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Ecology of a small mammal community on a rocky outcrop in the Namib Desert

by
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Aethomys
Petromyscus
Petromus
Elephantulus
Apr '77 - Feb '78

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ABSTRACT

The small mammal community of Tumasberg, an inselberg on the gravel plains of the Namib Desert, was studied by mark-release-recapture methods. The principal small mammals present on a 6 hectare live-trapping grid were: *Petromyscus collinus* (rock mouse), *Aethomys namaquensis* (rock rat), *Petromus typicus* (dassie rat) and *Elephantulus rupestris* (rock elephant-shrew). This study summarises climatic and micro-climatic data for Ganab, 3 km from Tumasberg, and the following ecological and demographic information for the small mammal community; abundance and distribution, home range, activity patterns, recruitment and mortality rates, diet, and reproductive cycles of the small mammals. These data are used to analyse the community structure and ecological interactions of the species.

1 INTRODUCTION

The Namib Desert stretches along the coast of South West Africa from Oranjemund northwards into Angola. Although the Namib Desert encompasses a remarkable variety of habitats, much of it is gravel plains and sand-dunes. The gravel plains are bounded to the east by a mountain escarpment (the Khomas Hochland), and numerous rocky areas (inselbergs and koppies) encroach into the plains.

The mammals occurring in the Namib Desert, their general distribution, and some aspects of their life habits, have been previously described (Shortridge, 1934; Roberts, 1951; Ellerman et al., 1953; Meester, 1962; Coetzee, 1969; Stuart, 1975). However, little is known concerning the detailed ecology of different species of small mammals in the Namib Desert, such as community structure, interspecific competition, niche partitioning, etc.

The present study forms part of a broad investigation into aspects of the physiological ecology, demography, and reproductive biology of the small mammal community found on the inselbergs (large rocky outcrops) which occur in the gravel plains region of the Namib Desert. The mammals of this habitat are of interest because they survive in a harsh desert environment, typified by low annual rainfall and high temperatures.

I report here the following aspects concerning the ecology of these small mammals present on a particular inselberg, Tumasberg; *Petromyscus collinus* Thomas and Hinton 1925 (rock mouse), *Aethomys namaquensis* Smith 1934 (rock rat), *Petromus typicus* Smith, 1831 (Dassie rat) and *Elephantulus rupestris* Smith, 1831 (rock elephant-shrew):

- (1) Population dynamics — abundance, distribution, home range, activity patterns, rates of birth, death, immigration, emigration
- (2) Diet and nature of digestive system
- (3) Reproduction

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PLATE I: (b) Study site after rain showing green plant growth.

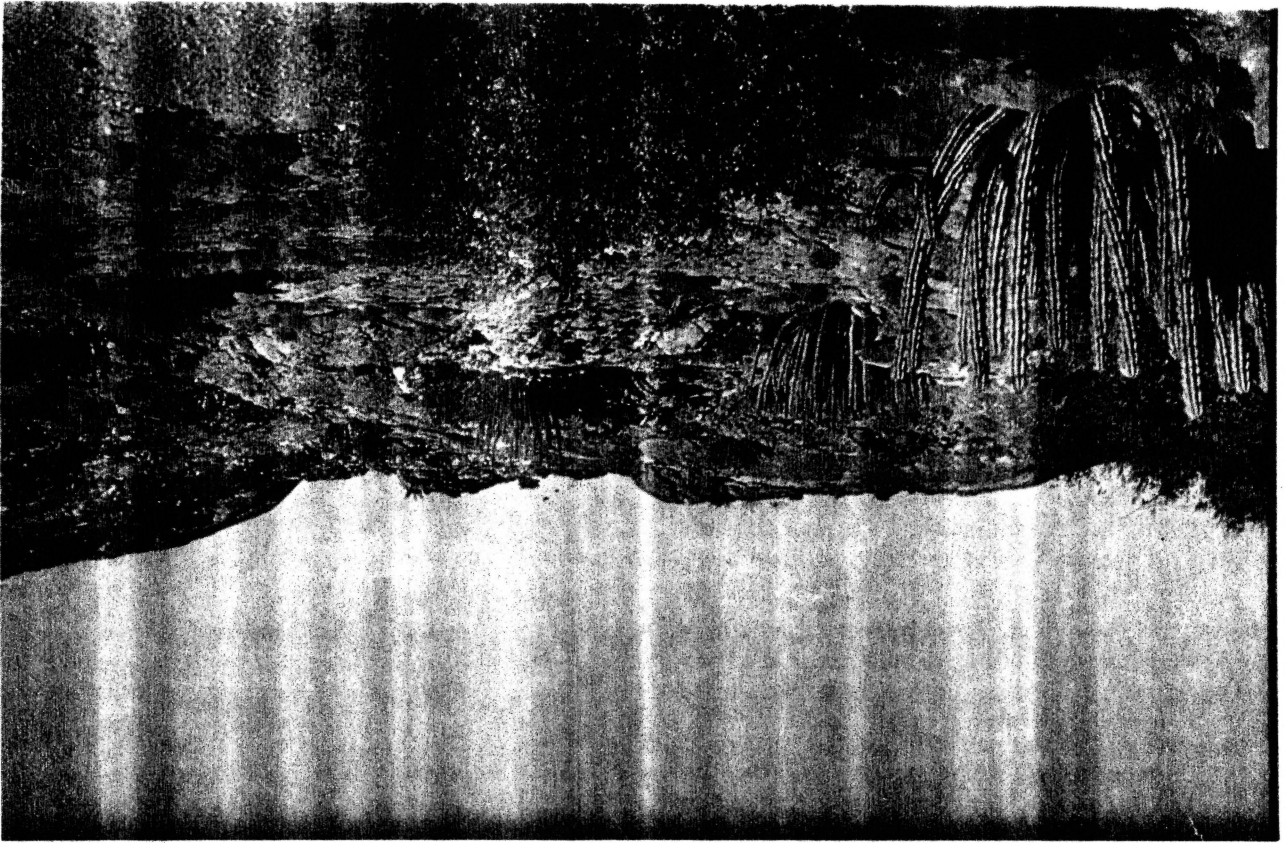
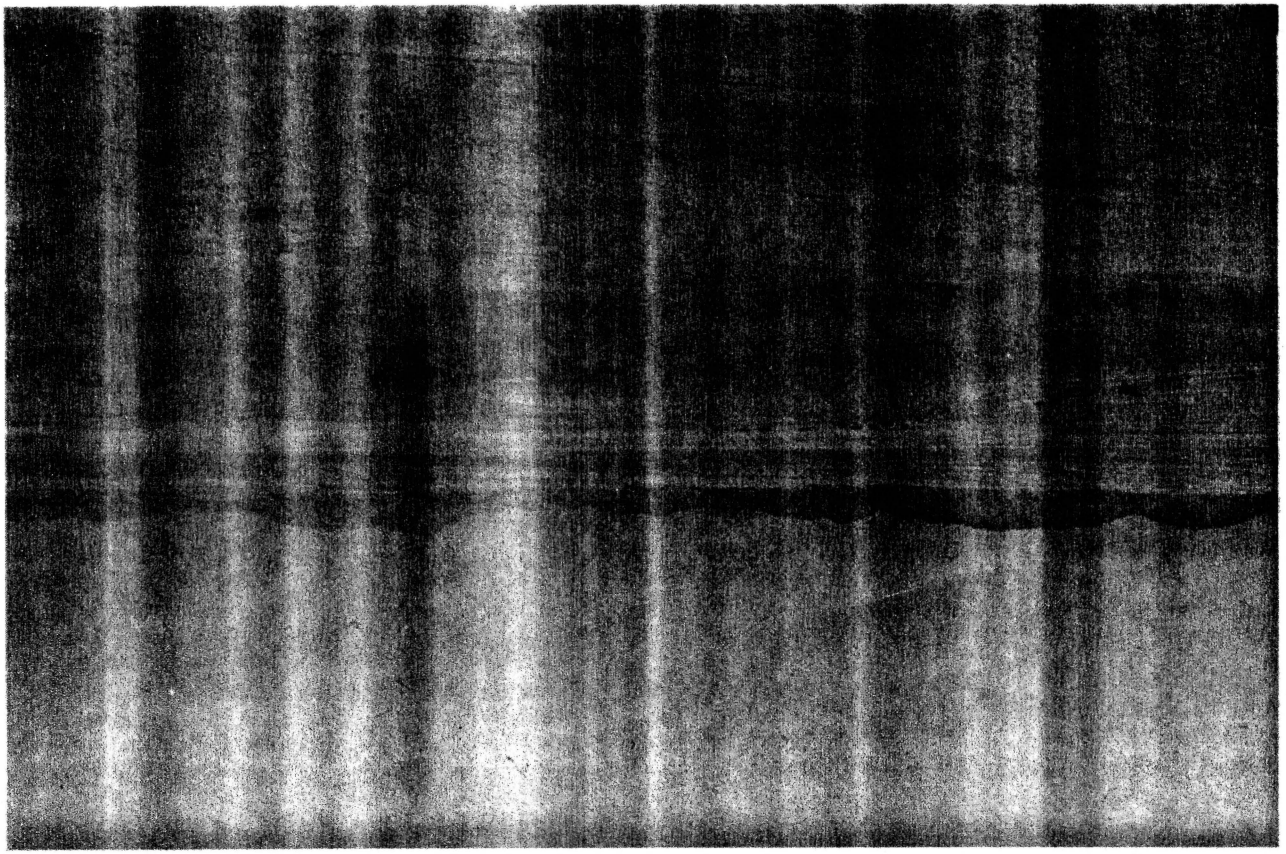


PLATE I: (a) General view of Turnasberg on gravel plains.



