations were made either parallel to or at right angles to the slope.

The reciprocal of the distance measured is directly related to the horizontal density of the vegetation. The two boards were therefore not moved further than 20 m apart as the change in the density reading after this becomes very small (,05).

Using these data the following were calculated:

1. Foliage density (D_i). This is simply the mean of the reciprocals for all 16 points ($1/x$) at each height class. $D_i = \sum 1/x_i/N$ with x in metres. D_{20} therefore expresses foliage density between 0 and 20 cm and D_{2040}, the sum of the reciprocals between 0 and 40 cm. (i.e. height class 20 and 40).
2. Proportion of foliage (P_i or $P_{i,j}$) at a specific height class or between specific height classes. This was determined from $Di/\sum_{i=1}^{n} Di$ or $\sum Di,j/\sum_{i=1}^{n} Di$ the sum of the reciprocal between height classes i and j divided by the sum of the reciprocal for all height classes. The proportion of the foliage between height classes 0 and 80 cm (P_{2080}) therefore indicates that the reciprocals for the four heights between 0 and 80 cm were summed and divided by the sum of the reciprocals as measured over the whole profile.
3. Relative amount of foliage ($F_{i,j}$). This is the relative amount of foliage between height classes i and j and is the mean of the reciprocals between height classes i and j multiplied by the distance between those height classes in metres. For example if the reciprocal at 0-20 cm is 1,5 and that at 20-40 cm is 0,65 then F_{2040} equals (1,5 + ,65)/2)

(,4 - ,2) = 0,215 (after Rosenzweig & Winakur 1969).

4. Area under the curve (A_i). Foliage profiles were drawn using D_i for every height class and the integral determined using spline functions $\int_{xi=1}^{x} (x)^n dx$ (Greville 1969). This then allows the calculation of the area under various sections of the foliage profile (Hewlett Packard 9820A MATH PAC undated).

5. Horizontal variation (S_i). The standard deviation of actual distance measurements at each height class i was used as a measure of the degree of homogeneity in the horizontal distribution of vegetation at that height class.

6. Horizontal foliage diversity. An index of horizontal foliage diversity was calculated using the two categories 50 cm or 50 cm for the actual distances measured at each height class and by using the Shannon-Wiener index of diversity, H.

7. Vertical foliage diversity. This was determined by:

   1. $V = (P_2 + P_3)^3 (P_2^2 + P_3^2)$ following Rosenzweig and Winakur (1969) where $P_2 = F_{2060} / F_{20200}$ and $P_3 = $ $= F_{60200}/F_{20200}$.

   2. Shannon-Wiener diversity index H of reciprocals of each height class $(D_i)_{i=1}^{n}$ which expresses foliage height diversity (FHD).

   3. ΣD_i for the layers, below 20 cm, between 20 cm and 60 cm and above 60 cm. using a Shannon-Wiener diversity index H on these data.

Point survey

Ground cover was surveyed at each site by a sample of 100 points, made by walking along the contour at measured intervals (5 m between lines), establishing a point every five paces, and recording the nature of the ground cover at each point. The point was simply a mark made on the observers boot, and the object at this point was placed in one of the following categories: termite heap, litter, graminoid (including restios and sedges), bare soil, rock, (in one of the following cm diameter classes 0-3, 3-6, 6-12, 12-25, 25-50, 50-100, 100-200, 200-400, 400 and parent material) and others. All other plant growth forms were included in this last category, i.e. succulents, shrubs, forbs and trees. Habitat diversity for each site was estimated by determining the Shannon-Wiener index of diversity (H) of the data based on the above categories.

TRAPPING AND HANDLING OF SMALL MAMMALS

Two rectangular grids, ca 100 - 200 m apart, of 50 trap stations each were established at every trapping site. Each grid consisted of five lines, 10 m apart, with 10 traps to a line, and ca 5 m between traps, giving a grid area of ca 0,18 ha.

At each site one grid was used to collect data on movement, density and survival of small mammals, using Sherman live traps (23 x 8 x 9 cm). Victor mouse traps were used on the other grid to kill trap animals to obtain data on feeding patterns from the stomach contents as well as reproductive data. Grids on the southern aspect, e.g. site 1-4 were trapped simultaneously and grids on the northern aspect were trapped the following week. Trapping was done in winter, spring and summer in 1978 and autumn, winter and spring in 1979. For details of trapping periods see Appendix 1.

Since kill trap grids were not run as frequently as live trap grids, these data were not taken into account when density or trap success for each trapping period was determined.

Traps were baited using a mixture of rolled oats, peanut butter and lard. Traps were set for four days and nights and checked once every 24 hours, in the morning. Live-trapped animals were released at the point of capture after measurements had been taken (mass, total length, hind foot length, ear length). Animals were marked by toe clipping before release (Twigg 1975).

All data were entered directly onto field data sheets which included a calendar of captures record (see Appendix 2 and 3).

Density estimates

The techniques for estimating the population size of organisms from capture-recapture and capture-removal studies, their underlying assumptions and shortcomings have been regularly reviewed (Giles 1971, Southern 1973, Delany 1974, Otis, Burnham, White & Anderson 1978, and Begon 1979).

It was assumed that all members of the small mammal community had an equal probability of being captured. It was also assumed that there were no physical or behavioural responses to being captured, marked and handled such as trap avoidance developing, increase in subsequent mortality or animals becoming trap addicted.

Given these assumptions any of the most commonly used density estimation techniques (e.g. Schnabel, Schumacher-Eschmeyer and the Peterson or Lincoln population estimate techniques) were suitable (Giles 1971, Begon 1979).

Giles (1971) and Carothers (1973) found that the Schumacher-Eschmeyer technique gave better results (in test situations) and it was therefore used in preference to other techniques. One of the advantages of this technique is that it allows for unequal probability of capture over time by summing captures over all occasions (Otis et al 1978, Begon 1979).

Population size was estimated from:

$$N = \frac{M^2 n}{Mx}$$

where

N = estimated population size

M = number of marked animals

n = number of animals trapped

and X = number of marked animals in trapped sample n

If no animals are retrapped the population size obviously cannot be estimated. In such cases it was assumed that the animals captured represented the total population (see French, Grant, Grodzinski & Swift 1976).

The mean distance between successive captures of all individuals was determined for every species. Effective grid area was determined (Begon 1979) by adding this distance to the actual grid perimeter. If an animal was recaptured at the same trap site, the distance moved was taken as 0 m.

Diet

Stomachs of animals captured in kill traps were removed and preserved in 70% alcohol. In the laboratory the stomach contents was removed and washed through a plankton net with a 0,1 mm^2 mesh. Remaining particles were transferred to a petri-dish with a 1 mm^2 grid background and evenly dispersed over the dish. All particles occurring on an intercept of the grid were counted as a strike until 100 strikes were recorded. This is a variation (Moolman & Breytenbach 1976) of the modified frequency of occurrence method as used by Chamrod & Box (1964).

The items were identified as representing remains of foliage, insects or seed. If any finer identification of particles was possible this was noted. The following categories could be distinguished under certain circumstances:

Insect: Hymenoptera, Coleoptera. Isoptera (Nasutitermes could be distinguished from other groups), Orthoptera and Blatidae.

Seeds: Protea, Restionaceae

Vegetation: Roots, bark, leaves, stem.

STATISTICAL METHODS AND INDICES

General statistical procedures, such as Student's t test, chi-square test of association, Spearman's rank correlation and Pearson's r, were used, as indicated in the text (see Sokal & Rohlf 1969).

Diversity indices

Before the indices are given, it is necessary to define the various components of diversity examined in this study, and the ways in which they can be expressed. MacArthur (1965, in Krebs 1972 : 516) suggested that in order to analise latitudinal gradients in species diversity, two components of diversity should be recognised viz. "within-" and "between-habitat-diversity". These concepts have been refined and are at present defined as follows:

1. Alpha diversity or community diversity describes the diversity within a single homogenous habitat (Whittaker 1972, Peet 1974, Cody 1975, Southwood 1978 and Kessel 1979). (Figure 7).
2. Beta diversity describes species turnover between habitats (after MacArthur 1965), but it is now recognised that beta diversity is best expressed as the species turnover along a gradient. By doing this it is possible to show whether species turnover along the same measured gradient is similar for different eco-systems (Whittaker 1975, Cody 1975, Southwood 1978 and Kessel 1979). Cody (1975) for example has shown that bird species

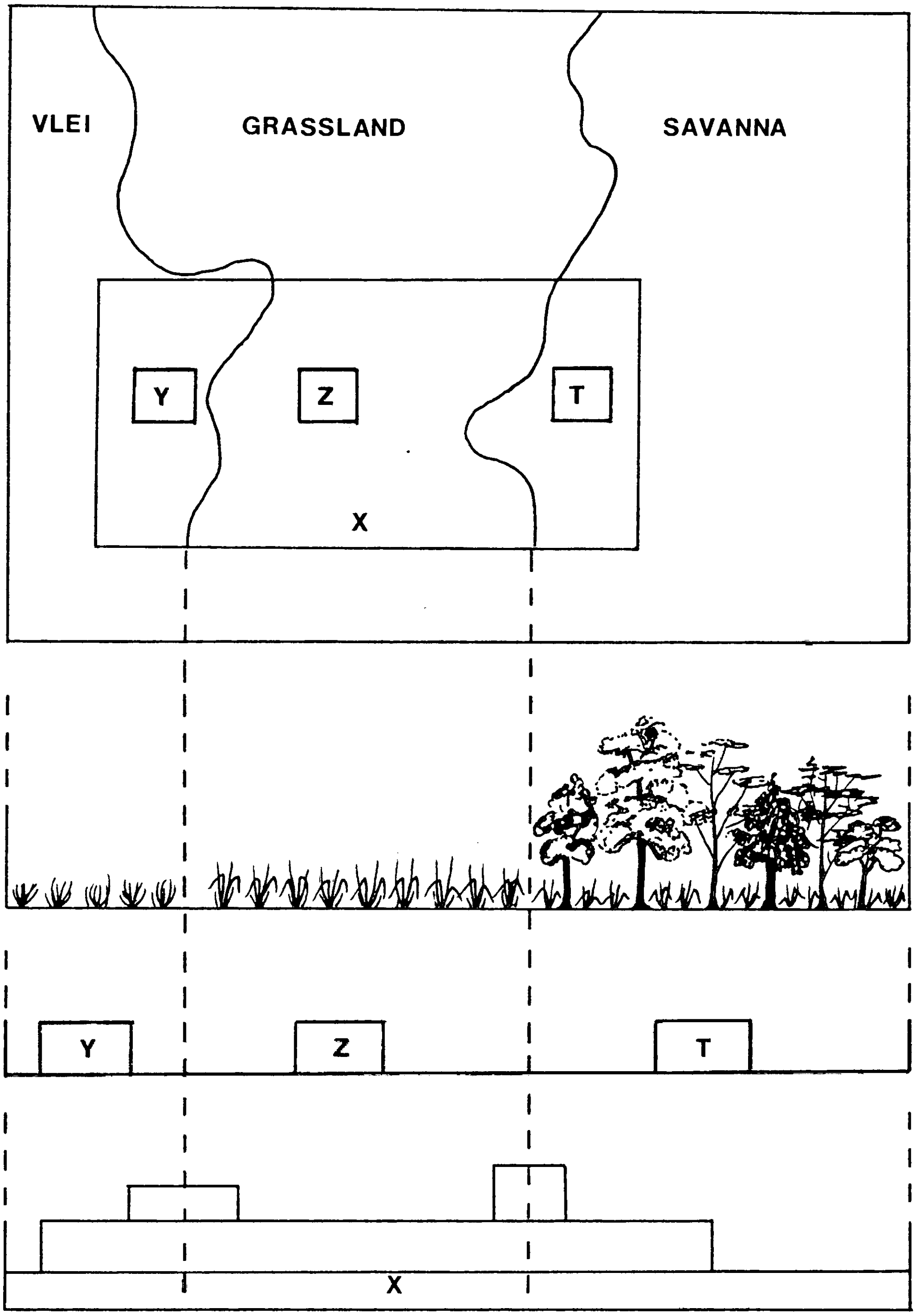


Fig. 7. Illustration of hypothetical grids sampling alpha and beta diversity. (Grids Y, Z and T sample alpha diversity only. Grid X samples both alpha and beta diversity.)

turnover in Mediterranean type ecosystems is fairly similar along a foliage profile gradient.

3. Gamma diversity describes diversity at landscape or ecosystem level and is therefore a function of both alpha and beta diversity (Whittaker 1975, Cody 1975, Southwood 1978 and Kessel 1979).
4. Delta diversity (not recognised by Cody 1975 or Southwood 1978) describes species turnover between similar habitats within the same landscape (Whittaker 1975).

Alpha diversity

According to Whittaker (1977) alpha diversity can be quantified as follows: The first is "... the number of species in communities or in samples of communities (diversity in this sense may also be termed richness)". The second is "that diversity is a synthetic characteristic comprising both richness and equitability (this concept may be termed mixed or total diversity)". Peet (1974) refers to this last concept as heterogeneity rather than diversity. Some authors restrict the term diversity to indices combining both number of spp. and equitability e.g. Krebs (1972). In this study, however, alpha and gamma diversity is expressed as diversity (richness and equitability) or as richness alone. Equitability expresses the uniformity of species abundances (Krebs 1972).

Peet (1975) has shown that most diversity indices respond dramatically to small changes in community composition.

When using these indices the following assumptions are made:

1. All individuals assigned to a respective class (or

species) are equal, irrespective of age and sex.

2. All classes or species, are assumed to be equally different (Peet 1974).

The Shannon-Wiener information function H was used to express alpha diversity:

$$H = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where H = index of species diversity

s = number of species

p_i = proportion of total sample belonging to the i th species (Shannon & Weaver 1949).

Beta diversity

The gradient along which sites were arranged was the density of foliage between 20 and 40 cm. It was decided to use this "resource" gradient as Bond _et al_ (1980) had shown that it has a strong influence on the alpha diversity of the Swartberg small mammals.

For comparison a matrix was drawn up showing beta diversity between all sites.

Beta diversity was determined by using Cody's (1980) species turnover

$$T = (Sl+Sg)/2$$

where T = turnover between consecutive sites along the gradient.

Sl = species lost

Sg = species gained

This method, however, ignores the combined species pool size of the two sites. A further index incorporating this facet was also used.

$$S = 2C/(A + B)$$

where S = similarity between samples
A = number of species in sample A
B = number of species in sample B
C = number of species common to both samples

This was changed to an index of dissimilarity I.D. = 1-S (Sörenson 1948). Species turnover between seasons for a single site was also determined by using the same two indices.

Gamma diversity

Gamma diversity was simply expressed as the number of species recorded.

Dominance indices

An index of dominance was used to estimate the degree to which a community was dominated by a few species

$$D = \sum (n_i/N)^2$$

where n_i = importance value for each species (this could be expressed either as number or biomass).
N = sum of importance values, n_i (Simpson 1949).

A further index of community dominance was used after McNaughton (1968).

$$Do = Y_1 + Y_2 / Y$$

where Y_1 = importance value of the species with the highest value

Y_2 = importance value of the species with the second highest value.

Y = sum of all the Y-values.

Ordination techniques and similarity indices

The relativized Czekanowski similarity coefficient as first developed in 1909 (Campbell 1978) was used to determine affinities between samples from all sites over all capture periods. The term sample is used throughout the study in the context of the results of a single trapping period from a single site. It was assumed that actual captures are indicative of community structure for each sample. The percentage difference between samples is determined by

$$PD_{jk} = 50 \mid X_{ij}/Q_j - X_{ik} / Q_k \mid$$

where PD_{jk} = percentage difference between sites j and k.

X_{ij} and X_{ik} = observed values (numbers, biomass) of species i in samples j and k, values being relativized between 0 and 1.

Q = the sum of the observed values of species i in the two samples

$$Q_j = \Sigma(X_{ij});\ Q_k = \Sigma(X_{ik}).$$

It was decided to use this technique since it is dominance weighted. Samples with the same dominant species would be identified as being more similar than a sample with the same species composition, but with a different species being dominant. (Campbell 1978).

Ordinations were done using the Bray-Curtis ordination technique

$$X_j = \frac{(DAJ + DBJ)\ (DAJ - DBJ)}{2\ DAB}$$

where X_j = is the location of site j on the ordination axis.

DAJ and DBJ = is the distance between site J and reference sites A and B.

DAB = is the distance between the two reference sites (Shimwell 1971).

Distance here refers to the degree of similarity between sites. Sites A and B, the reference sites, are selected so that they are greatly dissimilar (the two sites scoring lowest on similarity coefficient). (For a discussion of ordination, and classification techniques see Orlóci 1975, Weaver 1979 and Webster 1979).

Once an ordination has been done it is possible to do an indirect gradient analysis. The relative positions of sites on the various ordination axes can be subjected to correlation analysis and those environmental factors that are related to the positioning of samples can be identified (Collier et al 1973).

Index of species occupation

This is the number of capture periods that species were present at a site, expressed as a proportion of the possible number of times that all the species at that site could have been present.

This index was calculated from:

$$SO = \sum_{i=1}^{n} S_i / \sum |S| n$$

where S_i = number of species present at a site during a capture period.

$\sum |S|$ = the sum of species captured during all capture periods

n = number of capture periods.

CLIMATE

There is a paucity of climatic data for the montane regions of southern Africa. There are virtually no data on temperature or rainfall for the Swartberg. Rainfall, temperature and potential evapotranspiration therefore had to be estimated for each site.

Precipitation was estimated from an isohyetal map (Govt. Printer 1965) and from regression analysis. A number of rainfall stations occur within a 50 km radius of the study area. Data from these stations were used but a station had to comply to the following requirements before being included:

1. Records had to be available for at least a five year period.
2. The recording site had to be under the direct influence

of the Swartberg (mountain) orographic regime and therefore only sites that were within 10 to 15 km from the mountain itself were included. (See Appendix 4 for stations included).

As temperature data were not available, data from Kango Grotte (Weather Bureau meteorological station number 48/383) were used to estimate temperature for Swartberg (45/57) by using a lapse rate of 0,0055^{o}C·m^{-1} (Smith & Geller 1979).

Thornthwaite's (1948) method was used to estimate potential evapotranspiration for Swartberg (45/51) and Kango Grotte (48/383). This technique requires the estimation of a monthly heat index (I) from

$$I = (t/s)^{1,514}$$

where t = mean temperature of the month under consideration

s = slope.

These indices are then summed to give I, an annual heat index. Potential evapotranspiration (PE) is then calculated from

$$s = 1,6\ b\ (19t/I)^{a}$$

where s = monthly PE in cms.

t = mean monthly temperature in ^{o}C

a = cubic function of I

b = a factor to correct for unequal day lengths between months.

Without nomograms and algorithms computation is, however, complex (Ward 1967). Nomograms and algorithms have fortunately been developed and were used after Israelson & Hansen (1962).

Bond's (1981) drought index was also used to estimate the severity of drought stress (See Appendix 5). This index combines length and severity of drought into a single figure that varies between 0 and 1, with 1 indicating maximum stress.

RESULTS

ENVIRONMENTAL GRADIENTS

General site characteristics

The altitudinal range covered was almost 600 m. On the south facing aspect the slope varied from 10 to almost 50 degrees and on the north facing aspect it varied from 15 to 45 degrees.

Site characteristics are given in Table 2. For brevity the names given to the plant communities are abbreviated as follows.

Site 1. The *Protea repens* - *Phylica paniculata low* elevation shrubland to *Phylica paniculata* shrubland.

Site 2. The *Protea repens* - *Willdenowia teres* low mid- elevation shrubland to *Protea repens* shrubland.

Site 3. The *Protea punctata* - *Stoebe cinerea* upper mid-elevation shrubland to *Protea punctata* shrubland.

Site 4. The *Protea montana* - *Cliffortia robusta* high elevation heathland to *Protea montana* heathland.

Site 5. The *Leucadendron album* - *Cliffortia tuberculata* high elevation heathland to *Leucadendron album* heathland.

Site 6. The *Protea lorifolia* - *Willdenowia teres* upper mid-elevation shrubland to *Protea lorifolia* shrubland.

Site 7. The *Protea lorifolia* - *Paranomus dregei* lower mid-elevation shrubland to *Paranomus dregei* shrubland.

Site 8. The *Portulacaria afra* - *Crassula rupestris* succulent Karoo shrubland to *Portulacaria afra* shrubland.

Since the Gleasonian concept of a biological continuum was accepted for this study (Gleason 19.26) no attempts were made to classify the sampled vegetation types into communities. Nevertheless the following general trends in community structure were noted and are discussed in conjunction with Bond's (1981) structural classification of the plant communities.

On the lower north facing slopes the plant community was characterised by the presence of taller shrubs, small trees, succulents and sub-tropical grasses, all of which decreased with increasing altitude. This is equivalent to Bond's (1981) K1 - Succulent Karroid Shrubland. Only one site was sampled in this community (Site 8, the Portulacaria afra shrubland).

This community is gradually replaced by arid fynbos which occurs within a narrow altitudinal zone (1100 m a.s.l. to 1200 m a.s.l.) on the north slopes. It in turn is fairly quickly replaced by proteoid shrublands at approximately 1300 m a.s.l. Towards the top of the mountain, above 1400 m, the proteoid cover decreases and the community becomes heath like with ericoid plants becoming more abundant.

TABLE 2. General habitat features of trapping sites on the Swartberg.

Site	Altitude	Aspect and Slope	Topography and soils*	Vegetation
1	900m	South with an approximate 30° slope	Situated below small rock outcrop. There were few rocks of small size. The soil at this site varied between shallow to moderately deep Glenrosa and Oakleaf forms, with a pH of 5,1-5,2	Community: The *Protea repens*-*Phylica paniculata* low elevation shrubland The emergent layer is well developed. *Protea repens* and *P. eximia* form a distinct canopy between 1,5 and 2 m. *P.lorifolia* frequently and *Leucadendron salignum* less frequently forms a second distinct layer at approximately 1 m. Other prominent shrubs include *Phylica paniculata*, *Anthospermum aethiopicum*, several *Stoebe* spp., *Erica* spp., and *Agathosma* spp. The herbaceous layer is dominated by restios, e.g. *Willdenowia teres*, *Cannamois dregei* and *Hypodiscus striatus*.
2	1150	South; Slope approximately 10°.	Gently sloping with small isolated outcrops and almost no loose rocks and/or boulders. Soils are mostly shallow or moderately deep loamy sands (Glenrosa or Hutton forms) with a pH of 4,8-5,2.	Community: The *Protea repens*-*Willdenowia teres* lower mid-elevation shrubland. Emergent layer well developed, but with an open clumped appearance. Vegetation c.2,5 m tall with *Protea repens* and *P.punctata* common and isolated *P. eximia*. Microphylls contribute the major cover to this layer. The field layer is not continuous and consists mostly of *Willdenowia teres*, *Cannamois dregei*, *Hypodiscus striatus*, *Cliffortia tubercula* *Metalasia muricata*, *Stoebe plumosa* and *Protea lorifolia*.
3	1220	South with an approximate 35° slope.	Steep, with some loose rocks, large isolated boulders and T.M.S. outcrops. Soils are normally moderately deep loam sands (Oakleaf or Hutton forms) with a pH of 4,8-5,5	Community: The *Protea punctata*-*Stoebe cinerea* upper mid-elevation shrubland. Site with best developed emergent layer, consisting almost exclusively of *Protea punctata*. *P.eximia* and *P. lorifolia* are also present. Field layer is dense with *Cliffortia tuberculata*, *Stoebe cinerea* and *Anthospermum aethiopicum* contributing the greatest cover.
4	1600	South with an approximate 40-50° slope	Very steep upper slope with T.M.S. outcrops, loose boulders and rocks. Soils are shallow (Mispah or Clovelly forms), with a pH of 4,1-4,6.	Community: The *Protea montana*-*Cliffortia robusta* high elevation heathland. Emergent layer almost absent with *Protea punctata* as the only emergent species. It reaches a height of c.1,75m. Field layer well developed and almost continuous, with the procumbent *Protea montana* common in this layer. *Erica* spp., dominate this layer with *Cliffortia robusta* also prominent.

Site	Altitude(m)	Aspect and slope	Topography and soils*	Vegetation
5	1460	North slope is approximately 20°.	Steep upper mid-slope with some loose rocks and a few boulders. Outcrops almost totally absent. Loose stones are, however, fairly common. Soils are moderately deep sandy loams (Mispah or Clovelly forms) with pH 4,2 - 4,3.	Community: The Leucadendron album- Cliffortia tuberculata high elevation heathland. Emergent layer poorly developed, low average height c. 1,75-2 m. Protea punctata and Leucadendron album major contributing species. Protea repens and P. lorifolia are also present. Field layer low but continuous consisting almost exclusively of ericoid and restioid growth forms. Cliffortia tuberculata and Hypodiscus synchroolepsis are the most common species in this layer.
6	1400	North with the slope approximately 20°.	Steep boulder-stream mid-slope just above plateau. Boulders common, rocks present and some T.M.S. outcrops. Soils are rocky loamy sands, shallow (Mispah or Glenrosa forms) with a pH 5,0-5,7.	Community: The Protea lorifolia-Willdenowia teres upper mid-elevation shrubland. Emergent layers well developed but open with Protea lorifolia and P. repens being the major contributing species reaching a height of 2,5-3m. Field layer consists largely of Restionaceae with Willdennowia teres and Hypodiscus striatus prominent. Ericoid elements are also present and Agathosma mundii and A. capensis are also common.
7	1280	North-north west, slope 15°.	Steep, very rocky slope below ridge of T.M.S. outcrop. Soils are shallow and sandy (Mispah form) with pH 4,4-5,6	Community: The Protea lorifolia-Paranomus dregei lower mid-elevation shrubland. Emergent layer poorly developed and suppressed with Protea lorifolia and P.repens the major contributing species, reaching only c. 1,5 m in height. The field layer is open with vegetation in clumps. Prominent species included Paranomus dregei, Restio fruticosus, Willdenowia teres and Agathosma mundii.

Site	Altitude	Aspect and slope	Topography and soils*	Vegetation
8	900	North-north west, slope 45°.	Very steep, very rocky lower slope. Rocks small to large (5-30 cm diameter) rounded. Soils were shallow and stony (Mispah form) with pH 4,3-6,9.	Community: The Portulacaria afra - Crassula rupestris succulent karoo shrubland. Vegetation has a clumped, mosaic appearance with the taller shrubs and trees being largely limited to termite mounds. Species occurring on these mounds were taller than surrounding vegetation, tended to be non-succulent and reached some 2 to 3 m in height. Major species contributing to this layer included Euclea undulata and Rhus glauca. Interspersed between these taller vegetation islands are succulents and grasses (tropical rather than temperate fynbos types): Portulacaria afra, Crassula rupestris, Pteronia incana, Eriocephalus africana, Aloe ferox, Cotyledon sp., Digitaria natalensis and Aristida diffusa. Geophytes were also common.

* Soil description from Bond 1981.

Bond (1981) identified two communities above his K1 type, an A1 S, which was Arid Fynbos and a R1 S, Restioveld. Site 7, the *Paranomus dregei* shrubland, was in the transitional zone between these two communities.

Site 6, the *Protea lorifolia* shrubland, differed from the plant community at Site 5, the *Leucadendron album* heathland, in the following ways; it had a greater cover of tussocked restio species growing quite tall (1 m) and a tall proteoid cover (2 - 3 m) whereas site 5 had shorter restio and proteoid cover, with proteas rarely exceeding 1,5 m in height.

The emergent proteoid component disappears on the south slopes and is replaced by procumbent species such as *Protea montana*. As altitude decreases, at about 1600 m a.s.l., the emergent proteas reappear. Site 4, the *Protea montana* heathland was in this transitional zone with both emergent and procumbent *Protea* spp. This site was placed in the transition between Bond's (1981) H1 S, High Montane Heathland and his P1 bS, Mesic Proteoid Shrubland with a heathy understory.

The emergent layer rapidly increases in height and density with decreasing altitude, reaching a height of 3 m at site 3, the *Protea punctata* shrubland, which falls within Bond's (1981) P1 bS type. Further down the slope (below 1200 m) the proteoid cover opens up and restio cover increases while the ericoid cover decreases.

Site 2, the *Protea repens* shrubland, fell within Bond's (1981) P1 bS community (a drier version of his P1 aS community).

Towards the bottom of the mountain, below 1100 m a.s.l., the grass component of the vegetation increases and Protea nitida appears on the steeper slopes. Site 1, the Phyllica paniculata shrubland was in the transitional zone with a P. nitida community above it on the steeper slopes, but it was still in Bond's (1981) Pl S communities.

Generally proteoid cover only starts to develop above 1100 m a.s.l. on the north facing slopes, increases in size and density up to 1400 m a.s.l. and then decreases to the crest of the mountain, and disappears at the uppermost peaks. On the south facing slopes emergent proteoid cover is present from the foot of the mountain, at 850 m a.s.l. up to approximately 1600 m a.s.l. Sub-tropical shrubs, trees and grasses occur predominantly on lower north facing slopes, below 1100 m a.s.l. and are only present on the south slopes below 850 m a.s.l. or on alluvial deposits up to 1100 m a.s.l. Restioid cover is generally higher on north facing slopes than on south facing slopes and ericoid heathland is dominant at high altitudes, above 1600 m a.s.l.

Foliage profiles

Foliage profiles describe the vertical distribution of foliage at 20 cm intervals along a horizontal plane and could probably be used as a surrogate measure of plant biomass. The results from the survey are given in Appendix 7. Various measurements and derived profile parameters are given in Table 3. The foliage profiles are illustrated graphically in Appendix 6 with accompanying photographs of habitats with density boards in the foreground.

TABLE 3. Density of foliage and various other derived foliage parameters and the location of sites on the X and Y axis of a Bray-Curtis ordination based on foliage density measurements of the various sites.

Site	Plant Community	Density of foliage in various height classes (D_i) in cm.				Proportional cover (P_i) at various height classes in cm.			Total area under cover	FHD	½H	Bray-Curtis ordination location on X and Y axis	
		20	40	60	80	20	40	60					
1	Phylica paniculata shrubland	1,2	1,1	0,88	0,59	0,21	0,19	0,15	127,8	1,52	55,8	-22,7	-22,0
2	Protea repens shrubland	2,32	1,07	0,7	0,58	0,39	0,18	0,12	140,9	1,57	32,1	-41	-6,8
3	Protea punctata shrubland	3,04	1,15	0,44	0,36	0,5	0,19	0,07	151,1	1,32	25,0	72	6,9
4	Protea montana heathland	3,9	1,01	0,34	0,2	0,66	0,17	0,06	157,1	1,23	19,8	22,7	18,0
5	Leucadendron album heathland	2,85	0,58	0,26	0,15	0,66	0,13	0,06	115,7	1,15	20,7	21,7	17,5
6	Protea lorifolia shrubland	2,57	0,62	0,44	0,4	0,35	0,14	0,1	151,2	1,55	30,3	- 2,6	- 4,6
7	Paranomus dregei shrubland	2,35	1,32	0,9	0,77	0,38	0,22	0,15	146,6	1,57	36,4	- 3,2	- 9,7
8	Portulacaria afra shrubland	1,61	1,12	0,54	0,3	0,38	0,27	0,13	100,2	1,55	31,8	- 1,8	- 3.7

The results of the various calculated measures of density of the foliage profiles (Appendix 6 e.g. D_i , F_i and Area under the drawn foliage profile) are all highly intercorrelated. For example the total area under the drawn foliage profile and the sum of actual density measures for all heights were correlated ($r = 0{,}902$; $p < {,}01$).

Sites at which the emergent layer was well developed (in height and/or in density) generally had a greater area under the drawn foliage profile curves than sites at which this foliage layer was poorly developed. The Protea punctata and Protea lorifolia shrublands (Sites 3 and 6) ranked second and third in this regard. Those communities in which this layer was sparse or absent, ranked low (e.g. the Leucadendron album heathland and Portulacaria afra shrubland, Sites 5 and 8). The exception to this general trend was the Protea montana heathland (Site 4). In this community the emergent proteoid layer was poorly developed, yet it had the greatest area under the drawn foliage profile curves. The ground layer in this community was extremely dense and exceeded the density of the foliage in the 0 - 20 cm layer at other sites by between 27% and 69%. Since this layer also contributed between 21% and 66% to the total foliage profile at all the sites, the high ranking of the Protea montana heathland (Site 4) as regards area under the foliage profile, is not surprising.

The height at which the foliage profile could be cut, at a horizontal plane, so that the two areas so achieved would be equal, was calculated. This is ½ height (½H terminology following Cody 1975).

½H was also not directly related to the emergent layer. At the Protea punctata shrubland for example the emergent layer was well developed, but the low shrub layer was also dense and more than 70% of the total area under the drawn foliage profile curve occurred below 80 cm. As can be seen from Table 3 half the area of the drawn foliage profile curves occurred within the first two height classes (D_{20} 0 - 20 cm and D_{40}, 20 - 40 cm) in all the communities except the Phylica paniculata shrubland, where it was in the 40 - 60 cm (D_{60}) height class. Thus area under the profile increased, but was compressed into the bottom layers, with increasing altitude (Figs. 8 a and b).

The density of the foliage in the 0 - 20 cm layer (F20) was highest in the three communities in which the ground layer was dominated by ericoid growth forms, that is at the two heathland communities (Sites 4 and 5) and the Protea punctata shrubland community (Site 3). The contribution of this layer to the total area under the drawn foliage profile curves was more than 60% for the two heathland communities, 50% for the Protea punctata shrubland community, and was lower than 40% for all other communities.

There was an inverse relationship between profile density below 20 cm and that between 20 and 60 cm, (D_{20} and D_{4060}) ($r = -,768$ $p < 0,05$).

Foliage height diversity (FHD) as determined from the density of the foliage in all 20 cm height classes was lowest in the heathland communities (Sites 4 and 5).

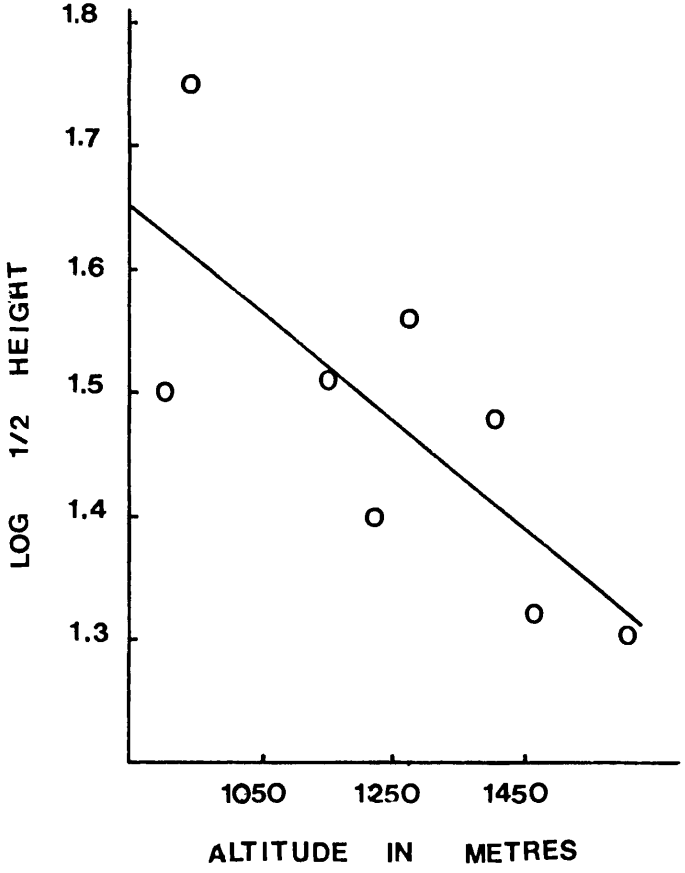


Fig. 8a. The relationship between log $^1/2$H of the foliage profile and altitude at Sites 1 - 8 on the Swartberg. (r = -0,75; y = 2,02-0,0004x.).

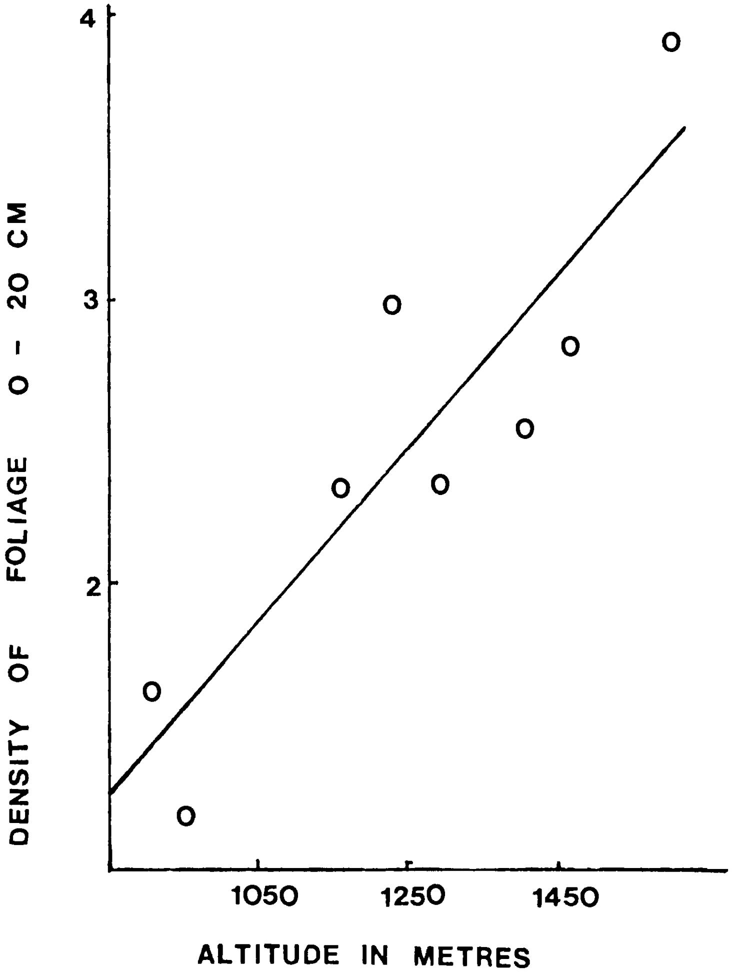


Fig. 8b. The relationship between the density of the foliage below 20 cm and altitude at Sites 1 - 8 on the Swartberg. (r = 0,895; y = 1,033 + 0,003x.).

Two ordinations for foliage profiles were done. The first was based on the densities measured for all height classes at all the sites. The two heathland sites (the *Protea montana* - and the *Leucadendron album* heathland, sites 4 and 5) were closely placed on the X-axis, as were the drier shrubland sites (The *Protea repens*-, *Protea lorifolia*-, *Paranomus dregei*- and the *Portulacaria afra* shrublands, sites 2,6,7 and 8) (Table 3). On the Y-axis, however, the *Phylica paniculata* shrubland was well separated from the other communities. This is due to the dense nature of the vegetation in this community in the 60 to 100 cm height classes.

The other ordination was based on the density of the foliage in the 0 to 100 cm height classes. Both axes gave similar results although differing from the first mentioned ordination. Regression of x on y gave $r = 0,999$ and $P < 0,001$. All the variation is therefore explained on the first axis.

Point survey

The results from the point survey are given in Table 4. Rockiness, as estimated, was between 30% and 67% higher at the *Portulacaria afra* shrubland (Site 8) and the *Paranomus dregei* shrubland (Site 7) than at any of the other communities sampled. On the south facing slopes there seemed to be an increase in rockiness with increasing altitude, while the opposite was true for the north facing slopes.

Bare soil cover showed less variation between sites. Between

TABLE 4. Percentage occurrence of rock, bare soil, litter, grass and "other" items as recorded in the point cover survey, as well as the location of sites on the X and Y axis of a Bray-Curtis ordination based on the survey data.

								Bray-Curtis ordination	
Site	Plant community	Rock	Bare Soil	Litter	Grass*	Other**	Habitat diversity	X axis location	Y axis location
1	Phylica paniculata shrubland	17	14	32	29	8	2.17	-23,5	3,1
2	Protea repens shrubland	23	11	27	28	11	2,21	-14,5	2,5
3	Protea punctata shrubland	20	9	25	11	35	2,16	-10,1	20,5
4	Protea montana heathland	35	4	21	12	28	2,07	7,6	5,1
5	Leucadendron album heathland	22	8	9	24	37	2,11	- 1,4	12,3
6	Protea lorifolia shrubland	17	4	34	33	12	2,04	-18,6	3,2
7	Paranomus dregei shrubland	51	5	16	21	7	1,88	10,2	-20,5
8	Portulacaria afra shrubland	58	3	9	16	14	1,74	23,5	-20,1

*Grass = Graminoid and includes Restionaceae, Cyperaceae and Poaceae.

** Other = Shrubs, herbs, trees and succulents.

3% and 14% of the points recorded fell into this category. Bare soil was recorded more frequently in the Phylica paniculata and Protea repens shrubland communities than elsewhere (Sites 1 and 2). Litter was recorded more commonly at sites with high proteoid cover, especially if Protea lorifolia was dominant in this layer. Litter was recorded more frequently in the Phylica paniculata - Protea lorifolia shrublands (Sites 1 and 6) than elsewhere. Litter was recorded at frequencies varying between 9% and 34% and was lowest in the Portulacaria afra shrubland and the Leucadendron album heathland communities. (Sites 8 and 5).

"Grass" cover, that is live plant cover with a graminoid growth form (including Poaceae, Restionaceae and Cyperaceae) made up between 1% and 33% of the cover at the sampled communities. There were no obvious trends between the various communities. Grass cover was below 20% at the Protea montana heathland, Protea punctata shrubland and the Portulacaria afra shrubland (Sites 4, 3 and 8). Grass cover seemed to be higher at sites where restios had a tussock growth form (Protea lorifolia, Protea repens and Phylica paniculata shrublands, Sites 6, 2 and 1).

"Other" plant growth forms were recorded at between 7% and 37% of the points in the sampled communities. These growth forms were recorded more frequently in communities with a heathy understory (the Protea montana-, and Leucadendron album heathlands and the Protea punctata shrubland, sites 4, 5 and 3).

To illustrate the relationship between degree of moisture stress and the percentage occurrence of "grass" and "other" growth forms, a three dimensional representation of the data is given in Fig. 9. "Grass" was more prevalent in the communities undergoing longer and more severe periods of moisture stress. (Bond's 1981 drought index, D_i, increases with increasing aridity).

A Shannon - Wiener index of diversity was determined for the data recorded in the point survey. This index of diversity may be interpreted as representing an index of habitat diversity. Habitat diversity was lowest in the Portulacaria afra shrubland (Site 8) and the Paranomus dregei shrubland (Site 7) communities. The low habitat diversity in these two communities can be attributed to the high rock cover recorded. Recorded habitat diversity varied between 1,74 and 2,21. Highest diversity was recorded at the Protea repens shrubland community (Site 2). The general trend in habitat diversity was one of decreasing diversity with increasing altitude on the south facing slopes and increasing with increasing altitude on the north facing slopes. There were therefore no consistent altitudinal trends in habitat diversity for the Swartberg as a whole.

The Bray - Curtis ordinations of the data showed a similar trend with communities on the two slopes being arranged in directly contrasting fashion on the X-axis. Those communities with a well developed emergent proteoid layer were closely grouped on the X-axis, as were the two heathland communities. Ordination on the Y-axis grouped the two low altitude communities of the north facing slopes close together (the Portulacaria afra -and the Paranomus dregei shrubland communities. When plotted the Protea punctata and Phylica paniculata south facing slope communi-

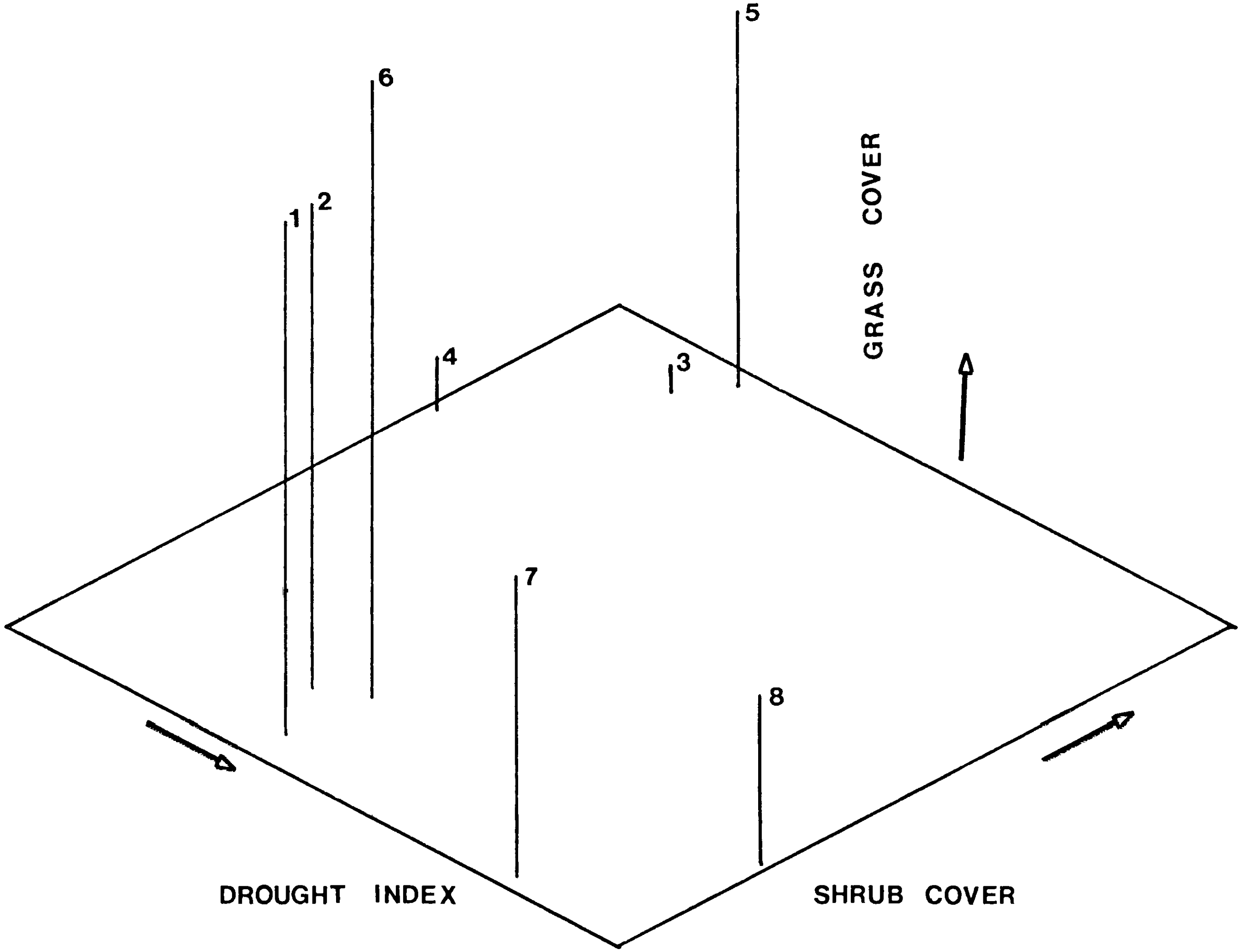


Fig. 9. Moisture availability and its effect on plant growth form on the Swartberg. There is an increase in shrub cover with decreasing drought. (Numbers indicate position of sites.).

ties were grouped with the Protea lorifolia community of the north facing slopes. (That is Sites 1,2 and 6). The two heathland sites were also fairly closely grouped (the Protea montana- and the Leucadendron album heathland communities, Sites 4 and 5).

Cover of various plant synusiae

Shrub cover was fairly high at all the sampled communities, varying between 70% and 90% (See Appendix 8). The shrubs were subdivided according to leaf size. Leptophyll cover was fairly high at all the south facing slope communities sampled, as well as the Leucadendron album heathland (Site 5), but was lower than at the other north facing slope communities. Nanophyll cover was less than 20% at all the sampled plant communities except at the Paranomus dregei shrubland (Site 7) where nanophyll cover was estimated to be 38%.

Microphyll cover increased from low to high altitude communities with the Phylica paniculata - and Protea punctata shrublands (Sites 1 and 3) having the highest microphyll cover (63% and 88% respectively). Mesophylls were scarce in the Protea montana heathland (Site 4) and absent in the Portulacaria afra shrubland (Site 8).

Succulents were common in the Portulacaria afra shrubland but scarce or absent from the fynbos communities. Succulents also occurred at high altitudes but were not a common feature in the heathland communities (Protea montana- and Leucadendron album heathlands).

Climate

The estimated altitude, rainfall, radiation and drought stress, expressed as a drought index, DI (after Bond 1981) for the different sites are given in Table 5.

The regression of rainfall on altitude is shown in Figs. 10 and 11. The rainfall isohyets (from the isohyetal maps, Govt. Printer 1965) did not show the rainfall shadow on the lower north facing slopes clearly. Rainfall at 900 m a.s.l. on the south facing slopes was between 500 and 550 mm per annum, and that on the north facing slopes for the same altitude was 450 mm according to the isohyets. Estimated rainfall from regression equations for this altitude, was 523 mm for the south facing and 342 mm for the north facing slopes.

The estimated rainfall in this latter case gave a far better impression of the actual situation as reflected by the plant communities e.g. at 900 m a.s l. on the south facing slopes fynbos plant communities occur while succulent karoo communities occur at the same altitude on the north facing slopes (irrespective of the angle of the slope).

TABLE 5. The altitude and estimated climatic data for each of the sampled communities.

Site	Plant community	Altitude	Rainfall Isohyets	Rainfall regression	Radiation Index	Drought Index *
1	Phylica paniculata shrubland	940	550	543,6	44,81	0,38
2	Protea repens shrubland	1150	650	651,8	48,4	0,38
3	Protea punctata shrubland	1220	700	687,9	46,88	0,25
4	Protea montana heathland	1600	850	883,8	44,3	0,15
5	Leucadendron album heathland	1460	850	811,6	56,7	0,28
6	Protea lorifolia shrubland	1400	750	653,4	51,66	0,39
7	Paranomus dregei shrubland	1280	550	578,7	55,24	0,63
8	Portulacaria afra shrubland	900	450	342	57,21	0,74

* from Bond 1981.

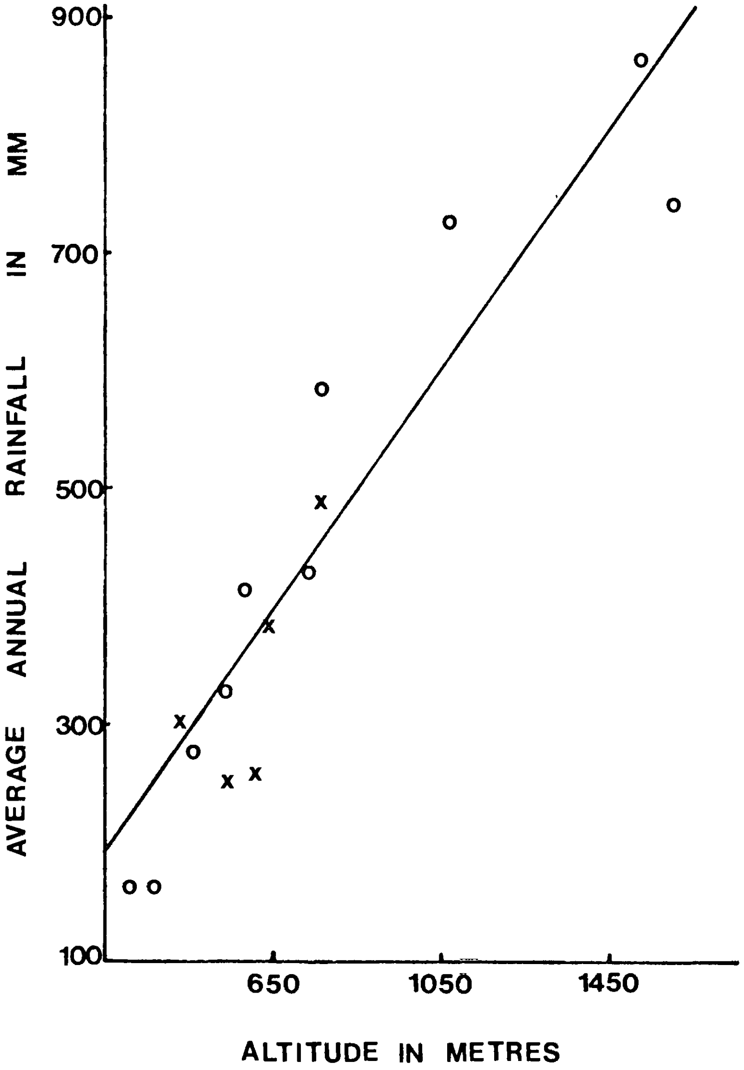


Fig. 10. The relationship between rainfall and altitude on south slopes. (r = 0,94; y = 59,05 + 0,515x.).

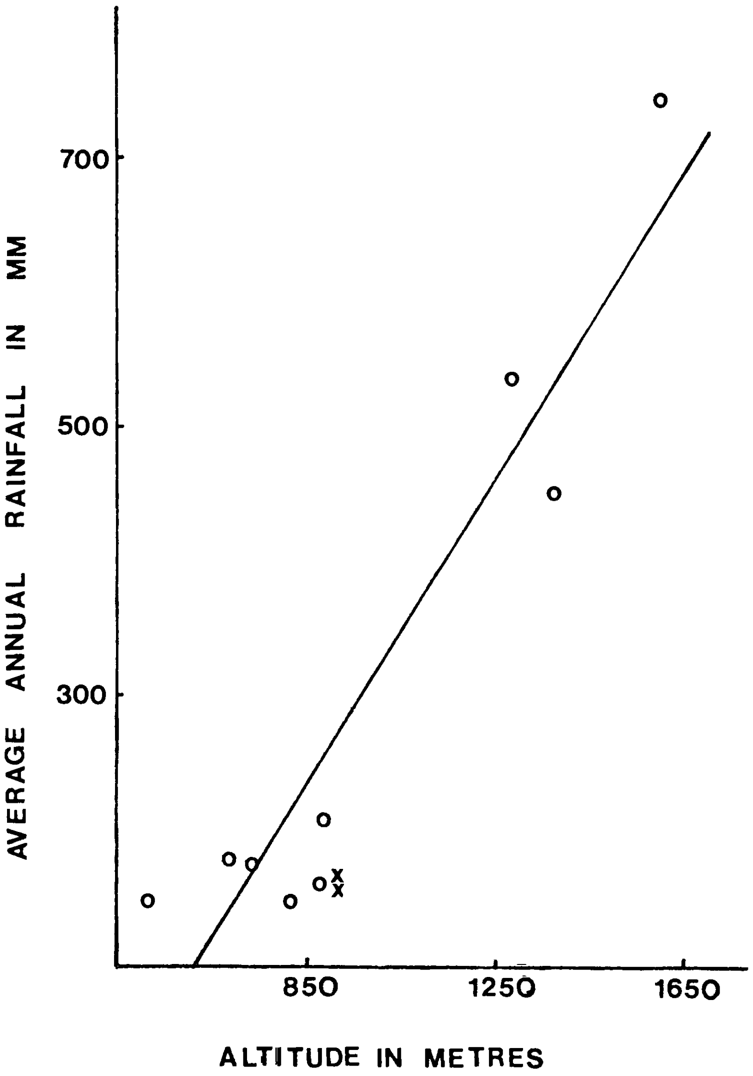


Fig. 11. The relationship between rainfall and altitude on north slopes. (r = 0,93; y = -218 + 0,622x.).

CAPTURE RESULTS

On the south facing slopes a total of seven small mammal species were captured. Only two species of Insectivora were captured (*E. edwardii* and *M. varius*). Five Rodentia were captured (*P. verreauxii*, *R. pumilio*, *A. subspinosus*, *O. irroratus*, and *D. mesomelas*). *E. edwardii* was not commonly captured on the south facing slopes, being present at two sites only. *M. varius* on the other hand was the most common species on these slopes. It was captured at all the sites with a total of 52 animals being captured. The most commonly captured rodent was *R. pumilio*, but it was only captured at three of the sample sites. Only *P. verreauxii* and *O. irroratus* were captured at all the sites. A total of 207 animals were captured during the various trapping periods. (Recaptures were not taken into account). No clear trends in species richness or in numbers captured were observed, generally however there seemed to be an increase in these parameters with an increase in altitude.

On the north facing slopes a total of 11 small mammal species were captured. In addition to the two species of Insectivora captured on the south facing slopes *Crocidura cyanea* was also captured. Similarly all the south facing slope rodents were captured on the north facing slopes as well as *D. melanotis*, *A. namaquensis* and *Petromyscus collinus*. The most commonly captured species on these slopes was *A. subspinosus*, a total of 55 individuals being captured. A total of 217 animals were captured on the north facing slopes. On these slopes there was a definite increase in species diversity and the number of animals captured with increasing altitude.

The north facing slopes therefore had more species and higher densities than the south facing slopes. None of the species were limited to the south facing slopes, but four of them only occured on the north facing slopes.

Small mammal community of the *Protea repens* - *Phylica paniculata* low elevation shrubland (Site 1).

Six species were captured in this community during the whole study period. The number of species present during any single capture period however varied between two and five. No single species was more numerous during all the sampling periods. Except for *E. edwardii*, each of the species captured were numerically dominant during at least one of the six capture periods. Over all the capture periods *R. pumilio* was the most common species, contributing 28,8% to the total number of animals captured. *M. varius* and *O. irroratus* contributed 24,5% and 22,1% respectively. *O. irroratus* and *R. pumilio* were only captured on four of the six trapping periods while *M. varius* was captured during all six. *P. verreauxii* and *A. subspinosus* were also recorded, but were present in low numbers only (Table 6).

Two insectivores were captured at this site. They constituted 25% of the total number of individuals captured during the study but only contributed 10,3% to the total biomass.

Because of its greater mass *O. irroratus* was the dominant species contributing 46,6% to the biomass over all capture periods,

TABLE 6. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 1. (The *Protea repens* - *Phylica paniculata* low elevation shrubland.)

Capture period	Trap success						Total small mammals					Rodentia only				
	Elephantulus edwardii	Myosorex varius	Praomys verreauxii	Rhabdomys pumilio	Acomys subspinosus	Otomys irroratus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	0,5	2	1	2,5	0	1,5	7,5	5	2,15	,93	292,2	5	3	1,49	,94	247,3
Spring 1978	0	0,5	0	0	1	0	1,5	2	0,92	,92	29,8	1	1	+	+	24,7
Summer 1978	0	0,5	0	0	1	1	2,5	3	1,52	,96	111,8	2	2	1,00	1,00	106,7
Autumn 1979	0	1	0	1	0	2	4	3	1,5	,95	208,5	3	2	,92	,92	198,3
Winter 1979	0	0,5	2	2	0	0,5	5	4	1,72	,86	191,9	4,5	3	1,39	,88	186,8
Spring 1979	0	1	0	1	0	0	2	2	1,00	1,00	44,5	1	1	+	+	34,3

followed by R. pumilio (25,4%) and P. verreauxii (13,2%).

There was a sharp decrease in the number of individuals trapped per 100 trap nights (hereafter referred to as percentage trap success) from the winter to spring sampling periods, both in 1978 and in 1979. The two winter sampling periods also yielded more species and higher species diversity H, both of which decreased sharply to the following spring sampling period.

Seasonality of captures was evident in certain species. O. irroratus was not present in two spring trapping seasons, and P. verreauxii was only present during the two winter trapping periods.

This was one of two sites where there was a correlation between species richness and the number of animals captured as well as diversity H and the number of animals captured (Pearson's $r = 0{,}968$, $p < 0{,}01$ and $r = 0{,}878$, $p < 0{,}05$) respectively. There was, however, no relationship between equitability and numbers captured.

Small mammal community of the Protea repens - Willdenowia teres lower mid-elevation shrubland (Site 2).

A total of four species were captured at this site. The number captured during a single season varied between two and four. Single species dominance was a feature of this community as 60% of the captures (over all capture periods) consisted of R. pumilio (Table 7). No clear seasonal trends in percentage

TABLE 7. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captures at Site 2. (The Protea repens - Willdenowia teres lower mid-elevation shrubland.)

Capture period	Percentage trap success				Total small mammals					Rodentia only				
	Myosorex varius	Praomys verreauxii	Rhabdomys pumilio	Otomys irroratus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978					NO TRAPPING									
Spring 1978	1	1	3,5	0,5	6	4	1,61	,81	209,9	4	2	,54	,54	199,7
Summer 1978	1,5	0	2,5	0	4	2	,95	,95	101,1	2,5	1	-	-	85,8
Autumn 1979	0,5	0	3,5	0,5	4,5	3	,99	,62	166,2	4	2	,54	,54	161,1
Winter 1979	0,5	0,5	0	0	1	2	1,00	1,00	24,4	0,5	1	-	-	19,3
Spring 1979	0	0,5	1	0	1,5	2	,92	,92	53,6	1,5	2	,92	,92	53,6

trap success occurred but there was a general decrease as the study progressed.

The number of *R. pumilio* captured was fairly high during the first three seasons but then declined sharply in the winter of 1979. Although only four species were captured at this site, a nest of *Dendromus mesomelas* was found within the grid and *A. subspinosus* was collected in a rocky area close by where the snap traps were set out. *M. varius* and *R. pumilio* were captured during four out of five trapping periods, *P. verreauxii* during three and *O. irroratus* during two.

Only one species of Insectivora was captured at this site (*M. varius*), which made up 26,5% of the total number of animals captured, but only 6% of the biomass. The species contributing most to the total biomass was *R. pumilio* (65,5%) which therefore dominated this *Protea repens* shrubland community both numerically and in mass.

Small mammal community of the *Protea punctata* - *Stoebe cinerea* upper mid-elevation shrubland (Site 3)

This community was characterised by its stability. Numbers and species composition stayed fairly constant over all capture periods. All five species present at this site were captured during at least five out of six trapping periods (Table 8).

Overall numerical dominance by a single species did not occur. Apart from *O. irroratus*, every species was most numerous during

TABLE 8. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 3. (The *Protea punctata* - *Stoebe cinerea* upper mid-elevation shrubland.)

Capture period	Percentage trap success					Total small mammals					Rodentia only				
	Myosorex varius	Praomys verreauxii	Rhabdomys pumilio	Acomys subspinosus	Otomys irroratus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	4	2	1,5	0,5	0,5	8,5	5	1,93	,83	222,9	4,5	4	1,75	,67	182,1
Spring 1978	0,5	1,5	3	0,5	0	5,5	4	1,62	,81	178,3	5	3	1,3	,82	173,2
Summer 1978	1	1,5	1,5	0,5	0,5	5	4	2,17	,93	173,0	4	4	1,81	,92	162,8
Autumn 1979	1	1	2	2	0,5	6,5	5	2,16	,93	207,8	5,5	4	1,82	,91	197,6
Winter 1979	2	2	0	2	0,5	6,5	4	1,85	,93	188	4,5	3	1,39	,88	167,6
Spring 1979	1,5	0	0,5	0	0,5	2,5	3	1,37	,86	73,5	1	2	1,00	1,00	58,2

one of the sampling periods. Over the whole study period M. varius contributed 28,9% to the total number of animals captured, while R. pumilio, P. verreauxii and A. subspinosus contributed a further 24,6, 23,1 and 15,9% respectively.

The highest number of small mammals were present in the winter of 1978, but the only real drop occurred during the final spring trapping session when trap success decreased from the previous season's 6,5% to 2,5%. Trap success also declined from the winter to spring 1978 sampling period, but the decline was less severe.

There was little variation in species richness over the study period but equitability varied from 0,81 to 0,93. Diversity was highest during the summer 1978 and autumn 1979 sampling period.

Only one insectivore (M. varius) was trapped at this site. It was the most common small mammal species, but only contributed 9,8% to the total biomass. P. verreauxii contributed the greatest biomass to the community (29%), followed by R. pumilio (28%) and O. irroratus (23%).

Small mammal community of the Protea montana - Cliffortia robusta high elevation heathland (Site 4)

A total of six species was captured at this site. The most species captured during a single season was five and the least three. O. irroratus totally dominated this small mammal community and R. pumilio was not captured here. O. irroratus was numerically dominant during four of six capture periods (44,9% of the total number of animals captured) and contributed most (nearly 77%) to the total biomass over all six sampling periods. *P. verreauxii* was only captured in winter and *M. varius* numbers declined from the first to the fourth trapping period (Table 9).

Two insectivores were present in this heathland community (*E. edwardii*, captured on two occasions, and *M. varius* captured during all six trapping periods). The Insectivora made up 30% of the total number of small mammals captured, but contributed only marginally to the total biomass of the community (9%).

One of the rarer species on the Swartberg, *D. mesomelas*, was captured in this plant community. Of the six species captured, three (*O. irroratus*, *M. varius* and *A. subspinosus*) were captured during all trapping periods.

Community composition was therefore stable and trap success did not fluctuate greatly, apart from a sharp decrease from the winter to spring 1979 sampling periods.

Small mammal community of the *Leucadendron album* - *Cliffortia tuberculata* high elevation heathland community (Site 5)

The large number of individuals captured, high species richness and lack of dominance by a single species characterised this community. Of the eight species captured, six were dominant or co-dominant during one of the capture periods. The number of species captured during a single capture period varied between two and seven (Table 10).

TABLE 9. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 4. (The <u>Protea montana</u> - <u>Cliffortia robusta</u> high elevation heathland.)

Capture period	Percentage trap success						Total small mammals					Rodentia only				
	Elephantulus edwardii	*Myosorex varius*	*Praomys verreauxii*	*Acomys usubspinosus*	*Dendromus mesomelas*	*Otomys irroratus*	Total traps success	Species richness	Species diversity H	Equitability E	Total biomass	Total traps success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	0,5	2,5	0	0,5	0	1,5	5	4	1,69	,84	135,4	2	2	,81	,81	185,4
Spring 1978	0,5	2	0,5	0,5	0	3	6,5	5	1,89	,81	277,7	4	3	1,06	,67	322,5
Summer 1978	0	1,5	0	0,5	0	2,5	4,5	3	1,35	,85	217,4	3	2	,65	,65	232,7
Autumn 1979	0	0,5	0	1	0	2,5	4	3	1,3	,82	229,9	3,5	2	,86	,86	235,0
Winter 1979	0	0,5	0,5	2,5	0	3,5	7	4	1,57	,79	375,8	6,5	3	1,3	,82	380,5
Spring 1979	0	1	0	0,5	0,5	0,5	2,5	4	1,92	,96	132,9	1,5	3	1,58	1,00	143,2

TABLE 10. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 5. (The Leucadendron album - Cliffortia tuberculata high elevation heathland.)

Capture period	Percentage trap success								Total small mammals					Rodentia only				
	Elephantulus edwardii	Myosorex varius	Praomys verreauxii	Rhabdomys pumilio	Acomys subspinosus	Dendromus mesomelas	Dendromus melanotus	Otomys irroratus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	0	2	1,5	5	3	0	0	0	11,5	4	1,85	,93	303,5	9,5	3	1,43	,9	323,9
Spring 1978	0,5	1,5	0,5	3	4	1	0	1	11,5	7	2,43	,86	317,8	9,5	5	1,96	,84	357,5
Summer 1978	0	2	0,5	3	2,5	0	0	2,5	10,5	5	2,17	,93	388,9	8,5	4	1,81	,9	409,4
Autumn 1979	0	1	0	2,5	2,5	0	0	2,5	8,5	4	1,92	,96	352,5	9,5	3	1,58	1,00	362,8
Winter 1979	0	1,5	1	0	0,5	0	0	0	3	3	1,46	,92	50,9	1	2			66,3
Spring 1979	0	0	0	0	1	0	1	0	2	2	1	1,0	35,3	2	2	1	1,00	35,3

A fire occurred just after the autumn 1979 sampling period. In spite of this P. verreauxii still reached its maximum density during the two winter capture periods. The M. varius population size remained constant over all pre-fire capture periods, but it disappeared three months after the fire had occurred. R. pumilio numbers declined steadily from the first to the fourth trapping period and it was not captured after the fire had occurred. O. irroratus also disappeared immediately after the fire. Of the eight species, only A. subspinosus was captured during all six capture periods. D. melanotis was only captured during the post fire period.

The fire had a considerable effect on the small mammal community. The mean number of species captured dropped from 5 to 2,5 per trapping period, while the biomass per 100 trap nights declined by 72% from 338,4 g to 50,8 g. A. subspinosus, P. verreauxii and M. varius all survived the fire, but it was only A. subspinosus that persisted. P. verreauxii and M. varius were not recorded three months after the fire.

During the pre-fire period two Insectivora were recorded (E. edwardii and M. varius). Together they made up 11,4% of the pre-fire population and 6% of the biomass.

Small mammal community of the Protea lorifolia - Willdenowia teres upper mid-elevation shrubland (Site 6).

The most outstanding feature of this community was the large number of species only captured during a single capture period (four out of seven species). Only one species, A. subspinosus was captured during all capture periods (Table 11). The mean number of species captured per trapping period was 3,5. This was the only sampled community at which more than two insectivores were captured and where *Crocidura cyanea* was collected. The three Insectivora made up 47% of the total numbers of the small mammal community and 20% of its biomass. The numbers of animals captured increased from summer 1978 to winter 1979. There was a positive correlation between number of individuals captured and species richness and diversity, respective Pearson r values being 0,94 and 0,98 ($p < 0,05$ in both cases). The number of *A. subspinosus* captured increased over the four capture periods, and it contributed 36% to the total number of individuals captured while *P. verreauxii* and *E. edwardii* contributed 28,9% and 13,3% respectively to the numbers captured.

Small mammal community of the *Protea lorifolia* - *Paranomus dregei* lower mid-elevation shrubland (Site 7)

The small mammal community of this shrubland was characterised by its low species richness (only three species), stability, presence of *Aethomys namaquensis* and high numbers of *E. edwardii*. The site was also burned after the autumn trapping period and as at Site 5 the subsequent trapping results were not taken into account when determining mean values (Table 12).

An average of 2,8 species was captured per trapping period. *E. edwardii* was trapped on all trapping periods and *A. namaquensis* and *A. subspinosus* were captured on four occasions. *A. namaquensis* numbers decreased during the study period whereas *A. subspinosus* numbers increased. There was only one member of the Insectivora

TABLE 11. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 6. (The Protea lorifolia - Willdenowia teres upper mid-elevation shrubland.)

Capture period	Percentage trap success							Total small mammals					Rodentia only				
	Elephantulus edwardii	Myosorex varius	Crocidura cyanea	Praomys verreauxii	Rhabdomys pumilio	Acomys subspinosus	Otomys irroratus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978										NO TRAPPING							
Spring 1978	0,5	0	0	2	0	0,5	0	3	3	1,25	,97	114	2,5	2	0,72	,72	89,6
Summer 1978	0,5	0	0	0	0	1,0	0	1,5	2	,92	,92	49,3	1	1	-	-	24,9
Autumn 1979	0	0	0,5	1,5	0	1,5	1,5	5	4	1,9	,95	223,4	4,5	3	1,58	1,0	217,9
Winter 1979	1,5	0,5	0	1,5	1,5	3,5	0	8,5	5	2,09	,9	274,3	6,5	3	1,46	,97	195,8
Spring 1979										NO TRAPPING							

TABLE 12. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 7. (The <u>Protea lorifolia</u> – <u>Paranomus dregei</u> lower mid-elevation shrubland.)

Capture period	Percentage trap success			Total small mammals					Rodentia only				
	Elephantulus edwardii	Aethomys namaquensis	Acomys subspinosus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	0,5	4,5	0	5	2	0,47	,47	233,1	4,5	1	-	-	208,7
Spring 1978	2,5	3,5	1	7	3	1,43	,9	309,4	4,5	2	,76	,76	187
Summer 1978	1,5	2,5	3	7	3	1,53	,97	263,4	5,5	2	,99	,99	190
Autumn 1979	0,5	1,5	3	5	3	1,33	,82		4,5	2	,92	,92	143,7
Winter 1979+	1,5	0	0,5	2	2	,81	,81	85,8	0,5	1	-	-	12,4
Spring 1979	NO TRAPPING												

at this arid shrubland community (*E. edwardii*) and it made up 20% of the number of individuals captured and 25% of the total biomass.

The fire that occurred had a marked impact on this community in spite of vegetated islands that did not burn occurring in the study area. *E. edwardii* numbers increased, *A. namaquensis* disappeared and *A. subspinosus* numbers declined. The impact would perhaps have been greater had all the vegetation been burned.

Small mammal community of the *Portulacaria afra* - *Crassula rupestris* succulent karoo shrubland (Site 8)

Only two species, *A. namaquensis* and *Petromyscus collinus* were present in this community, (Table 13) with the first species being dominant during all trapping periods. The number of *A. namaquensis* captured declined over the total study period after remaining nearly constant for the first three capture periods.

Seasonal trends in numbers of the different species captured in the study area for all sites combined

There were no apparent trends in the number of individuals captured for some of the species. *O. irroratus* and *E. edwardii* fall within this category. Mean trap success for *O. irroratus* was 0,9% and for *E. edwardii*, 0,33%.

TABLE 13. Percentage trap success, species richness, diversity and biomass (in grams) of small mammals captured at Site 8. (The *Portulacaria afra - Crassula rupestris* succulent karoo shrubland.)

Capture period	Percentage trap success		Total small mammals				
	Aethomys namaquensis	Petromyscus collinus	Total trap success	Species richness	Species diversity H	Equitability E	Total biomass
Winter 1978	4	0	4	1	-	-	185,5
Spring 1978	3,5	1	4,5	2	0,76	,76	177,3
Summer 1978	4	0	4	1	-	-	185,5
Autumn 1979	2	2	4	2	1,00	1,0	122,8
Winter 1979	1	0	1	1	-	-	46,4
Spring 1979	NO TRAPPING						

Only one of the species seemed to reach its highest densities in winter (*P. verreauxii*). A sharp decline was recorded for this species in both spring capture periods. Mean trap success for this species over all capture periods was 0,7%.

M. varius was most numerous during the first winter capture period (2,6% trap success). After this the numbers captured dropped sharply, reaching the lowest level in spring 1979. Mean trap success was 1,1%. Two of the species (*R. pumilio* and *A. namaquensis*) showed a steady decrease from the first to the last capture period, e.g. the trap success for *R. pumilio* decreased from 3% to 0,6%. Mean trap success for *R. pumilio* was 1,6% and for *A. namaquensis* it was 2,7%.

A. subspinosus on the other hand showed the opposite trend, increasing over the first five capture periods. Mean trap success for this species over all capture periods was 1,2%.

The percentage trap success at all sites combined decreased from 6,9% or 110 captures, to 4,8% or 77 captures per season. Within the whole Swartberg small mammal community the most prominent species during the various seasons were the following:
From the summer 1978 to winter 1979, *A. subspinosus* was the most commonly captured species, contributing 21% to the total numbers captured. In winter 1978 and spring 1979, *M. varius* was the most common species (24,1% and 39,8% respectively). In spring 1978. *R. pumilo* was captured most often (20,9% of the trapped animals).

The three species trapped most often during each season was determined and six species fell into this category on one or more occasions: *M. varius*, *P. verreauxii*, *R. pumilio*, *A. namaquensis*, *A. subspinosus* and *O. irroratus.*

Survival of individuals

Individual animals were not often recaptured during consecutive capture periods. The scanty data does however give an indication of the potential longevity of individuals (see Table 14).

These data should, however, be interpreted with caution. Some of the species such as *M. varius*, died more frequently in the traps than any other species. Because of differential trap mortality rates these data are therefore not directly comparable.

The number of *M. varius* surviving more than one season was ten. Taking into consideration that, of the almost 50 individuals captured, nearly 25% succumbed in the traps, it is remarkable that they still survived for such extended periods of time. One individual at Site 4 was present for nearly 12 months. The longest recorded period that individuals of each species survived were: *E. edwardii* 12 months (Site 7); *A. subspinosus* 12 months (Sites 3 and 5); *A. namaquensis* 15 months (Site 8); *P. verreauxii* 12 months (Sites 1 and 2); *R. pumilio* 15 months (Site 5) and *O. irroratus* 12 months (Site 4).

Effectiveness of trapping procedure

Species richness in the different plant communities

TABLE 14. The number of individuals of each species that were present at a site for two or more consecutive capture periods (or seasons) at each site.

	SPECIES							
	Site	Myosorex varius	Elephantulus edwardii	Acomys subspinosus	Praomys verreauxii	Aethomys namaquensis	Rhabdomys pumilio	Otomys irroratus
Present for more than two seasons	1	1	0	0	0	-	1	1
	2	1	-	-	0	-	2	0
	3	3	-	1	1	-	0	0
	4	1	0	1	0	-	-	2
	5	0	0	1	0	-	2	1
	6	0	0	0	0	-	0	0
	7	-	2	1	-	1	-	-
	8	-	-	-	-	3	-	-
Present for two seasons only	1	0	0	0	0	-	0	0
	2	0	-	-	0	-	0	0
	3	0	-	4	2	-	1	0
	4	2	0	0	0	-	-	3
	5	2	0	2	0	-	0	1
	6	0	0	1	0	-	0	0
	7	-	2	4	-	3	-	-
	8	-	-	-	-	3	-	-
TOTAL		10	4	15	4	10	6	8

The number of species and the consistency of their occurrence varied considerably between sample sites (Table 15).

The total number of species that occurred at a site varied between two and eight. The lowest number of species were recorded at Sites 7 and 8 which were representative of xeric north slope fynbos and spekboomveld. (The Paranomus dregei and Portulacaria afra shrublands). Most species were captured on the mesic north facing slope sites (Sites 5 and 6, the Leucadendron album heathland and the Protea lorifolia shrublands). The mean number of species captured per season at all sites varied between

TABLE 15 Number of species present at the various trapping sites during different seasons.

Site	Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Winter 1979	Spring 1979	Mean	No. of different spp captured
1	5	2	3	3	4	2	3,2	6
2	+	4	2	3	2	2	2,6	4
3	5	4	5	5	4	3	4,3	5
4	4	5	3	3	4	4	3,8	6
5	4	7	5	4	3^{++}	2	5,0	8
6	+	3	2	4	5	+	3,5	7
7	2	3	3	3	2^{++}	+	2,75	3
8	1	2	1	2	1	+	1,4	2
Mean	3,5	3,75	3,0	3,38	3,33	$2,75^{++}$		
No of different spp. captured	7	9	7	9	8	6		

$^{+}$ No sampling was done during the seasons marked.

++Fire occurred. Means calculated did not include these samples or samples collected subsequently.

three and 3,75, whilst the total number of species captured seasonally varied between seven and nine.

The increase in the number of species captured at each site during consecutive trapping periods is given in Table 16.

The number of capture periods required before all the species trapped at a site was recorded, varied considerably: at Site 4 and 5, for example, the full species complement was only reached after five seasons.

Almost three capture periods were needed (2,75) to record all the captured species at each site. When species were accumulated from the period when the lowest number of species was captured at each site, 3,75 trapping periods were required to record all species (Table 17). Of the 11 species captured overall, 9 were captured during the first two capture periods.

Persistence of a species in a community also varied. The index of species occupation (Table 18), shows that species seemed capable of maintaining themselves at some sites. At Site 3 (*Protea punctata* shrubland) for example, the five species recorded were present at the site for nearly 90% of the time. The mean index of species occupation was 0,66. This means that at all the trapping sites combined the recorded species were present at the sites for nearly 70% of the time.

TABLE 16. Number of new species captured at each site during consecutive trapping periods.

		Capture period						
Site	Plant Community	Winter	Spring	Summer	Autumn	Winter	Spring	Number of capture periods required to trap all species at a site.
1	Phylica paniculata shrubland	5	1	0	0	0	0	2
2	Protea repens shrubland	-	4	0	0	0	0	1
3	Protea punctata shrubland	5	0	0	0	0	0	1
4	Protea montana heathland	4	1	0	0	1	0	5
5	Leucadendron album heathland	4	3	0	0	1	0	5
6	Protea lorifolia shrubland	-	3	0	2	2	0	4
7	Paranomus dregei shrubland	2	1	0	0	0	0	2
8	Portulacaria afra shrubland	1	1	0	0	0	0	2

TABLE 17. The number of new species captured at a site during consecutive trapping periods, starting at that capture period when the lowest number of speceis were recorded.