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PLATE 1: (c) Study site during heavy fog.

These data are used here to classify the general position of each of the species in the community, to reveal possible areas of overlap (or competition) between the species, and to show how these four species partition the natural resources available to them and coexist in the harsh desert environment. Additional information concerning bio-energetics and ionic regulation will be published subsequently (Withers, Louw and Henschel, in preparation).

2 METHODS

Tumasberg is a typical, large inselberg which is located at approximately 23°10'S; 15°32'E; it is about 115 km from the coast.

Temperature, humidity, rainfall and fog data were compiled from records for the Ganab weather station, which is about 3 km from the trapping grid. The weather station is maintained by the Division of Nature Conservation and Tourism, SWA, and the Namib Research Institute, Gobabeb. Additional ambient temperature, relative humidity, and microclimate data were measured using a Bailey Batt thermocouple meter with wet and dry thermocouples.

An approximately square trapping grid, consisting of 64 traps arranged in an 8 × 8 grid, and set 30 m apart, was established on Tumasberg. The grid area included a variety of terrain, from steep rocky areas to flat gravel or rock areas (Plate 1). Grid points were marked with small pieces of nylon rope, and red reflective tape, for ease of identifying grid points particularly at night.

The small mammal grid was trapped for a total of 24 nights throughout 1977/78 during six different periods (April, June, September, November, January and February). The trapping grid had one live trap placed at each grid point, and the grid was trapped for at least three consecutive nights on the six separate occasions during 1977/1978. A mixture of peanut-butter, rolled oats and honey was primarily used as bait, though mixed bird seed was also used with equal success. On the first trapping occasion (April), wooden traps were used with limited success, and on all subsequent occasions Sherman aluminium live traps were used. Small mammals on the grid were toe-clipped for subsequent identification, weighed using Pesola scales (0 – 50 g and 0 – 500 g), then released. A number of commercially available steel snap traps were also set well away from the grid in order to obtain animals for stomach content analysis.

Body weight data for each species were analysed separately for each of the 6 trapping sessions; mean \pm s.e. was calculated, the data were arranged into frequency histograms, and normal distributions were fitted to the data where possible.

The stomachs of kill trapped mice were preserved in 4 % formalin or dilute $H_2SO_4/MgSO_4$, and examined in the laboratory. Stomach contents were first washed in a fine sieve (500 μ mesh) to remove small particles, and the remaining contents were washed into a glass petri dish and examined using a binocular microscope for seed, plant stem, leaf tissue, insect, and other material. The "other" category was usually hair and parasitic worms. The approximate % coverage of an ocular grid was estimated for each of the food items, for five different portions of the petri dish (about $\frac{1}{4}$ of total area of dish), in order to obtain a quantitative estimate of the proportions of different items in the diet.

The digestive systems of the four species were dissected from the animals and photographed for subsequent analysis of the relative proportions of the stomach, foregut, caecum and hindgut.

The abundance of the small mammal species at different points of the trapping grid were tested for randomness, clumping or dispersion using Morisita's Index of Dispersion (Morisita, 1962). The distribution data were also analysed using a General Purpose Contouring Program (GPCP) which interpolates the 8×8 distribution into a 90×90 grid, and the GPCP output was used to draw 3-D representations of the distributions. Possible interactions between the four species were investigated by association analysis, using presence or absence of the species at each grid site (Pielou, 1969). The distribution of each species was compared with that of each other species.

The distribution and abundance of the major plant species on the grid were pooled with annual estimates of animal abundances, and the data were analysed using similarity analysis (see Field, 1969). These distributional data of small mammals and plants were also analysed using multiple linear regression techniques.

The small mammal recapture data were analysed for various population parameters. Population size for *Petromyscus* was estimated using Schumacher and Eschmeyer's (1943) explicit solution which determines the rate at which the proportion of marked animals increases as more mice are marked each night. This estimate also allows the testing of one underlying assumption for use of trapping data, equal trapability of mice. A stochastic analysis (Jolly, 1965; Seber, 1965) was also used for calculation of population size (\pm standard error), combined immigration/birth rate (\pm s.e.) and emigration/death rate (\pm s.e.). A Fortran computer program for Jolly-Seber estimates was developed and tested with data from Jolly (1965).

The reproductive condition of the live trapped mice was examined, and the following categories recognised:

for males, whether the testes were non-descended, partially or completely descended, and presence/absence of peri-anal flap; for females, the absence/presence and number of teats, whether there was swelling of the base of the teats indicating lactation, whether the vagina was perforate/imperforate, and whether embryos could be detected by palpitation.

All computer analyses were completed using the UCT Computer Department facilities.

3 RESULTS

3.1 Climate

There was a pronounced seasonal cycle for 1977/1978 in mean monthly temperatures (maximum, mean, minimum), with lowest temperatures in June and July and highest temperatures in March and April (Fig 1); similar climatic data are reported for 1969 by Bessler (1972). The maximum and minimum temperatures for February, 1977, were lower than would be expected,

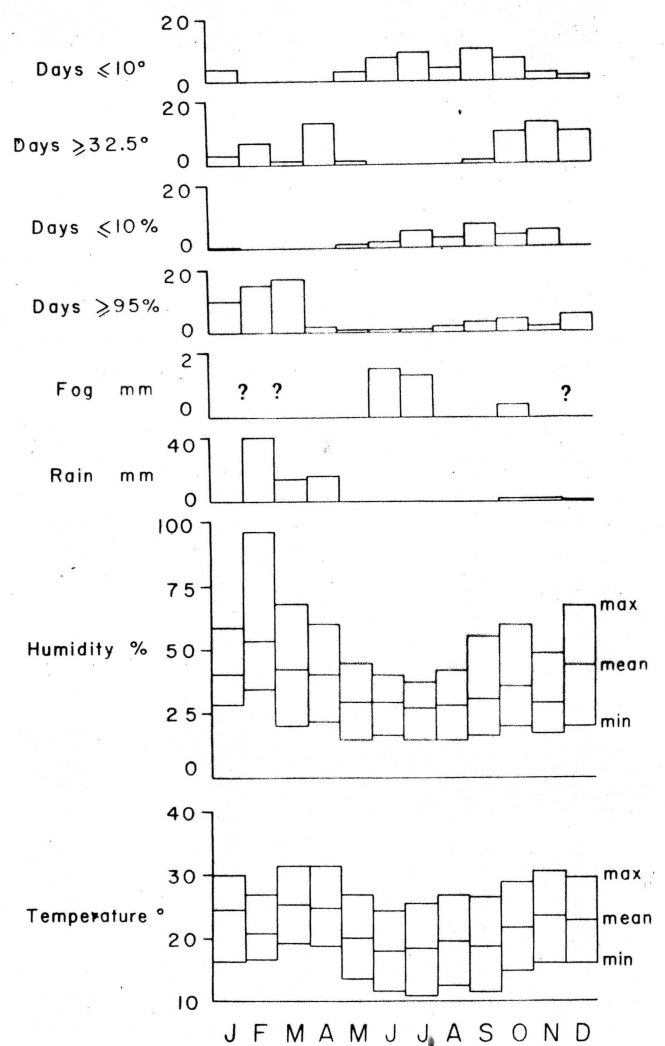


FIGURE 1: Monthly macroclimatic data from Ganab weather station, about 3 km from study site, for 1977.

but this is probably because of the high rainfall which would indicate overcast conditions. The number of days per month with temperatures greater than 32.5°C, and less than 10°C, also show a marked seasonal cycle corresponding to the mean monthly temperature data (Fig 1).

The relative humidity at Ganab for 1977 also showed a seasonal cycle, with highest humidity in February and lowest in June – July (Fig 1). The warmest months of the year (November – April) were also the most humid, whereas the coldest months (May – October) were the driest. The number of days with relative humidity greater than 95 %, and less than 10 %, also showed a similar pattern to the mean humidity data (Fig 1).

Yearly rainfall patterns at Tumasberg are typical of a desert. Mean annual rainfall is 110 ± 40 mm ($n = 8$) and rain is highly seasonal, sporadic and tends to fall in many light showers (mean = 4.6 ± 2 mm per rainfall, $n = 8$). Over an eight year period, only two months (July and August) had no recorded rain (Fig 2) but the majority of the rain fell in four months, January to April. Rainfall for 1977/1978 is shown in Fig 1.

In addition to rain, there is significant precipitation due to fog. Advective fog forms over the cold Benguella Ocean current and moves rapidly across the gravel plains from the west, for over 115 km. Advective fog is much less common at Tumasberg than at Gobabeb,

and there appears to be no correlation between day to day occurrences of fog at the two locations. Local fog can form as a result of the marked nocturnal radiation on clear nights which results in low ambient temperatures and formation of low-lying, stationary fog common at night.