Site	Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Winter 1979	Spring 1979	Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Number of capture periods required to trap all species at a site.
1		2	1	1	1	0	1				6
2				2	1	1	-	0	0		3
3		4	1	0	0	0	0				2
4			3	0	2	0	1	0			5
5				4	2	0	0	2	0		5
6			2	3	2	0	-	0			3
7					2	0	0	1	0	0	4
8	1	1	0	0	0	0					2

TABLE 18. Number of trapping sessions for which each species was recorded at every site. (For key to plant communities at each site see Table 17)

	Sites							
Species	1	2	3	4	5	6	7	8
Myosorex varius	6	4	6	6	5	1	0	0
Crocidura cyanea	0	0	0	9	0	1	0	0
Elephantulus edwardii	1	0	0	2	1	4	5	0
Otomys irroratus	4	2	5	5	3	1	0	0
Dendromus melanotis	0	0	0	0	1	0	0	0
Dendromus mesomelas	0	0	0	1	1	0	0	0
Petromyscus collinus	0	0	0	0	0	0	0	2
Rhabdomys pumilio	4	4	5	0	4	1	0	0
Acomys subspinosus	2	0	5	6	6	4	4	0
Aethomys namaquensis	0	0	0	0	0	0	4	5
Praomys verreauxii	2	3	5	2	4	3	0	0
Index of species occupation	,52	,65	,87	,61	,52	,54	,87	,7
Number of sampling periods	6	5	6	6	6	4	5	5

It is evident (see Table 18), that some sites (e.g. Site 3 and 7 the Protea punctata and Paranomus dregei shrublands) maintained their full species complement to a far greater degree than the other sites.

The rate at which new unmarked individuals were captured during consecutive days is shown in Table 19. The mean for all sites indicates that by day 2 nearly 75% of the total known population at a site had been captured, and by day 3 more than 90%. The number of animals re-captured also varied between sites (Table 20). By day four between 29% and 70% of the individuals had been captured more than once.

TABLE 19. Mean percentage of unmarked animals captured on consecutive days (standard deviation is given in parentheses) at each site during all the different trapping periods.

Site	Day 1	Day 2	Day 3	Day 4
1	41,6	25,6	20,3	12,3
	(19,9)	(15,4)	(13,7)	(12,9)
2	53,8	37,3	5,9	3,5
	(17,4)	(16,8)	(6,8)	(5,2)
3	42,9	26,8	14,4	16,1
	(16,0)	(8,6)	(15,4)	(14,3)
4	42,4	33,9	14,5	9,1
	(8,4)	(14,9)	(9)	(6,5)
5	35,5	27,6	22,3	13,8
	(6,4)	(13,1)	(11,9)	(10,9)
6	42,9	24,3	31,4	1,5
	(12,1)	(8,9)	(9,5)	(2,9)
7	47,7	31,4	15,3	5,6
	(19,7)	(14,7)	(13,6)	(6,9)
8	56,7	29,9	10,3	3,1
	(15,3)	(5,3)	(6,9)	(6,3)

TABLE 20. Mean number of animals (expressed as a percentage) recaptured during a single trapping period at every site (s represents standard deviation)

Site	Plant community	mean	s
1	Phylica paniculata shrubland	32,3	10,3
2	Protea repens shrubland	38,8	18,9
3	Protea punctata shrubland	29,9	11,8
4	Protea montana heathland	40,2	25,9
5	Leucadendron album heathland	52,9	33,0
6	Protea lorifolia shrubland	44,8	16,4
7	Paranomus dregei shrubland	60,3	27,2
8	Portulacaria afra shrubland	69,6	21,2

Body mass and breeding patterns

It was assumed that animals with a body mass lower than the mean mass for the particular species minus one standard deviation represented young animals, rather than adults suffering from malnutrition. The mean mass of each species was determined from both live and kill trapped individuals (Table 21).

TABLE 21. Mean mass (in grams) for several species of small mammals captured on the Swartberg mountains. (s represents the standard deviation and N the number of individuals).

Species	mean mass in grams	s	N
Elephantulus edwardii	49,8	7,4	39
Myosorex varius	10,2	3,2	154
Acomys subspinosus	24,7	3,1	144
Praomys verreauxii	38,6	7,4	102
Aethomys namaquensis	46,4	11,2	127
Rhab domys pumilio	34,3	5,4	219
Dendromus mesomelas	14,7	2,1	3
Dendromus melanotis	13,2	2,4	6
Petromyscus collinus	15,0	1,8	9
Otomys irroratus	82	11,7	132

The general trends in size (mass) classes of individuals of each species was examined using only the data from the live trap grids. The lowest mean mass of M. varius was recorded in winter 1978. Eight of the 21 M. varius captured then had a mass lower than 8 g (Table 22). During winter 1979, however, none of the animals had a mass below 8 g.

TABLE 22. Distribution of Mysorex varius individuals in various mass classes during consecutive capture periods in the Swartberg. (Only midpoint of mass class is given).*

Capture period	Midpoint of mass class in grams 4	5	6	7	8	9	10	11	12	13	14	>14	$\bar{x}$	N	sub-adults	median
Winter 1978	0	4	2	9	1	4	1	0	0	0	0	0	7,1	21	8	7,1
Spring 1978	0	0	0	1	1	2	4	0	1	0	0	0	9,5	9	0	9,8
Summer 1978	0	1	0	1	0	0	0	0	1	2	5	5	14,2	15	2	14,1
Autumn 1979	1	0	2	0	2	5	8	4	1	3	0	0	9,7	26	3	9,9
Winter 1979	0	0	0	0	4	3	7	4	1	1	2	0	10,3	22	0	10,1

*Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 10,2 ± 3,2 g. Individuals weighing less than 7 g were regarded as sub-adults.

The mean and median body mass was consistently lower during the cooler moister periods (winter, spring and autumn). Pregnant females were, however, captured throughout the year. (Three in winter, one in spring, two in autumn and one in summer). From the mean body mass, the distribution of the median and the number of sub-adults, it seemed that breeding probably occurred predominantly in winter and autumn, with some recruitment also occurring during the rest of the year. The number of foetuses recorded varied between four and six.

The mean and median body mass of P. verreauxii individuals was highest during the spring and summer capture periods (Table 23). Only three pregnant females were captured, one during the autumn and two during the winter capture periods. Three foetuses were found on two occasions and four on one occasion. The number of sub-adults captured was highest during the autumn trapping period. No sub-adults were captured during the spring and summer capture periods. It therefore seems as if recruitment to the population takes place during autumn and winter, in this species.

TABLE 23. Distribution of Praomys verreauxii individuals in various mass classes during the consecutive capture periods in the Swartberg. (Only midpoint of mass class is given).*

Capture period	Midpoint of mass class in grams 10	15	20	25	30	35	40	45	50	55	60	$\bar{x}$	N	sub-adults	Median
Winter 1978	0	0	0	1	3	3	0	1	0	0	0	32,6	8	3	32,5
Spring 1978	0	0	0	0	0	2	1	3	3	1	1	46,5	11	0	47,5
Summer 1978	0	0	0	0	0	0	0	3	1	1	0	46,6	5	0	47,5
Autumn 1979	1	1	0	1	3	0	4	0	0	0	0	29,7	10	5	31,6
Winter 1979	0	0	0	0	3	8	3	2	0	0	0	36,8	16	1	35,9

*Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 38,6 ± 7,4 g. Individuals weighing less than 31 g were regarded as sub-adults.

Mean body mass of R. pumilio individuals captured was highest in spring and summer (Table 24). Animals falling in or below the mass class with a midpoint of 20g were recorded in all seasons, except winter 1979. The median body mass, however, remained constant for both winter capture periods but was considerably lower in autumn and in winter than in summer. Pregnant females were not captured in summer. A total of 21 pregnant females were captured (11 in winter, eight in autumn and two in spring). The mean number of foetuses recorded was 4,5 (range 2 - 6). The presence of sub-adults and the low median and means in autumn and winter indicates that recruitment occurred largely in autumn and winter.

TABLE 24. Distribution of Rhabdomys pumilio individuals in various mass classes during the consecutive capture periods in the Swartberg. (Only midpoint of mass class is given.)*

Capture	Midpoints of mass class in grams														sub-	
period	10	15	20	25	30	35	40	45	50	55	60	65	$\bar{x}$	N	adults	median
Winter 1978	0	0	3	0	6	7	4	1	1	0	0	0	33,4	22	5	34,3
Spring 1978	2	0	0	0	2	1	4	5	3	2	1	0	44,8	20	3	44
Summer 1978	0	2	1	1	0	1	0	1	2	1	2	1	40,9	12	4	47,5
Autumn 1979	2	0	1	4	8	11	4	2	3	0	0	0	33	35	10	33,8
Winter 1979	0	0	0	1	4	6	2	0	2	0	0	0	35,6	15	2	34,9

*Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 34, 3 ± 5,4 g. Individuals weighing less than 29 g were regarded as sub-adults.

Eight pregnant A. namaquensis females were captured and the mean number of foetuses was 3,1 (range 2 - 4). Of the eight, three were captured in spring, one in summer, two in autumn and two in winter. Sub-adults were, however, recorded only in the winter of 1978 and autumn of 1979. The mean and the median body mass were highest in summer. Recruitment to the population therefore seemed to take place throughout the year, with lower numbers being added to the population in summer (Table 25).

There was no distinct seasonal pattern in the mean mass of A. subspinosus individuals or in the distribution around the median in mass classes (Table 26). The number of animals captured per trapping period increased during the whole study. From this one may conclude that recruitment was occurring throughout the study period. This is borne out by the mass data. Mean body mass of individuals decreased from the first to the last trapping session as did the mass class in which the median fell, although in the latter case the trend is not so clear. Pregnant females (8) were collected in snap traps (three in autumn, two in winter, one in spring and two in summer) and the mean number of foetuses was 3,1 (range 2 - 4).

TABLE 25. Distribution of Aethomys namaquensis individuals in various mass classes during the consecutive capture periods in the Swartberg. (Only midpoint of mass class is given).*

Capture period	Midpoint of mass class in grams 25	30	35	40	45	50	55	60	65	70	$\bar{x}$	N	sub-adults	median
Winter 1978	0	2	4	5	5	4	0	0	0	0	41,8	20	5	42
Spring 1978	0	0	0	1	7	3	0	1	1	0	48,3	13	0	46,7
Summer 1978	0	0	1	1	1	2	2	5	4	3	57,5	19	0	61,5
Autumn 1979	1	0	3	4	1	1	0	1	0	0	40,5	11	3	40
Winter 1979	0	0	0	0	1	3	1	2	0	0	51,1	7	0	51,6

*Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 46,4 ± 11,2 g. Individuals weighing less than 35 g were regarded as sub-adults.

TABLE 26. Distribution of Acomys subspinosus individuals in various mass classes during the consecutive capture periods in the Swartberg. (Only midpoint of mass class is given.)*

Capture period	Midpoint of mass class in grams 9	12	15	18	21	24	27	30	33	$\bar{x}$	N	sub-adults	median
Winter 1978	0	0	1	2	0	3	0	0	2	23,6	8	3	23,5
Spring 1978	0	0	1	3	3	3	1	0	0	21,5	11	6	21,5
Summer 1978	2	0	0	2	3	3	2	4	1	22,9	17	6	24,5
Autumn 1979	0	0	5	3	4	1	0	0	0	18,2	13	10	18,5
Winter 1979	0	0	3	9	11	3	1	0	0	19,9	27	17	20,1

*Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 24,7 ± 3,1 g. Individuals weighing less than 21 g. were regarded as sub-adults.

Mean and median body mass for O. irroratus were at their highest in the spring of 1978. Only two pregnant females were captured during the autumn of 1979. Both had three foetuses. The sub-adult population was at its highest during the winter of 1979 but sub-adults were present during all the capture periods except in the spring of 1978. The total population also increased in numbers over the whole capture period and the general impression was gained of reproduction taking place throughout the year. (Table 27).

Actual grid area trapped

The grid area occupied by the traps was similar for each site (40 x 45m, or 0,18 ha). The mean distance moved by individual animals between successive recaptures was used to determine the actual grid area trapped.

Mean distance moved by each species at each trap site was compared but no statistically significant differences between sites could be detected. Because of this, data were lumped for each species, and the mean distance so determined for each species was used as a perimeter area around the grid (Table 28). These data were used to determine density per hectare from capture recapture data and the actual area trapped.

TABLE 27. Distribution of Otomys irroratus individuals in various mass classes during the consecutive capture periods in the Swartberg. (Only midpoint of mass class is given.)*

Capture Period	Midpoint of mass class in grams																			$\bar{x}$	N	sub-adults	median
	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140				
Winter 1978	0	0	0	0	2	0	0	1	0	0	1	0	1	0	0	0	0	0	0	87,2	5	2	87,5
Spring 1978	0	0	0	0	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	101,9	9	0	107,5
Summer 1978	0	0	0	0	5	1	0	5	0	2	4	0	3	0	2	1	0	0	0	94,3	23	3	96,3
Autumn 1979	1	2	0	0	3	1	5	8	4	0	1	1	1	0	0	0	0	0	1	81,1	28	4	83,8
Winter 1979	0	0	0	1	2	3	0	3	2	1	0	0	1	0	0	1	0	1	0	99,7	15	2	85,8

* Mean mass for this species in the Swartberg (including individuals from the kill trap grids) was 82 ± 11,7 g. Individuals weighing less than 70 g were regarded as sub-adults.

TABLE 28. Mean distance (and standard deviation(s)) moved by recaptured individuals between successive captures for each species as well as the actual number of recaptures and the actual area trapped.

Species	Mean distance in m	s	N	Actual area trapped in ha
Elephantulus edwardii	24,4	15,5	7	0,446
Myosorex varius	21,1	10,3	41	0,404
X Acomys subspinosus	25,5	13,0	36	0,462
Praomys verreauxii	13,8	9,4	20	0,316
Aethomys namaquensis	17,6	11,9	47	0,361
Rhabdomys pumilio	21,2	13,8	46	0,405
Petromyscus collinus	12,5	3,5	2	0,302
Dendromus melanotis	18,5	-	1	0,371
Dendromus mesomelas	22,5	-	1	0,423
Otomys irroratus	17,6	8,1	23	0,361

In comparing species no definite trends could be detected in the mean distance moved by individuals during successive captures.

There seemed to be no difference between species using or those not using pathways, or between those from open and closed dense environments.

Diet

The small mammals in the Swartberg had species specific dietary requirements (Fig. 12). *A. subspinosus* and *P. verreauxii* feed predominantly on seeds, with *P. verreauxii* feeding largely on *Protea* seeds and *A. subspinosus* feeding extensively on Restionaceae, though some dietary overlap occurred.

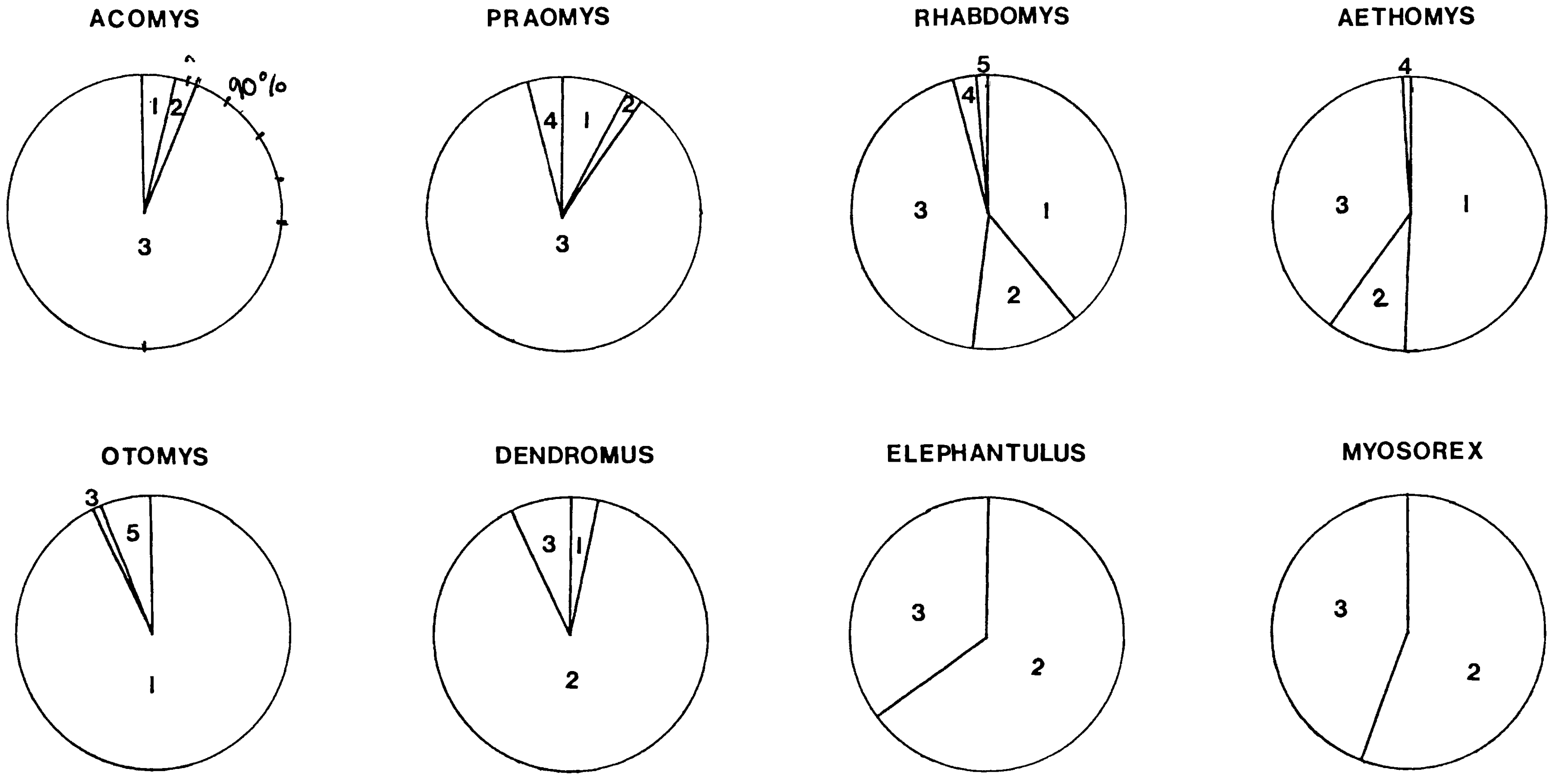


Fig. 12. The percentage contribution of green material (1), insects (2), seed (3), Protea seed hairs (4) and stem (5) to stomach contents of small mammal genera captured in the Swartberg.

O. irroratus fed extensively on green plant material such as leaves and stems, and in captivity it readily fed on bark and roots as well, which only occurred sporadically in the diet of free ranging animals. O. irroratus therefore specialises on a diet consisting almost entirely of green plant material.

A. namaquensis and R. pumilio were omnivorous with seed, green plant material and insect remains featuring prominently in their stomach contents. E. edwardii and M. varius stomachs contained seed and insect material. Seed remains occurred in fair quantities in their stomachs, throughout the year. No green plant material was found in their stomachs.

Only four stomachs of D. mesomelas were investigated and they all contained large amounts of insects. It was noted that a few stomachs of R. pumilio, A. subspinosus, A. namaquensis and E. edwardii contained feathers. Meat, however, was only recovered from one stomach.

Differentiation within food categories could be made in some cases. E. edwardii and M. varius for example, utilised specific invertebrates. M. varius fed extensively on the larval stages of Lepidoptera and adult Coleoptera, as well as general litter Arthropoda such as Blattidae. E. edwardii on the other hand occurred on the drier north facing slopes of the mountain where litter buildup is slow. Up to 90% of the insects found in some stomach samples of E. edwardii consisted of the soldiers of Trinervitermes spp. Workers were practically never found in the stomachs. The length of the post stomach digestive tract (the caecum was included when calculating the length of the gut), showed a correlation with the fibre content of the diet. In those small mammal species with a high fibre content diet (here taken as being green material, stem, bark and roots), the proportional contribution of the caecum to the post-stomach digestive tract increased (Fig. 13, $y = 9,2 + 3,82\ x$; $r^2 = 0,91$; $p < 0,01$). Similarly the proportional contribution of the large intestine also increased (Fig. 14, $y = 69,36 + 4,2\ x$; $r^2 = 0,799$; $p < 0,05$).

The proportional contribution of the small intestine to the total post-stomach digestive tract length increased with an increase in the protein content of the diet. (Protein is here assumed to be directly proportional to the amount of seed and insects in the diet). (See Fig. 15, $y = 82,4 + 2,3x$; $r^2 = 0,958$; $p < ,01$).

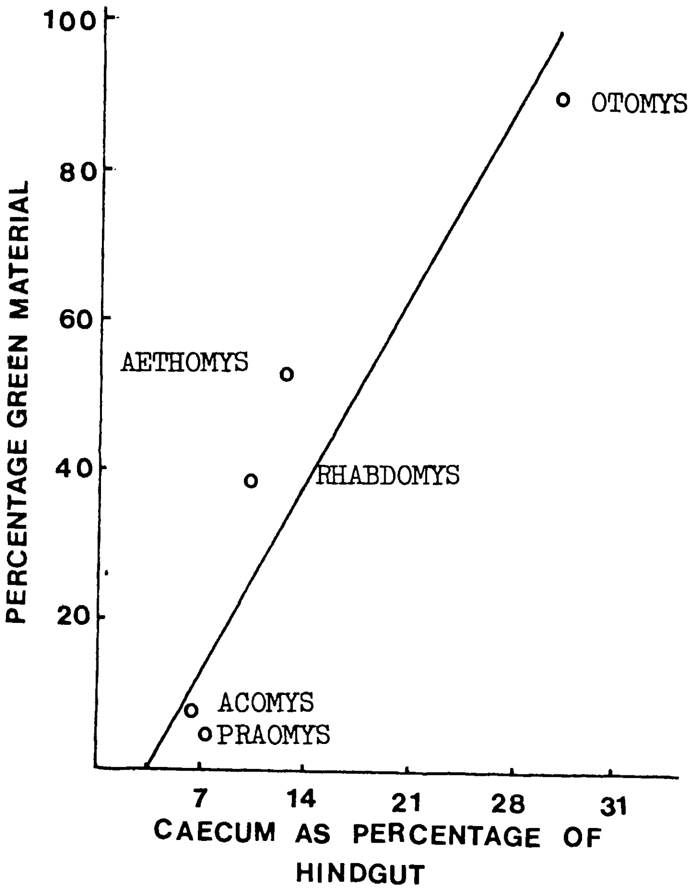


Fig. 13. The relationship between the percentage green material in stomach contents and the proportional contribution of the caecum to the hingut length in various small mammal species captured in the Swartberg.

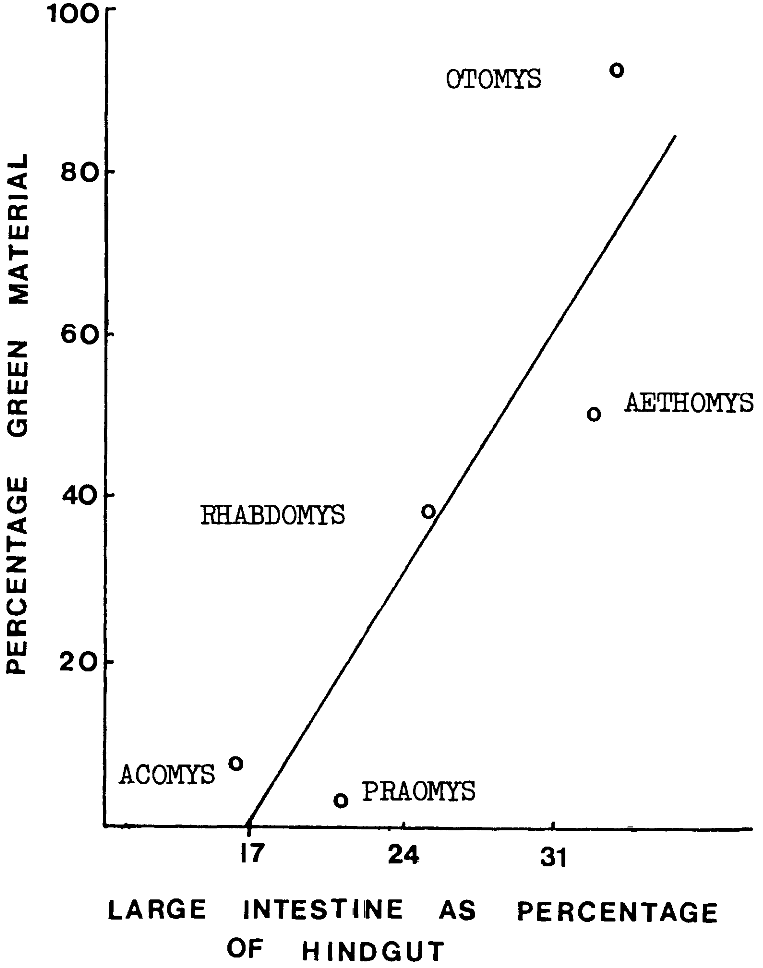


Fig. 14. The relationship between the percentage green material and the proportional contribution of the large intestines to the hindgut length in various small mammal species captured in the Swartberg.

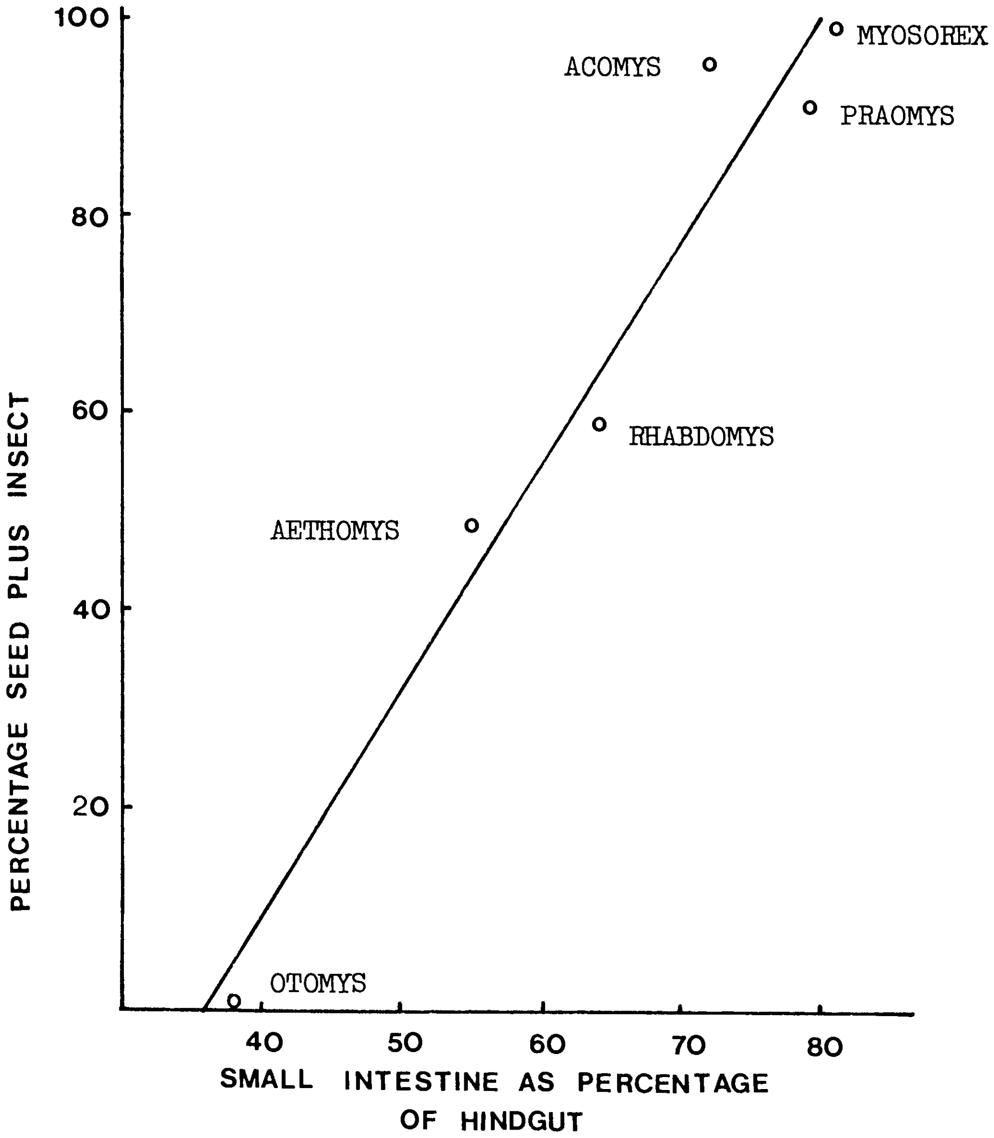


Fig. 15. The relationship between the percentage seed and insect in the stomach contents and the proportional contribution of the small intestines to hindgut length in various small mammal species captured.

Environmental controls on species distributions

Elephantulus edwardii (A. Smith, 1838)

This species was captured most frequently on the north facing slopes. On these slopes it was more common at those sites with a good restioid cover. It did not occur in the *Portulacaria afra* shrubland (Site 8) and was therefore only captured at fynbos sites. This elephant shrew is also rupicolous, and was captured at sites with a high rock cover, especially if the rocks were exposed to the direct sunlight. It was not captured in the *Protea repens* or the *Protea punctata* shrublands (Sites 2 and 3). At the first mentioned site the rocks were half buried in the colluvial soils and there were no loose boulders. In the *Protea punctata* shrubland on the other hand the rocks were suitable but because of the dense vegetation, the litter and soil were always damp. It is therefore possible that the cool damp conditions excluded this species from this community as *E. edwardii* was often observed sitting and basking in the sun at other sites.

Myosorex varius (Smuts, 1832)

M. varius was captured at all the sampled communities on the south facing slopes, but was absent from the *Paranomus dregei* and *Portulacaria afra* shrublands (Sites 7 and 8). It was not captured at sites receiving less than an estimated 500 mm of rainfall per annum. The number of *M. varius* captured was negatively correlated to the density of foliage between 20 and 60 cm (D_{4060}). The numbers captured were positively correlated to the shrub, shrub plus litter cover and microphyll cover (Fig. 16 and 17). Correlations between the number of M. varius captured and these various measured environmental parameters are given in Table 29.

TABLE 29. Correlation matrix of the relationship between the number of M. varius individuals captured and several measured environmental parameters.

Variable	Spearman's r	P
P_{4060}	-0,898	,05
Shrub cover	+0,994	,01
Shrub plus grass cover	+0,851	,05
Shrub plus litter cover	+0,78	,05
Microphyll cover	+0,857	,05

Cover per sé may not be the ultimate controlling factor. M. varius was captured at the Leucadendron album heathland community after the fire had destroyed all the available cover. During this period all M. varius individuals had fat deposits around the kidneys and the dorsal section of the hindquarters, and this was the only time that animals with fat deposits were recorded. It is during this immediate post fire period that the serotinous plants release their seed from the serotinous capitula. Animals surviving the fire therefore had a superabundant food source.

Praomys verreauxii (A. Smith, 1834)

This species was captured most frequently in the Protea punctata shrubland (Site 3) and was absent from the Paranomus dregei

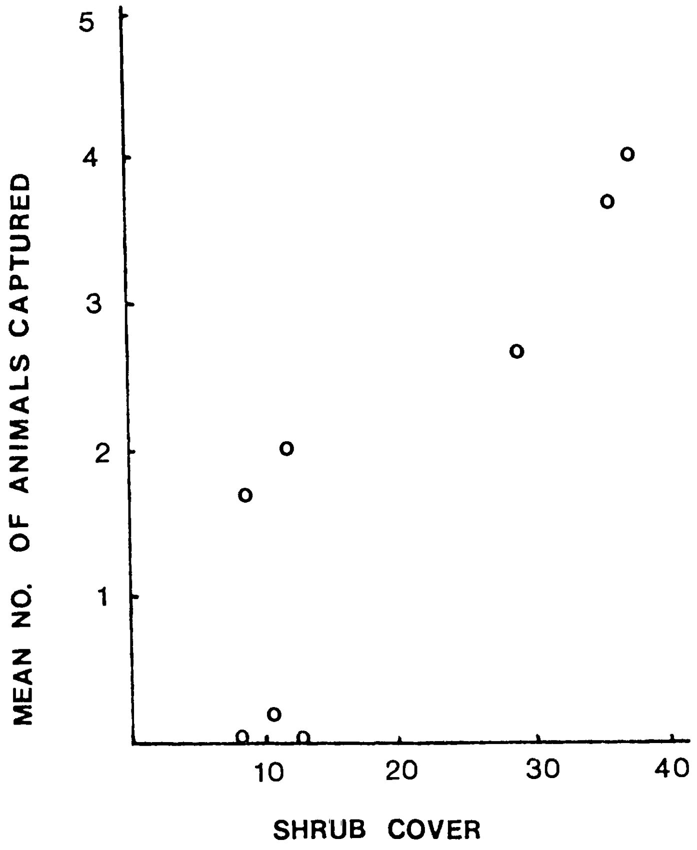


Fig. 16. Scatter diagram of the mean number of <u>Myosorex varius</u> captured per 200 trap nights in relation to shrub cover.

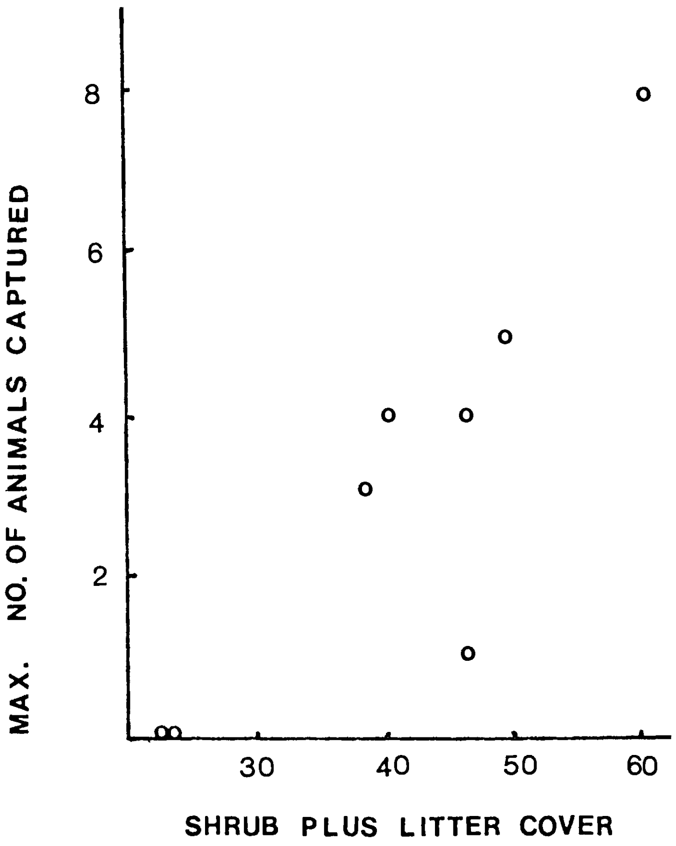


Fig. 17. Scatter diagram of the maximum number of <u>Myosorex varius</u> captured in 200 trap nights in relation to shrub plus litter cover.

and the Portulacaria afra shrubland (Sites 7 and 8).

The number of P. verreauxii captured was correlated to the P_i of the foliage profile above 160 cm (Fig. 18, Spearman's r = 0,875) and to foliage density at 140, 160 and 200 cm. This relationship was significant when using Pearson's correlation coefficient but not always so when using Spearman's rank correlattion coefficient.

The numbers of P. verreauxii were therefore higher in areas where the emergent layer was well developed, but only if the emergent layer was proteoid.

The number of P. verreauxii captured were also negatively correlated to total rock plus bare soil and positively to litter. (Respective Spearman's r = 0,899 with $p < 0{,}01$ and r = 0,862 with $p < 0{,}01$).

Aethomys namaquensis (A. Smith, 1834)

This species was only captured in the Paranomus dregei - and the Portulacaria afra shrublands (Sites 7 and 8), on the north facing slopes. This made the use of correlation analysis unpractical.

A. namaquensis were not captured at sites where total rock cover was less than 50% or where cover by rocks with a diameter of less than 13 cm was less than 30%. They were also absent from all sites where shrub cover was more than 75% and they preferred areas with low cover in the 0 - 60 cm layer.

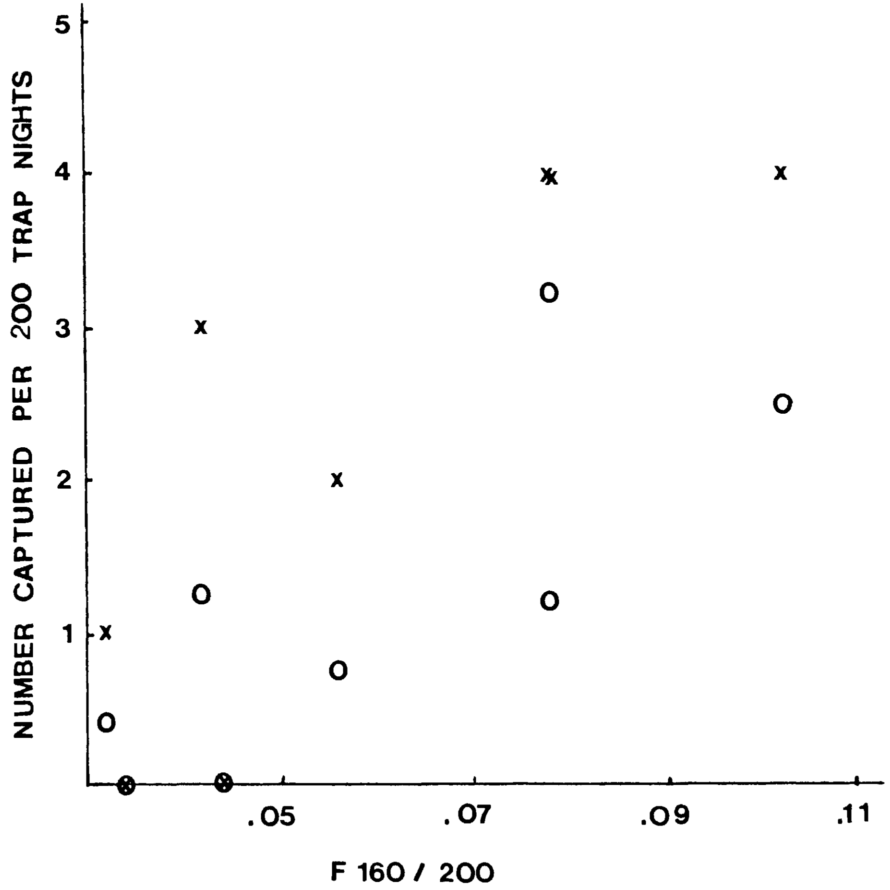


Fig. 18. Scatter diagram of the mean number of <u>Praomys verreauxii</u> captured in 200 trap nights in relation to foliage cover between 160 and 200 cm. (O = mean number captured, x = maximum number captured).

Rhabdomys pumilio (Sparrmann, 1784)

The numbers of *R. pumilio* captured increased with an increase in total live plant cover as estimated in the point survey. Therefore as the number of "grass" and "other" cover points increased so did the density of *R. pumilio*. (Spearman's r = 0,813 with p $< 0{,}05$; Fig 19). *R. pumilio* was not captured at the *Protea montana* heathland, *Paranomus dregei*- and the *Portulacaria afra* shrublands (Sites 4,7 and 8), (Fig. 20).

The general decrease in the number of *R. pumilio* captured over time is clearly shown in Fig. 19. The results from Bond *et al* (1980), were included since they sampled the same communities at the same intensities.

Acomys subspinosus (Waterhouse, 1838)

Acomys subspinosus numbers captured were correlated to altitude but not significantly so (Fig 21). Of all the other measured variables only the measured levels of N and P as determined for the foliage of *Protea* spp. at the sampled communities were correlated to *A. subspinosus* numbers captured. This species was not captured in the *Portulacaria afra*- or the *Protea repens* shrublands (Sites 8 and 1). Highest numbers were captured in the *Paranomus dregei* shrubland (Site 7).

Petromyscus collinus (Thomas and Hinton, 1925)

P. collinus was only captured at Site 8 in the *Portulacaria afra* shrubland but it was not present during all capture periods.

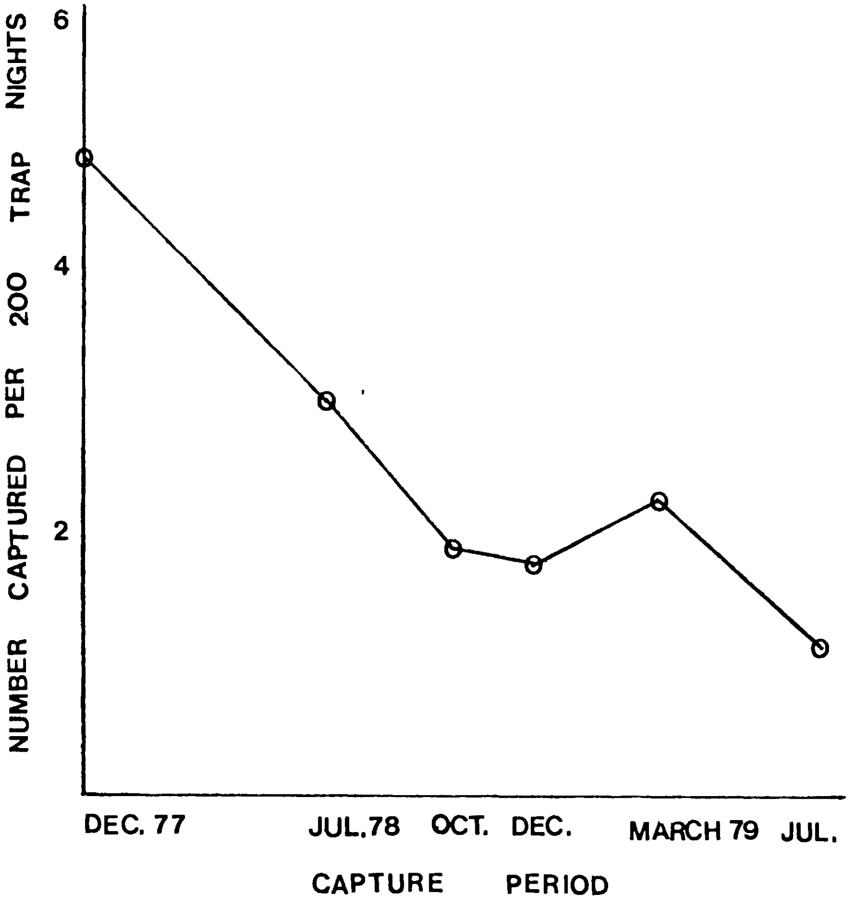


Fig. 19. The number of Rhabdomys pumilio captured per 200 trap nights from December 1977 (Bond et al 1980) to July 1979.

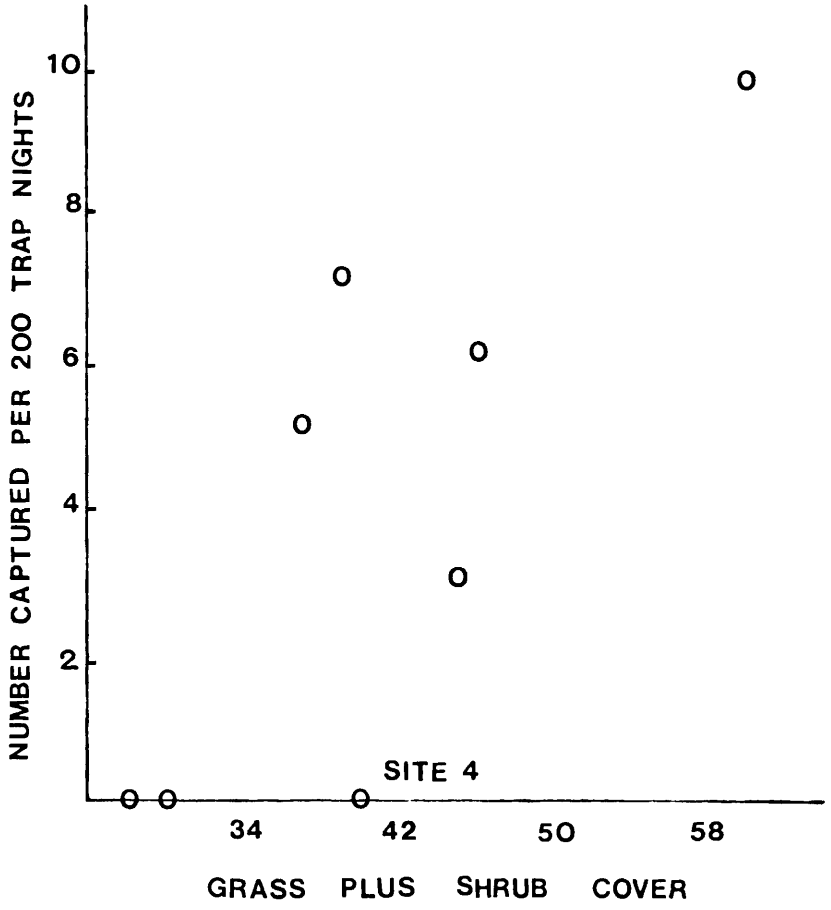


Fig. 20. Scatter diagram of the maximum number of Rhabdomys pumilio captured per 200 trap nights in relation to grass plus shrub cover.

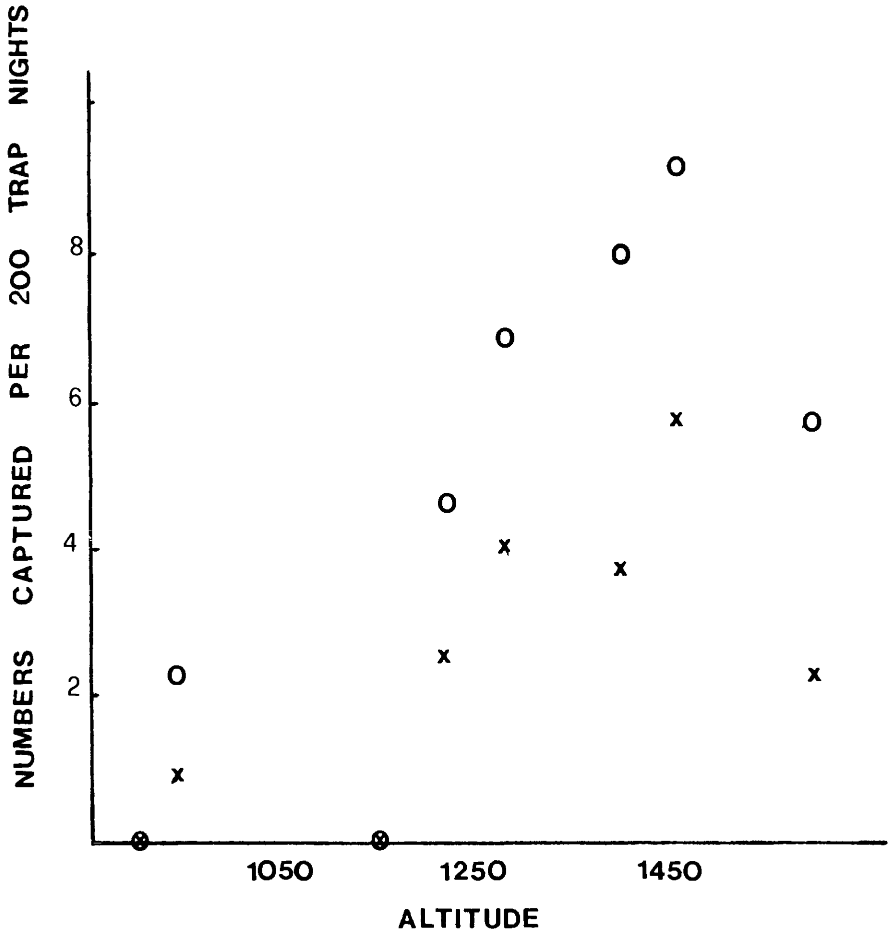


Fig. 21. Scatter diagram of the number Acomys subspinosus captured per 200 trap nights in relation to altitude. (O = maximum number, x = mean number per 200 trap nights.

It was only present in low numbers but were readily trapped.

Dendromus mesomelas (Brants, 1827)

This species was only trapped on three occasions in the Protea montana and Leucadendron album heathlands (Sites 4 and 5). A nest with a lone female in it was found near Site 2 (the Protea repens shrubland) in a Protea lorifolia bush. The nest was constructed primarily from Thamnocortus argenteus fillodiums and was lined with Protea seed "down".

Dendromus melanotis (A. Smith, 1834)

D. melanotis was only captured at Site 5 (the Leucadendron album heathland) during the post fire period, when grass, though sparse, was the dominant plant cover type.

Otomys irrotatus (Brants, 1827)

The number of O. irroratus captured was correlated with various environmental variables. The results show that the greater the live cover the higher the number of O. irroratus (Fig 22). Live cover here refers to the point survey's "grass" and "other" category. O. irroratus was therefore most commonly captured at the two heathland sites (the Protea montana- and Leucadendron album heathlands, Sites 4 and 5).

The numbers of O. irroratus also responded to the foliage density gradient. If the density of the foliage was high between 0 and 20 cm then the number of animals captured was high (Fig.

23). On the other hand numbers showed a negative relationship with proportion of foliage between 20 and 60 cm (P_{4060}).

There was also a positive correlation between numbers of *O. irroratus* captured and cover of the microphyll layer.

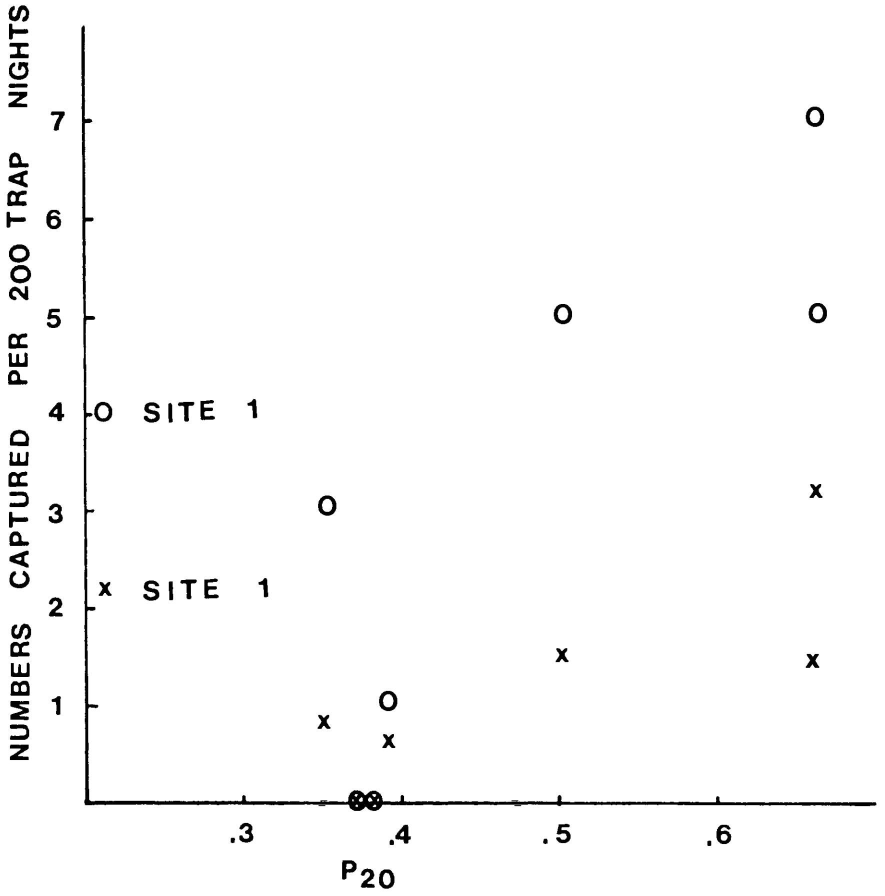


Fig. 22. Scatter diagram of the number of <u>Otomys irroratus</u> captured per 200 trap nights in relation to increasing density of foliage below 20 cm. (0 = maximum; X = mean).

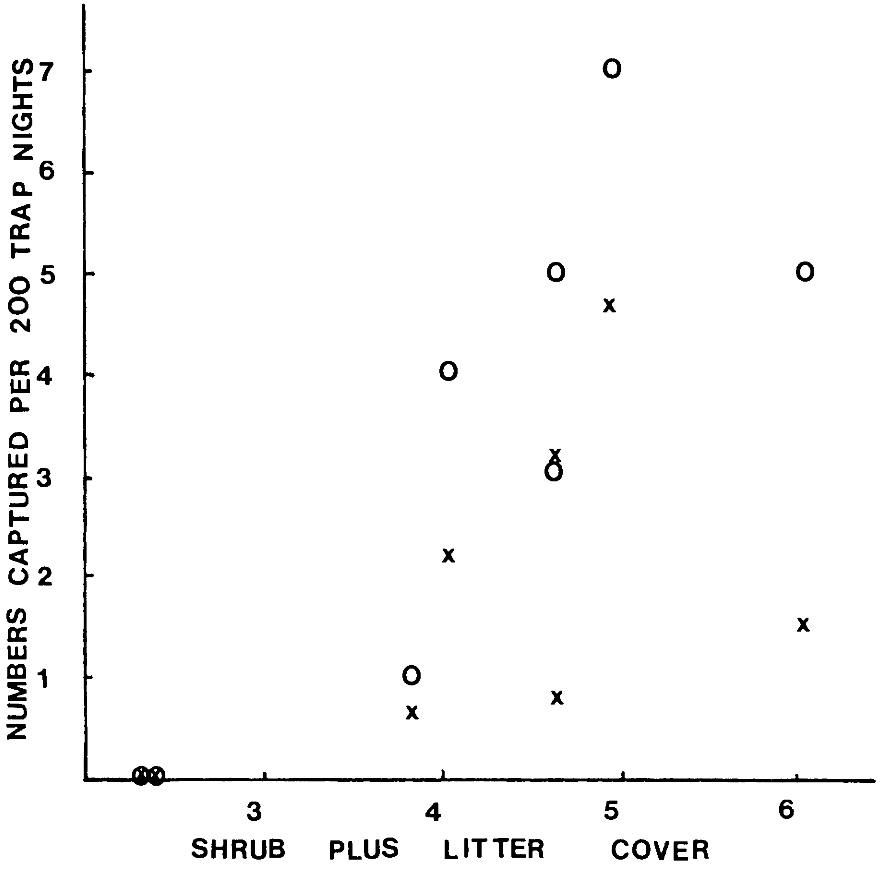


Fig. 23. Scatter diagram of the number of <u>Otomys irroratus</u> captured per 200 trap nights in relation to shrub plus litter cover. (0 = maximum; X = mean).

DIVERSITY

Alpha diversity

A null hypothesis that stated that none of the trap stations within a trap site should capture one or more species more frequently than expected, was postulated. (This was done to test that the number of species captured was a function of alpha diversity only).

Only in one case, at Site 5, was it possible to show that A. subspinosus was trapped more frequently than expected at four out of 50 trap stations during one of the trapping periods. The results from these four trap stations were, however, included since A. subspinosus was captured elsewhere on this site and the inclusion of these data did not influence species richness or diversity to any large extent. Alpha diversity as expressed by species richness and diversity H for each of the sampled trapping sites, is shown in Table 30.

TABLE 30. Alpha diversity for each of the sampled communities, as expressed by species richness and diversity H. (Mean over all capture periods).*

Site	Plant community	Richness	Diversity H
1.	Phylica paniculata shrubland	3,2	1,12
2.	Protea repens shrubland	2,6	1,14
3.	Protea punctata shrubland	4,3	1,95
4.	Protea montana heathland	3,8	1,61
5.	Leucadendron album heathland	5	2,09
6.	Protea lorifolia shrubland	3,5	1,54
7.	Paranomus dregei shrubland	2,8	1,18
8.	Portulacaria afra shrubland	1,4	0,88

*Mean did not include post fire results at Site 5 and 7.

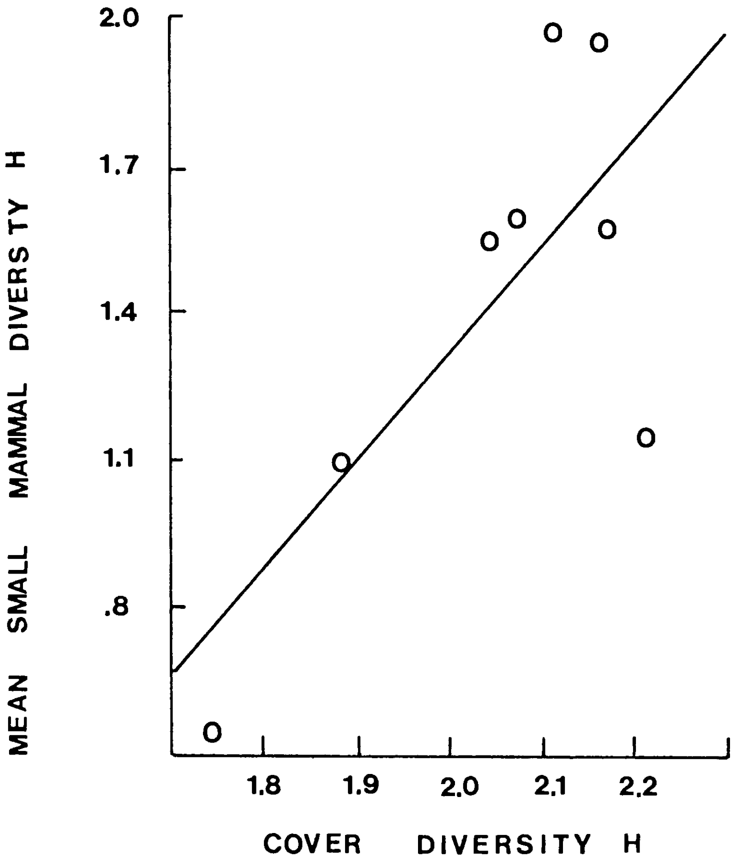


Fig. 24. The relationship between mean small mammal diversity H and cover diversity H. (r = 0,744; y = -2,47 + 2.11x.).

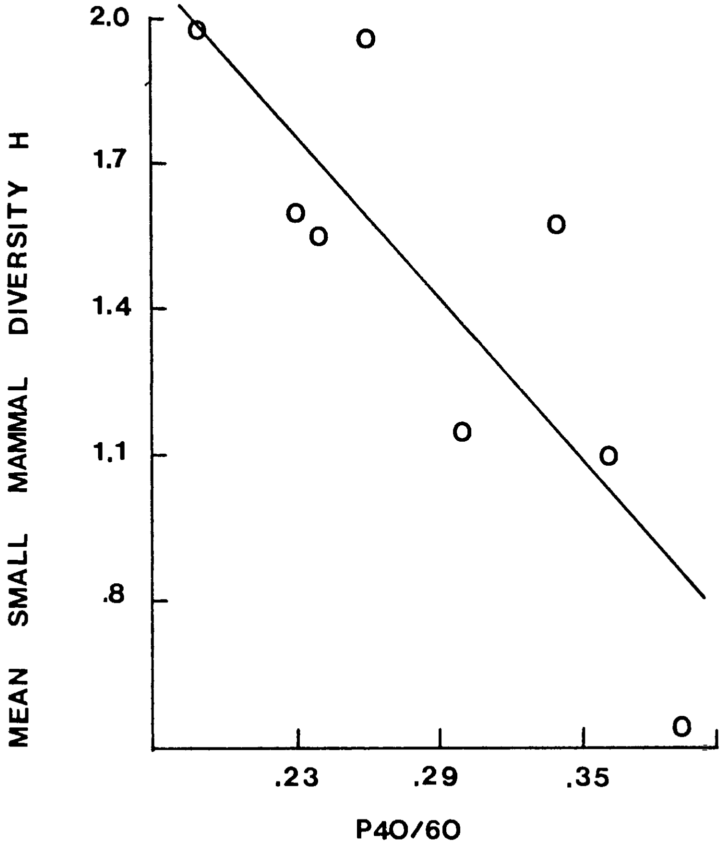


Fig. 25. The relationship between mean small mammal diversity H and the proportion of the foliage profile that lies between 40 and 60 cm. (r = 0,886; y = 2.94 - 5,17.).

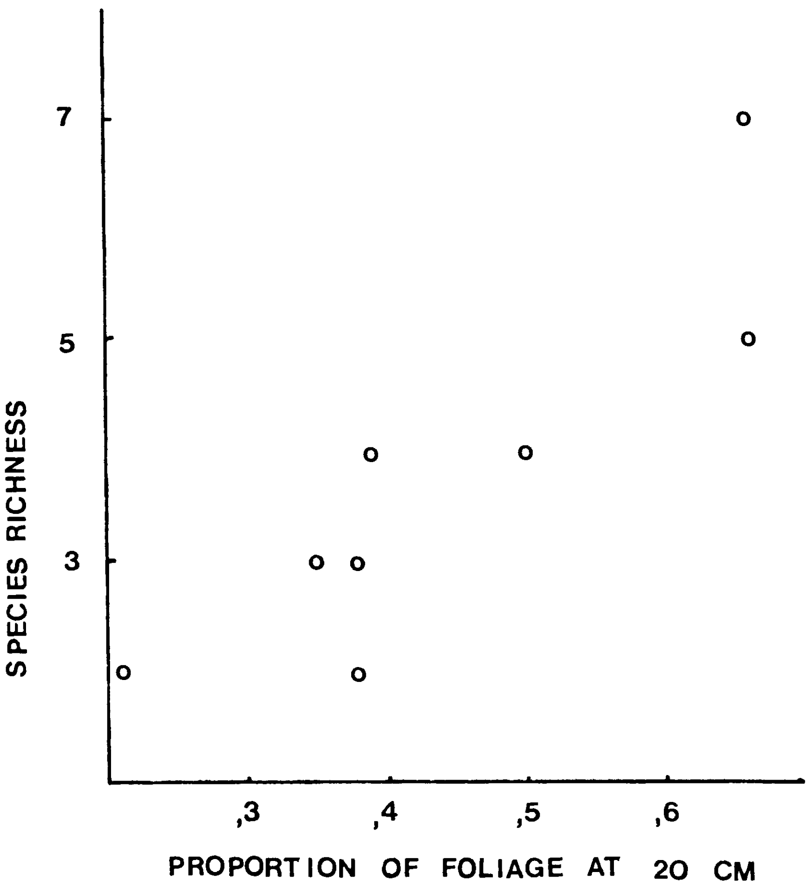


Fig. 26. Scatter diagram of the relationship between maximum species richness and the proportion of the foliage profile occuring below 20 cm.

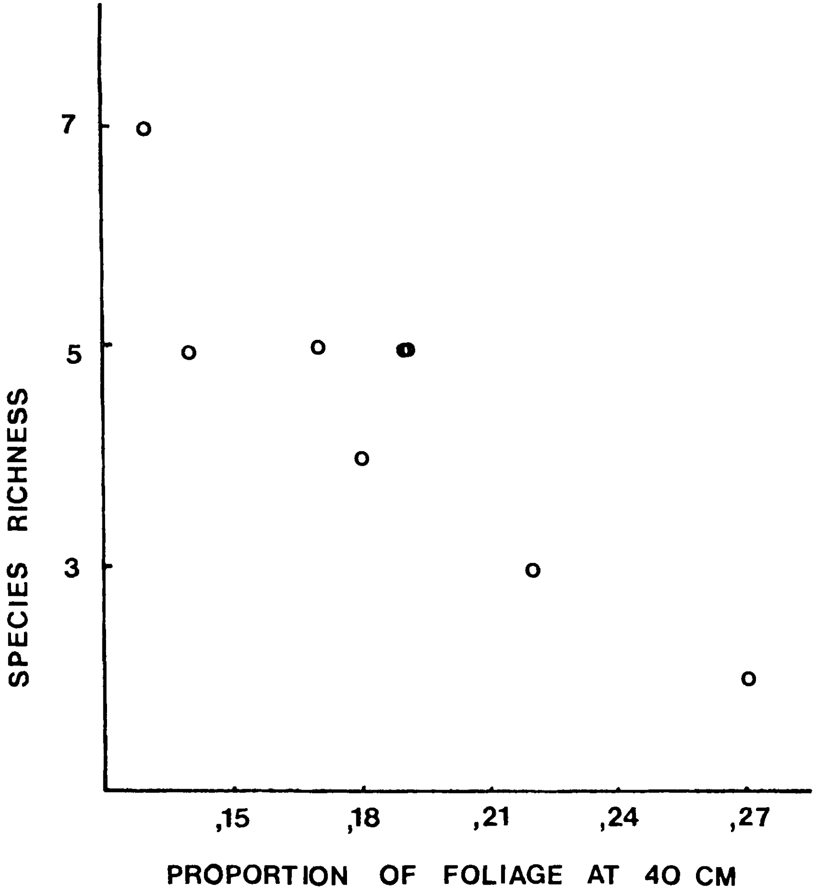


Fig. 27. Scatter diagram of the relationship between maximum species richness and the proportion of the foliage profile between 20 and 40 cm.

Alpha diversity of the small mammal community as expressed by species richness and diversity H was highest in the Leucadendron album heathland community (Site 5). It was low in the Portulacaria afra shrubland (Site 8). Alpha diversity therefore generally increased from low to high altitudes, with this trend more obvious on the north facing slopes. On the south facing slopes, however, slpha diversity in the Protea montana heathland was lower than would be predicted from the north slope results.

Alpha diversity of the small mammal communities increased with increasing cover. It was correlated to grass plus shrub cover as estimated in the point survey, and negatively correlated to the rock and bare soil cover. It was also positively correlated to the habitat (point survey) diversity (Fig. 24) and negatively correlated to the density of foliage in the 20 to 40 cm foliage layer (Table 31). The maximum number of species captured at a site was positively correlated to the proportion of the foliage recorded in the 0 - 20 cm layer and negatively to the proportion of the foliage recorded in the 20 to 60 cm foliage layer (Figs. 25 - 27).

There was also a positive correlation between small mammal alpha diversity and the Bray-Curtis ordination of the structural attributes of the various plant communities (Data from Bond 1981). Both diversity H and species richness were influenced by the number of individuals captured (Figs. 28 and 29).

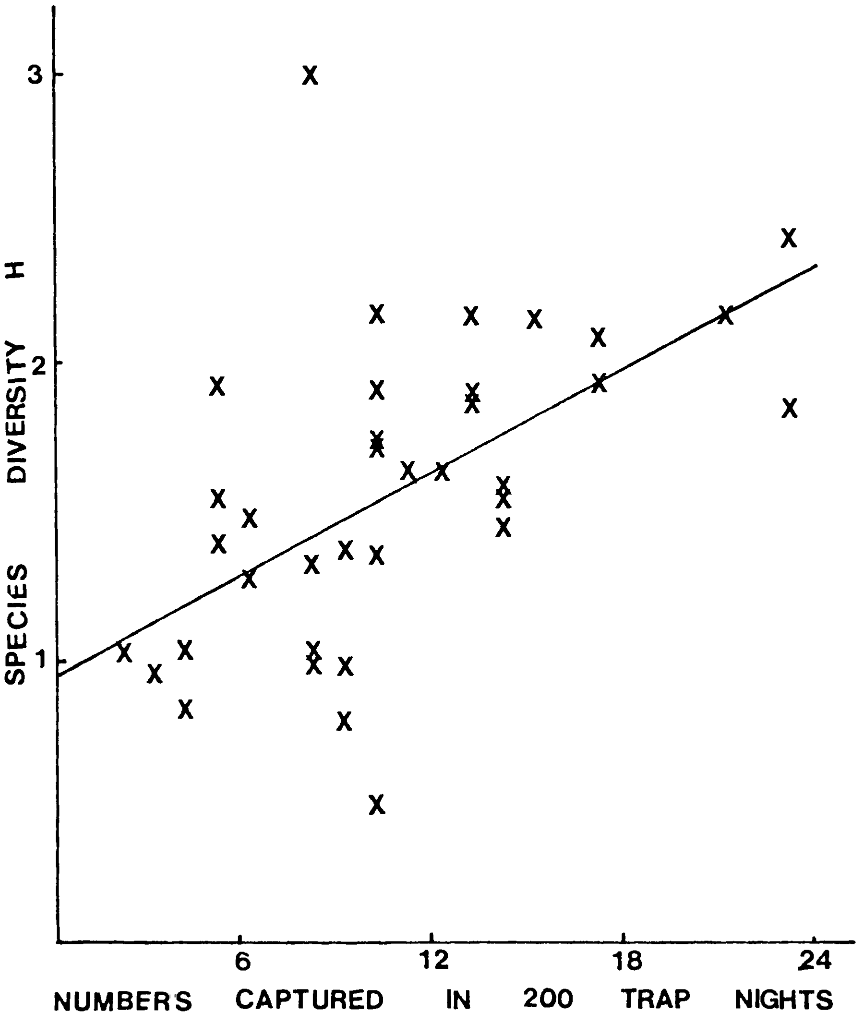


Fig. 28. The relationship between species diversity H and the total number of animals captured per 200 trap nights. (r=0,604; y=0,927+0,059x.).

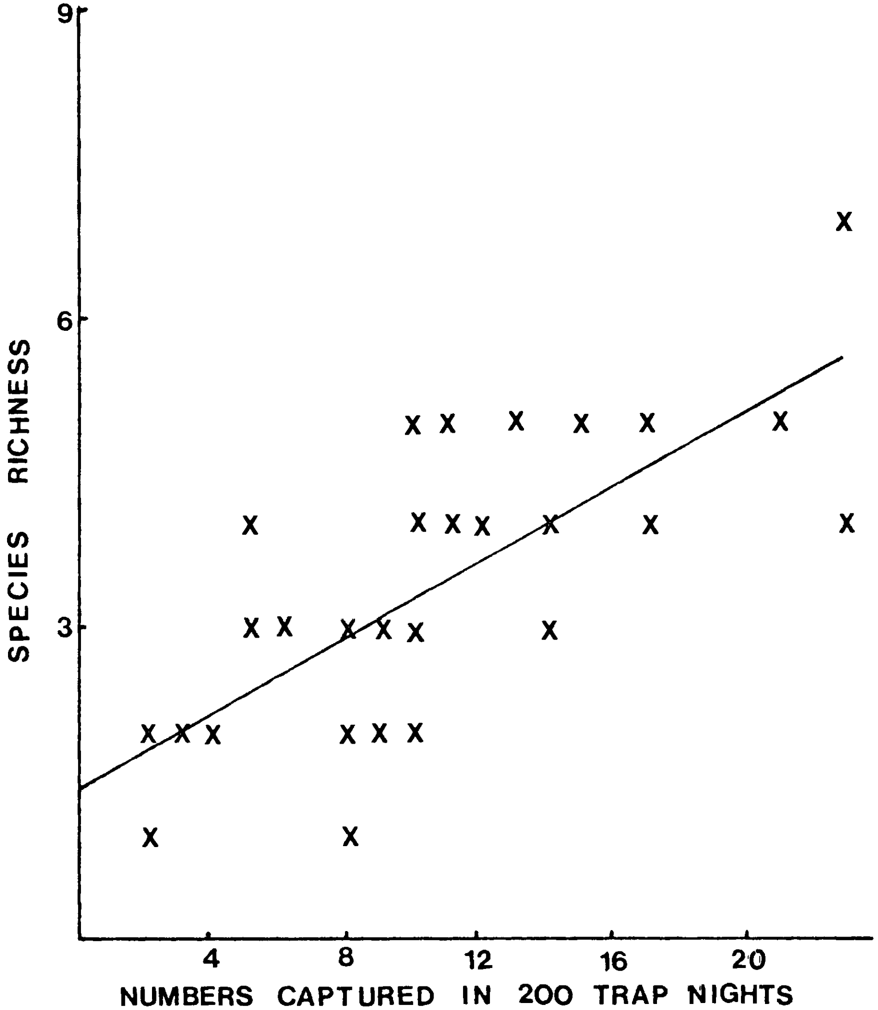


Fig. 29. The relationship between species richness and the total number of animals captured per 200 trap nights. (r=0,742; y=1,459+0,183x).

Foliage height diversity (FHD) was negatively correlated to the small mammal alpha diversity.

TABLE 31. Correlation matrix for habitat variables and alpha diversity as expressed by richness and diversity H. (Mean over all capture periods).

Habitat variables	Richness	Diversity H
P_{40}	-,792	-,804
P_{4060}	-,860	-,821
Total rock cover	-,72	-,78
Total rock plus bare soil	-,75	-,996
Grass plus shrub cover	,803	,802
Grass plus shrub plus litter cover	,75	,796
Plant diversity H*	n.s.	-,761
Bray-Curtis ordination of structural variables*	,871	,871
Diversity (H) point cover survey	,707	n.s.
Equitability point cover survey	,716	n.s.
FHD	-,778	n.s.

*From Bond 1981

Species turnover

It is realised that trap success was not high and the results may not reflect actual community composition. The results given below must therefore be seen as a first approximation against which future studies can be compared.

Turnover with time

Temporal turnover of species was high at some sites and low at others. This means that at some sites many species may be recorded over all the capture periods, but the actual number of species present at any one time may be low. Turnover between capture periods was calculated. The mean turnover between seasons (Table 32) was not correlated to alpha diversity in any way.

Beta diversity

Beta diversity was determined for the sampled small mammal communities (Table 33).

Beta diversity was lower between the south facing slope small mammal communities than between those on the north facing slopes. The beta diversity between the small mammal communities in the Portulacaria afra- and Paranomus dregei shrublands and the other sampled small mammal communities were much higher than between any of the others.

TABLE 32. Seasonal species turnover and Index of Dissimilarity for the small mammal community at each trapping site. (Turnover is given in the first and Index of Dissimilarity in the second column beneath each trapping period. Mean values and standard deviation (s) are also given.

		Trapping period													
Site	Plant community	1		2		3		4		5		mean		s	
1	Phylica paniculata shrubland	0	0	2,5	0,71	0,5	0,2	1	0,33	0,5	0,14	1,13	0,35	0,95	0,26
2	Protea repens shrubland	-	-	0	0	1	0,33	0,5	0,2	1,5	0,6	1,00	0,38	0,5	0,2
3	Protea punctata shrubland	0	0	0,5	0,11	0,5	0,11	0	0	0,5	0,11	0,38	0,08	0,5	0,6
4	Protea montana heathland	0	0	0,5	0,11	1	0,25	0	0	1	0,25	0,38	0,12	0,25	0,12
5	Leucadendron album heathland	0	0	1,5	,27	1	0,17	0,5	0,11	-	-	1,0	0,18	0,5	0,08
6	Protea lorifolia shrubland	-	-	0	0	0,5	0,2	1,4	0,43	2,4	0,15	0,67	0,26	0,76	0,15
7	Paranomus dregei shrubland	0	0	0,5	0,2	0	0	0	0	0,5	0,2	0,29	0,1	0,29	0,12
8	Portulacaria afra shrubland	0	0	0,5	0,33	0,5	0,33	0,5	0,33	0,5	0,33	0,5	0,33	0	0

TABLE 33. Beta diversity between all sampled small mammal communities (Index of Dissimilarity given above and turnover below diagonal).

Site		1	2	3	4	5	6	7	8
1	Phylica paniculata shrubland	-	0,2	0,09	0,17	0,14	0,08	0,56	1,0
2	Protea repens shrubland	1	-	0,11	0,2	0,33	0,27	1,0	1,0
3	Protea punctata shrubland	0,5	0,5	-	0,27	0,23	0,17	0,75	1,0
4	Protea montana heathland	1	2	1,5	-	0,14	0,23	0,56	1,0
5	Leucadendron album heathland	1	2	1,5	1	-	0,2	0,64	1,0
6	Protea lorifolia shrubland	0,5	1,5	1	1,5	1,5	-	0,6	1,0
7	Paranomus dregei shrubland	2,5	3,5	3	2,5	3,5	3	-	0,6
8	Portulacaria afra shrubland	4	3	4,5	4	5	4,5	1,5	-

To determine whether a gradient has a substantial influence on beta diversity, beta diversity has to be expressed as a function of the gradient itself (Cody 1975). It was decided to use the DI value (drought index after Bond 1981) as one gradient, because this index probably reflects the total change in the plant communities to a far greater extent than any of the plant community parameters (e.g. foliage density) measured in this study (Table 34).

There was a strong relationship between the degree of change in the D.I. gradient and beta diversity. (Pearsons $r = 0.839$; $P<0,05$).

Beta diversity was also expressed as a function of a "total live cover" gradient (i.e. "grass" and "other" cover as determined in the point cover survey Table 34).

The large change in the live cover gradient between the Protea punctata shrubland and the Leucadendron album heathland (Sites 3 and 5) was not reflected in the beta diversity trends between the two small mammal communities. There was therefore no distinct relationship between the live cover gradient and the observed beta diversities. Nevertheless the large beta diversity between the small mammal communities in the Paranomus dregei and Portulacaria afra shrublands (Sites 7 and 8) and the others were associated with large changes in the total live cover.

TABLE 34. Comparison of the changes in beta diversity between small mammal communities and the relative changes along a Drought Index gradient and a "live cover" gradient.

Site	Plant community	DI* GRADIENT Percentage change in DI gradient	Percentage change in beta diversity
4	Protea montana heathland	0	0
3	Protea punctata shrubland	16,7	11,7
5	Leucadendron album heathland	5,1	10,0
2	Protea repens shrubland	16,9	14,3
1	Phylica paniculata shrubland	0	8,7
6	Protea lorifolia shrubland	1,7	3,5
7	Paranomus dregei shrubland	40,7	26
8	Portulacaria afra shrubland	18,6	26

Site	Plant community	"LIVE COVER" GRADIENT Percentage change in LC*gradient	Percentage change in beta diversity
5	Leucadendron album heathland	0	0
3	Protea punctata shrubland	45,5	8,8
6	Protea lorifolia shrubland	3,0	6,4
4	Protea montana heathland	15,2	8,8
2	Protea repens shrubland	3,0	7,6
1	Phylica paniculata shrubland	6,1	7,6
8	Portulacaria afra shrubland	21,2	38
7	Paranomus dregei shrubland	6,1	22,8

* Live cover

DENSITIES, BIOMASS AND ENERGETIC REQUIREMENTS OF SMALL MAMMAL COMMUNITIES.

The estimates of density, biomass and energy requirements (Table 35) should not be regarded as absolute values, but as a reflection of relative changes along the altitudinal gradient. The amount of energy consumed by the small mammal communities were estimated by using the following two equations drawn up by French, Grant, Grodzinski & Swift (1976).

Rodents $\quad$ ADMR Kcal. $g^{-1} = 2{,}297\ W^{-0{,}5}$

Insectivores $\quad$ ADMR Kcal. $g^{-1} = 3{,}087\ W^{-0{,}5}$

where ADMR = average daily metabolic rate

W = mass in g.

The two different equations were used since insectivores and rodents have distinctly different metabolic rates (Wunder 1975, French et al 1976).

Although only densities are discussed here it also applies to the biomass and the estimated energy requirements of the small mammal communities since they are auto-correlated.