Although it is technically difficult to measure precipitation due to fog, the rain recorder at Ganab was fitted with a fog screen, and data for fog precipitation are included in Figs. 1 and 2. The precipitation due to fog appears to be orders of magnitude less than rainfall. Fog, like rain, appears to be sporadic. The interpretation of these fog data are difficult, however, since it is not possible to tell the difference between fog and light rain from the rain records. Furthermore, a particularly heavy fog observed at Tumasberg was not detected by the rain/fog recorder, so the fog data in Figs. 2 and 3 are somewhat unreliable. The distribution of fogs throughout the year at Gobabeb, where complete visual records are available, indicate a greater frequency of fogs in September to November (Schulze, 1969). I assume that a similar seasonal pattern for fog exists at Tumasberg, particularly in view of the seasonal distribution of days with relative humidity greater than 95 % (Fig 1).

3.2 Microclimate

Microclimate is an essential aspect of the ecology of small animals, particularly in deserts, because the extremes of the macroclimate are considerably different near the ground.

Ambient air temperature and humidity were measured in the shade, and under rocky areas facing east and west. Substrate temperature was measured at the surface of a layer of sand overlying granite. The substrate temperature altered markedly (by over 40°C) during a 24 hour period, whereas the air temperature changed by considerably less (Fig 3). The temperature under the east-facing rocks increased earlier in the morning, and decreased sooner in the evening, than under the west-facing rocks, but there were only slight differences in air temperature between the ambient air and under the rocks. The relative humidity under the rocks was similar to that at the surface, and changed by about 25 % during the day.

3.3 Vegetation

The vegetation of Tumasberg is described as a *Commiphora glaucescens-Anthepora pubescens* community which is typical of inselbergs and rocky outcrops east of Mirabib (Robinson, 1976). About 80 species of plants are associated with this community on Tumasberg (Robinson, 1976).

The common, large plants found on the grid were *Commiphora glaucescens* (Burseraceae), *Euphorbia virosa* (Euphorbiaceae) and *Aloe dichotoma* (Kokerboom tree, Liliaceae). A few species of grasses and

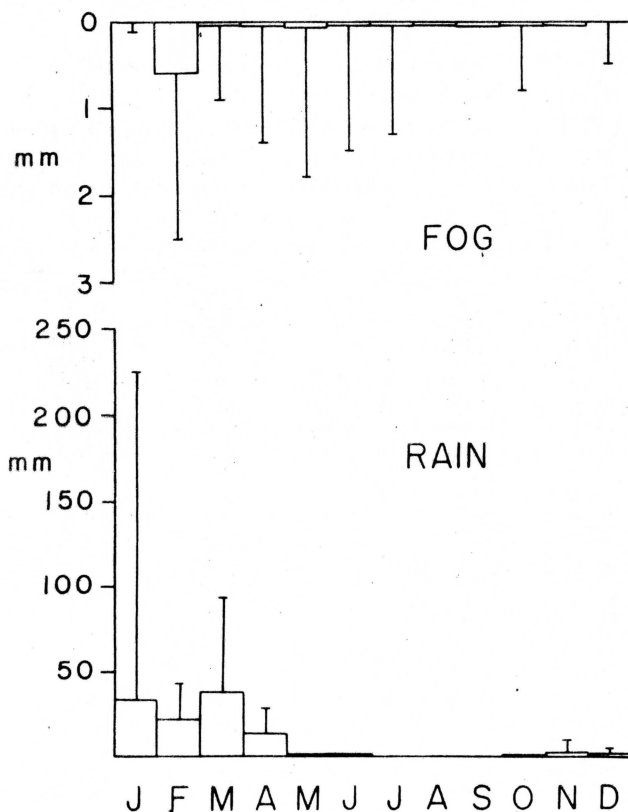


FIGURE 2: Monthly summary of fog and rain data for Ganab weather station, 1970 - 1977.

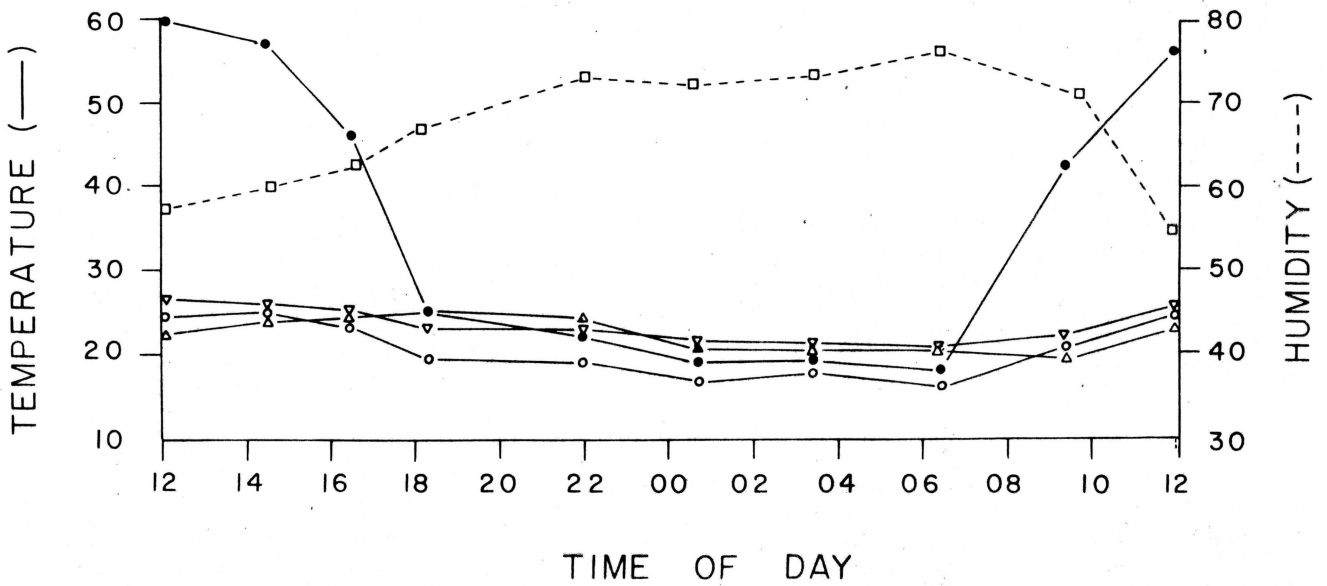


FIGURE 3: Soil surface temperature (●), ambient air temperature (○), air temperature under east facing rocks (∇), air temperature under west facing rocks (Δ) and relative humidity (□) during 24 hours, in January, 1977.

perennials were widespread on the grid, but none were particularly abundant (i.e. greater than 5 – 10 % coverage).

The vegetation covering each of the grid areas was examined, and the abundance for each of the species was subjectively rated from 0 (absent) to 4 (abundant) in terms of per cent cover for the smaller species; the larger species (*Euphorbia*, *Aloe*, *Commiphora*) were rated higher to partly compensate for their large biomass. A total of 39 species was recognised on the trapping grid and identified where possible.

Three species of plant, two grasses and one scrophularia, predominated in terms of total coverage/biomass, and with four other species comprised greater than 70 % of all vegetation cover. These seven plants in order of decreasing abundance are: *Stipogrostis*, *Enneapogon*, *Anticharis*, *Commiphora*, *Ruellia*, *Euphorbia*, *Blepharis*.

3.4 Mammals

A high diversity of mammals is found either on the inselberg, or on the gravel plains near the base of the inselberg. These species have been listed by previous authors (Shortridge, 1934; Roberts, 1951; Coetzee, 1969; Stuart, 1975). The species observed at Tumasberg during this study, which do not appear to have been previously recorded here, are: slender mongoose (*Herpestes sanguineus*), pigmy mouse (*Leggada minutoides*), and spotted hyaena (*Crocuta crocuta*).

The small mammal community studied at Tumasberg included *Petromyscus collinus*, *Aethomys namaquensis*, *Petromus typicus* and *Elephantulus rupestris*. Two pigmy mice (*Leggada minutoides*) and one lesser gerbil (*Gerbillus paeba*) were captured on Tumasberg.

3.5 Population size

From a total of 1 536 trap-nights, *Petromyscus* were captured 224 times (14,6 % trap success), *Aethomys* 85 times (5,5 %), *Petromus* 53 times (3,5 %) and *Elephantulus* 16 times (1,0 %). The sexes and numbers of individuals captured at the different times during the year are shown in Table 1.

Certain of the individual mice were frequently recaptured, whereas others were never recaptured. The recapture history for the individuals of the four species are summarised in Table 2. A large proportion of *Petromyscus* were recaptured on subsequent trapping sessions (i.e. at least 1 month later, not during the next few nights) whereas most of the *Aethomys* were

TABLE 1: Numbers of small mammals captured on trapping grid during 1977/1978.

Date	Petromyscus		Aethomys		Petromus		Elephantulus	
	♂	♀	♂	♀	♂	♀	♂	♀
1 – 3								
April	2	2	0	1	1	1	1	0
13 – 16								
June	10	20	8	13	1	1	1	1
1 – 3								
September	14	17	6	3	3	2	1	1
22 – 28								
November	12	13	9	1	16	3	1	0
16 – 19								
January	13	14	2	1	8	4	1	1
22 – 24								
February	10	12	2	3	0	0	1	0

Footnote:

1 *G. paeba*, June
1 *L. minutoides*, January.

TABLE 2: Recapture history of small mammal individuals captured on trapping grid (excluding new animals captured on last trapping session since they have no recapture history). Values are actual numbers of individuals, and values expressed as a % of total in parentheses.