Overall density remained fairly constant between seasons, mean density varying between 28,6 and 36,1 animals per hectare. The density as estimated for individual trapping sites, however, showed great seasonal variability. (As can be seen from Tables 6 to 13, capture rates show the same variability at a trapping site). the seasonal changes in density are illustrated in Fig. 30a and b. In some of the small mammal communities, densities were fairly stable, e.g. the Paranomus dregei and Portulacaria afra shrublands (Sites 7 and 8), while in others

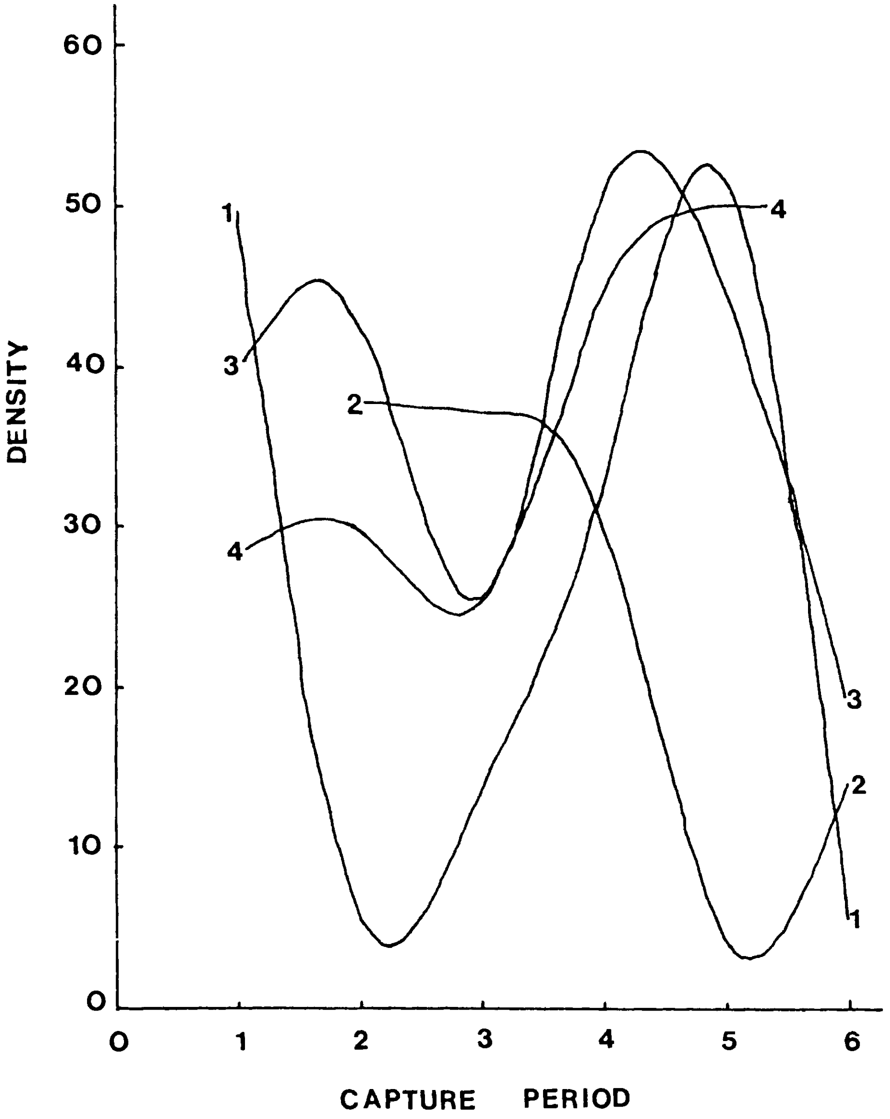


Fig. 30a. Seasonal fluctuation in density of small mammals (numbers per hectare) on the south slope. Numbers refer to trapping sites.

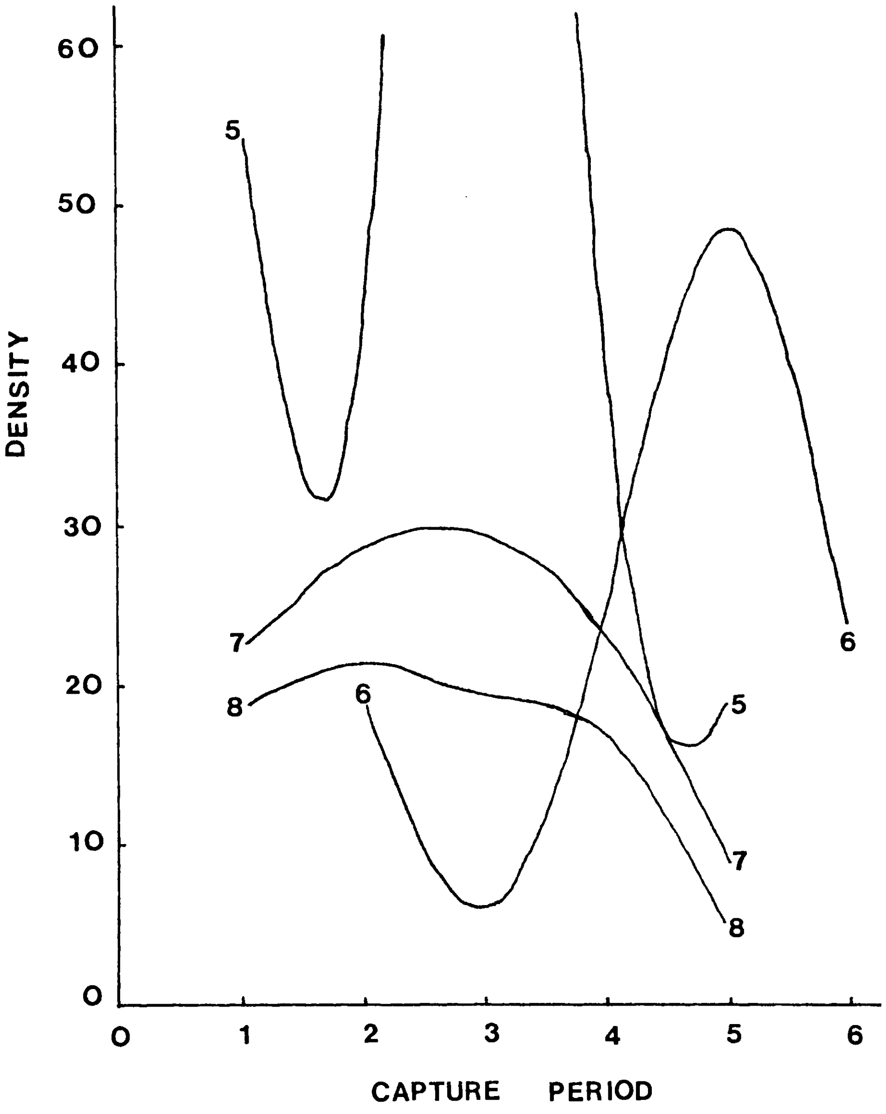


Fig. 30b. Seasonal fluctuations in density of small mammals (numbers per hectare) on the north slope. Numbers refer to trapping sites.

TABLE 35 Estimated density, biomass and energetic requirements of the small mammal communities in the Swartberg during the different trapping periods. (For key to trapping site and plant com= munities see Table 36).

ESTIMATED NUMBER OF ANIMALS PER HECTARE

		SPECIES											
Site	Capture period	Elephantulus edwardii	Myosorex varius	Crocidura cyanea	Praomys verreauxii	Rhabdomys pumilio	Aethomys namaquensis	Acomys subspinosus	Petromyscus collinus	Dendromus mesomelas	Dendromus melanotis	Otomys irroratus	Total
1	Winter 1978	0	9.1	0	5.7	18.2	0	2.81	0	0	0	8.7	44.5
	Spring 1978	0	1.8	0	0	0	0	4.4	0	0	0	0	6.17
	Summer 1978	0	2.1	0	0	0	0	5.3	0	0	0	5.5	12.9
	Autumn 1979	0	5.4	0	0	8.8	0	0	0	0	0	14	28.2
	Winter 1979	0	3.4	0	16.8	21.7	0	0	0	0	0	4.3	46.2
	Spring 1979	0	1.8	0	0	0	0	0	0	0	0	2.3	4
2	Spring 1978	0	3.5	0	6.9	26	0	0	0	0	0	2.7	39.1
	Summer 1979	0	8.9	0	0	31	0	0	0	0	0	0	39.8
	Autumn 1979	0	2	0	0	28.5	0	0	0	0	0	3	33.4
	Winter 1979	0	1.7	0	2.2	0	0	0	0	0	0	0	3.9
	Spring 1979	0	2.5	0	3.3	5.3	0	3.3	0	0	0	0	14.4
3	Winter 1978	0	20.7	0	5.2	10.2	0	4.6	0	0	0	2.5	43
	Spring 1978	0	3.4	0	13.7	23.6	0	3	0	0	0	0	43.8
	Summer 1978	0	5.2	0	7.8	7.6	0	2.3	0	0	0	2.5	25.4
	Autumn 1979	0	8.3	0	8.3	16.2	0	14.7	0	0	0	3.9	51.4
	Winter 1979	0	14.6	0	14.6	0	0	13	0	0	0	3.5	45.6
	Spring 1979	0	12.2	0	0	4	0	0	0	0	0	3.9	20.1
4	Winter 1978	3.31	10.3	0	0	0	0	4.1	0	0	0	7.8	25.5
	Spring 1978	2.3	4.2	0	2.46	0	0	2.83	0	0	0	16	27.9
	Summer 1978	0	4.9	0	0	0	0	3.3	0	0	0	8.2	16.4
	Autumn 1979	0	3.1	0	0	0	0	12.5	0	0	0	29.4	45
	Winter 1979	0	9.1	0	9.4	24.9	0	14.5	0	0	0	0	58
5	Winter 1978	0	4.2	0	0	11.6	0	18	0	4.7	0	6.1	44.6
	Spring 1978	0	22.6	0	7.8	37.1	0	30	0	0	0	40.9	138.3
	Summer 1978	0	4.1	0	0	11.3	0	11	0	0	0	14.9	41.3
	Autumn 1979	0	8.9	0	8.2	0	0	3.2	0	0	0	0	20.2
	Winter 1979	2.3	0	0	16.7	0	0	3.6	0	0	0	0	22.6
6	Spring 1978	2.1	0	0	0	0	0	3.2	0	0	0	0	5.3
	Summer 1978	0	0	2.3	9.3	0	0	5.1	0	0	0	9.6	26.2
	Autumn 1979	7.8	2.2	0	11.1	12.9	0	14	0	0	0	0	47.9
	Winter 1979	2.1	0	0	0	0	21.6	0	0	0	0	0	23.7
7	Winter 1978	11.5	0	0	0	0	16.1	2.4	0	0	0	0	30
	Spring 1978	6.2	0	0	0	0	12	12.9	0	0	0	0	31.1
	Summer 1978	2.3	0	0	0	0	8.1	14.4	0	0	0	0	24.8
	Autumn 1979	6.3	0	0	0	0	0	2.2	0	0	0	0	8.5
	Winter 1979	0	0	0	0	0	19.2	0	0	0	0	0	19.2
8	Winter 1978	0	0	0	0	0	20.9	0	6.5	0	0	0	27.4
	Spring 1978	0	0	0	0	0	20.2	0	0	0	0	0	20.2
	Summer 1978	0	0	0	0	0	10	0	8.2	0	0	0	18.1
	Autumn 1979	0	0	0	0	0	4.7	0	0	0	0	0	4.7
	Winter 1979	0	1.92	0	3.3	0	0	19.1	0	3.1	0	25.2	52.7

TABLE 35 (cont.)

ESTIMATED BIOMASS IN GRAMS PER HECTARE

		SPECIES											
Site	Capture period	Elephantulus edwardii	Myosorex varius	Crocidura cyanea	Praomys verreauxii	Rhabdomys pumilio	Aethomys namaquensis	Acomys subspinosus	Petromyscus collinus	Dendromus mesomelas	Dendromus melanotis	Otomys irroratus	Total
1	Winter 1978	0	93	0	218	626	0	70	0	0	0	712	1718
	Spring 1978	0	18	0	0	0	0	109	0	0	0	0	127
	Summer 1978	0	22	0	0	0	0	131	0	0	0	446	598
	Autumn 1979	0	56	0	0	301	0	0	0	0	0	1141	1498
	Winter 1979	0	34	0	649	744	0	0	0	0	0	353	1780
	Spring 1979	0	18	0	0	0	0	0	0	0	0	186	204
2	Spring 1978	0	39	0	308	1013	0	0	0	0	0	212	1571
	Summer 1978	0	96	0	0	1208	0	0	0	0	0	0	1304
	Autumn 1979	0	21	0	0	1111	0	0	0	0	0	232	1364
	Winter 1979	0	18	0	98	0	0	0	0	0	0	0	116
	Spring 1979	0	28	0	147	207	0	82	0	0	0	0	463
3	Winter 1978	0	224	0	198	419	0	92	0	0	0	223	1155
	Spring 1978	0	37	0	524	973	0	61	0	0	0	0	1594
	Summer 1978	0	56	0	297	315	0	46	0	0	0	224	938
	Autumn 1979	0	90	0	316	670	0	294	0	0	0	356	1725
	Winter 1979	0	158	0	551	0	0	259	0	0	0	314	1289
	Spring 1979	0	132	0	0	165	0	0	0	0	0	351	649
4	Winter 1978	162	101	0	0	0	0	86	0	0	0	730	1082
	Spring 1978	111	42	0	105	0	0	61	0	0	0	1504	1823
	Summer 1978	0	48	0	0	0	0	71	0	0	0	773	892
	Autumn 1979	0	31	0	0	0	0	268	0	0	0	2765	3064
	Winter 1979	0	19	0	142	0	0	412	0	46	0	2376	2994
5	Winter 1978	0	85	0	327	933	0	370	0	0	0	0	1714
	Spring 1978	0	40	0	0	432	0	451	0	69	0	493	1491
	Summer 1978	0	212	0	270	1386	0	763	0	0	0	3293	5924
	Autumn 1979	0	39	0	0	422	0	279	0	0	0	1203	1942
	Winter 1979	0	83	0	284	0	0	80	0	0	0	0	447
6	Spring 1978	126	0	0	693	0	0	72	0	0	0	0	891
	Summer 1978	113	0	0	0	0	0	65	0	0	0	0	177
	Autumn 1979	0	0	23	387	0	0	100	0	0	0	788	1297
	Winter 1979	418	24	0	461	441	0	279	0	0	0	0	1622
7	Winter 1978	103	0	0	0	0	1002	0	0	0	0	0	1105
	Spring 1978	574	0	0	0	0	745	52	0	0	0	0	1371
	Summer 1978	309	0	0	0	0	557	282	0	0	0	0	1148
	Autumn 1979	116	0	0	0	0	375	316	0	0	0	0	807
	Winter 1979	314	0	0	0	0	0	48	0	0	0	0	361
8	Winter 1978	0	0	0	0	0	991	0	0	0	0	0	991
	Spring 1978	0	0	0	0	0	1077	0	98	0	0	0	1174
	Summer 1978	0	0	0	0	0	1043	0	0	0	0	0	1043
	Autumn 1979	0	0	0	0	0	514	0	123	0	0	0	637
	Winter 1979	0	0	0	0	0	242	0	0	0	0	0	242

TABLE 35 (cont.)

ESTIMATED ENERGETIC REQUIREMENTS IN JOULES PER HECTARE PER DAY

Site	Capture period	SPECIES											Total
		Elephantulus edwardii	Myosorex varius	Crocidura cyanea	Praomys verreauxii	Rhabdomys pumilio	Aethomys namaquensis	Acomys subspinosus	Petromyscus collinus	Dendromus mesomelas	Dendromus melanotis	Otomys irroratus	
1	Winter 1978	0	374	0	337	1026	0	134	0	0	0	757	2630
	Spring 1978	0	73	0	0	0	0	210	0	0	0	0	283
	Summer 1978	0	87	0	0	0	0	252	0	0	0	473	814
	Autumn 1979	0	224	0	0	493	0	0	0	0	0	1213	1931
	Winter 1979	0	138	0	1004	1221	0	0	0	0	0	375	2739
	Spring 1979	0	73	0	0	0	0	0	0	0	0	197	270
2	Spring 1978	0	150	0	443	1560	0	0	0	0	0	226	2383
	Summer 1978	0	377	0	0	1859	0	0	0	0	0	0	2237
	Autumn 1979	0	82	0	0	1711	0	0	0	0	0	251	2045
	Winter 1979	0	71	0	140	0	0	0	0	0	0	0	212
	Spring 1979	0	56	0	211	318	0	157	0	0	0	0	795
3	Winter 1978	0	878	0	307	627	0	197	0	0	0	225	2236
	Spring 1978	0	145	0	814	1455	0	131	0	0	0	0	2547
	Summer 1978	0	220	0	462	472	0	99	0	0	0	226	1479
	Autumn 1979	0	351	0	491	1001	0	631	0	0	0	360	2836
	Winter 1979	0	619	0	866	0	0	557	0	0	0	317	2361
	Spring 1979	0	519	0	0	247	0	0	0	0	0	354	1121
4	Winter 1978	299	416	0	0	0	0	183	0	0	0	723	1623
	Spring 1978	205	171	0	154	0	0	125	0	0	0	1490	2148
	Summer 1978	0	199	0	0	0	0	146	0	0	0	766	1111
	Autumn 1979	0	126	0	0	0	0	556	0	0	0	2739	3422
	Winter 1979	0	77	0	209	0	0	853	0	114	0	2353	3608
5	Winter 1978	0	360	0	533	1465	0	704	0	0	0	0	3064
	Spring 1978	0	167	0	0	679	0	871	0	173	0	528	2420
	Summer 1978	0	893	0	440	2179	0	1455	0	0	0	3527	8495
	Autumn 1979	0	162	0	0	663	0	531	0	0	0	1288	2646
	Winter 1979	0	352	0	462	0	0	152	0	0	0	0	967
6	Spring 1978	221	0	0	1033	0	0	154	0	0	0	0	1410
	Summer 1978	198	0	0	0	0	0	138	0	0	0	0	337
	Autumn 1979	0	0	69	576	0	0	215	0	0	0	834	1696
	Winter 1979	736	93	0	686	725	0	601	0	0	0	0	2843
7	Winter 1978	188	0	0	0	0	1416	0	0	0	0	0	1604
	Spring 1978	1051	0	0	0	0	1052	107	0	0	0	0	2211
	Summer 1978	566	0	0	0	0	787	578	0	0	0	0	1931
	Autumn 1979	211	0	0	0	0	529	649	0	0	0	0	1391
	Winter 1979	573	0	0	0	0	0	97	0	0	0	0	671
8	Winter 1978	0	0	0	0	0	1325	0	0	0	0	0	1325
	Spring 1978	0	0	0	0	0	1440	0	243	0	0	0	1683
	Summer 1978	0	0	0	0	0	1395	0	0	0	0	0	1395
	Autumn 1979	0	0	0	0	0	688	0	304	0	0	0	992
	Winter 1979	0	0	0	0	0	323	0	0	0	0	0	323

there were great variation, e.g. the Leucadendron album heathland (Site 5).

There were no distinctive patterns on variation in densities in all the trapping sites combined. The Phylica paniculata and Protea repens shrublands (Sites 1 and 2), for example, varied in exactly the opposite manner. When site 1 population densities increased, those at Site 2 decreased and vice versa; the same applies to the Leucadendron album heathland and the Protea lorifolia shrublands (Sites 5 and 6). To get an impression of the change between seasons, the magnitude of change between seasons were calculated for each trapping site. For example, estimated density for the Phylica paniculata shrubland (Site 1) during winter and spring 1978 was 49,4 and 5,9 animals per hectare respectively. Magnitude of change was 49,4/5,9 = 8,4. Since the population decreased from the first to the second season the magnitude of change is given as -8,4 (Table 36). Populations at Site 1 varied considerably during the study period. The range of magnitude of change recorded between successive seasons was 1,6 to 11,4 (mean 5,22).

The change in density was far less pronounced at other sampled communities on the south facing slopes (Sites 2 - 4), and there was a general decrease in the magnitude of change from low to high altitudes (Table 36).

On the north facing slopes the trends in magnitude of change are greatest at high, and least at low altitudes, it is therefore the reverse of the results for the south facing slope. Because of the great variation between trapping sites no general statements

TABLE 36. Magnitude of change in density at a trapping site between consecutive seasons. Decrease in density is indicated with a minus and an increase with a plus.

Site	Plant community	Season Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Winter 1979	Spring 1979	Mean magnitude of change
1	Phylica paniculata shrubland	0	-8,4	+2,3	+2,4	+1,6	-11,4	5,22
2	Protea repens shrubland	-	0	-1,01	-1,22	-6,8	+3,2	3,66
3	Protea punctata shrubland	0	+1,07	-1,7	+1,89	-1,1	-2,4	1,65
4	Protea montana heathland	0	+1,04	-1,16	+1,75	+1,13	-1,67	1,35
5	Leucadendron album heathland	0	-1,28	+3,08	-3,28	-2,09	-	2,43
6	Protea lorifolia shrubland	-	0	-3,1	+4,13	+1,93	-	3,05
7	Paranomus dregei shrubland	0	+1,29	+1,03	-1,27	-2,64	-	1,56
8	Portulacaria afra shrubland	0	+1,16	-1,1	-1,15	-3,74	-	1,79

on trends in seasonal variation could be made. At five out of eight sample sites, maximum densities were recorded during one of the two winter and spring capture periods. On the other hand minimum densities were also recorded during the same seasons, at seven of the eight sample sites.

The variation between seasons, however, may simply te random. A null hypothesis that maximum densities were higher in any specific season was discarded, as was the same hypothesis for minimum densities when using

From Table 36 it was, however, calculated that the magnitude of population increases were lower than for population decreases. The mean magnitude of seasonal change in increasing populations was only 1,94 against 2,97 for population decreases.

A correlation matrix showing the relationship between various environmental parameters and small mammal density, biomass and energy requirements are given in Table 37.

Density, biomass and energetic requirements were correlated to various parameters that could be a reflection of productivity, at the various trapping sites, e.g. "grass" plus "other" cover points, "other" plus litter cover points, "other" cover points, density of the foliage profile below 20 cm (D_{20} , P_{20}), foliar and soil P and N levels, profile diversity and habitat diversity. (The latter based on the point survey). There was also a positive correlation with nitrogen in the A1 soil horizon.

(Soil data from Bond 1981, see Appendix 9), and with the Bray-Curtis ordination of the structural attributes of the sampled plant communities as done by Bond (1981).

All three these parameters were also increasing with altitude and in relation to an increase in the denseness of the plant community. As was the case with alpha diversity, productivity, standing biomass and distribution of the biomass in space seemed to be the factors of overriding importance in determining the density of the small mammal communities at the trapping sites.

TABLE 37. Environmental parameters significantly correlated to mean and maximum density, biomass and energetic requirements. (Pearson's correlation coefficient was used in all cases).

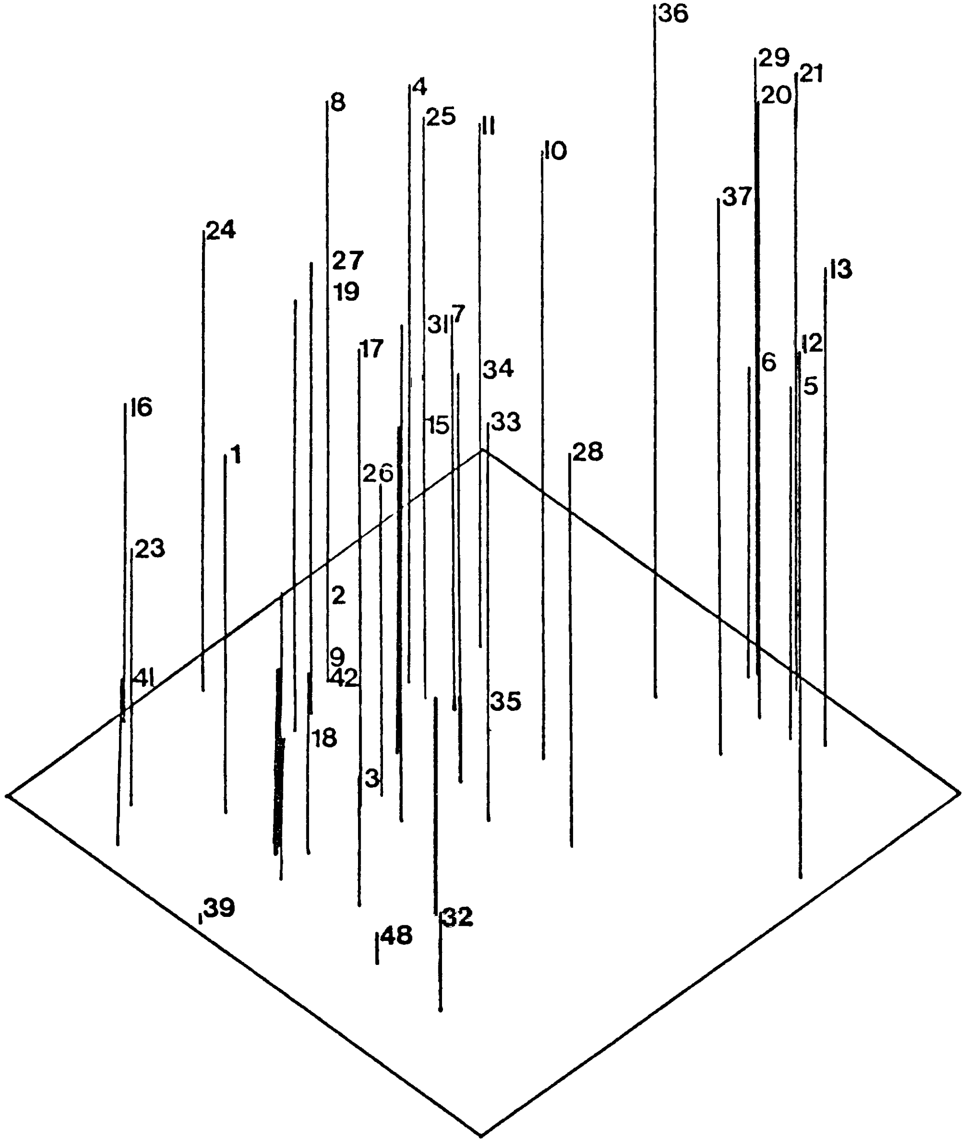
Environmental parameters	Numbers per ha^{-1}		Biomass ha^{-1}		J ha^{-1}	
	Mean	Maximum	Mean	Maximum	Mean	Maximum
Grass plus shrub cover points	,837	,763	n.s.	n.s.	n.s.	n.s.
Shrub plus litter cover points	,715	,856	n.s.	n.s.	n.s.	,763
Shrub cover points	,869	n.s.	n.s.	n.s.	n.s.	,77
Bray Curtis structural ordination	,781	,814	n.s.	n.s.	,79	,845
D_{20}	n.s.	n.s.	,81	n.s.	,82	n.s.
P_{20}	,769	n.s.	,777	n.s.	,827	n.s.
$P_{40\ 60}$	-,836	-,803	n.s.	n.s.	-,786	-,717
Foliar P Mg/Cm^2	,943	n.s.	n.s.	n.s.	,821	n.s.
Foliar N %	,78	n.s.	,702	n.s.	,809	n.s.
Profile diversity H	n.s.	n.s.	-,827	n.s.	-,819	n.s.
Profile equitability E	n.s.	n.s.	-,821	n.s.	-,813	n.s.
Habitat diversity H	n.s.	,798	n.s.	n.s.	n.s.	,715
Habitat equitability E	n.s.	,802	n.s.	n.s.	n.s.	,714

SMALL MAMMAL COMMUNITIES AND THEIR DISTRIBUTION ALONG THE SAMPLED GRADIENT

A Bray-Curtis ordination was done using the relativized Czekanowski similarity coefficient as estimator of percentage similarity existing between samples. The number of captures were low and the community composition as reflected by the data may be incorrect. Nevertheless it was assumed that the captures represent the community at a capture site during that capture period. The results can however only be seen as a first approximation of the distribution patterns in the small mammal communities of the Swartberg. Two distinct communities were identified, a lower north facing slope small mammal community and a mesic fynbos small mammal community (Overlay 1, Fig. 31).

The lower north facing slope small mammal community.

All the samples (data from different trapping sessions) from the *Paranomus dregei*- and the *Portulacaria afra* shrublands (Sites 7 and 8), were placed in this small mammal community as were three of the four *Protea lorifolia* shrubland (Site 6) small mammal samples. These samples were placed close together in the ordination largely because of the dominance of either *A. namaquensis* or *A. subspinosus* in conjunction with sub-dominance by *E. edwardii*. The small mammal samples from the *Protea lorifolia* shrubland (Site 6) can be seen as transitional between the lower north slope small mammal community and the mesic fynbos small mammal community.



BRAY CURTIS ORDINATION OF ALL SAMPLES

Fig. 31. Bray-Curtis ordination of all samples with overlay showing position of identified small mammal communities. (Numbers represent sequential samples for sites and seasons . See fig. 32).

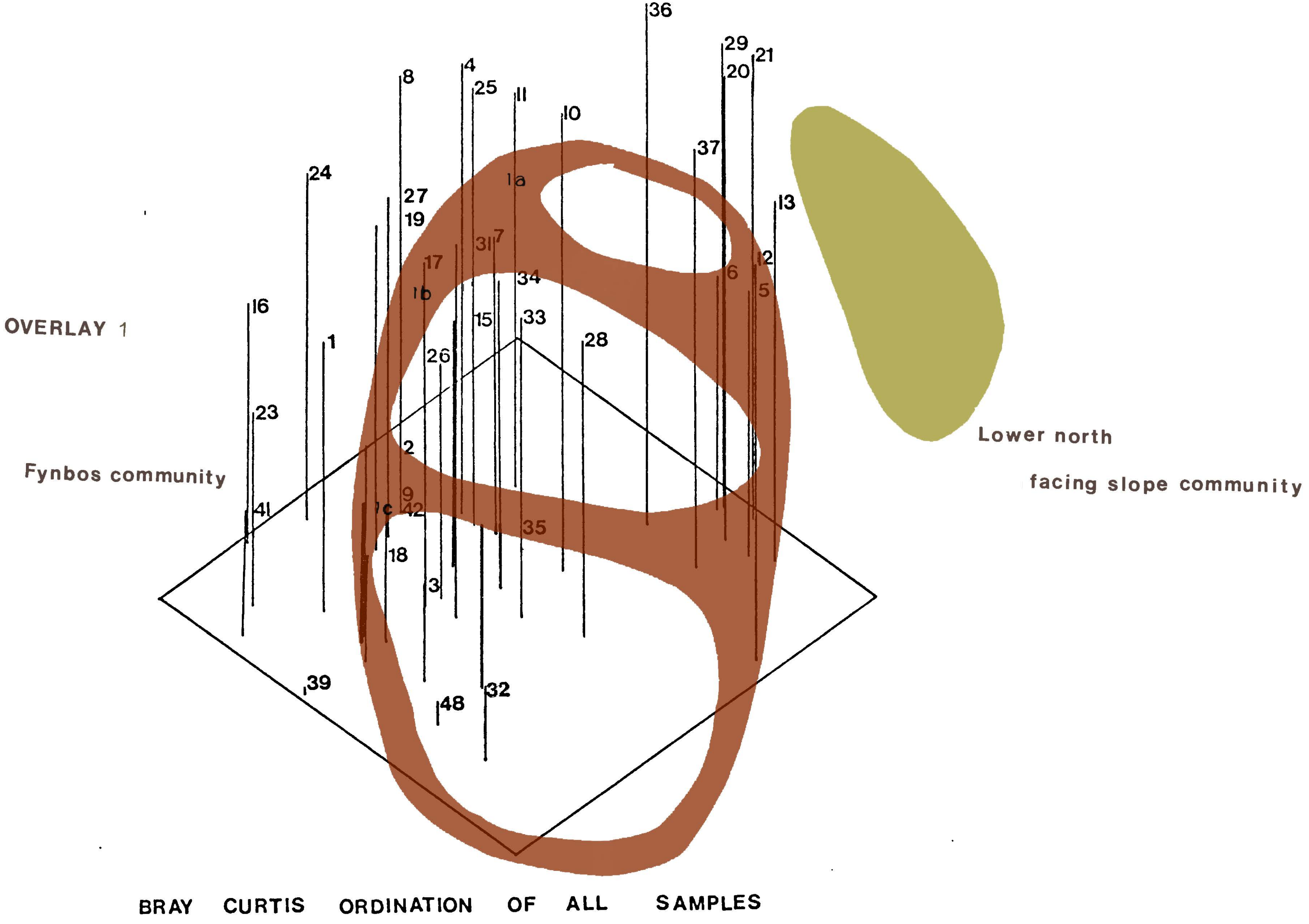


Fig. 31. Bray-Curtis ordination of all samples with overlay showing position of identified small mammal communities. (Numbers represent sequential samples for sites and seasons. See fig. 32).

This community can probably best be described as an *Aethomys namaquensis*, *Acomy subspinosus*, *Elephantulus edwardii* small mammal community. Any small mammal assemblage in the Swartberg in which *A. namaquensis* is dominant, or in which *A. subspinosus* and *E. edwardii* are co-dominants can be regarded as forming part of this community.

The mesic fynbos small mammal community

The mesic fynbos small mammal community can be subdivided into three sub-communities; each of these were dominated by a different species or group of species, but none of these species were limited to a specific sub-community.

The first sub-community (1a Overlay 2, Fig. 31), consisting of five samples, contain three samples from the spring 1978 capture period, and included samples from the *Protea repens*-*Protea punctata* shrublands, *Protea montana*- and *Leucadendron album* heathlands (Sites 2,3,4 and 5). This small mammal sub-community was characterised by the partial dominance of *A. subspinosus* and/or *R. pumilio*, and/or the presence of *M. varius* in reasonably large numbers.

The second small mammal sub-community (1b Overlay 2, Fig. 31) contained 12 samples, 11 of which come from the summer to winter 1979 capture periods and represent samples from the *Phylica paniculata* shrubland and the *Leucadendron album* heathland (Sites 1 and 5). This sub-community was characterised by the dominance of *A. subspinosus* and/or *O. irroratus* and fairly high numbers of *M. varius* and *P. verreauxii.*

The third small mammal sub-community (1c Overlay 2, Fig. 31) contained 11 samples, four of which came from Spring 1979 sampling periods. Samples from *Protea punctata* shrubland and *Protea montana* heathland (Sites 3 and 4) were prominent in this sub-community and it was characterised by the dominance of *M. varius* and the presence of *P. verreauxii* and/or *O. irroratus* in fairly large numbers.

The mesic fynbos small mammal community can not be characterised by any single species or group of species. Species that occur in this community include *M. varius*, *A. subspinosus*, *P. verreauxii*, *R. pumilio* and *O. irroratus*. Any one or more of these species could assume a dominant position in this small mammal community.

Only two small mammal communities were therefore identified, one on the lower north facing slopes and another occuring over the rest of the mountain. The first mentioned community was fairly stable and the species characteristic of this community were always present. The ordinal position of samples from this community in the ordination were therefore fairly constant. The other community had a wider distribution occurring right across the rest of the mountain. There was no single dominant species in this community and the samples from the various seasons and from the various trapping sites did not occupy a constant ordinal position in the ordination. There were therefore only two small mammal communities that were readily identifiable in the Swartberg, in spite of an altitudinal range of 700 m and a rainfall gradient of almost 500 mm being covered. The variability in the ordinal position of the samples does not allow one to do a satisfactory indirect gradient analysis.

The ordinal position of small mammal trapping sites along the x and y-axis of an ordination based on the mean and maximum number of individuals of each species at each trapping site were used to try and identify environmental factors that influence small mammal community composition.

There were negative relationships between the ordinal position along the x-axis and total rock cover ($r = -0,918$ and $r = -0,892$ for the ordination based on mean and maximum numbers captured, $p < 0,05$). There were positive correlations ($r = 0,872$ and $0,82$ respectively) between the ordinal position along the x-axis and shrub plus litter cover and grass cover. Community composition was therefore apparently influenced by total plant cover.

Seasonal variation in small mammal community structure

The consecutive position of the seasonal samples from each trapping site in the ordination were determined and the distance between the ordinal positions measured (See Fig. 32, Overlay 1 and 2).

A second set of two dimensional ordinations were drawn, but in this case the samples in each ordination were from a single trapping site. The distance between the ordinal position of samples 1 and 2, and 5 and 6 are greater in nearly all of the ordinations than that between samples 2,3,4 and 5 are. This means that in the winter to spring trapping sequence (samples 1 and 2, and 5 and 6) the small mammal samples changed quite dramatically whereas the changes between the other seasons were less dramatic. (Fig. 33).

The distance between the ordinal position of successive samples from each trapping site in the ordination was measured and ranked from the smallest to the greatest. (Table38).

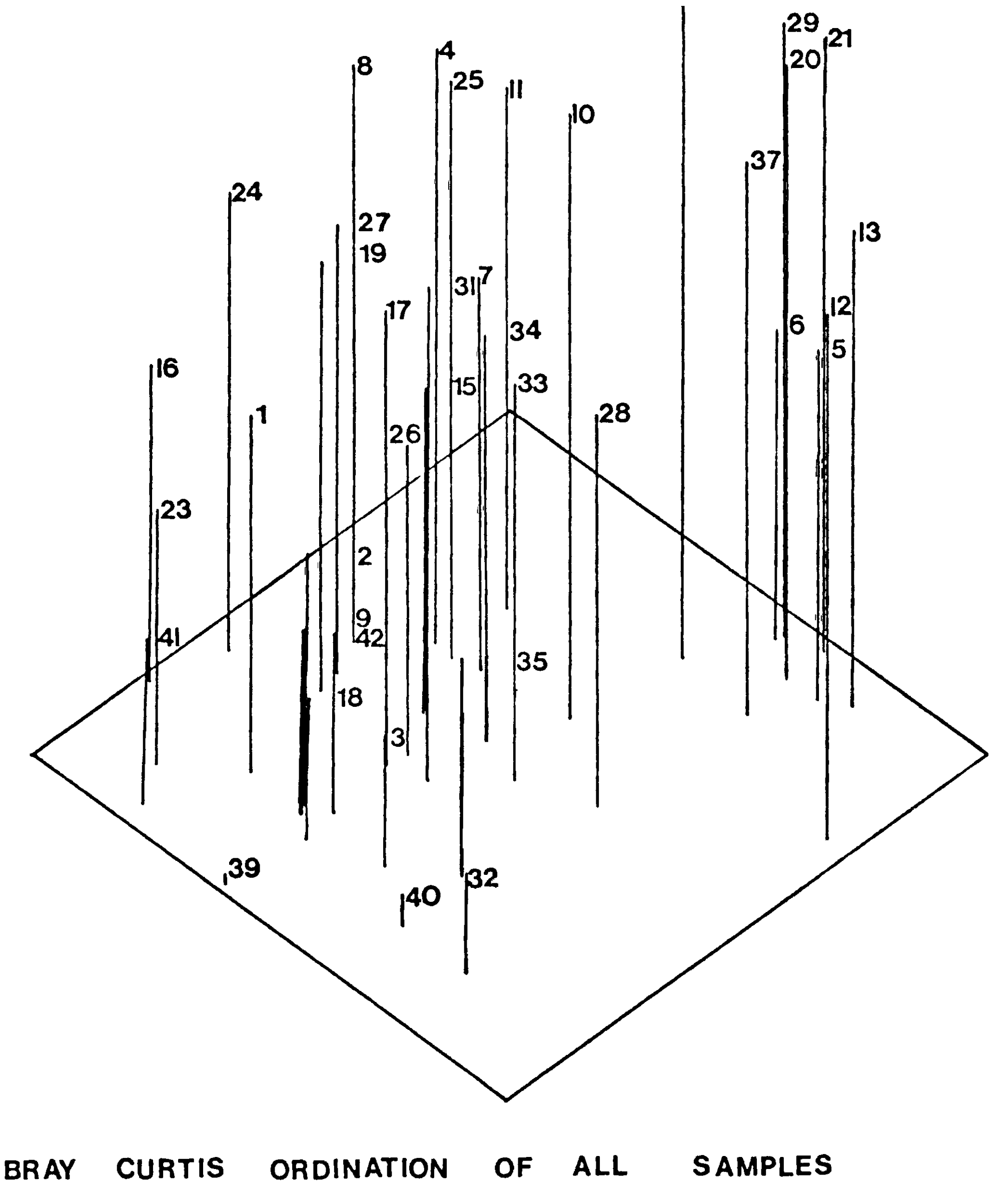


Fig. 32. Bray-Curtis ordination of all samples with overlays showing the ordinal position of sites during consecutive seasons. (Key to sites on overlays).

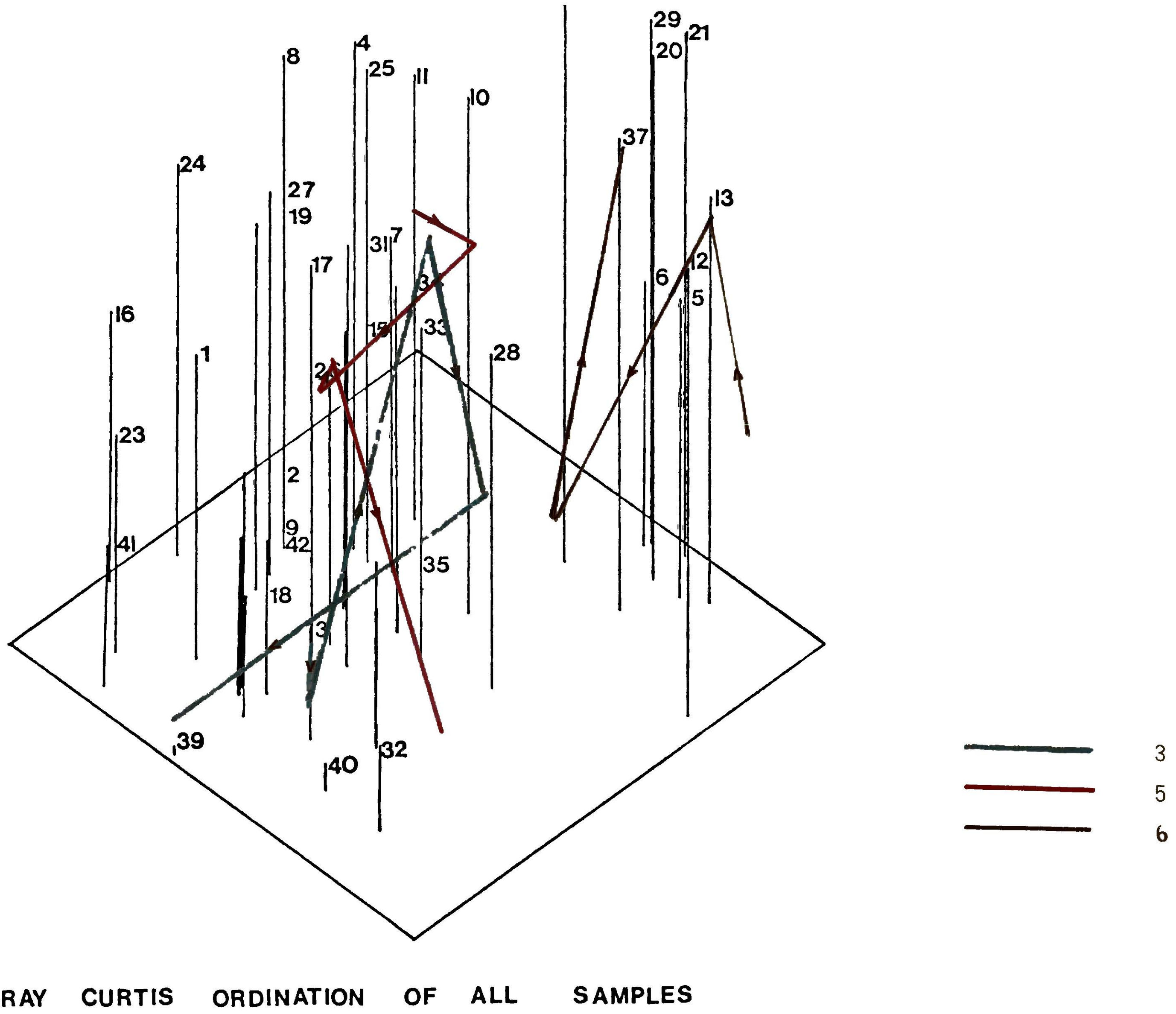
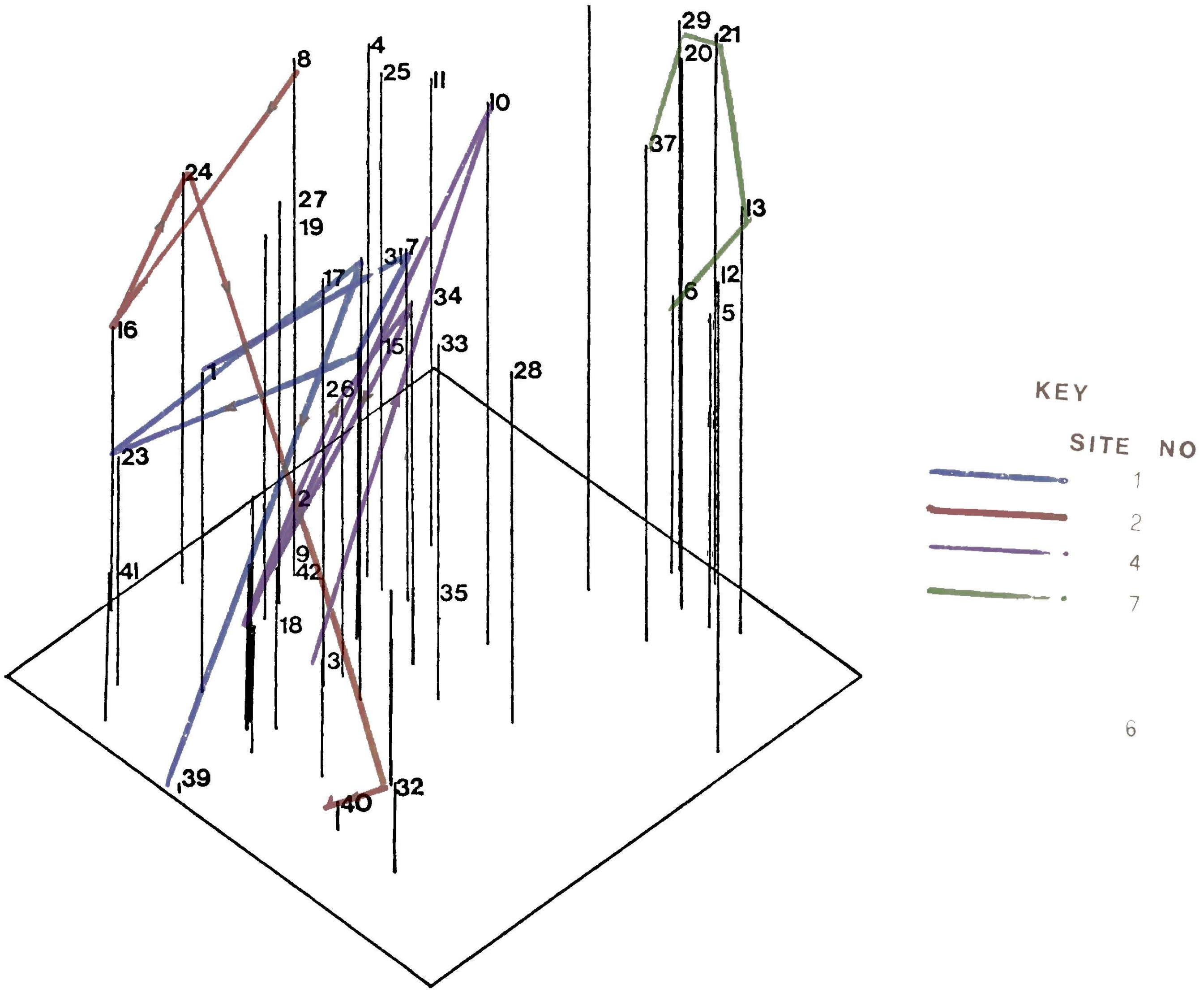


Fig. 32. Bray-Curtis ordination of all samples with overlays showing the ordinal position of sites during consecutive seasons. (Key to sites on overlays).



BRAY CURTIS ORDINATION OF ALL SAMPLES

Fig. 32. Bray-Curtis ordination of all samples with overlays showing the ordinal position of sites during consecutive seasons. (Key to sites on overlays).

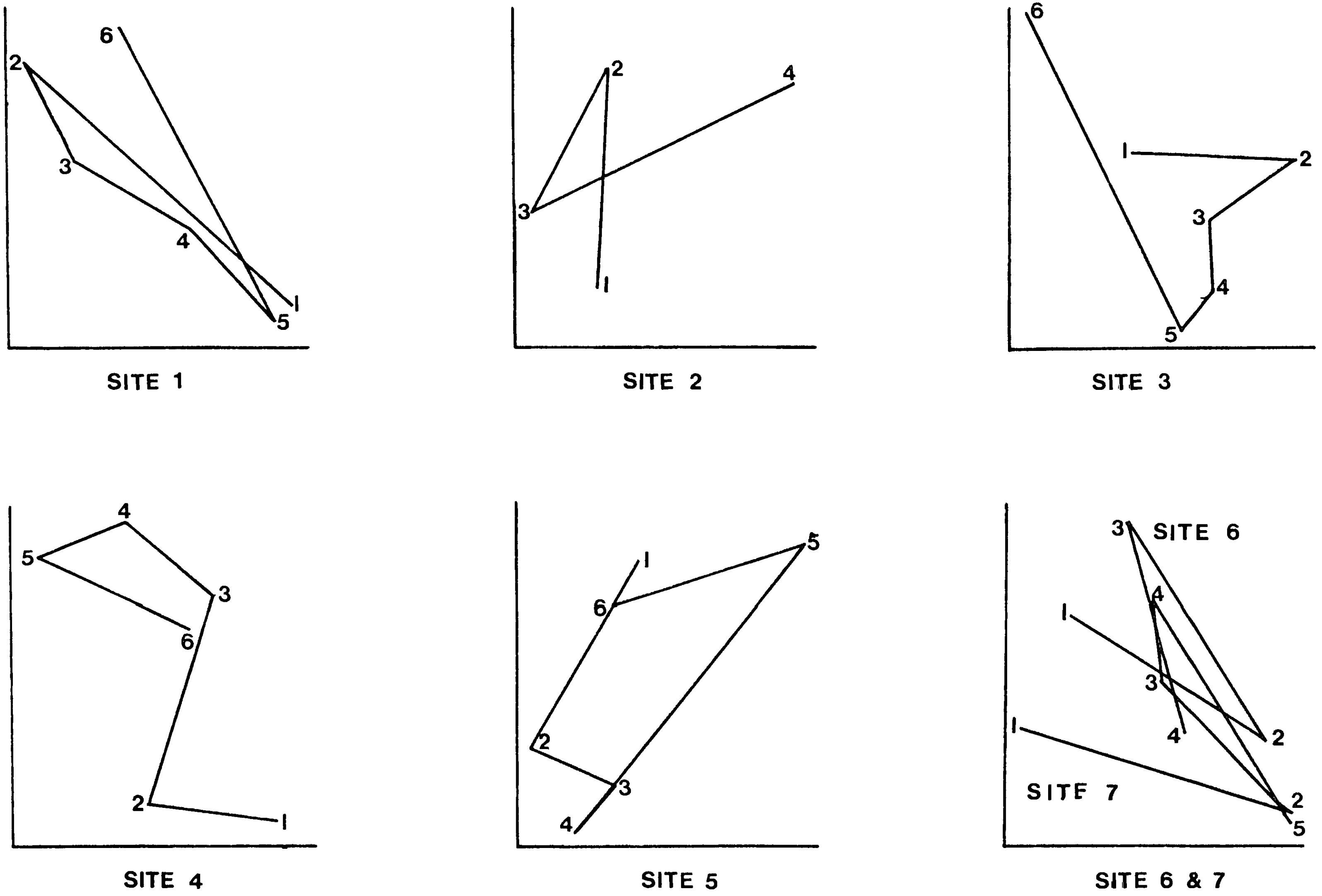


Fig. 33. Ordination of seasonal samples from each site. Seasonal samples are numbered consecutively and joined by lines.

TABLE 38 . Ranking from greatest to smallest seasonal changes in community structure between samples as derived from the distance between the ordinal position of consecutive samples from the same trapping sites.

A. From single site ordinations (Fig.33).

Site	Plant community	Seasons					
		Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Winter 1979	Spring 1979
1	Phylica paniculata shrubland	0	5	1	2,5	2,5	4
2	Protea repens shrubland	-	0	3	2	4	1
3	Protea punctata shrubland	0	4	3	2	1	5
4	Protea montana heathland	0	3	5	2	1	4
5	Leucadendron album heathland	0	3,5	2	1	5*	3,5*
6	Protea lorifolia shrubland	-	0	2	3	1	-
7	Paranomus dregei shrubland	0	4	2	1	3*	-
	Mean	0	3,9	2,6	1,9	1,9	3,5

*Sites burned down, not included in mean.

TABLE 38 (Continued).

B. From the all sample ordination (Fig. 32)

Site	Plant community	Winter 1978	Spring 1978	Summer 1978	Autumn 1979	Winter 1979	Spring 1979
1	Phylica paniculata shrubland	0	3	1	2	4	5
2	Protea repens shrubland	-	0	3	2	4	1
3	Protea punctata shrubland	0	1	4	2	3	5
4	Protea montana heathland	0	4	1	2	3	4
5	Leucadendron album heathland	0	2	3	1	4*	3,5*
6	Protea lorifolia shrubland	-	0	1	2	3	-
7	Paranomus dregei shrubland	0	2,5	4	1	2,5*	-
	Mean	0	2,5	2,4	1,7	3,4	3,8

* Sites burned down, not included in mean.

The results show that greatest change (as far as community structure and/or composition is concerned) took place during the winter and spring capture periods, both in 1978 and 1979. The mean ranking was 3,9 and 3,5 respectively and 2,8 overall for the single ordinations.

The results from the all sample ordination were not as clear (this could be expected because of the unassociated end points), but the winter to spring 1979 samples were still the most different.

It seems that certain species may become dominant during certain seasons and this explains why so many samples from the same season, but from different small mammal trapping sites, are grouped together in the ordination.

Dominance patterns in the small mammal communities

The dominance index (Do.I) of all samples are shown in Table 39. The Do.I was correlated to alpha diversity (both species richness and species diversity H). (Figs. 34 and 35). There was, however, no relationship between the Do.I and total trap success.

Between 50% and 100% of the animals in each sample were members of two species only, while the most commonly captured animal in each sample contributed between 29% and 100% to the sample.

TABLE 39. Degree of numerical and **biomass** dominance in each sample for the most, and **second** most dominant species. (Numbers and biomass).

	Most common species Sample number **							Actual numbers captured Second most common species							Sum of first and second most common species						
Site	1	2	3	4	5	6	$\bar{x}$	1	2	3	4	5	6	$\bar{x}$	1	2	3	4	5	6	$\bar{x}$
1	,33	,67	,4	,43	,4	,67	,48	,27	,33	,4	,29	,4	,33	,34	,5	1	,8	,72	,8	1	,8
2	-	,58	,62	,78	,5	,67	,63	-	,17	,38	,11	,5	,33	,3	-	,75	1	,89	1	1	,93
3	,47	,55	,3	,31	,31	,6	,42	,24	,27	,3	,31	,31	,2	,27	,81	,82	,6	,62	,62	,8	,71
4	,5	,46	,56	,7	,47	,4	,51	,3	,31	,33	,2	,33	,4	,31	,69	,77	,89	,9	,80	,8	,83
5	,43	,35	,29	,29	,5*	-	,34	,26	,26	,24	,29	,33*	-	,26	-	,61	,53	,58*	,83*	-	,6
6	-	,67	,67	,3	,41	-	,52	-	,17	,33	,3	,18	-	,25	1	,84	1	,6	,59	-	,76
7	,9	,5	,43	,67	,75*	-	,63	,1	,36	,36	,22	,25*	-	,26	1	,86	,79	,89	1*	-	,91
8	1	1	1	5	1	-	9	0	0	0	5	0	-	1	1	1	1	1	1	1	1

	Sample number **							Biomass													
Site	1	2	3	4	5	6	$\bar{x}$	1	2	3	4	5	6	$\bar{x}$	1	2	3	4	5	6	$\bar{x}$
1	,47	,83	,73	,79	,4	,58	,63	,21	,17	,22	,16	,36	,27	,68	,68	1	,95	,95	,76	,85	,87
2	-	,57	,77	,72	,79	1	,77	-	,2	,23	,25	,21	0	,18	-	,77	1	,97	1	1	,95
3	,35	,58	,33	,33	,41	,44	,41	,23	,32	,3	,24	,26	,21	,26	,58	,9	,63	,57	,67	,65	,67
4	,66	,76	,88	,87	,75	,57	,74	,14	,08	,07	,11	,16	,27	,14	,8	,84	,95	,98	,91	,84	,9
5	,53	,29	,5	,57	,58*	-	,51	,23	,28	,25	,24	,23*	-	,25	,76	,57	,75	,81	,81*	-	,72
6	-	,68	,5	,55	,32	-	,51	-	,21	,5	,26	,27	-	,31	-	,89	1	,81	,59	-	,82
7	,89	,52	,44	,44	,86*	-	,57	,11	,4	,28	,41	,14*	-	,3	1	,92	,72	,85	1*	-	,87
8	1	,91	1	,76	1	-	,93	0	,09	0	,24	0	-	,11	1	1	1	1 -	1	-	1

* Not included. Abnormal because of accidental fires.

Key to sample numbers :

1	Winter 1978
2	Spring 1978
3	Summer 1978
4	Autumn 1979
5	Winter 1979
6	Spring 1979

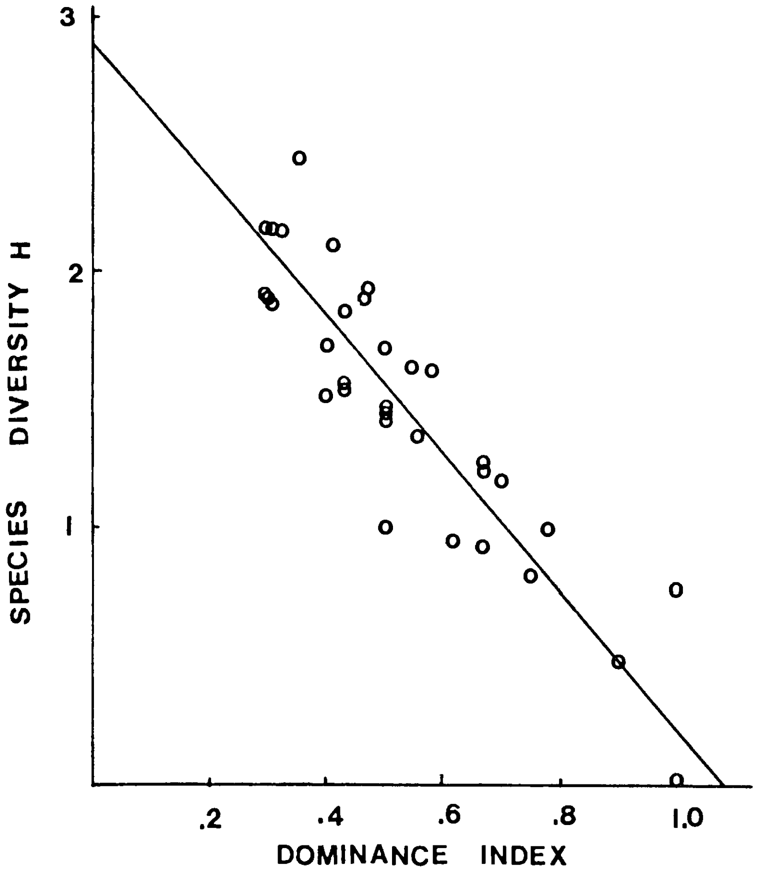


Fig. 34. The relationship between dominance and species diversity H of the sampled small mammal communities.

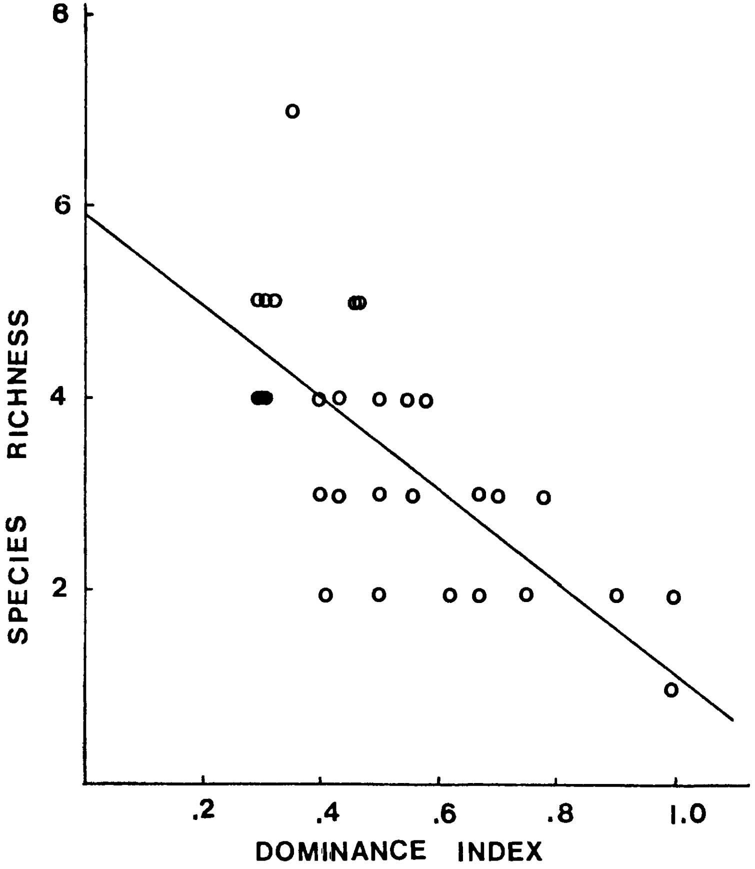


Fig. 35. The relationship between dominance and species richness of the sampled small mammal communities.

DISCUSSION AND CONCLUSIONS

SELECTION OF THE STUDY SITES

Huston (1979) postulated that competition in communities should be at a minimum directly after a perturbation event had occurred and that species diversity and density should therefore increase for some time after the perturbation event as conditions improve, but reach an asimptote and decrease as competition increases.

This model certainly seems to be applicable in the fynbos vegetational patterns (Bond 1980b, van Wilgen 1980) and likewise for small heathland mammals in Australia (Fox & McKay 1981, Catling & Newsome 1982) and therefore could not be excluded as a complicating factor. Since the objective of this study was to establish the possible environmental conditions that are conducive to high species richness and population densities on a broad geographical scale it was deemed necessary to sample only "undisturbed" mature adult vegetation. In the Swartberg for example, winter or spring fires, which are considered to be "unnatural" result in extreme reductions of Protea spp. (Bond 1980a). Such sites could therefore be excluded a priori.

The effect of perturbations on small mammals have been shown in many studies (Neal 1970, Sheppe 1972, Christian 1977, Kern 1977, Newsome and Catling 1979, Fox 1981 and Fox & McKay 1981, Catling and Newsome 1982). Since it would not be possible to differentiate between pertubation and ecosystem and/or site effects, sites were subjectively chosen so that areas with obvious human impact were excluded. Because of these factors and accessibility problems, sites could not be ideally spaced along the altitudinal gradient and the coverage of the gradient was therefore not even.

The two trapping grids at every site were placed within 100 to 200 m of each other. It is known that small mammals cover greater distances than this (Sheppe 1972), but only one marked animal was ever captured on a snap trap grid and the decision to place these grids so close together was fortuitously proven correct.

ENVIRONMENTAL GRADIENTS

The gradient sampled was a complex one, with many environmental conditions changing along the pre-selected altitudinal gradient. Temperature for example decreased with altitude in the Swartberg (Bond 1981) and closely followed the lapse rate as estimated by Smith & Geller (1979).

Precipitation increased with altitude but the rainfall isohyets as given on the isohyetal maps were found to be inadequate, as they followed topographic features and the rainshadow on the north slope was obscured. Rainfall as estimated from regression analysis and Bond's (1981) D.I. were usefull comparative gradient measures and placed trapping sites along a moisture gradient in a way that seemed to correspond to the vegetation patterns observed.

The soils (Bond 1981), also conformed to expected fynbos patterns being acidic, low in exchangeable bases and having extremely low P and N levels (Cowling & Cambell 1980, Bond 1981). Along the gradient, however, N and P levels in the soils showed trends opposite to that expected. N and P are both substances that are leached fairly easily as acidic compounds (Buckman & Brady 1971), but were highest in the higher rainfall zones. This could be an artefact of soil genesis (Bond 1981), a closed nutrient cycle (Van Daalen 1980, Bond 1981), or may be the result of soil hydrophoby (Bond pers comm), however, this latter phenomenon needs further investigation.

The foliage profile was assumed to be a surrogate measure of plant biomass and conformed to the finding that increasing rainfall results in greater plant biomass (Phillipson 1975, Rutherford 1978, 1980). The foliage profile can be measured quickly and can with practice even be estimated accurately. The relationship between foliage profiles and the actual biomass should be established before they are applied as such but they are useful measures that have much wider potential application.

In this study foliage profiles were found to be extremely useful parameters, since many of the foliage profile measures had a direct bearing on various of the small mammal parameters, i.e. D_{20} was correlated to density, biomass and alpha diversity.

The height of the plant community was not positively correlated to the area under the drawn foliage profile. Plant height and foliage density decreased with increasing altitude as was shown by ½H. (The height at which the surface under the drawn foliage profiles can be bisected). This is probably due to increasing wind velocity and duration with altitude, resulting in different plant growth forms (Grace 1977).

In this study several calculations were made so as to express the measured foliage density in various ways. It was found that the foliage density measure as proposed by Rosenzweig and Winakur (1969) (F_i) is simply the actual density (D_i) multiplied by a constant and F_i and D_i were auto-correlated. It was therefore far easier to simply use the actual density measurements. Similarly the area under the drawn foliage profile was highly correlated to the actual density measure. They were, however, handy since this was the only way in which ½H or any similar measure relating the foliage density to foliage height could be determined.

The results from the point cover survey also indicated that the density of total live cover increased with increasing altitude (Total live cover was taken as being "grass" plus "other" cover, and included all plant growth forms). This again conforms to the notion that cover (biomass) increases with increasing rainfall (Phillipson 1975).

Plant growth forms also varied along the sampled gradient. These patterns have been examined in detail by Bond (1981). He was able to show that there is a close resemblance between floristic composition and the structural attributes of his various identified plant communities.

The general trend observed in this study was that plant leaf size within the sampled plant communities tended to decrease with increasing altitude. This is interpreted as a response of plants to an increase in ultra-violet radiation (Scriba pers comm.). There was also a decrease in leaf size with increasing drought conditions which is seen as an adaptation to drought. As expected succulents also increased with increasing drought stress.

Gradient analysis as technique

The relationships between the small mammal parameters (e.g. density, diversity) and environmental gradients (e.g. altitude, foliage density), were identified by simple correlation analysis.

This means (at the 5% level of significance) that for every 100 such correlations found there is a probability that five may be spurious (Sokal & Rohlf 1969), or it may be the result of a single outlying point. To guard against the last contingency the relationships were all drawn graphically and inspected for outliers and use was made only of those with no outliers.

The biggest problem encountered in this study was to decide which small mammal parameters to use in these analyses, since seasonal samples showed considerable variation e.g. in density and species composition. The problem of local variation in data has been discussed by Rotenberry & Wiens (1980) and Wiens (1981). Wiens (1981) used various combinations and random itterations of a data set and came to the conclusion that variation on a local scale complicates interpretation and analysis. "The results of this exercise suggest some caution and skepticism are in order when reviewing the results of *broad* comparative analyses based upon single-year surveys over a variety of sites. The conclusions that emerge may not really apply to the system under study, and the generality of their application to other systems at other times, in other places may be quite limited ......". "The difficulty I have emphasised here is in a sense one aspect of an ecological paradox: Rather consistently, ecological patterns are discerned on board geographic or temporal scales of resolution, but when one looks at the dynamics of local populations and species assemblages for mechanisms to explain them, the patterns are missing, swamped by local variability" (Wiens 1981).

The broad geographic patterns in density of various rodents and the factors controlling their density in two southern Cape areas were established by Bond et al. (1980). They however, based their findings on a single survey during the summer of 1977 - 1978. In spite of the great variability recorded over time in the present study (whether this is due to inadequate sampling or actual patterns must still be determined) most of their findings were borne out by some of the present results. The density or percentage capture of a species, for example, was not always significantly correlated to the same environmental patterns over time. The general trends were however constant over time. (Paper delivered to the A.G.M. of the South African Association of Botanists, 1982, Breytenbach).

It is realised that far better multi-variate techniques are available for determining the relationship between animals and their habitats (e.g. stepwise multiple linear regression has been used with great success Sturman 1968, Robbins 1978, Anderson 1980 and even better still discriminant functions analysis Anderson & Shugart 1974, Bertin 1977). Nevertheless these techniques were not used because of the limited number of trapping grids used and because the reliability of the data may be questionable.

SMALL MAMMAL CAPTURES

Density estimates

The technique used proved to be satisfactory, and the assumption that the captured population represented the total population was only necessary on a few occasions. The total sampled population was then also invariably very small (less than four animals).

Effectiveness of trapping techniques

In order to determine the number of trapping nights required to trap the majority of animals in the various study sites it is necessary to trap for extended periods of time. De Witt (1972), for example, trapped for 21 days during a trial period and found that the majority of animals in his study area were trapped within the first seven days.

Because of logistic problems, however, it was not possible to trap for more than four consecutive nights at any trapping site during the present study. The results, however, indicate that this gave a fair coverage of the community. For example, the cumulative number of all known individuals (over all trapping sites) captured during the first two nights was 75% and after three trap nights it was 91,8%, based on a four-night trapping period, but will of course be less if taken over a longer trapping period. The percentage of animals captured more than once at a particular site during a single trapping season varied considerably (between 29,9% and 69,6%). The fact that nearly one third of the animals were captured at least twice, also indicates that trapping efficiency was fairly high and that the majority of animals were probably captured.

Since the major emphasis of this study was directed towards identifying how small mammal density and diversity responds to environmental gradients, determination of absolute densities were not needed. Delany and Happold (1979) point out that an index of abundance, e.g. a time relative index of abundance such as number of captures over time or a per unit effort index of abundance, such as numbers captured per unit trap nights, is also acceptable, provided that precisely the same method of obtaining estimates is used, especially if some indication of the accuracy limits exists or can be calculated.

It is therefore not wholly acceptable to do inter-study comparisons using trap success as criterion for density since each researcher tends to use different trap spacing, bait, trapping period and trap type. Furthermore, grids or traplines are not deployed in the same fashion. De Wit (1972), Rautenbach & Nel (1975), Nel (1978), Davis (1974), Jooste (1980), for example, used grids or lines covering more than one habitat. Large grids even if placed in what is considered homogenous habitats may be sampling within habitat or pattern diversity (Engström & James 1981). Trap success has also been expressed in such a fashion that it included recaptures (e.g. Hockings 1981) and this is not always stated clearly.

Densities were therefore also estimated, but it is recognised that the derived densities are far from satisfactory, nevertheless, they are useful for comparing results between studies. When the results of one study are going to be compared to those of another study it is important that the same sampling techniques are used. The techniques as used by Bond et al. (1980) were followed in this study and direct comparisons could therefore be made between the two data sets.

One of the major points of emphasis of this study was to get a fairly accurate indication of species richness and it was therefore important to identify the whole small mammal species complement that occurred at a trapping site.

Small mammal species known to occur at a site are almost never all recorded at the same time (e.g. see results from Rautenbach & Nel 1975, Kern 1977, Nel 1978). In the present study all the known species at a site were recorded within a mean of 2,75 trapping periods. Starting at the time when the lowest number of species were captured the mean number of trapping periods needed to record all species was 3,75. It was therefore assumed that the total number of sampling periods (4-6) were adequate. A randomized approach for determining the number of required trapping periods (see Wiens 1981, Fox 1981) would have been more appropriate than the above technique.

That all the species present at a trapping site at a specific point in time, were all captured is unlikely. In the Protea repens shrubland (Site 2) for example, a lone *D. mesomelas* nest was found close to the trapping site with an animal in it, but this species was never captured there.

A major premises was that animals of all species had an equal probability of being captured. The fact that certain species were captured consistently at some sites, but only occurred rarely at others, indicate that such species are readily captured in the traps used and that they are probably absent from sites when not captured there. *M. varius* for example, was only captured once in the *Protea lorifolia* shrubland (Site 6), but was present nearly 100% of the time at all the other mesic fynbos trapping sites (Sites 1 - 5) (see Table 18).

The relative ease with which species were captured and the consistency of captures also did not indicate poor sampling. For example, *O. irroratus* was present at extremely low densities in the *Protea punctata* shrubland (Site 3), but in spite of this was captured consistently at this site (Table 18).

Density and species composition remained constant at some sampled communities over time but varied considerably at others. The index of species occupation was lowest at the *Phylica paniculata* and the *Protea lorifolia* shrubland (Sites 1 and 6). These two trapping sites were similar in regard to the local environmental conditions (e.g. foliage profiles were reasonably similar as were the point survey results). The variability in the trapping results and the similarity in environmental conditions may be coincidental but it may also be indicative of an existing pattern.

In summary;

Species that are captured readily when at high densities are also captured consistently at low densities.

Trapping sites that display variability in regard to species occupation are similar in regard to environmental conditions.

Some of the species are captured consistently at some of the sites, even at low densities, but are almost never captured at other sites.

It is therefore concluded that even though there is great variability that remains to be explained, the observed patterns in diversity and density along the sampled gradient can be seen as a good first approximation of small mammal community patterns. It must also be remembered that mean diversity and density were used in the correlation analysis which may result in a decrease in the possible sampling errors.

The complex altitudinal gradient (complex because not only altitude varied) can best be summarised as one along which rainfall, wind and radiation had a strong influence on plant community structure, height, density and composition. The consumers within the ecosystem, of which the small mammals formed a small but significant part, showed strong relationships with these various measured gradients and are discussed in the following section.

SMALL MAMMAL POPULATIONS

Distribution of species in relation to environmental gradients

Elephantulus edwardii

Rautenbach and Nel (1980) reported this species from grassy slopes with rocks and from among boulders and rock debris, devoid of any vegetation in the Cedarberg. In the Rooiberg it was confined to the north and north-east slopes that were more rocky than the south facing slopes (David 1978).

The present results support the above findings. *E. edwardii* preferred rocky areas, but were not readily trapped in areas with grass cover as stated by Rautenbach & Nel (1980). They did, however, survive the fires in the *Paranomus dregei* shrubland (Site 7), and occupied this site during the post fire "grassy" period. (Grass "Poaceae" form a dominant part of the cover in certain areas during the immediate post fire period. These are later replaced by Restionaceae and shrubs). *E. edwardii* was not captured in the *Portulacaria afra* shrubland (Site 8). This site was in a very rocky environment, but had no Restionaceae or evergreen C3 grasses (Bond 1981). In the Swartberg this species therefore seems to be limited to fynbos vegetation and it seems that the same may be true for this species in the Cedarberg (Rautenbach and Nel 1980). Rautenbach & Schlitter (1977) have, however, reported it from the non-fynbos area at Fraserburg-Sutherland, probably from mountain renosterbosveld.

Mysorex varius.

This is a species with a wide distribution and it prefers a mesic micro-climate (Brain & Meester 1964, Bigalke 1978). It has a wider distribution range and greater habitat tolerance than either of the other two sympatric *Myosorex* species, *M. cafer* and *M. longicau-*

datus (Meester & Dippenaar 1978). M. varius has been recorded from grassland (Rautenbach 1976, 1982), dense undergrowth near rivers and streams (Shortridge 1934), shrublands (fynbos) (David 1978, Bond et al. 1980, Rautenbach & Nel 1980, Nel et al 1980) and forest (Meester & Dippenaar 1978, Rautenbach 1982). Two specimens from a dry arid karoo site (Bond et al 1980) are probably misidentifications.

In the present study relationships between numbers captured and various foliage profile parameters e.g. foliage density below 20 cm, indicate that the primary requirement of this species seems to be dense cover and largely confirms the above findings.

The association with dense cover could be explained in several ways. M. varius in the Southern Cape feeds extensively on seeds (Nel et al. 1980, this study), but cannot utilise the available seed resources in the same way as rodents. A. namaquensis, R. pumilio, P. verreauxii, and possibly A. subspinosus, gnaw through the stems of seed bearing plants. They then drag the seed to a "safe" feeding site, where they can feed undisturbed.

M. varius probably cannot do this and is dependent on seeds that have already been dropped from the plants, or it has to feed on individual seeds in the canopy. From this then one would expect M. varius numbers to be high in areas where seeds are available, and where cover offers adequate protection against predators. It would, therefore, be absent from the drier areas where cover is insufficient and where litter build up and insect populations are smaller.

M. varius was captured at all sites on the south facing slopes but was absent from the drier sites on the north facing slopes (*Paranomus dregei-* and *Portulacaria afra* shrubland plant communities "Sites 7 and 8), and has not been captured in any area that receives less than 500 mm rain per annum.

As stated in the results cover per sé may not be as important as is stated above since animals do not move out of newly burnt veld during the post fire seed glut. It may therefore simply be that *M. varius* populations are limited by food resources and that cover plays a minor role. This aspect, however, needs further investigation.

Praomys verreauxii

This species is endemic to the south-west Cape Biotic Zone (Rautenbach 1978a) and in spite of having been collected in forest areas, is normally associated with fynbos. David (1978) is of the opinion that since some ground proteas depend on *P. verreauxii* for pollination and all of the captures during his study were from protea stands, *P. verreauxii* is dependent on proteas for its existence.

From the results it was evident that *P. verreauxii* was more common in areas where the cover above 120 cm was dense. *Protea*, *Leucadendron* and *Leucospermum* dominates this layer at Swartberg and David's (1978) observation that *P. verreauxii* is dependent on *Protea* for its existence, is confirmed. *Protea* seeds form a substantial part of the diet of *P.verreauxii*. The dependence of *P. verreauxii* on protea seeds was also illustrated by the fact that they survived for at least a month in the *Leucadendron album* heathland (Site 5), after the fire had occurred. During this period of superabundant protea seed supply *P. verreauxii* actually built up fat reserves. After three months, however, when the available protea seed resource had largely been depleted, *P. verreauxii* disappeared from the burned areas.

Proteas in the Swartberg normally germinate during the late winter and/or spring following a fire. Depending on the phenology of the species and soil moisture conditions no flowering occurs during the first 8 to 16 years after the fire. *P. verreauxii* was captured only once in an area where proteas were present but not flowering, but in this instance mature flowering proteas were within 100 m of the capture site.

Several variables e.g. foliage profile above 160 cm and litter, also reflected the state of the proteoid layer to some extent. Proteas all have long leaf duration and it is only when flowering starts that leaf senescence and leaf fall is prominent and litter accummulates. Thus after a fire it takes some 4 - 12 years before microphylls, and in this case the Proteaceae, start losing their leaves. There is therefore a negative relationship between the amount of "bare soil and rock" and litter with increasing age.

P. verreauxii numbers were therefore showing a primary response to the phenology and presence of proteas. Since protea density decreases towards the xeric end of the gradient, this could explain the absence of *P. verreauxii* from the arid sites.

P. verreauxii has also not been captured in areas where the emergent layer is non-proteoid such as valley bushveld, renosterbosveld, karoo and ericoid heathlands (Bond et al 1980). They do, however, occur in the forests of the south-west Cape (Setzer 1975), but have never been encountered at high densities. Animals trapped in forest areas have also always been captured near the forest-fynbos ecotone.

Aethomys namaquensis

This species has been reported as being rupicolous (Sclater 1901, Roberts 1954, De Graaff 1981) and Bond et al (1980) reported this species' presence to be correlated with the number of rocks up to 13 cm in diameter.

They have, however, also been reported from non-rocky sites such as dry river banks and dunes (Smithers 1971, Nel & Rautenbach 1975), where they probably nest in trees, logs or fallen piles of debris (Smithers 1971). Normally nests are found in crevices or under loose boulders (Pienaar 1964, Smithers 1971). Nel & Rautenbach (1975) also reported that this species is limited by available nesting material (grass) in the Kalahari.