	Petro- myscus	Aethomys	Petromus	Elephan- tulus
not recaptured	20(37)	19(70)	7(44)	1(25)
recaptured over 1 session	9(17)	4(15)	4(25)	1(25)
recaptured over 2 sessions	3(6)	3(11)	1(6)	1(25)
recaptured over 3 sessions	7(13)	0(0)	3(19)	1(25)
recaptured over 4 sessions	14(28)	1(4)	1(6)	0(0)
recaptured over 5 sessions	1(2)	0(0)	0(0)	0(0)
Total # recaptured	54(100)	27(100)	16(100)	4(100)

not. A high proportion of the *Petromus* and *Elephantulus* were also recaptured on subsequent trapping sessions.

Such recapture data can be used to estimate population size in a number of ways. The simplest method is to use the total number of mice captured as a minimum estimate of population size; trapping for three or four nights in succession as was done in the present study

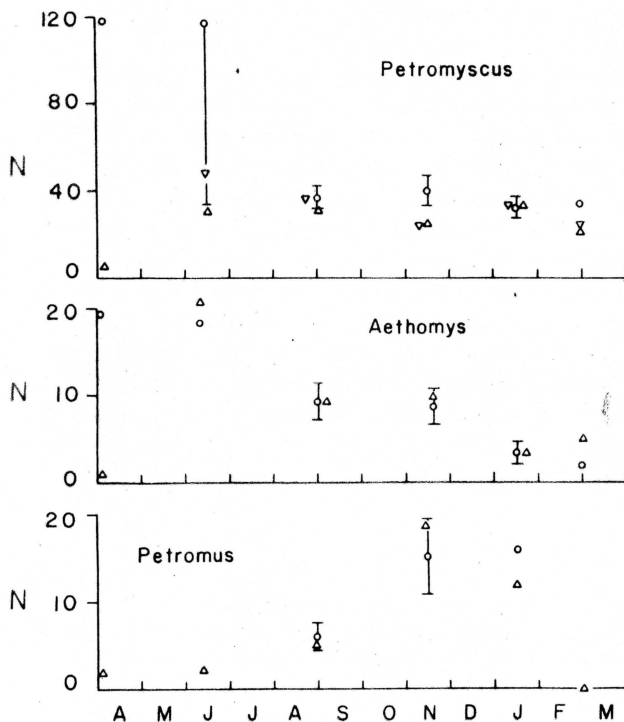


FIGURE 4: Various population estimates for rodents on trapping grid during study period, 1977 - 1978. N is total number of mice on the grid (~6 hectare). Data are numbers of individual mice actually captured per trapping session (Δ); population estimates calculated from Schumacher-Eschmeyer (1943) (∇ , *Petromyscus* only); and population estimates (mean \pm s.e.) calculated using Jolly's (1965) stochastic method (\circ).

increases the usefulness of such an estimate, particularly if the recapture rate is high. The numbers of mice captured per trapping session in this study are shown in Fig 4 and Table 1.

Better population estimates can be obtained using a variety of methods for analysing mark-release-recapture data such as Schumacher and Eschmeyer's (1943) method. A more sophisticated population estimate, based upon a stochastic, statistical model, is afforded by Jolly (1965) and Seber (1965) analysis. This method requires substantial recapture data and did not prove suitable for data from the present study in many respects. This technique does not provide population estimates for the first and last trapping sessions and so values for the first and last sessions were extrapolated from the second and third sessions, and the second and third to last sessions (Caughley, 1977). The technique does, however, provide measures of immigration/birth and emigration/death rates, and confidence limits for all population parameters (Fig 4; Table 3).

TABLE 3: Population estimates from Jolly-Seber analysis; population size (number of mice, \pm s.e.), survival rate (fraction of mice surviving between trapping sessions, \pm s.e.) and immigration/birth rate (number of mice, \pm s.e.).

Population size	Petromyscus	Aethomys	Petromus
1-3 April	117*	19*	--
13-6 June	116 \pm 104	18	--
1-3 September	37 \pm 6	\pm 2	6 \pm 1
22-28 November	38 \pm 7	8 \pm 2	15 \pm 4
16-19 January	32 \pm 6	3 \pm 1*	16*
22-24 February	32*	--	--
Survival rate			
April - June	.77 \pm .30*	1*	1*
June - September	.73 \pm .10	.28 \pm .11	1
Sept. - Nov.	.87 \pm .10	.56 \pm .27	1.1 \pm 0.2
Nov. - Jan.	.76 \pm .11	.13 \pm .12	--
Jan. - Feb.	--	--	--
Immigration/Birth rate			
April - June	--	--	--
June - September	-47 \pm 75	4	--
Sept. - Nov.	6.1 \pm 2.6	4	7.9 \pm 4.4
Nov. - Jan.	2.6 \pm 2.4	2	--
Jan. - Feb.	--	--	--

* Indicates value extrapolated using logarithmic growth assumptions (see Caughley, 1977).

There are a number of underlying assumptions involved with population estimates because of various sources for unequal catchability, both for different species and different individuals of single species. Three major sources of unequal trapability are: 1) an inherent bias of particular species, or individuals not to be captured; 2) the result of learning which can make an animal become trap-shy, or trap-prone; and 3) unequal opportunity of capture.

The first assumption is difficult, or almost impossible, to evaluate since certain individuals may never be captured. The second effect can be evaluated using Schumacher and Eschmeyer's (1943) method for testing equal recatchability. Data for *Petromyscus* indicate equal recatchability, but there were not sufficient data to evaluate the other species. *Petromyscus* were significantly ($P < 0.05$) less prone to kill trapping (5.6 % success) than live trapping (14.6 %) whereas the other species did not favour either type of trap. *Petromyscus* were probably less prone to be kill-trapped because they are lighter and less likely to trigger the relatively insensitive steel snap traps. Since kill trapping allows for no learning, either there was no effect of learning for *Aethomys* and *Petromus*, or any learning effect was counteracted by a bias towards live or kill traps.

The third effect, unequal opportunity for capture, was discounted for two reasons. Firstly, on one occasion an additional 40 traps were incorporated into $\frac{1}{4}$ of the grid by placing them between existing grid points. The effect on the numbers of mice captured, and the individuals involved, was negligible. This indicates that there most likely were no mice which could not be caught because no traps were placed in their vicinity. Further, most mice were recaptured at different grid sites, indicating that the distance between traps was not greater than the size of home ranges, and no one mouse was likely to "monopolise" a trap site.

Although the numbers of *Petromyscus* and *Aethomys* caught in live traps appear to not be biased by unequal trapability, the seasonal pattern for numbers of *Petromus* suggest that their trapability altered. The population size of *Petromus* appeared to increase during the year, although none were caught on the last trapping session (Fig 4). Because *Petromus* are diurnal, their numbers could be estimated visually, and the population appeared to be constant throughout the year. Evidence for the reproductive cycle of *Petromus* (see below) contradicts the possibility of births during the year (see later) and a net immigration of animals is difficult to explain. The most reasonable explanation for this increase in numbers of *Petromus* during the year is a change in trapability such that the *Petromus* are more readily captured in baited traps in mid-year. After the rains in February, no *Petromus* were trapped although they were commonly seen on the grid. Hence, it is likely that *Petromus* are more prone to enter a trap in search of food during the drier parts of the year when their natural diet was diminishing.

The population estimates for *Petromyscus*, *Aethomys* and *Petromus* calculated using the method of Jolly (1965) and Seber (1965) are generally similar to the numbers of animals captured, and for *Petromyscus*, to the Schumacher-Eschmeyer estimates. *Petromyscus* was the most abundant rodent captured in terms of total numbers (both individuals present and total recaptures), with decreasing numbers of *Aethomys*, *Petromus* and *Elephantulus*. The larger *Petromus*, however, had the highest biomass density on the grid (431 g hectare⁻¹), about twice that of both *Petromyscus* and *Aethomys* (174 and 199 g hectare⁻¹), and that of *Elephantulus* was the least (18 g hectare⁻¹). The numbers of *Petromyscus* and *Aethomys* appeared to continually decline throughout the year, although the population size of *Petromyscus* appeared to decline less over the year than that of *Aethomys*. Such declines in population size are clearly associated with mortality/emigration. *Petromyscus* has a higher survival rate (≈ 0.9) than *Aethomys* (≈ 0.6). The survival rates of *Petromus* and *Elephantulus* would appear to be much greater than even for *Petromyscus* (between 0.9 and 1.0).

Equal proportions of male and female *Petromyscus* and *Aethomys* were captured throughout the year, but the sex ratio for *Petromus* was significantly skewed ($P < .05$) towards males (12) compared to females (4). The sex ratio of *Petromyscus* for different trapping sessions was never significantly different from 1:1, and on only one trapping session was the sex ratio of *Aethomys* significantly skewed towards males (November; 9 males, one female). The sex ratio of *Petromus* on different trapping sessions indicated more males, whenever sufficient animals were captured to allow statistical comparison.

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3.6 Population distribution

The number of individuals captured for each of the four species over the trapping grid was tested to determine whether the distribution of the individuals was at random, aggregated, or evenly dispersed, using Morisita's Index of Dispersion (Morisita, 1962). Individual capture records for all species were significantly clumped (Table 4). The individual animals were also classified as "residents" and "non-residents", according to whether they were recaptured on one or more subsequent trapping session ("residents") or whether they were never recaptured on a different trapping session although they may have been captured on subsequent nights of the same trapping session ("non-residents"). The distribution of captures for all resident species were also clumped whereas the non-residents were distributed at random, over the trapping grid (Table 4).