A. namaquensis was captured only on the low altitude sites on the north facing slopes, in the Paranomus dregei and Portulacaria afra shrublands (Sites 7 and 8). The relationship between environmental parameters and densities could therefore not be determined by using regression or correlation analysis. The relationship with rocks smaller than or equal to 13 cm in diameter as found by Bond *et al*. (1980) was supported by the present limited data. They were not captured in areas with less than 30% and 50% of ground cover consisting of rocks $<$ 13 cm in diameter and total rock cover respectively. As found by Bond *et al*. (1980) *A*. *namaquensis* was also not captured in areas with more than 75% shrub cover and it occurred in areas with low total foliage cover.

It was not clear why *A*. *namaquensis* should be limited to the xeric sites. Restios bearing nutlet like fruits (e.g. *Willdenowia teres* and *Hypodiscus* spp.), were utilised as food in the *Paranomus dregei* shrubland (Site 7). Similar fruit bearing plants were common elsewhere along the gradient and food was abundant. Unlike the Kalahari population that uses only grass, sticks and restios were also used as nesting material in the present study area. Nesting material was therefore available all along the gradient, but it is not known whether vegetation density could limit the movement of such material from collecting points to nest sites. It, therefore, remains to be shown what the actual limiting factor for this species is.

Rhabdomys pumilio

R. *pumilio* is an ubiquitous species. It is common throughout South Africa, but is absent from eastern lowveld areas such as Zululand and Mozambique. Davis (1974) suggested that it is replaced here by *Lemniscomys griselda*. It is not limited to any vegetation type and is absent only from forests (Davis 1974).

Suitable cover seems to be an essential requirement for *R. pumilio* (Smithers 1971, Nel & Rautenbach 1975, Swanepoel 1979, Jooste 1980, Bond *et al*. 1980, De Graaff 1981, Rautenbach 1982) and the importance of "grass" cover has been stressed by Rautenbach (1976, 1982) and Bond *et al*. (1980). The decrease in *R. pumilio* densities during the study period was a wide-spread phenomenon. This decrease occurred at all three study areas (Swartberg, Baviaanskloof and Robinson's Pass) and therefore occurred synchronously throughout a region, of some 100 x 300 km. These results therefore supports Nel's (1975) hypothesis that cyclic fluctuations in population density of South African rodents are synchronised and occur over large areas.

Although the numbers of *R.pumilio* trapped, decreased over the study period relative density along the sampled gradients could have been expected to remain constant. The strong relationship between *R. pumilio* numbers trapped and various environmental parameters as detected by Bond *et al*. (1980), were not confirmed as the relative density along the sampled gradient had changed. The general predictability, and the utilisation of environmental variables as estimator of rodent density therefore seems trivial (see Wiens 1981).

Nevertheless Anderson (1970) has shown that colonizing and survival habitats support different population levels during the various phases in the population cycle in some small mammals. If his findings have general application, it is possible that "colonizing" habitats could have been oversaturated during Bond *et al*'s. (1980)

study, and that "survival" habitats could have supported comparatively more individuals during the low population period of the present study.

If cover is as important as suggested in the literature, highest densities should have been recorded at Site 4, (*Protea montana* heathland) where cover was highest. No *R. pumilio* was trapped here. This was attributed to micro-climatic conditions, especially in winter when this site did not receive more than three hours of sunlight daily due to local topography and steep slopes. In addition because of *R. pumilio's* poor insulation (Haim & Fourie 1980) extreme windy conditions, rain, prolonged misty periods, low temperatures and persistence of snow probably also contributed towards making this site unsuitable for *R. pumilio*.

Acomys subspinosus

Davis (1974), in contrast to Setzer (1975), considers *A. subspinosus* as being endemic to the south west Cape Biotic Zone, and found this species to be limited to shrublands. There have, however, been reports of this species being captured in forest and woodlands (Andrews *et al*. 1975 in Avery 1979).

Most species of *Acomys* are rupicolous and Rautenbach & Nel (1980) have suggested that *A. subspinosus* may be limited to rocky areas. At Swartberg, however, *A. subspinosus* nests in holes rather than in cracks and crevices, or under exfoliating slabs of rock like some other species of *Acomys* (Smithers 1971). *A. subspinosus* has also been captured in areas almost totally devoid of rocks

(Bond et al. 1980, this study). Thus even though rocky areas may be considered to be optimal for these animals, they do occur in other habitats as well.

This study supported Bond et al's (1980) findings that captures increased with altitude. Numbers captured at the Protea montana heathland (Site 4) the highest altitude site, were however lower than those at the Leucadendron album heathland and Protea lorifolia shrublands. There is some indication that like R. pumilio, A. subspinosus may be influenced by micro-climatic conditions. A. subspinosus, however, also feeds extensively on nutlets of restios. Its low dlensity at the Protea montana heathland (Site 4) may therefore be the result of the absence of a good restio cover with the above seed characteristics.

A. subspinosus has only been captured at sites (in all three of the major study areas) that support a fynbos vegetation and can therefore be considered to be a true fynbos endemic.

Petromyscus collinus

P. collinus has been widely collected in the south-west Arid Zone, extending from Williston in the south to north of the Kunene river. It is a rupicolous species and was thought to be confined to the rocky zone east and west of the great escarpment (Davis 1962, 1974, De Graaff 1981).

In a detailed study done at Tumasberg in the Namib-desert, Withers

(1979) found that *P. collinus* preferred rocky areas where there are rock overhangs, crannies, cracks and vegetation to provide hiding places. They also showed a preference for areas with a grass cover consisting of *Stipagrostis cilliata* and *Enneapogon brachystachys*.

P. collinus was captured only in the *Portulacaria afra* shrubland (Site 8). This is a dry rocky area where succulence of the vegetation is prominent and it is interesting that all records of this species in southern Africa (see Davis 1974) are from veldtypes (Acocks 1953) with a high degree of succulent plants. This could explain its absence from all the fynbos areas in the Swartberg which have almost no succulent plant species.

This is the most south-eastern record of this species, and is also the first record from the Cape folded belt. Avery (1979, 1982) has found no record of this species during the last c.32 000 years at Boomplaats some 15 km to the east of this study area or other S.W. Cape archeological sites (Avery 1982). *P. collinus* have been recorded from Mirabib in the Namib dating back nearly 8 000 years (Brain & Brain 1977). This species is therefore actively colonising new areas.

Dendromus mesomelas and *Dendromus melanotis*.

Insufficient data precludes discussion on these two species.

Otomys irroratus

Several species of *Otomys* occur sympatrically in the mountains of the southern and south-western Cape, *O. irroratus*, *O. laminatus* and *O. saundersiae* (Davis 1974, Setzer 1975, Avery 1979, Rautenbach & Nel 1980, Nel *et al*. 1980). Since the species cannot be distinguished in the field most workers, e.g. Bond *et al*. (1980), refers to the *Otomys* complex rather than referring to a single species. Recognition of species-specific habitat preferences is therefore impossible in live capture studies and leads to confusing results where these species occur sympatrically.

O. irroratus inhabits dense vegetation on the banks of streams and edges of swamps (Roberts 1954, Delany 1972, De Graaff 1981, Rautenbach 1982), but has also been captured some distance from water (Shortridge 1934, Swanepoel 1979, Bond *et al*. 1980). Bond *et al*. (1980) records this species as being limited to areas with at least 75% shrub cover in the mountain fynbos. This does not hold true for the total distribution range of *O. irroratus*. In moist areas such as vleis and swamps, shrubs are replaced by grass and this is also a preferred habitat.

During the present study both kill and live trap techniques were used. All *Otomys* specimens collected from kill trap sites were *O. irroratus*. Because of this it is assumed that only *O. irroratus* was trapped and that the habitat preference discussed here, refers only to this species. The possibility that other *Otomys* species were also trapped cannot be excluded. If present, however, they would probably only represent a small number of individuals and would not materially have affected the correlations that were found.

This is the only fynbos study that has failed to reveal more than one Otomys species, e.g. see Rautenbach & Nel (1980), Nel et al. (1980) Willan (1979 a & b.) None of the trap sites in the present study were placed along drainage lines, swampy areas or scree slopes where the other species may still be collected.

After fire in fynbos, seedlings are established and resprouting species start sprouting and growing. After this initial input of species from seed into the system, stabilisation occurs and new seedlings become an unusual phenomenon after two years. After some time during the postfire period, geophytes and Poaceae become less obvious, while Restio spp. and shrubs become more conspicuous. It is only after some six to eight years that the emergent layer starts developing, Proteaceae start flowering and leaf senescence occurs. It is during this period that O. irroratus becomes established. Bond (1980) has shown that leaf duration (in Protea) is shorter at higher elevations and that leaf P and N also increase. Brooks (1974) and Davis (1973) have shown that O. irroratus and R. pumilio numbers are inversely related. Similar trends were detected during the present study. The high numbers of O. irroratus recorded in the Protea montana heathland (Site 4) might therefore be the direct result of decreased competition because of R. pumilio's absence from this site.

Why the Phylica paniculata shrubland (Site 1) had higher Otomys numbers than was predicted from the general trend, is not clear.

This was the only site where the foliage profile had more cover at intermediate heights (80 - 100 cm) than at 40 and 60 cm. It was also the only site where plant senescence had started, litter had accumulated and the field layer had opened up.

A senescent site sampled during a succession study also showed an above average number of *O. irroratus*. This site was some 35 years old and other small mammal species densities were low. Senescence might therefore reduce the competition factor as identified by Brooks (1974) and Davis (1973). This site was sampled only once and seasonal variation was not monitored.

The relationship between *Otomys* numbers and the microphyll layer found by Bond *et al*. (1980) was only partially substantiated. No relationship with total microphyll cover was found but the correlation with microphyll cover between 1,0 m and 2,5 m was confirmed. Feeding data show that *O. irroratus* do not utilise the microphylls as a food resource (Proteaceae in the Swartberg). It is therefore assumed that as in the case of *P. verreauxii* the relationship with microphyll cover is an indication of successional and postfire status of a stand and that *O. irroratus* only start utilising the area when microphyll cover starts developing in the overstory.

DIVERSITY

Study sites were. selected on a subjective basis and were placed out in what was supposed to be homogenous habitat. This assumption of homogeneity was tested and in only one case was it found that micro-habitat selection by a small mammal species had occured. (A. subspinosus was captured more frequently at 4 out of 50 trap sites at the Leucodendron album heathland (Site 5) during one of the six trapping periods). Since this species was captured elsewhere on this site during that period species richness and diversity were not materially influenced. Trapping results therefore confirmed that homogenous habitats were trapped at each trapping site and that the alpha and beta diversity components of diversity were not mixed at a site.

Alpha diversity of the Swartberg small mammal communities

Several workers have put forward hypotheses to explain trends in small mammal alpha diversity. (Alpha diversity as expressed by richness and/or by diversity indices). Rosenzweig & Winakur (1969) found that horizontal foliage complexity and soil resistance (measured as depth of penetration of a metal rod under a given pressure) had the greatest effect on small mammal alpha diversity. Brown (1973, 1975) found that the mean annual productivity of a habitat (measured as the predictable amount of annual precipitation; mean annual rainfall minus one standard deviation) accounted for about 70% of the variation in rodent species diversity in American desert rodent communities. Hafner (1977) pointed out that he did not find it possible to distinguish between rainfall (productivity) and habitat complexity and vegetation density.

The importance of competition and niche space along a seed resource gradient as a control on alpha diversity has been stressed by several workers, e.g. Brown & Lieberman (1973), Brown & Davidson (1977), and Munger & Brown (1981). All the above studies were done in arid environments in the U.S.A., mostly in desert ecosystems.

In Australian heathlands, Fox (1981) was able to show that species diversity and richness was a function of habitat complexity. Bond et al. (1980) working in the mountains of the south-west Cape found that there was a strong negative relationship between alpha diversity and the proportional contribution of foliage between 20 and 60 cm above ground level to the total foliage profile.

Results from the present study showed a negative relationship between foliage height diversity (FHD) and small mammal diversity as measured by H, in contrast to the positive relationship found by Rosenzweig & Winakur (1969). These contradictory results could be an artefact of local variation in community composition (Wiens 1981) or may simply be the result of the incorrect assumption that the diversity (H) of categorised data (density in three foliage layers in this case), is an accurate reflection of habitat complexity. It is also possible that the factors controlling alpha diversity in the two systems are simply different.

The present results, however, support the findings by Brown (1973), that rainfall (or some surrogate moisture index) is possitively correlated with alpha diversity (both richness and diversity H). As found by Hafner (1977) rainfall could not be separated from FHD, "grass", "shrub" and litter cover and plant community structure, since there were strong positive correlations between them all. In a principal component analysis context, these variables could be construed to represent the first principal component in the variation of alpha diversity. The reliability of rainfall estimates for each site may also be questioned.

Fox (1981) defined habitat complexity by the number of habitats recognised in his sample sites. Beta diversity was therefore not excluded and his hypothesis is therefore not valid in the present case. Alpha diversity, richness and diversity H were nevertheless positively correlated to the habitat diversity expressed as H of the point cover survey. It is, however, again not reasonable to assume that diversity H of categorised data represents habitat diversity.

The total number of individuals captured was positively correlated to species diversity. This is in contrast to the findings of Nel & Rautenbach (1975) in the Kalahari.

There was no obvious reason to investigate the role of seed size in niche partitioning as a possible causal factor in alpha diversity since the animals were well separated in their trophic requirements, e.g. *Omnivores:* *R. pumilio* and *A. namaquensis* did not occur at the same trap sites and were therefore spatially separated.

Granivores: *A. subspinosus* and *P. verreauxii* predominantly utilised totally different seed resources (*Restio* and *Protea* respectively).

Granivores - insectivores: *M. varius* and *E. edwardii* occurred at the same sites, but *M. varius* was largely confined to the south and E.edwardii to the north slopes.

Herbivores: Only one species was present, O. irroratus.

The findings of Bond et al. (1980) that alpha diversity of small mammals in the south-west Cape was influenced by proportion of foliage between 20 and 60 cm ($P_{40.60}$) was supported by this study. There was, however, a strong negative correlation between $P_{40.60}$ and proportion of foliage below 20 cm (P_{20}) and density of foliage below 20 cm (D_{20}) (r = -,715 and r = -,739 respectively). Mean small mammal alpha diversity (expressed as diversity H) was also correlated to P_{20} and D_{20}. It therefore seems that foliage profiles and especially density within the lower layers play an important part in niche partitioning.

The positive correlation of alpha diversity with rainfall, high cover below 20 cm, high grass, shrub and litter cover, Bray Curtis ordination of plant structural variables, diversity H of point cover data and equitability of these data could be explained in several ways, i.e.

1. Greater protection against predators. Predators are, however, few, and are poorly represented in mountain fynbos. Raptors would also have very little chance of capturing small mammals in the dense vegetation. At Swartberg pass for example during 100 "carnivore trap nights" only 1 Felis lybica was captured during the whole study period and rock kestrels and martial eagles were observed once only (Falco tinnumculus and Polemaetus bellicosus) The only common raptors were the black eagle and augur buzzards

(Aquila verreauxii and Buteo augur). These have large territories and feed largely on dassies.

2. With more cover in the "living space" of the small mammal community (foliage density below 20 cm) the frequency of interspecific encounters are likely to decrease and direct interference competition would be lower.

3. The denser the cover below 20 cm, and shrub and grass cover the greater the trophic resources, and the higher the population densities possible. There is, however, no evidende to support this hypothesis and food production and availability will have to be monitored in future studies.

An increase in available trophic resources allows greater resource overlap between species and/or more dietary specialization (Pianka 1978), and from the data it seems as if the latter suggestion holds true for the Swartberg small mammal community. (Species have well defined trophic niches with seemingly little overlap).

One of the shortcomings of this study was the inability to define a parameter by which the diversity of the habitat could be described. Diversity indices are not suited for use with categorised data and the best results were achieved by using similarity coefficients and doing indirect gradient analysis. This is, however, an undesirable process since the "positions" of sites can not be pinpointed in the landscape or described in terms of landscape characteristics.

Species turnover

Turnover with time.

Sampling efficiency was low and the results must therefore be interpreted as only giving an indication of patterns to be tested in future studies.

Considerable variation in species composition was recorded at some sites during different seasons e.g. in the *Phylica paniculata* shrubland (Site 1), but it was low at others e.g. in the *Protea punctata* shrubland (Site 3) (Table 32). The reasons for these fluctuations are not understood. Cody (1980) was able to show that species turnover in bird communities could be ascribed to changes in foliage profile parameters and insect biomass.

Turnover at xeric sites where seasonal stress is high, was low. It was not clear, however, whether this could be attributed to low species carrying capacity, since only a few species were captured and turnover therefore could not be high.

At mesic sites however, turnover was greatest at those sites with a longer seasonal stress period (stress here seen as duration of drought), than at those with a shorter drought period.

Beta diversity

Beta diversity expresses the change-over in species along a gradient. Cody (1975) opted for an indirect gradient analysis, using a habitat variable based on three foliage parameters and doing a principal component analysis. A direct gradient was used in this study, and two gradients were chosen, Bond's (1981) DI and profile density between 20 and 40 cm (D_{40}). These two parameters were selected because of the detected importance they had in relation to populations, alpha diversity and overall density.

Two separate indices were used to determine turnover along the gradient. Because Cody's (1980) turnover rates do not take species pool size into consideration, it means that a turnover of 6 species between two sites have a similar turnover value, whether the species pool size is 10 or 100. It was therefore decided to use 1-Sörrensens index of similarity as well (Mueller-Dombois & Ellenberg 1974), since it gives an indication of the magnitude of change in relation to species pool size.

Turnover along the gradient

In the present study, beta diversity was directly correlated to the degree of change that had taken place along the selected gradients (a moisture and a horizontal foliage density gradient), and especially so in the case of the moisture gradient. Beta diversity therefore did not show a sudden increase when phytosociological boundaries were crossed i.e. going from a fynbos to a karoo veldtype. It therefore seems that the Swartberg small mammals were responding to the physical features of the environment i.e. plant cover and height, rather than plant species composition. The _Leucadendron album_ heathland (Site 5) supported eight of the 10 species captured in fynbos plant communities. It is therefore evident that beta diversity contributed little to the total species pool (gamma diversity) of the fynbos small mammal community. It is also evident from the work done by others (Bond et al 1980), Nel et al 1980, Raubenbach and Nel 1980) that delta diversity (species turnover between landscapes) is also unlikely to do so. This is in direct contrast to the fynbos plant communities (Kruger & Taylor 1978) where delta diversity was found to be one of the most important components of gamma diversity.

The higher gamma diversity recorded in non-fynbos biomes (Rautenbach 1978) can probably be ascribed to higher beta and delta diversity in these other ecosystems. The species turnover that has been recorded in other South African studies certainly point to this (De Wit 1972, Nel 1978, Jooste 198o).

DENSITIES, BIOMASS AND ENERGETIC REQUIREMENTS

Factors influencing density may be density dependent or independent, they may operate simultaneously or separately, e.g. climate, trophic resources, floods, fire, disease, parasitism and intra- and inter-specific competition (Krebs 1972, MacArthur 1972, Pianka 1978, Delany & Happold 1979, Hansson 1979). There are also intra-specific factors which influence population densities (Krebs et al. 1975, Delany & Happold 1979, Southern 1979).

Rainfall and primary productivity are closely related, especially in more arid environments (Walter 1939, Rutherford 1978, 1980). Rainfall also influences the quality of primary production (as reflected by N and P levels in foliar samples) (Hanks 1972, Phillipson 1975, Strugell & Piggot 1978, Botha & Botha 1980). These relationships do not necessarily cross phyto-geographic and geological boundaries (Rutherford 1978). The quality of productivity may also be influenced by secondary compounds especially in areas with nutrient poor soils (Janzen 1974).

The factors apparently influencing small mammal densities in this study (Table 37) are interpreted as reflecting a productivity gradient. None of the habitat parameters measured have a proven relationship with productivity and standing biomass, nevertheless it can be shown that most of them show a relationship with estimated annual rainfall as did the estimated density biomass and energetic requirements of the small mammals at each of the habitats.

The estimated seasonal density showed considerable variation at some of the trapping sites (Tables 35 and 36). Sample size was also small and the reliability of the data is therefore open to questioning. Nevertheless it was observed that density and hence biomass and energetic requirements increased with increasing altitude, rainfall and hence productivity. At each of the trapping sites the community structure was different with animals with totally different diets being dominant in each of the communities (tables

6 to 13). It must be remembered that each of the small mammals had a different diet and therefore occupied a different trophic category.

How is it therefore possible that density, biomass and energetic requirements of the small mammal community can increase with rainfall (and it is assumed productivity) when communities dominated by species occupying totally different trophic levels are involved? If primary productivity is the major determinant of density, how does it, for example, change from being available as green material in one locality, to being available as seed at another?

The data therefore indicates that when numbers of animals in one "trophic group" were low, the other group compensated by increasing in numbers. On islands where mainland species are absent, other community members responded by increasing their densities. This process (density compensation) is the result of an increase in the realised niche and habitat utilization (Diamond 1970) of the species concerned. Theoretically, however, density on islands should never exceed those on the mainland since the efficiency of utilization of new resources by a species not adapted to using that resource must be lower. A study of density compensation processes in island situations has shown that "excess density compensation" has taken place in some situations. This has been ascribed to over-exploitation (Diamond 1975) and interference competition (Case & Gilpin 1974).

In the present study "density compensation" was taking place across trophic boundaries. It was at first assumed that interference competition was playing a role. Davis (1973) and Brooks (1974) have shown that there is an inverse relationship between the numbers of *O. irroratus* and *R. pumilio*. Bond *et al*. (1980) suggested that they are probably competing for a spatial resource since both are diurnal, and use runways.

From the present data no definite conclusions could be reached, but it seems likely that productivity influences density of small mammals and hence biomass and energetic requirements of the small mammals along the altitudinal gradient.

The change in species composition along the gradient, i.e. dominance of *O. irroratus* at the *Protea montana* heathland community (Site 4) and the dominance of *A. namaquensis* at the *Portulacaria afra* shrubland community (Site 8) indicates that the relationship between density and productivity is not necessarily related to food resources. The roll of interference competition needs careful investigation in future studies.

SMALL MAMMAL COMMUNITIES AND THEIR DISTRIBUTION ALONG THE GRADIENT

Communities are never stable in space or time (Elton & Miller 1954). For the purposes of this study a small mammal community is, therefore, seen as a loose assemblage of species, that occupy a site at a particular point in time. The community can, therefore, best be described by its component parts and it is assumed that species are equally different and that individuals of a species are equals irrespective of sex and age.

It was also assumed that trap avoidance and/or selectivity did not materially influence the species composition of a sample. It was also accepted that local environmental conditions within a habitat such as soil, water, vegetation and microclimate can never by themselves explain community structure (Elton & Miller 1954), and that inter- and intra-specific interaction could influence community composition. Each sampling period was therefore considered to be a separate sample, representative of the community at that site, for that capture period. A relativized Czekanowski similarity coefficient was used to determine similarity between samples and a Bray-Curtis ordinational procedure was used to arrange sites in a three-dimensional space (Fig. 31). (The actual number of animals captured for each species was used to determine similarities).

The ordinations made, showed two distinct communities that could be defined as xeric and mesic. Xeric communities differed from the mesic communities in relation to the presence or dominance in the community of *A. subspinosus*, *A. namaquensis* and *E. edwardii.*

This means that in spite of the fact that an altitudinal gradient of 1 300 m was covered and a rainfall gradient of nearly 600 mm only two distinct communities could be identified, a xeric (D.I. above 0,4) community and a mesic community. *A. namaquensis* features prominently in the first. In the mesic community several species were prominent, e.g. *R. pumilio*, *P.verreauxii*, *A. subspinosus*, *O.irroratus* and *M. varius.*

The fynbos trapping sites covered an extensive gradient (altitude varied between 950 - 1600 m, rainfall varied between 550 - 850 mm, and there was a nearly 100% plant species turnover between several of the sites (Bond 1981). In spite of this large variation only a single small mammal community could be identified. Within most other biomes such an extensive gradient in which the total environment changed would have resulted in several distinctive communities. In Gorongosa for example with a similar degree of change the plant communities changed from grassveld to forest to heathland (see Tinley 1977).

The lack of change in small mammal community structure along the sampled gradient can probably be attributed to the lack of gross structural change in the plant communities and the homogeneity of plant growth form within these communities. Therefore, in spite of the very definite changes in plant community species composition along the sampled gradient and the concommitent changes in the structural attributes (Bond 1981) these changes are not reflected in the small mammal communities.

Seasonal variation in small mammal community structure

The ordinations showed that small mammal community structure changed seasonally, some species becoming more common in certain seasons and this resulted in seasonal sample aggregation. It must again be stressed that samples were small and may not reflect the true state of affairs.

Praomys verreauxii, for example, was more numerous during winter.

If seasons were influencing community structure, one would expect a cyclical pattern to emerge, with communities dominated by certain species during specific seasons. Even if the patterns were not synchronous along the altitudinal gradient a cyclical pattern for a single site could still be expected.

The results from the two techniques used (single site vs. all sites) differed because the ordination is based on the affinities of samples to end point samples. The position of a sample in the ordination therefore portrays how similar it is to a sample from the same site taken during a different season. It is a well known phenomenon from various environments that annual cycles in population density and community structure do occur (Delany & Happold 1979). If this was the case in the Swartberg one would predict that samples from the same plot for a similar season would be placed closer together than those from a different season. Thus a cyclical pattern should emerge. However, only in the Paranomus dregei shrubland (Site 7) was such a pattern observed (Fig. 33). Seasonally bound changes were therefore largely absent in the fynbos small mammal communities.

Dominance patterns in the communities

There is ample evidence in the literature that small mammal communities are often dominated by one or two species, e.g. Hanney (1965), Handley (1967), Coe (1972), Fleming (1973, 1975), Nel & Rautenbach (1975). All these authors found that in the small mammal communities they investigated 55%- 90% of the community consisted of only three or fewer species.

The one aspect of community structure that must still be considered is the equitability or dominançe aspect. Røv (1975) and Nel (1978) for example, found that diversity (that is diversity of a community as expressed by a diversity index), is lower in communities with single species dominance.

In this study between 50% and 100% of the animals in each community were members of two species only. The most commonly captured animal from each community contributed between 29% and 100% to the community. The trapping sites along the sampled gradient also varied considerably in respect of the species being dominant at each.

It was evident however that single species dominance did occur at some of the trapping sites, e.g. in the Protea montana heathland (Site 4), O.irroratus was dominant during all the trapping seasons. No general pattern existed however and it was therefore not possible to construct any general hypotheses regarding dominance patterns in the sampled small mammal communities.

SYNTHESIS

In the introduction it was stated that findings can only be interpreted correctly if the peculiarities of the specific ecosystem is taken into account.

In an attempt to make some generalisations from the data, the present results are compared to those from other ecosystems and biomes.

Densities and biomass

Densities as recorded in the Swartberg (3,9 to 131,4 animals per hectare were extremes as estimated seasonal mean density for all sites combined varied between 28,6 to 36,1 animals per hectare) exceeded those from most other areas (see Table 40). Densities in these studies were not always calculated by the various authors and where necessary were estimated from the published data. In these cases an arbitrary 25 m boundary strip was added to the grid areas and actual trap success was used as a parameter where densities on the grid were not estimated. Small mammal densities for different ecosystems are given in Table 40.

From the above table it would then seem that fynbos has a relatively high small mammal density which must be explained in some way.

Cheeseman & Delany (1979) have put forward a hypothesis that explains differences in small mammal densities in certain central African areas. They suggest that in areas with bimodal productivity densities are higher than in areas with a unimodal rainfall pattern.

Therefore in the Swartberg where rain occurs throughout the year small mammal densities should be higher than in the western Cape where rain only occurs in the winter. This is especially so if one takes into consideration that the fynbos plants are evergreen and that there is always at least one of the plants that are growing at any one point in time. Those in the western Cape should therefore not be growing as well in the summer as those in the Swartberg.

TABLE 40 Small mammal densities in different ecosystems

ECOSYSTEM	RANGE (number per hectare)	MEAN	AUTHOR
Savanna			
Roodeplaat Pretoria	9,1-48	18,5	De Wit 1972
Kruger National Park	7,5-17,8		Kern 1977
Nylsvley	10		Tembe 1979
Ivory Coast	1,5-21		Bellier in Cheeseman & Delany 1979
Kenya	193-212		Delany & Robberts in Cheeseman & Delany 1979
Desert			
Namib		9,34	Christian 1977
Namib		9,34	Withers 1979
America (shrubland)		16,7	Chew & Chew 1979
Grassland			
Uganda	16,6-63,3		Cheeseman & Delany 1979
Heathland			
Australia	13-15		Barnett *et al*. 1978
Australia	14,5-22,5	18,76	Braithwaite & Gullan 1978
Australia	7-8		Dwyer *et al*. 1979
Chaparral		10,2	Quinn 1978
Fynbos (W.Cape)		17,0	De Hoogh 1968
Fynbos (S.Cape)	25-87	41,5	Bond *et al*. 1980
Fynbos (S.Cape)	3,9-138,3	31,3	Present study
Forest			
Zaire	236-361		Dieterlin in Delany 1972

There is only scanty data available from the western Cape area (de Hoogh 1968). The estimated number of small mammals in the western Cape was lower than that recorded in this study and in that of Bond et al (1980). Unfortunately the more comprehensive data from Rautenbach & Nel (1980), could not be adapted for use in this comparison since it was not possible to estimate densities from their study. Nevertheless it seems that the Cheeseman & Delany (1979) hypothesis may also be applied to systems where rainfall occurs throughout the year.

It has been shown that primary productivity in fynbos is reasonably similar to that in other South African biomes given a similar annual rainfall (Rutherford 1980). The major difference in small mammal community density can therefore not be sought at this level. What is of interest though are the peculiarities of the fynbos ecosystem.

The "grassy plants" in fynbos are characterised by Restionaceae and Cyperaceae which are evergreen, as are the C3 grasses (Bond 1981). C4 grasses only occur in arid fynbos communities (Kruger 1979). Because of the evergreen plant communities and the peculiar phenology (Kruger 1975, Bond 1980), trophic resources are available to grazers and browsers throughout the year. The granivores have the added advantage that serotony (maintaining seeds in the canopy for a long period i.e. several years) is fairly predominant in fynbos. Certain of the nutlet bearing Restionaceae species -also retain their seed in the canopy for a reasonable extensive period.

The small mammals are able to utilise these resources continuously throughout the year and are therefore living in an environment in which abundant trophic resources are available irrespective of the season. The mean seasonal density of small mammals in the Swartberg as a whole (mean over all trapping sites) was fairly constant in comparison to those from other biomes (e.g. see the results from De Wit 1972, Swanepoel 1972, Davis 1973, Brooks 1974, Kern 1975 and Nel 1978).

Habitat complexity, continuous availability of trophic resources and winter breeding may therefore be the primary factors responsible for the maintenance of such high densities in the southern Cape fynbos.

Diversity

It has already been pointed out that diversity trends can only be interpreted correctly if the various components of diversity can be distinguished (Cody 1966, 1975).

From the available literature on African small mammals it is almost impossible to identify either alpha or beta diversity. As an approximation attempts were made to distinguish between the various components of diversity (see Table 41). The diversity at alpha and gamma levels were identified. In those cases where the presence of beta diversity components could not be excluded, the number of species recorded were taken to represent an estimate of alpha diversity and are identified in the table as "alpha".

TABLE 41. Diversity of small mammal communites (Diversity expressed as richness).

Veld Type & Region	Alpha			Alpha?			Gamma			Source
	Rodentia	Insectivora	Total	Rodentia	Insectivora	Total	Rodentia	Insectivora	Total	
Grasslands Transvaal							15	7	7	Rautenbach 1978b
Namib	5								5	Christian 1977
Uganda	5-11						12		12	Flemming 1975
U.S.A.	±4,8(n=6)						18		18	French et al 1976
Fynbos Swartberg	2-6	1-3	4,5				10	3	13	Present study
Rooiberg						4,5	8		8	David 1978
Cedarberg				4-8	2-3				18	Rautenbach & Nel 1980
Chaparral U.S.A.				3-7					9	Quin 1978
Heathlands Australia				6-4	3-4	4-8				Cockburn & Lee 1978
Desert shrublands										
Namib	5	1	6							Withers 1979
U.S.A.				3-9		9				Chew & Chew 1970
Savanna										
Pretoria				6-9	1-2				12	De Wit 1972
Kalahari				19-4	1-2				18	Nel 1978, Rautenbach & Nel 1975
Kruger Nat. Park				4-6	2					Kern 1977
Botswana North							25			Smithers 1971
Botswana South							16			Smithers 1971
Sweet Arid Bushveld							21	10	31	Rautenbach 1978b
Nylsvlei	1,3								21	Tembe 1977
Uganda									15	Neal 1970
Forest										
Malabigambo				4	0	4				Delany 1964
Palm Forest Q.E. Park				6	2	8				Delany 1964
Kalimu Forest				7	1	8				Delany 1964
Bamboo forest				1	0	1				Delany 1964
Montane for est										
Mayanja				14		14				Delany 1971 in Flemming 1975
Southern Cape				2	2	4				Personal observations.

The mean alpha diversity (expressed as richness) of small mammal communities in various African biomes was found to be the following (based on literature):

Grasslands: 5,5 (5-6)
Shrublands: Fynbos 6 (2-8) "Desert" 6,3 (6-7)
Savanna: 6,7 (1-12)
Forest: 8,5 (1-18)

As has already been stated the influence of beta diversity on sample diversity is not known. Delany (1964), for example, even moved his traps around during sampling periods thus increasing the likelihood of including components of beta diversity in his samples.

Disregarding these variations it is nevertheless interesting to note that average alpha diversity is not remarkably different between biomes. The range over which the data varies, especially the upper end of the scale seems to be much greater in complex habitats as opposed to structurally simple habitats. It is evident from Table 41 that the diversity of small mammal communities are fairly similar in all habitats at alpha diversity level. It is only rarely that more than 6 species are recorded within the same habitat at the same time. Bigalke's (1979) statement that fynbos with generally 6 species is species poor, can therefore not be accepted. He also quotes Flemming (1975) as a reporting that most tropical habitats contain ten to sixteen species of rodents. Flemming (1975), however, made no distinction between alpha and beta diversity. His data unfortunately does not allow one to distinguish between these different components of diversity.

From Table 41 it is evident that tropical forests seem to have a more diverse small mammal fauna at some sites, e.g. Mayanja and Lake Kivu. At other sites, however, the diversity is much lower (e.g. Delany 1964). Again it is difficult to assess whether beta diversity had perhaps not been included in the samples. In spite of the fact that Delany (1964), for example, at times moved traps between trapping periods; he still recorded low diversity.

Because of the inadequacy of the data it is suggested that at this stage one should test the hypothesis that small mammal alpha diversity depends on structural criteria (O'Connel 1980) rather than trophic resource levels.

At gamma diversity level, however, certain landscapes or systems support more species than others. Cody (1980) has speculated that for the avifauna at least, the paucity of fynbos birds can be attributed to size of the source area.

The large number of Gondwana relics (both plant and animal) that occur in the temperate climatic area of the Cape suggests that the northward movement of the continent (Endrödy-Younga 1978) has resulted in a compression of available mesic temperate habitat. (Habitat here referring to "climatic habitat"). It seems unlikely that a group that evolved largely after the breakup of Gondwanaland and has a largely northern tropical origin (Meester 1965) should be influenced by this. Nevertheless, the structure, growth form and peculiar chemical properties of fynbos plants (Kruger 1978, Puttick & Glyphis 1980), plus the climatic conditions, make this an extraordinary habitat. Animals would have to adapt specifically to the habitat and from the following section it will be clear that the largely tropical small mammal savanna fauna has not been able to do so successfully.

The mammal community of the South West Cape Biotic Zone is not as depauperate as one would have expected (see Table 42).

TABLE 42 The number of mammal species occurring in South African Biomes (Data was derived from various literature sources, especially Rautenbach 1978b and Stuart & Lloyd 1978)

	Size in km^2	Number of species	Number per km^2
Forest biome	2000 (actual) (50 962 veld type)	74	0,037
Fynbos biome	62054	106	0,0017
Grassland biome	280047	92	0,0003
Karoo biome	369946	138	0,0004
Savanna biome	305799	210	0,0005
Total R.S.A.		276	0,00023

A random even distribution of species would have resulted in 0,00023 species per km^2. It is quite clear, however, that all the biomes support a more diverse fauna than what would have been predicted from a random distribution.

It seems that the smaller the biome the more species are encountered. This would suggest that all animals (as has been suggested by Rautenbach 1978a) do not recognise biotic zones or biomes per sé, but tend to spill over and occupy adjacent biomes. Using island biogeographic terminology it is here suggested that dissimilar biomes act as source areas and that the predicted gamma diversity, that is an average species density of 0,00023 species per km^2, is not achieved since species from adjacent biomes occupy "foreign biomes" and "emigrate" into them at a greater rate than they go "extinct".

If the above statement is true one should be able to show that species from adjacent biomes that do not cross phytogeographic boundaries are limited to the adjacent biome because of definite and distinct ecological barriers. For such species the "island boundary" is therefore a distinct barrier that cannot be crossed.

In a comparative approach the fynbos biome species will be compared to those from the South West Cape Biotic Zone. No comprehensive work has been done to show which of the species occurring in the South West Cape Biotic Zone does not cross over into fynbos per sé.

This was indeed found to be the case: Petromyscus collinus did not cross the phytogeographic boundary, probably because of a lack of succulent plants in fynbos. Saccostomus campestris has only been captured in areas with Acacia karoo. This association is not a recent one. S. campestris densities as recorded in archaelogical deposits at Boomplaats has been fluctuating synchronously with the amount of A. karoo pollen in the same deposit (Avery 1982).

Graphiurus murinus requires large trees with holes for nesting and often eats fleshy fruit, both of which are lacking in fynbos.

Otomys unisulcatus prefers flat terrain with deep heavy red soils, and open vegetation. Again none of these are features of the fynbos landscape.

It therefore seems that fynbos supports fairly high densities of rodents in the southern Cape and that the alpha diversity of the communities fall within the normal range of small mammal communities and that structural physical attributes of the fynbos vegetation and landscape play an important part in controlling density, diversity and species distributions.

SUMMARY

The small mammal communities of the Groot Swartberg were sampled between July 1978 and October 1979. Eight trapping sites covering an altitudinal gradient of nearly 700 m, with four sites on the south and four on the north facing aspect, were sampled between four and six times during this period for small mammals.

A total of 11 small mammal species were captured. Although seasonal trends in population size were detected, the patterns were inconsistent. *Rhabdomys pumilio* and *Aethomys namaquensis* populations for example decreased during the whole study period while *Acomys subspinosus* and *Otomys irroratus* populations increased. Breeding seemed to occur throughout the year but young animals were captured more frequently during autumn, winter and spring.

Each small mammal species had a specific diet: *A. subspinosus* for example fed predominantly on restio seeds and especially those with elaiosomes that are ant dispersed. *Praomys verreauxii* also had a granivorous diet but it fed predominantly on *Protea* seeds. *Elephantulus edwardii* and *Myosorex varius* also consumed a fair amount of seed. *M. varius*, however, fed largely on litter arthropods whereas *E. edwardii* fed extensively on termites. *R. pumilio* and *A. namaquensis* were omnivorous, feeding on insects, seeds and green plant material.

There was a strong relationship between diet and the gut morphology of the various species. The small mammals with a low protein

content in their diet (few seeds and insects) had a relatively longer large intestine and caecum, while those with a high protein diet had a relatively longer small intestine.

Factors influencing population densities along the sampled gradient were identified and it was found that *E. edwardii* preferred rocky habitats with a good restionaceous cover. *M. varius* on the other hand preferred the denser vegetation of the more mesic trapping sites at which a fair amount of litter had accumulated. *A. subspinosus* populations seemed to increase with an increase in altitude. *P. verreauxii* was closely related to a well developed proteoid layer and is probably related to its preference for *Protea* seeds. *R. pumilio* preferred habitats with a good "grass" cover (that is Restionaceae, Cyperaceae and Poaceae). They were however absent from sites with an adverse micro-climate. For example they were absent from the high cool south facing aspects. *A. namaquensis* was limited to hot xeric rocky sites. *Petromyscus collinus* was captured on several occasions in spekboomveld. This is the first time that it has been collected from the Cape folded mountains. *Dendromus melanotis* was only captured in newly burnt veld with low cover.