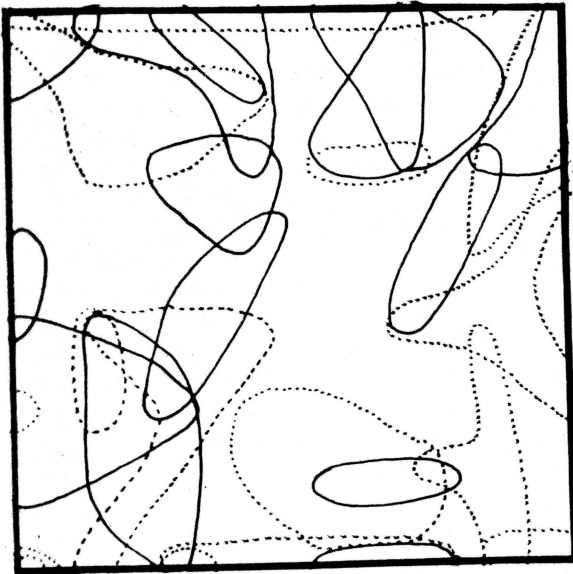
TABLE 4: Analysis of distribution of small mammals over trapping grid using Index of Dispersion (Morisita, 1962).

	Total animals	Residents	Non-residents
<i>Petromyscus</i>	clumped*	clumped*	random
<i>Aethomys</i>	clumped*	clumped**	random
<i>Petromus</i>	clumped**	clumped**	†
<i>Elephantulus</i> †	clumped***	--	--

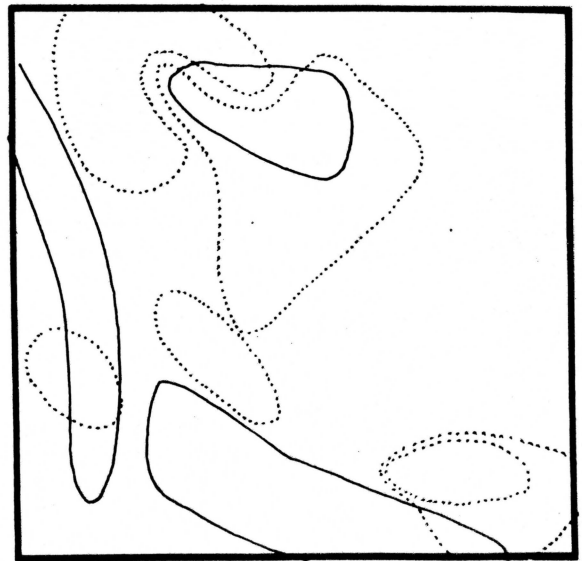
† Insufficient #s; † essentially all *Elephantulus* were resident; * $P < .01$; ** $P < .005$; *** $P < .001$

The distribution pattern for individual, resident mice over the trapping grid showed definite home ranges, which in many cases were maintained stable throughout the year (Fig 5). The home ranges of individual male *Petromyscus* showed little overlap with other males, and some of the overlap was temporally separated, i.e. the males may have been at the same grid site, but not on the same trap session. However, there was some overlap of males over single trapping sessions, and on

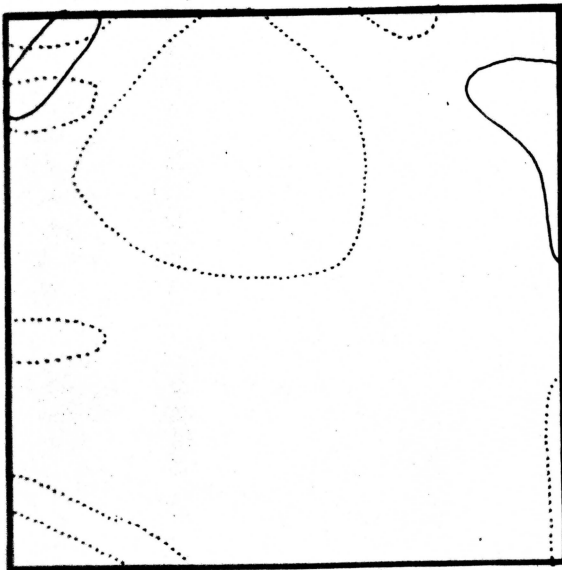
one occasion two male *Petromyscus* were found in the same trap; The home ranges of female *Petromyscus* showed considerable variation in size and overlap; some female home ranges were totally enclosed within those of other females. There was also marked overlap of male and female *Petromyscus* home ranges. These patterns could be interpreted as evidence for agonistic behaviour between males, but no male-female and female-female agonistic behaviour.



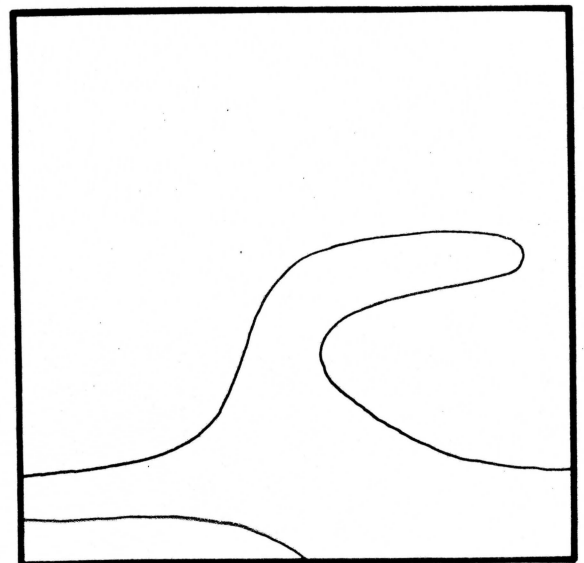
Petromyscus



Petromus



Aethomys



Elephantulus

FIGURE 5: Home ranges of male (---) and female (—) small mammals on the trapping grid, as determined from point of capture. Data for female and male *Elephantulus* were pooled.

Aethomys were less abundant, and their population less stable than *Petromyscus*, as fewer of the *Aethomys* were residents. *Aethomys* home ranges were not maintained for as long as those of *Petromyscus*. The home ranges of the six resident male *Aethomys* did not overlap. Although the home ranges of the two resident *Aethomys* females did not overlap, they did overlap with those of the males.

Petromys appeared to be quite sedentary, although interpretation of the trapping data is made difficult because of the apparent alteration in trapability. The home ranges of three resident male *Petromys* showed total overlap in one case, and non-overlap in the other; the three female *Petromys* had distinct home ranges, but did overlap with the males.

The *Elephantulus* were present in low numbers, and there were never more than two *Elephantulus* (1 male and 1 female) caught on the grid at any one time. There is not sufficient data to delimit their home range, but it is apparently very large; one male was accidentally kill-trapped over 200 metres from the trapping grid.

Mean home range sizes for the four species were: *Petromyscus*, 0,27 hectare; *Aethomys*, 0,31 h; *Petromys*, 0,31 h; *Elephantulus*, >1.2 h.

Association analysis of presence/absence for the four species indicated that *Aethomys* and *Elephantulus* were

negatively associated ($P < 0.05$) i.e. these species tended to avoid each other. None of the other possible interactions of the four species showed any significant tendency for positive or negative association.

It is also of interest to look at the distribution of total numbers of animals caught (including recaptures of the same individuals) over the trapping grid. The data for numbers of captures of *Petromyscus*, *Aethomys*, *Petromys* and *Elephantulus* are summarised in Figure 6 as 3-dimensional graphs. Data for residents and non-residents, the plant species, and substrate-type and microhabitat-abundance data can be expressed in the same manner.

The relative abundance for 39 plant species, the nature of the substrate (rock-gravel-sand), the abundance of suitable hiding places for small rodents, the total number of times that individual animals were caught at each trap site, the number of residents at each site, were combined for the 64 grid sites. These 51 different parameters (39 plant species, 2 habitat measures, 10 mammal parameters) for each of the 64 trap sites were analysed, using multiple correlation techniques and step-wise multiple linear regression techniques, to determine whether there were significant correlations between the various parameters. A 51×51 table of correlation coefficients was produced, and the significant correlations are summarised in Table 5. Every animal species was correlated, or associated,