Alpha diversity was correlated to productivity (rainfall), and a dense plant cover below 20 cm. Beta diversity was higher at the xeric end of the sampled gradient but appeared to be constant both in relation to moisture and foliage profile gradients.

Density and biomass was higher at high altitudes where rainfall and hence productivity was higher. Percentage trap success was directly correlated to alpha diversity. Density and percentage trap success increased along the altitudinal rainfall gradient in spite of changes in community structure. This was interpreted as representing density compensation taking place across trophic boundaries.

Alpha diversity and density was equal to or higher than that from most other African small mammal communities. Gamma diversity of the mammal community was exceptionally high. Differences between fynbos and other biomes probably lie at beta and delta diversity levels.

OPSOMMING

Die kleinsoogdier gemeenskap van die Groot Swartberge in die suid-Kaap is gemonster tussen Julie 1978 en Oktober 1979. Agt plotte, wat so uitgeplaas was dat 'n hoogte gradient van bykans 700 m gedek is, met vier plotte op die suidelike en vier plotte op die noordelike hange, is almal tussen vier en ses keer gedurende hierdie periode vir klein soogdiere gemonster.

'n Totaal van 11 species is versamel. Ten spyte daarvan dat seisoenale fluktuasies in bevolkings digthede waargeneem is, was daar geen konstante patrone nie. Gedurende die hele studieperiode byvoorbeeld, het *Rhabdomys pumilio* en *Aethomys namaquensis* bevolkings afgeneem terwyl die van *Acomys subspinosus* en *Otomys irroratus* toegeneem het. Dit wil voorkom asof die diere reg deur die jaar teel, maar jong diere is meer dikwels in die herfs, winter en lente gevang.

Die kleinsoogdiere wat teëgekom is, het spesifieke voedselvoorkeure gehad: *A. subspinosus* het byvoorbeeld hoofsaaklik saad van restios gevreet en veral die wat elaiosome besit en deur miere versprei word. *Praomys verreauxii* het weer hoofsaaklik saad van *Protea* spp. gevreet. *Elephantulus edwardii* en *Myosorex varius* het ook baie saad gevreet, en tot 100% van sommige van die maaginhoude het uit saad bestaan. *M. varius* het hoofsaaklik arthropoda wat in die humuslae voorkom gevreet terwyl *E. edwardii* hoofsaaklik termiete gevreet het. *R. pumilio* en *A. namaquensis* was omnivore en het insekte, saad en groen materiaal geredelik gevreet. *O. irroratus* het net groen materiaal, stingels en bas gevreet.

Daar was 'n sterk verband tussen maaginhoud en dermkanaalstruktuur. Die kleinsoogdiere met 'n lae proteien dieet (min saad en insekte) het 'n relatief langer caecum en dikderm gehad, terwyl die met 'n hoë proteien dieet weer 'n relatief langer dunderm gehad het.

Faktore wat bevolkingsdigthede langs die gemonsterde gradient beïnvloed het, is geïdentifiseer. *E. edwardii* het byvoorbeeld 'n klipperige habitat met 'n redelike digte restiobedekking verkies. *M. varius* daarenteen het in die digbegroeide meer gematigde klam dele voorgekom en was veral volop waar daar 'n opbou van humus was. *A. subspinosus*-getalle het toegeneem met hoogte. *P. verreauxii*-populasies was groter in gebiede met 'n goed ontwikkelde protea-bevolking en hou verband met die dier se voorkeur vir protea-saad. *R. pumilio* verkies habitatte met 'n goeie "grass" (d.w.s. Restionaceae, Cyperaceae en Poaceae) bedekking, maar was afwesig indien die mikro-klimaat ongeskik is. Hulle het byvoorbeeld nie voorgekom op die hoë koel suidelike hange nie. *A. namaquensis* verkies droë areas met 'n goeie klipbedekking en *O. irroratus* bevolkings was hoër in gebiede waar daar 'n goeie struik bedekking was. *Petromyscus collinus* is op verskeie geleenthede in spekboomveld gevang. Dit is die eerste keer dat hierdie spesie in die Kaapse-voubergreekse versamel is. *Dendromus melanotis* is slegs in veld gevang wat onlangs gebrand is.

Alpha diversiteit was gekorreleer met produktiwiteit (reënval), en 'n hoë plantegroei-bedekking in die 0-20 cm laag. Beta diversiteit was hoër tussen plotte op die droë punt van die bemonsterde vogtigheids gradient, maar was konstant in verhouding tot die plantegroeiprofiel- en vogtigheidsgradiente, m.a.w. as daar 'n groot verandering is in beta diversiteit dan is daar ook dieselfde mate van verandering in die gradient.

Digtheid en biomassa was hoër by die hooggeleë plotte waar reënval en dus ook produktiwiteit hoër was. Valsukses was positief gekorreleer met alpha diversiteit. Beide digtheid en valsukses het langs die hoogte-reënval gradient toegeneem ten spyte van die feit dat die speciesamestelling van die gemeenskap by die agt plotte verskil het. Die vertolking wat hieraan geheg is, is dat digtheidskompensasie plaasgevind het, ongeag die trofiese vlak waarin die dominante species van die gemeenskap geval het.

Alpha diversiteit en digtheid van die gemeenskap was gelyk aan of selfs hoër as die wat in ander Afrika kleinsoogdier gemeenskappe aangetref word. Gamma diversiteit van die soogdier gemeenskap was egter besonder hoog. Verskille tussen fynbos en ander biome lê moontlik by verskille in beta en delta diversiteit.

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APPENDIX 1. Trapping periods, number of trap nights for each trapping period and told number of trap nights for each site over all trapping periods.

Site	Plant community	June-July 1978	Sept. 1978	Dec. 1978	March 1979	July 1979	Oct. 1979	Total no. of trap nights
1	Phylica paniculata shrubland	200	200	200	200	200	200	1200
2	Protea repens shrubland	0	200	200	200	200	200	1000
3	Protea punctata shrubland	200	200	200	200	200	200	1200
4	Protea montana heathland	200	200	200	200	200	200	1200
5	Leucadendron album heathland	200	200	200	200	200	200	1200
6	Protea lorifolia shrubland	0	200	200	200	200	0	800
7	Paranomus dregei shrubland	200	200	200	200	200	0	1000
8	Portulacaria afra shrubland	200	200	200	200	200	0	1000

Site: No.______ Grid Reg.______________ Photo____________ Date______________

Species	Sex No.	Mass	Tot.	L Tail	L Hind	Ear	Lact	Scrot	Ing	Perf	Foot	Loc

APPENDIX [illegible]. Field data sheet.

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APPENDIX 4. Rainfall stations used in regression analysis for estimating rainfall at each site.

South facing slopes

Station No.	Station	Alt.	Period Years
47/359	Calitzdorp-DAM	366	36
47/360	Besemkop	305	22
47/716	Kruisrivier	579	32
48/51	Dewetsvlei-BOS	1525	10
48/79	Swartberg-BOS	1600	12
48/83	Matjiesrivier-SKL	732	30
48/42	Albertberg-BOS	1067	10
48/449	Schoemanshoek	457	37
48/624	Rust-en-Vrede	762	37
49/60	De Rust-POL	533	46

North facing slopes

Station No.	Station	Alt.	Period Years
47/436	Weltevreden	511	26
47/801	Kliphuisvlei-BOS	1370	10
48/43	Prince Albert-TNK	686	83
48/275	Zachariasfontein	815	18
48/406	Willow Glen	884	26
49/50	Klaarstroom-POL	732	44
49/71	Zwartskraal	876	36
48/81	Zwartberg	1600	16

APPENDIX 4. Rainfall stations used in regression analysis for estimating rainfall at each site.

South facing slopes

Station No.	Station	Alt.	Period Years
47/359	Calitzdorp-DAM	366	36
47/360	Besemkop	305	22
47/716	Kruisrivier	579	32
48/51	Dewetsvlei-BOS	1525	10
48/79	Swartberg-BOS	1600	12
48/83	Matjiesrivier-SKL	732	30
48/42	Albertberg-BOS	1067	10
48/449	Schoemanshoek	457	37
48/624	Rust-en-Vrede	762	37
49/60	De Rust-POL	533	46

North facing slopes

Station No.	Station	Alt.	Period Years
47/436	Weltevreden	511	26
47/801	Kliphuisvlei-BOS	1370	10
48/43	Prince Albert-TNK	686	83
48/275	Zachariasfontein	815	18
48/406	Willow Glen	884	26
49/50	Klaarstroom-POL	732	44
49/71	Zwartskraal	876	36
48/81	Zwartberg	1600	16

APPENDIX 5. Procedure for calculating Drought Index. Calculations were programmed on a Hewlett Packard 9820 Calculator.

1. Obtain monthly PE and rainfall (R) data using slope, aspect and altitude adjustments if required.

2. Calculate monthly surplus/deficit.

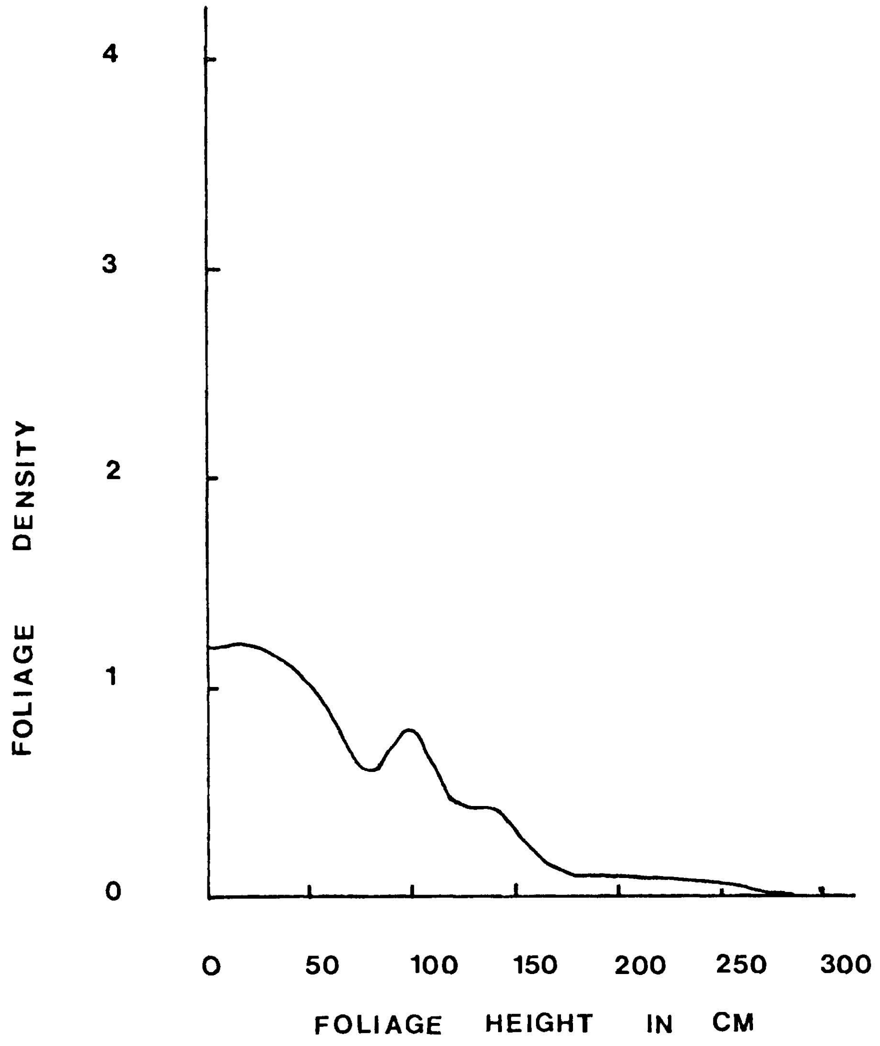
3. Sum the number of months with deficits falling into five classes with 20 mm increments and divide by the potential number of months with a deficit (i.e. No. of classes x 12). The index ranges from 0 - no deficit, to 1 - severe and prolonged deficit (80 mm throughout the year).

Example

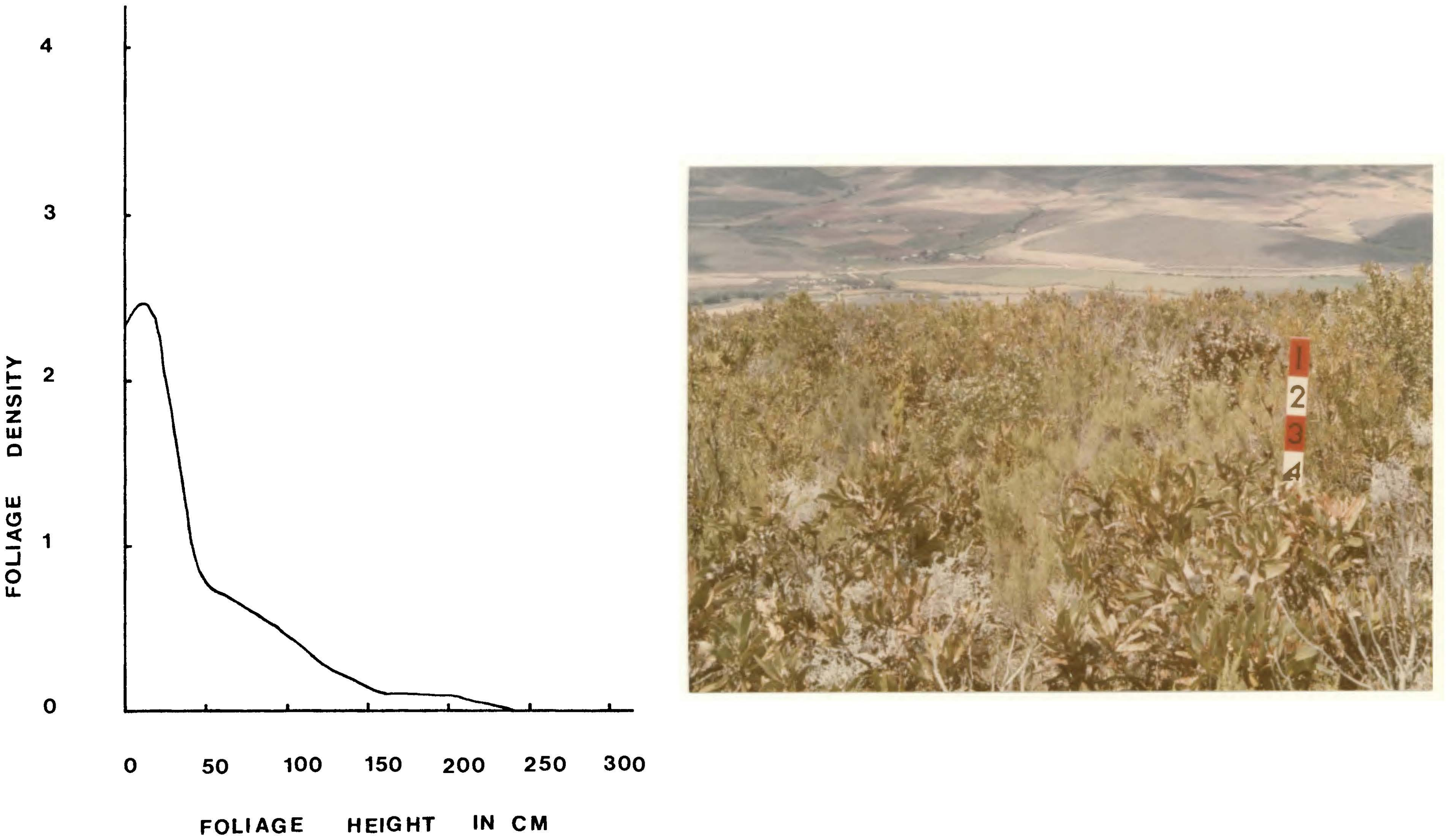
	J	F	M	A	M	J	J	A	S	O	N	D
R	60	60	60	60	60	60	60	60	60	60	60	60
PE	100	110	90	70	60	50	50	60	70	80	90	100
Deficit (R-PE)	-40	-50	-30	-10	0	0	0	0	-10	-20	-30	-40

No. of months with deficit exceeding			Potential number of months
1.	0 mm	8	12
2.	20 mm	5	12
3.	40 mm	1	12
4.	60 mm		12
5.	80 mm		12
	TOTAL	14	60

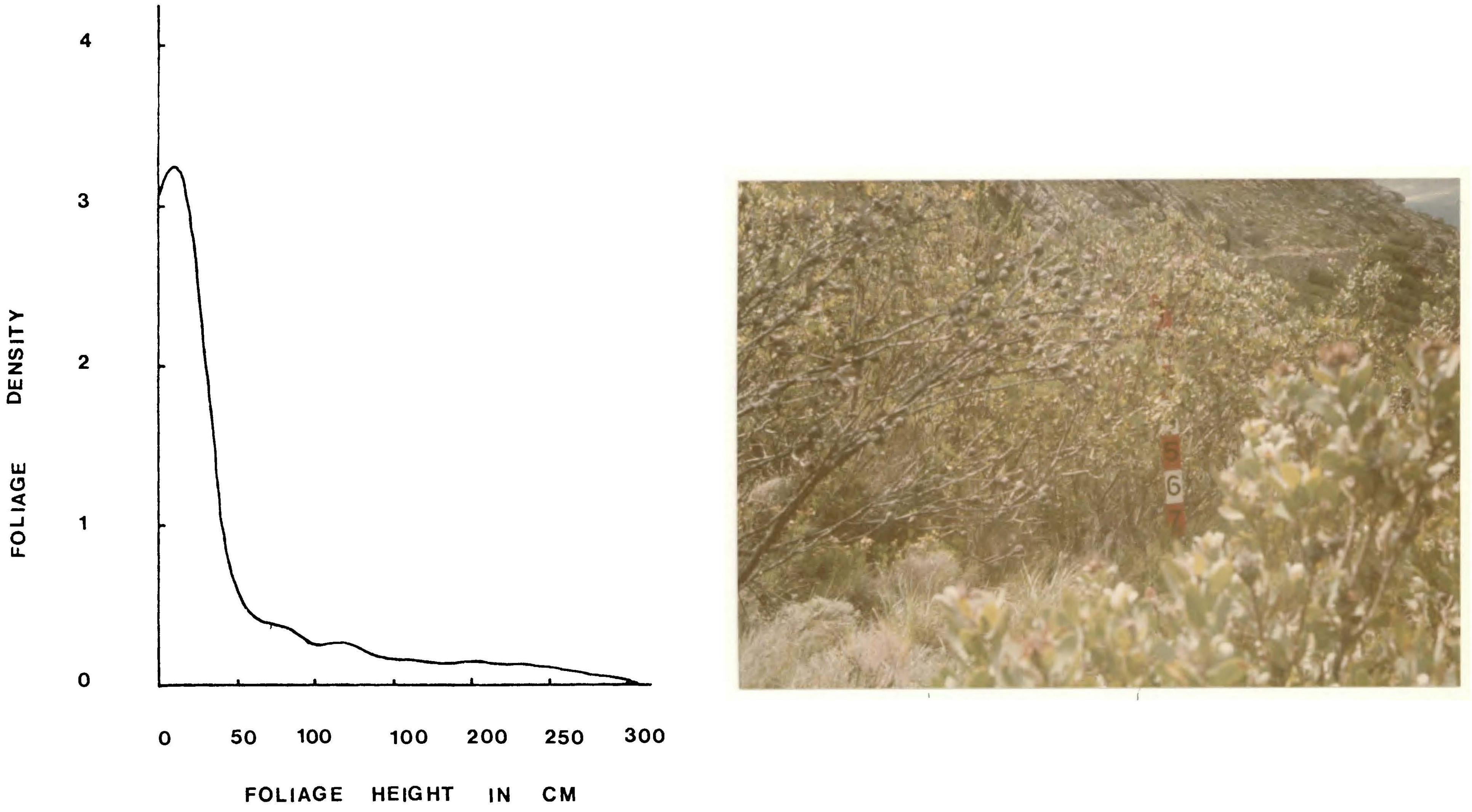
Drought Index = $^{14}/60$ = ,23



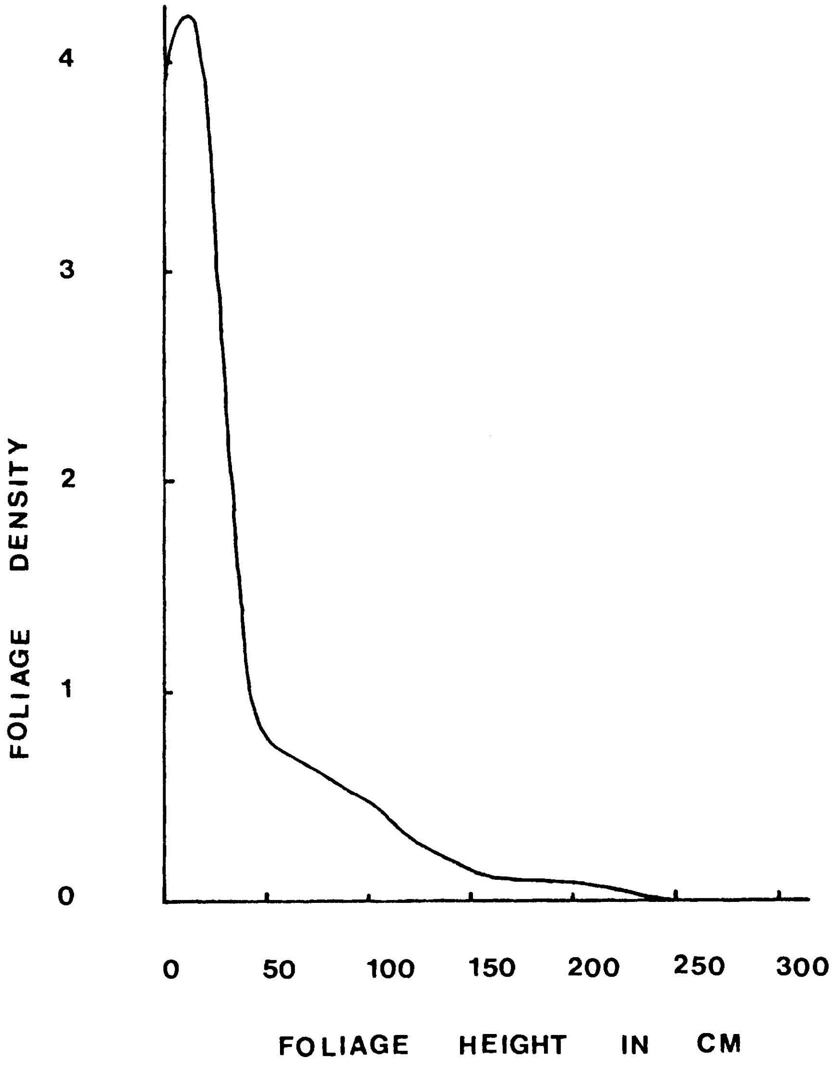
APPENDIX 6a. Foliage profile for Site 1 (The *Phylica paniculata* shrubland) with accompanying photograph.



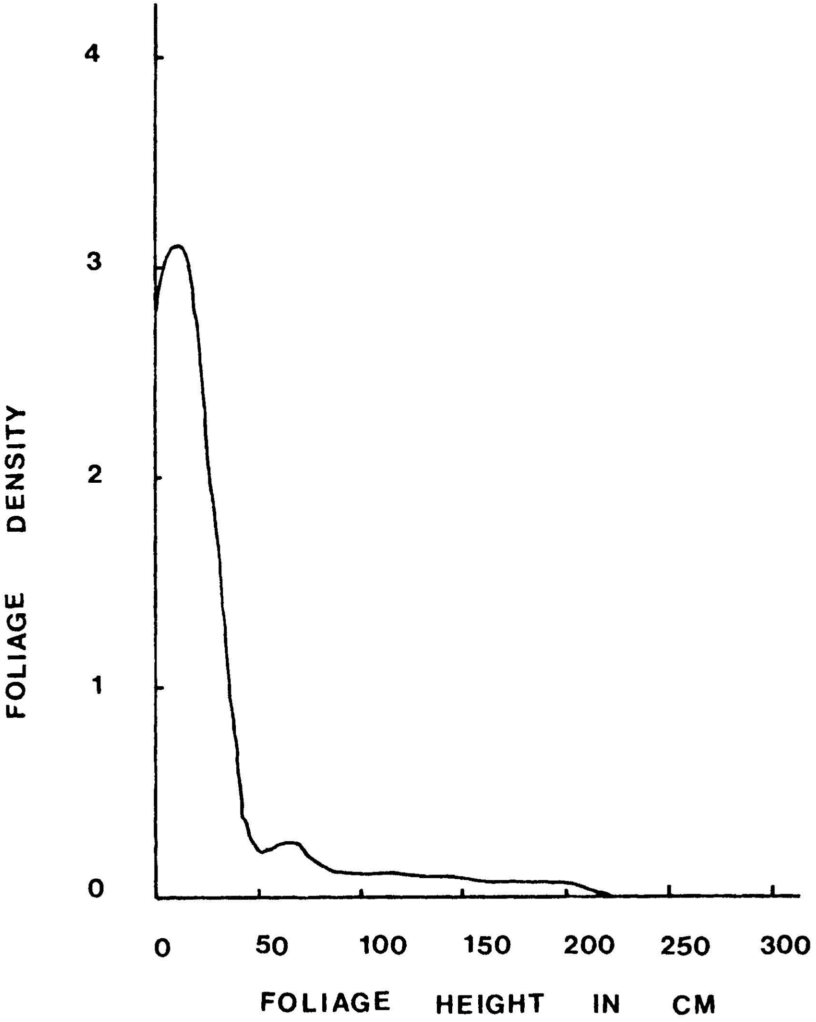
APPENDIX 6b. Foliage profile for Site 2 (The *Protea repens* shrubland) with accompanying photograph.



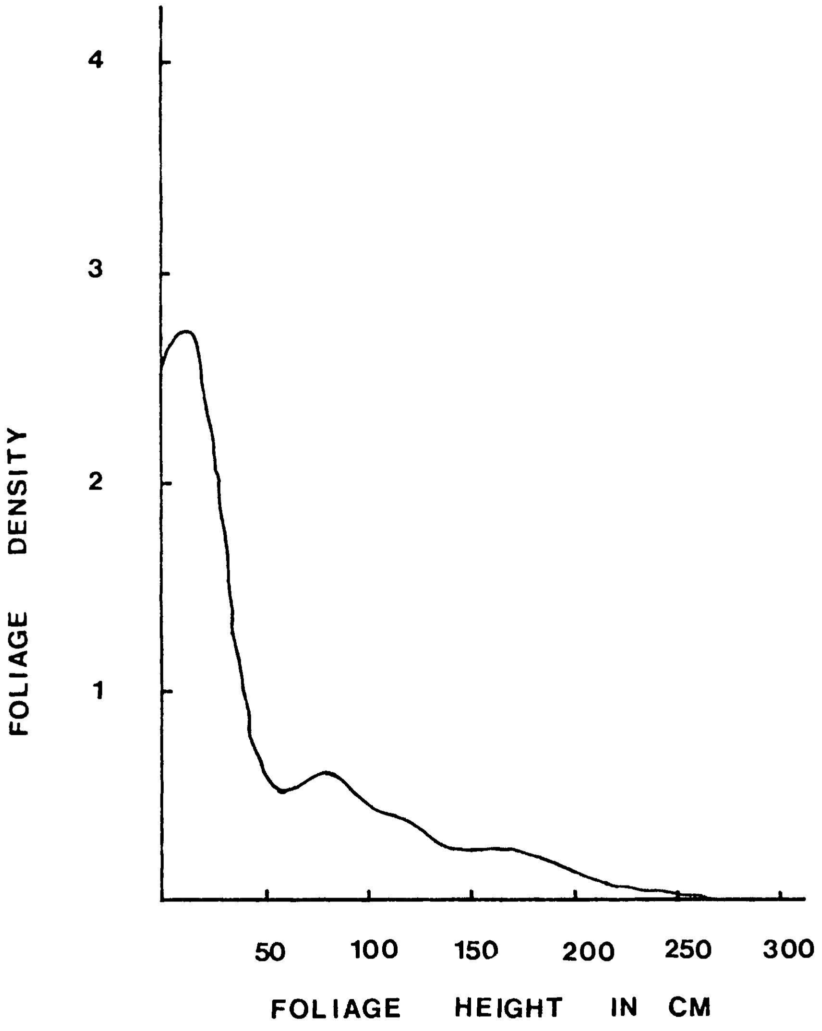
APPENDIX 6c. Foliage profile for Site 3 (The *Protea punctata* shrubland) with accompanying photograph.



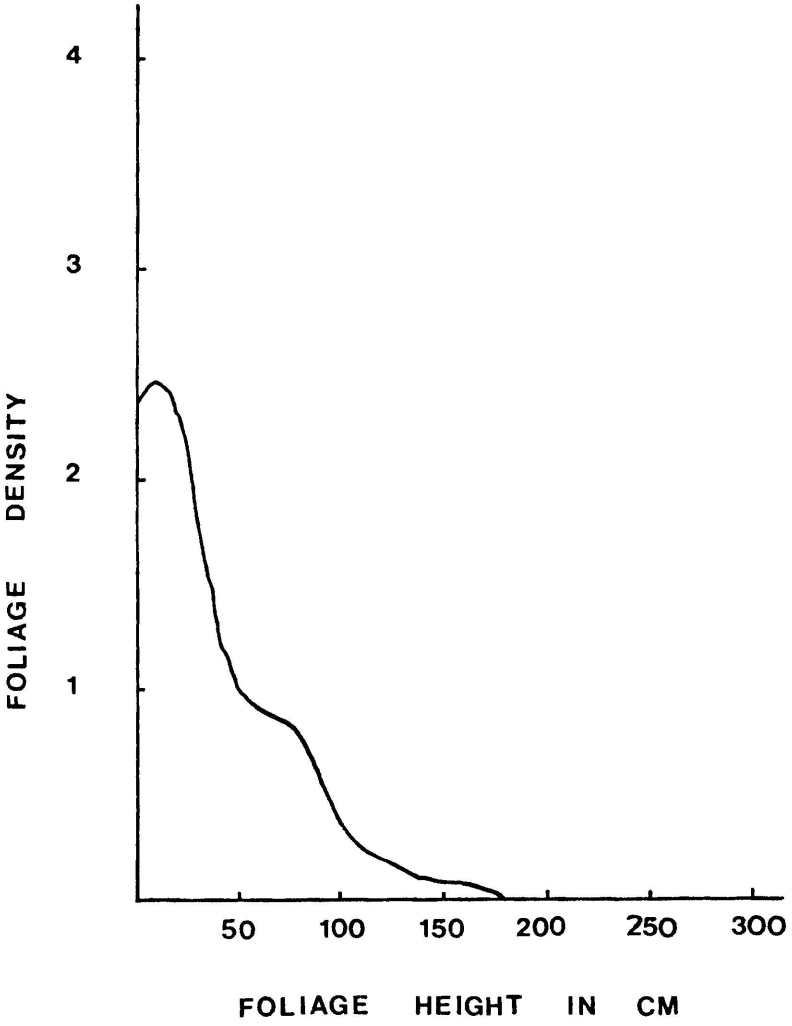
APPENDIX 6d. Foliage profile for Site 4 (The Protea montana heathland) with accompanying photograph.



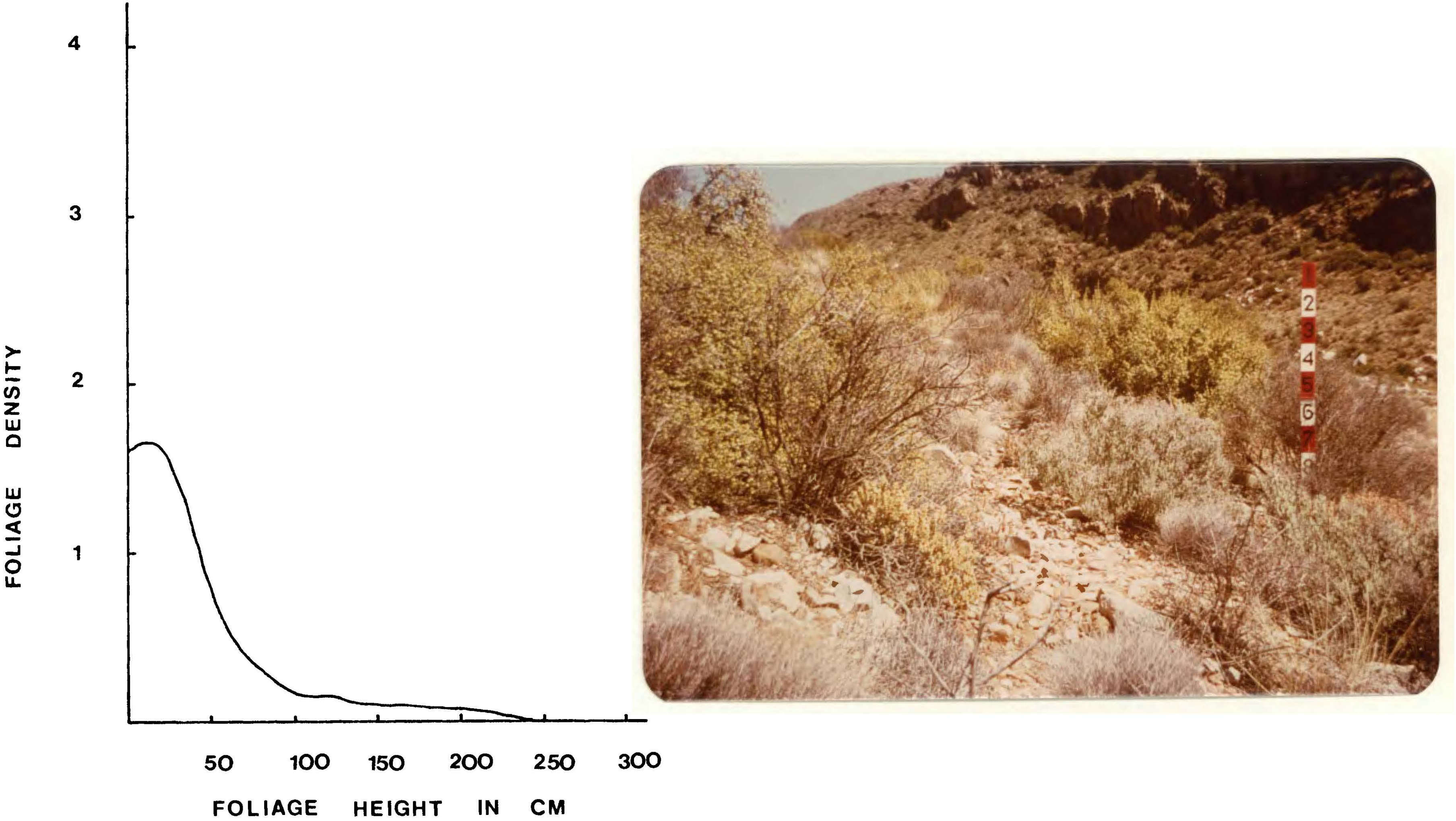
APPENDIX 6e. Foliage profile for Site 5 (The Leucadendron album heathland) with accompanying photograph.



APPENDIX 6f. Foliage profile for Site 6 (The *Protea lorifolia* shrubland) with accompanying photograph.



APPENDIX 6g. Foliage profile for Site 7 (The *Paranomus dregei* shrubland) with accompanying photograph.



APPENDIX 6h. Foliage profile for Site 8 (The Portulacaria afra shrubland) with accompanying photograph.

APPENDIX 7. Various foliage profile parameters for the various sites. (for key to plant communities see appendix 1)

Foliage density in various height classes

Site	D20	D40	D60	D80	D100	D120	D140	D160	D180	D200
	0-20	20-40	40-60	60-80	80-100	100-120	120-140	140-160	160-180	180-200
1	1.2	1.1	.88	.59	.80	.46	.41	.2	.1	.09
2	2.32	1.07	.7	.58	.46	.3	.19	.11	.09	.08
3	3.04	1.15	.44	.36	.25	.25	.18	.15	.12	.12
4	3.9	1.01	.34	.2	.13	.08	.06	.06	.05	.05
5	2.85	.58	.26	.15	.11	.1	.09	.08	.07	.06
6	2.55	.97	.52	.6	.45	.36	.24	.25	.2	.12
7	2.35	1.32	.9	.77	.36	.19	.1	.07	.05	.05
8	1.61	1.12	.54	.30	.17	.15	.11	.08	.08	.07

Standard deviation of the actual density measurements in various height classes

Site	0-20	20-40	40-60	60-80	80-100	100-120	120-140	140-160	160-180	180-200
1	.63	.37	.59	3.88	.37	1.84	2.0	4.36	6.05	6.24
2	.44	.59	.96	.94	1.09	2.13	4.2	5.32	5.36	5.58
3	.2	.43	2.24	2.32	3.23	2.23	3.39	5.31	6.91	6.89
4	.16	.64	1.79	3.14	5.63	7.3	5.76	4.98	4.13	4.17
5	.40	1.18	2.69	4.74	6.07	5.79	6.61	7.36	8.01	7.2
6	.29	.61	1.3	.7	1.2	1.45	3.53	3.43	3.96	5.49
7	.19	.47	.34	.6	3.95	4.58	6.04	4.6	3.7	2.52
8	.34	.52	1.48	1.98	4.31	4.06	5.57	6.09	5.73	5.77

Proportional contribution of the foliage density in each layer to the total foliage profile

Site.	P20	P40	P60	P80	P100	P120	P140	P160	P180	P200
	0-20	20-40	40-60	60-80	80-100	100-120	120-140	140-160	160-180	180-200
1	.206	.189	.151	.101	.137	.079	.07	.034	.017	.015
2	.393	.181	.119	.098	.078	.051	.032	.019	.015	.014
3	.502	.19	.073	.059	.041	.041	.029	.025	.02	.02
4	.663	.172	.058	.034	.022	.014	.01	.01	.009	.009
5	.655	.133	.059	.035	.025	.023	.021	.018	.016	.014
6	.342	.241	.149	.079	.045	.034	.034	.032	.025	.02
7	.382	.214	.146	.125	.058	.031	.016	.011	.008	.008
8	.38	.264	.127	.071	.04	.035	.026	.021	.019	.017

APPENDIX 8. The estimated cover of various plant synusiae at the various study sites.

No	Site	Shrub	Restio	Graminoid	Ground	Leptophyll	Nanophyll	Microphyll	Mesophyll
1	Phylica paniculata shrubland	86	38	5	1	63	1	63	38
2	Protea repens shrubland	88	65	5	1	65	5	35	1
3	Protea punctata shrubland	87	37	5	1	88	18	88	22
4	Protea montana heathland	82	38	18	5	88	22	38	0
5	Leucadendron album heathland	86	40	5	5	90	16	39	5
6	Protea lorifolia shrubland	63	64	18	1	17	0	18	64
7	Paranomus dregei shrubland	65	62	5	0	40	37	5	19
8	Portulacaria afra shrubland	62	0	38	0	37	5	0	0

APPENDIX 9 Selected soil analyses for A1 soil horizons in the Swartberg (Data from Bond 1981)

Site	Plant community	pH	Nett extractable cations mg kg^{-1}			Total N and P mg kg^{-1}	
			Ca	Mg	Na	Total N	Total P
1	Phylica paniculata shrubland	3,9	233	87	57	784	75
2	Protea repens shrubland	4,1	117	45	17	896	129
3	Protea punctata shrubland	3,9	51	35	21	1498	191
4	Protea montana heathland	3,95	177	63	23	1428	138
5	Leucadendron album heathland	4,2	104	38	18	1092	119
6	Protea lorifolia shrubland	3,6	199	81	23	1148	75
7	Paranomus dregei shrubland	4,5	718	212	35	246	98
8	Portulacaria afra shrubland	4,5	758	102	20	630	169