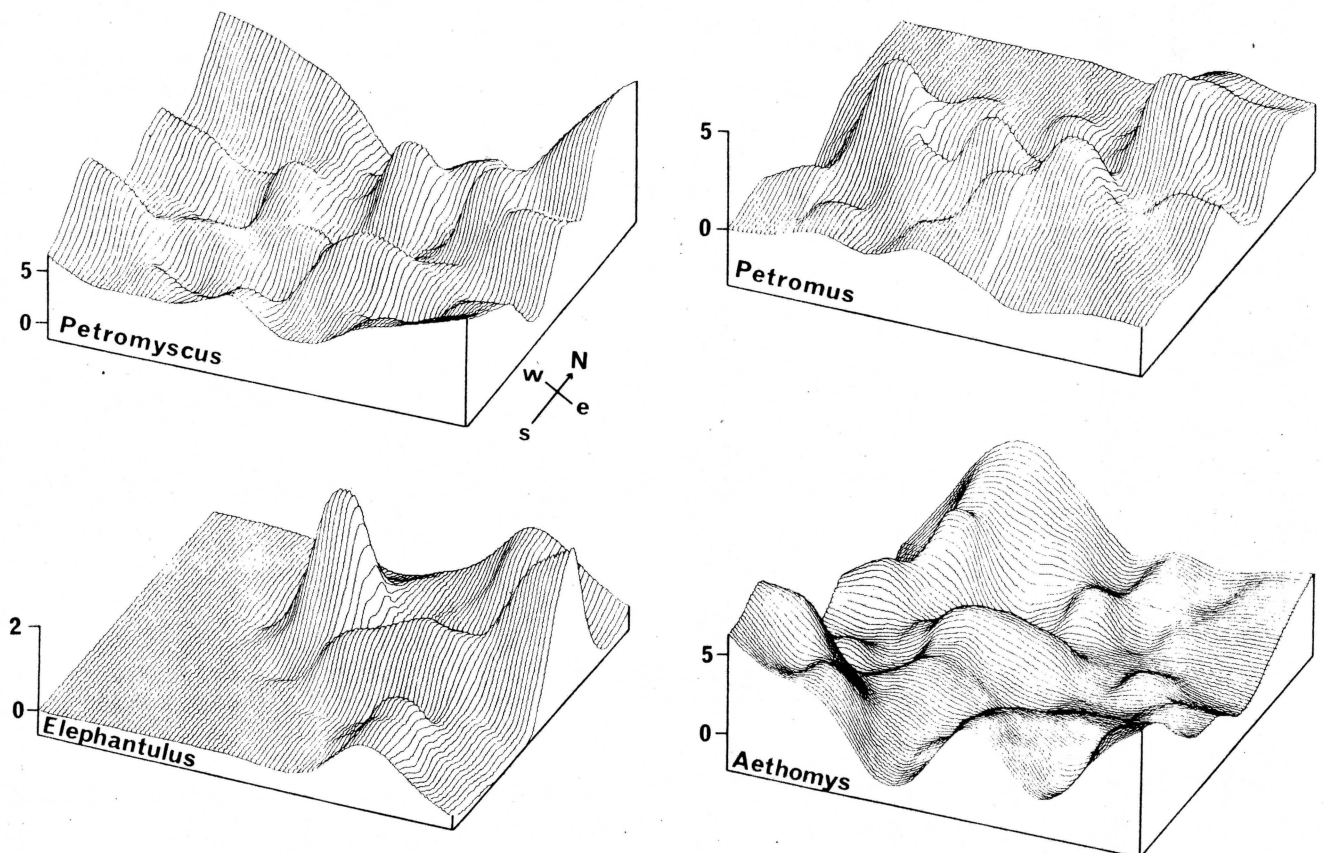


FIGURE 6: Three dimensional representation of distribution patterns for the four small mammal species on the trapping grid. X and Y coordinates indicate trapping grid coordinates; Z scale indicates the numbers of captures on grid. See text for method involved with interpolating data for 8×8 grid into 3-D representations.

TABLE 5: Comparison of associations of small mammal species with other small mammal species, plant species, microhabitat suitability, and nature of substrate, using similarity analysis (logarithmic transformed data) and multivariate regression analysis. For similarity analysis, all small mammal associations of >60 % similarity are shown; for multivariate regression analysis, all correlations significant of $P < .05$ ($r > 0.25$) are shown.

	Similarity Analysis	Multivariate Regression*
<i>Petromyscus</i>	abundant micro-habitat, plants 1, 2, 3, 4, 5	abundant microhabitat ⁺ , rocky substrate ⁺ , plants 3 ⁻ , 5 ⁺ , 8 ⁻ , 14 ⁻ , 17 ⁺ , 20 ⁻ , 22 ⁻ , 36 ⁻
<i>Aethomys</i>	plant 39	plants 2 ⁻ , 11 ⁺ , 17 ⁺ , 20 ⁺ , 37 ⁺
<i>Petromus</i>	----	abundant microhabitat ⁺ , plants 16 ⁺ , 21 ⁺ , 28 ⁺ , 35 ⁺
<i>Elephantulus</i>	----	<i>Petromyscus</i> ⁻ , <i>Aethomys</i> ⁻ , plants 2 ⁺ , 29 ⁺

* + indicates positive correlation, - indicates negative correlation.

Plant 1 = <i>Commiphora glaucescens</i>	Plant 17 = unidentified Compositae
2 = <i>Anticharis linearis</i>	20 = <i>Rhus marlothii</i>
3 = <i>Stipogrostis ciliata</i>	21 = <i>Dyerophytum africanum</i>
4 = <i>Enneapogon brachystachyus</i>	22 = <i>Blepharis grossa</i>
5 = <i>Ruellia diversifolia</i>	28 = <i>Eragrostis</i>
8 = <i>Zygochloa simplex</i>	29 = unidentified Graminae
11 = <i>Sarcocaulon mossamedense</i>	35 = unidentified
14 = <i>Triraphis ramosissima</i>	36 = <i>Boscia foetida</i>
16 = <i>Abutilon pycnodon</i>	37 = <i>Pergularia daemia</i>
	39 = <i>Euphorbia virosa</i>

with some other variable, either plant species, micro-habitat, or substrate, or another animal species.

Similarity analysis using untransformed data clearly associated the most abundant animals (*Petromyscus*, *Aethomys*) with micro-habitat, and the abundant plant species 1 – 5. However, using logarithmic transformed data (which compensates for different abundances) associated *Aethomys* with *Euphorbia* (>55 % similarity), *Petromyscus* with plant species 3 and 4, and micro-habitat availability (>75 % similarity); *Elephantulus* and *Petromus* were poorly associated with other species (Table 5). Some interactions between the small mammal species and plant species were shown by similarity and correlation analysis but the interpretation of these associations is unclear. Firstly, correlation does not imply causation. Further, the low abundances of both plants and mammals on the grid, the heterogeneous habitat of the grid, the ability of the rodents to move between grid points (for example, one grid site had no vegetation or rocky cover, but *Petromyscus* was captured there), and the somewhat arbitrary distinction between resident and non-resident animals tend to obscure causal relationships. A simplistic,

correlative approach also cannot account for factors being multiplicative. For example, the presence of a required vegetation type might not assure the presence of a rodent if there are not sufficient rocky niches to ensure protection against predators.

Consequently, few realistic correlations between the mammals and plants were noted. *Petromyscus* appear to be found in rocky areas where there are numerous rock overhangs, small cracks, crannies, and vegetation to provide hiding places. Their distribution may be causally related to that of some plant species. *Aethomys* appear to be found at the periphery of rocky areas and flatter, gravel or sand areas; their home ranges may be related to the presence of *Aloe*, *Euphorbia*, or other plants. *Petromus* appear to also prefer rocky areas, but are particularly common where there are numerous large boulders which provide more spacious hiding places, safe sunning-areas, and also access to grassy areas. *Elephantulus* range widely, but noticeably utilise the open, gravel areas which the other species avoid. Being insectivores, they are understandably poorly correlated in distribution with any plants.

Interestingly, the distributions and abundances of the different species were not positively associated, or correlated, using any of the mathematical techniques, although there was clearly some overlap for all species. This would suggest that the four species are utilising particular areas of the grid to different extents, thereby avoiding direct competition. This is most apparent for *Aethomys* and *Elephantulus* which (statistically) avoid each other.

3.7 Body mass

The body mass of individual animals caught throughout the year can provide valuable information concerning the reproductive cycle and growth patterns. Histograms summarising the body masses of the three rodent species throughout the year with normal distributions fitted to the data where appropriate, are shown in Fig 7.

There was a clear increase in the mean body mass of *Petromyscus* and *Aethomys*, and the body mass distributions become progressively more like normal distributions throughout the study. The early skewness of body mass (towards lower values) clearly indicates the presence of juveniles.

A similar pattern of change in body mass was not apparent for *Petromus*. In fact, *Petromus* individuals showed a remarkable stability of body mass throughout the year, regardless of their initial mass. For example, a 110 g male and female were still about 110 g after 7 months, whereas other (older?) *Petromus* maintained mass at over 200 g (Fig 7). The body masses of *Petromus* thus do not indicate a discreet breeding season but do indicate that the growth rate is probably not equivalent for all individuals up to adult body mass.

Distribution factors

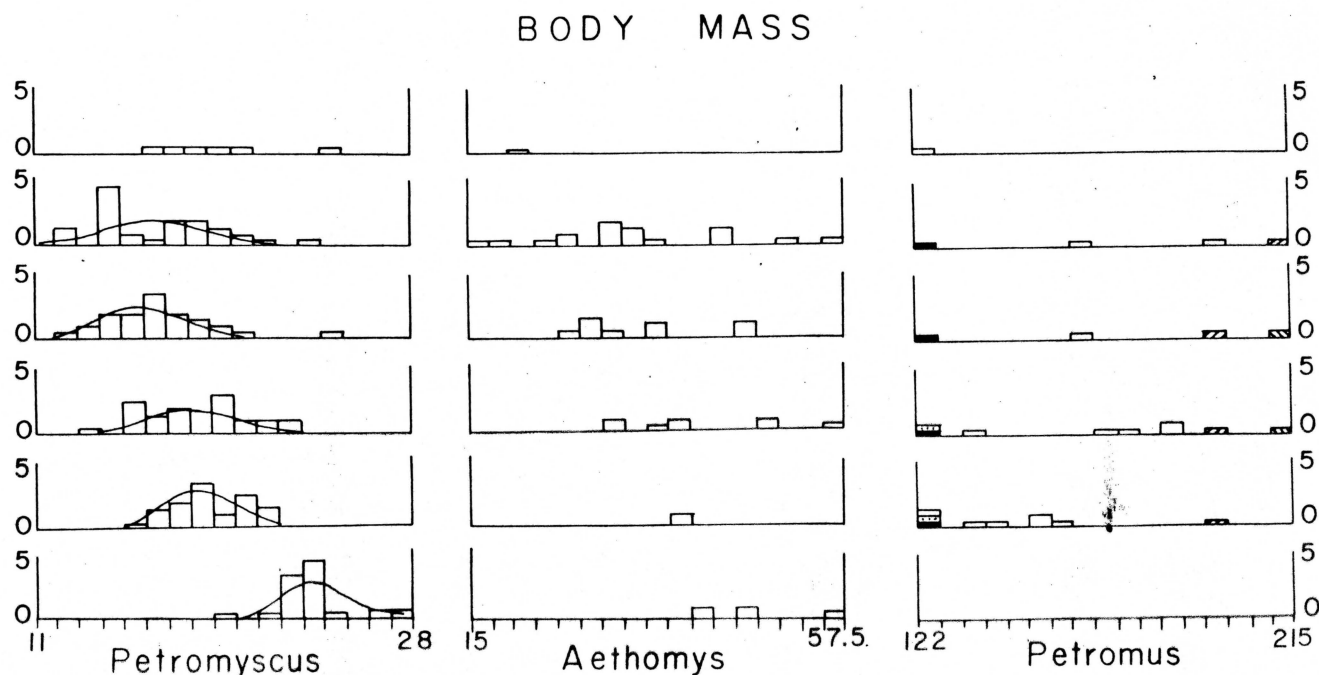


FIGURE 7: Frequency histograms for body mass of the three rodent species, and normal distributions where appropriate. Ordinate indicates number of individuals within weight classes. Weight classes are 1 g intervals for *Petromyscus*, 2.5 g for *Aethomys*, and 5.5 g for *Petromus*. Some particular *Petromus* individuals are indicated.

3.8 Stomach contents and digestive systems

The mean proportions of different food categories observed in stomachs of *Petromyscus*, *Aethomys* and *Petromus* are summarised in Table 6. There were no apparent seasonal trends, so data was pooled for all six trap sessions. It is likely that more insect material was taken in February after the rains, but the sample sizes are too small to test this statistically. All species of mice appear to be opportunistic feeders, particularly when the ranges of the stomach contents are considered. However, *Petromus* in general had a significantly higher proportion ($P < .05$) of stem and leaf material (often entirely monocotyledenous) and significantly less seed ($P < .05$) than *Petromyscus* and *Aethomys*. All species consumed similar proportions of insect. The proportions of insect, seed, leaf and stem comprising the diets of *Petromyscus* and *Aethomys* were statistically indistinguishable, although the actual composition of the diet (i.e. plant and insect species eaten) may be different.

The food preferences of rodent species are often reflected by the structure of their digestive systems (Kostelecka-Myrcha and Myrcha, 1964; Baker, 1971), and this is also apparent for the small mammals investigated here (Table 7). *Petromus* has the relatively largest caecum, which would be associated with post-gastric bacterial fermentation of its plant (particularly grass) diet; *Petromus* is also highly coprophagous. *Petromyscus* and *Aethomys* have relatively smaller caecae, and their diets comprise less vegetation and

TABLE 6: Proportion of seed, leaf, stem and insect in the stomach of rodents. Values are mean \pm s.e. (range). n = number of stomach analysed.

	Petromyscus (n = 16)	Aethomys (n = 16)	Petromus (n = 13)
Seed	28.4 \pm 7.9 (0-100)	32.3 \pm 8.8 (0-94)	3.0* \pm 1.1 (0-13)
Leaf	14.8 \pm 5.5 (0-80)	19.1 \pm 5.3 (0-94)	24.8† \pm 8.5 (1-95)
Stem	31.6 \pm 8.4 (0-97)	27.2 \pm 8.0 (0-92)	49.7† \pm 9.9 (4-96)
Insect	25.3 \pm 9.4 (0-100)	21.3 \pm 9.4 (0-98)	21.9 \pm 9.5 (0-88)

* Significantly lower ($P < .05$) than seed content for both *Petromyscus* and *Aethomys*, using analysis of variance.

† Sum of leaf and stem for *Petromus* is significantly greater ($P < .05$) than for *Petromyscus* and *Aethomys*, using analysis of variance.

more seed, which is easier to digest. *Elephantulus*, an insectivore, has a caecum but it is relatively the smallest of the four species.

3.9 Activity patterns

Estimates of the time of capture for the different species were obtained by checking the traps frequently throughout the day, and occasionally during the night. On certain occasions, individuals were observed during the

TABLE 7: Relative proportions of stomach, small and large intestine, caecum and hindgut for Namib Desert rodents.

Relative length*	Petro- myscus	Aethomys	Petromus	Elephan- tulus
Stomach	14 %	11 %	5 %	8 %
Small & large Intestine	56 %	58 %	47 %	65 %
Caecum	16 %	15 %	31 %	9 %
Hindgut	30 %	31 %	48 %	27 %

* Relative length expressed as % of (stomach + small intestine + large intestine + hindgut). Caecum is not included in total length for this calculation.

day (notably *Petromus*), or the exact time of capture determined by hearing the trap shut. Data for estimates of time of capture, and times of observation, are summarised in Fig 8. *Petromus* are conspicuously active throughout the day, may be crepuscular, but do not appear to be active at night. *Petromyscus* are crepuscular (at dusk) and nocturnal. They are caught early in the evening rather than just before sunrise, and this is independent of whether the sky is moonlit early or late at night. *Aethomys* are primarily nocturnal, but were caught during the day on three occasions. On two of these occasions, the diurnal activity could not have been an artefact of having released the animal that same morning. *Aethomys* also were less commonly caught in the hours before dawn, being active more early in the evening. *Elephantulus* were caught at night and also observed at dusk and during the day.

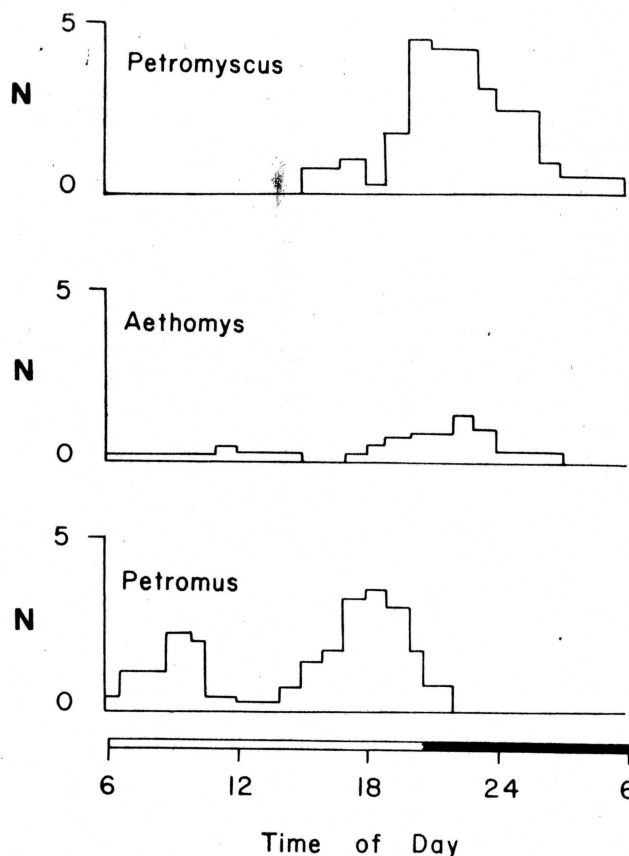


FIGURE 8: Temporal activity cycles of the three rodents. Ordinate is numbers of individuals captured per hour.

TABLE 8: Reproductive status of female and male rodents.

		April	June	Sept.	Nov.	Jan.	Feb.
Female							
<i>Petromyscus</i> ,	#	2	20	17	13	14	12
	% teats	0	35	35	54	43	83
	% vp	0	0	0	15	7	90
	% preg.	0	0	0	0	0	44
<i>Aethomys</i> ,	#	1	13	3	1	1	3
	% teats	0	8	33	0	100	100
	% vp	0	0	0	0	0	33
	% preg.	0	0	0	0	0	33
<i>Petromus</i> ,	#	1	1	2	3	4	0
	% vp	0	0	0	0	100	--
	% preg.	0	0	0	0	25	--
Male							
<i>Petromyscus</i> ,	#	2	10	14	12	12	9
	% dt	50	0	0	42	100	100
<i>Aethomys</i> ,	#	0	8	6	9	2	2
	% dt	--	0	0	67	100	50
<i>Petromus</i> ,	#	1	1	3	16	8	0
	% dt	0	0	0	13	19	--

is total number of rodents caught; % teats is number of females with teats; vp is perforate vagina or pregnant; preg. is pregnant; dt is descended testes.

3.10 Reproduction

Some male *Petromyscus* and *Aethomys* had descended testes in November, and all males had descended testes and prominent peri-anal flaps by January; testes of some individuals were descended in April (Table 8). The testes of *Petromus*, even when descended, were never so apparent as with the other species, and a much lower proportion (20 %) had visibly descended testes. *Elephantulus* have abdominal testes.

The numbers of female *Petromyscus* and *Aethomys* with teats tended to be greatest in January and February, but this does not provide a clear indicator of breeding. The lateral teats of *Petromus* were often difficult to see, and were not consistently noted. Whether the vagina was perforate or imperforate provides a more reliable indicator of breeding; the females were perforate primarily in January and February, which coincided with the sexual cycle of the males. Females with embryos were found in January (*Petromus*) and February (*Petromyscus*, *Aethomys*).

It appears that female and male *Petromyscus* and *Aethomys* become sexually active at about the time the fogs begin, but pregnancies do not occur until later. *Petromus*, which relies more upon grasses as a major portion of its diet, apparently breed slightly earlier than the other species.

Elephantulus may breed throughout the year, as the female was perforate on all occasions when captured (June, September, January). A juvenile *Elephantulus* was captured in April. *Elephantulus* males have abdominal testes, so whether they show a sexual cycle could not be determined.

4 DISCUSSION

The present study is concerned with the small mammal community found at Tumasberg, an isolated rocky outcrop in the gravel plains of the Namib Desert. A prime objective of the study was to investigate community structure, and determine how the small mammals partition the various habitats and limited food resources of Tumasberg in order to avoid excessive competition. The potential conflicts due to competition within a small mammal community would be exacerbated in a desert environment where low rainfall and low plant productivity would provide limited resources for the mammals.

The small mammal community of Tumasberg is composed almost entirely of *Petromyscus*, *Aethomys*, *Petromus* and *Elephantulus*, with rare occurrences of *Leggada* and *Gerbillurus*. Dassies are also a conspicuous faunal element in certain parts of Tumasberg, but were never noted on the trapping grid; red rock hare were occasionally observed on the grid. The three main rodent species of Tumasberg are very different in their taxonomy, and also have different geologic histories. *Petromus*, the sole genus of the unique family Petro-

myidae, appears to be an archaic element of the African mammal fauna (Meester, 1965). *Petromyscus*, a cricetid rodent, also appears to be an old group with few relatives in the southern African fauna. *Aethomys* is a murid, closely allied with the *Rattus* group, and would appear to be a recent faunal element in southern Africa. *Aethomys namaquensis* is extremely widespread throughout southern Africa and occupies a wide range of habitats, unlike the other species (*Petromyscus*, *Petromus*). *Elephantulus*, an elephant shrew (Insectivora: Menotyphla) is widespread in southern Africa, and is probably an old faunal element in the Namib.

A significant means for species to attain niche separation, particularly when having similar diets, is to select different sized food items (e.g. Brown and Lieberman, 1973; MacArthur, 1972). This is often reflected by non-overlapping body masses, and such separation in body mass is apparent for the Tumasberg mammals (Fig. 9). *Leggada* has a mean body mass of 6,8 g (range 5,0 – 9,0 g) in Botswana (Smithers, 1971); *Petromyscus* is 18,3 g (12,0 – 27,0 g); *Aethomys* is 36,8 g (15,0 – 55,0 g); *Elephantulus* is 50,7 g (28 – 58 g); *Petromus* is 155,0 g (103 – 210 g); red rock hare weigh about 2 175 g (Smithers, 1971); Dassies are about 3 890 g (Smithers, 1971). Such avoidance of body mass overlap provides potential niche separation for all species except *Aethomys* and *Elephantulus* through preferences for different size seeds, differing foraging strategies related to size, or differences in insect prey size which can be captured and subdued. The diets of the rodents were similar; all species appear to be opportunistic and omnivorous feeders, although *Petromus* consumes more grass than the other species, which consume more seed. The rodents are, therefore, partitioning the resources of Tumasberg through dietary preferences to some extent. However, such diet analyses do not indicate true dietary preferences, e.g. what type of seeds, or size, are preferred by different species, what type of insects and size are caught and eaten, what species of plants are preferred. *Elephantulus* is mainly insectivorous, and thus competes with all three rodents and particularly *Aethomys*. It is significant that *Elephantulus*, although overlapping in distribution to some extent with all three rodents, was negatively associated (i.e. avoided) *Aethomys*, and utilised the open, gravel areas which the other species strongly avoided.

Dassies and red rock hare are potential competitors, to some extent, with the smaller mammals. Dassies were not found on the trapping grid, but occurred near it, and coexisted with all other species nearby. Dassies would compete most directly with *Petromus*, but are also browsers in large bushes and acacia trees, and eat *Euphorbia* stems. Red rock hare were rarely seen on the grid, and appeared to feed in the more open areas, but not very far from the rocks.

The dietary preferences of small mammals are clearly reflected in the structure of their digestive systems. This is also apparent for the Namib species; *Petromus*, which eats significantly more plant stem and leaf

material than the other species, has a large caecum and is conspicuously coprophagous, both adaptations for a predominantly herbivorous diet.

It is theoretically possible for similar species to avoid direct competition by being active at different times of the day. However, the activity patterns of desert mammals are typically correlated with the daily temperature/insolation cycle so as to avoid the extreme temperatures. Even moderately rocky cover on Tumasberg does not provide protection against desiccating conditions or ameliorate ambient temperature, but the wide fluctuations of surface temperature are damped. *Petromyscus*, *Aethomys* and *Elephantulus* shelter from the extreme surface conditions for most of the day. Both rodent species probably also utilise aestivation (summer dormancy in response to heat and water deprivation) as a physiological means of avoiding unfavourably hot and dry conditions (see Withers, Louw and Henschel, in preparation). *Petromus*, although diurnal, appears to have a bimodal activity pattern, and avoids the extreme midday temperatures. *Petromus* do not appear to regulate body temperature precisely (personal observation; J. Henschel, personal communication). Such observations agree with the propensity of *Petromus* to sunbathe, but to avoid being active around midday.

Activity patterns could also reflect to some extent the foraging patterns of potential predators. Black eagles (*Aquila verreauxi*) which are active by day, prey on dassies at Tumasberg (personal observation) and probably also on *Petromus*. A number of other smaller raptorial birds were also observed at Tumasberg. Foxes, mongooses and jackals are also potential predators during the day and night. Owls also prey upon the small rodents at night.

It appears that temporal activity patterns are not an important factor in enabling the four small mammals to coexist at Tumasberg.

Examination of various aspects of distributional patterns of the small mammals show marked habitat partitioning. Individuals of all species had specific home ranges which in some cases were maintained over the year of observation. It is likely that male *Petromyscus* defend their home ranges against other males, whereas males tolerate the presence of females, as do other females. This is probably true also for *Aethomys*. The paucity of data for *Petromus* make interpretation hazardous, but it suggests female-female interaction, perhaps indicating a matriarchal social organization.

Association analysis of the presence/absence of the different species throughout the trapping grid indicated only one negative association, between *Aethomys* and *Elephantulus*. These species are the most likely to be in direct competition, since they are of similar sizes; *Elephantulus* is a specialised insectivore and *Aethomys* also eats significant amounts of insect material. It is therefore not surprising to find that these two species occupy different portions of the grid area. The multi-

variate regression analyses further suggest a lack of correlation in distribution of the three rodents, and a negative association of *Aethomys* and *Elephantulus*. This analysis also provided correlations of the rodent distributions with various plant species. Whether there are causal relationships here can only be determined by more detailed study of feeding preferences of the rodents, or perhaps by similar correlative studies in other areas of the Namib Desert where the rodent communities are different to that at Tumasberg.

Of the possible means of obtaining niche separation which have been considered here (selection of different food items by virtue of body size, or dietary preference, and temporal or spatial separation) none provides complete potential separation of the species. However, it is apparent that a combination of various facets of their ecology provides sufficient separation of the species to avoid competitive exclusion. Another important aspect in this regard which was not studied here is behavioural differences. The trapping studies provide evidence of interspecific aggression (between males) for *Petromyscus* and *Aethomys*, but no evidence for interspecific aggression. *Petromyscus* is timid and unaggressive, whereas *Aethomys* is highly aggressive and active. Shortridge (1934) reports that *Petromyscus* forages by creeping stealthily between boulders by night, unlike the more active *Aethomys*. *Petromus* clearly has some social organisation. They are usually seen in groups. Large individuals will utter warning calls to the rest of the group (personal observation; also, Roberts, 1951). Their maintenance of size classes possibly indicates social hierarchy. Their patterns of home ranges indicate perhaps a matriarchal social system. Such conclusions are, however, tentative, and further specific field studies are required in order to clarify these issues.

The life cycles of the small mammals at Tumasberg, like all other desert organisms, are closely associated with rainfall. An additional factor of some significance to the Namib Desert fauna is the advective fog which often extends more than 100 km from the coast. This fog is utilised by many of the insects and reptiles, which directly ingest the condensed water (Louw, 1972; Seely and Hamilton, 1976; Hamilton and Seely, 1976). The rodents also assimilate fog water, but it is not known whether they drink the water or eat succulent vegetation (Withers, Louw and Henschel, in preparation). *Petromyscus* and *Aethomys* showed signs of breeding activity as early as November, but no pregnancies were noted until February. It is clear that reproduction is limited to those periods after rain, but it is likely that fogs provide sufficient stimulus for attaining breeding condition. There appeared to be little regrowth of vegetation at Tumasberg after the fogs, but there was conspicuous growth of annuals and perennials after the rains. The females might not, however, come into oestrous until after the rains cause extensive growth of annuals and perennials. The physiological data of Withers, Louw and Henschel (in preparation) clearly show that *Petromyscus* and *Aethomys* uti-

lise fog precipitation. *Petromys* do not appear to use fog water, and are less dependent upon exogenous water in that they have lower water turnover rates than *Petromyscus* and *Aethomys*. Female *Petromys* were pregnant in January, before *Petromyscus* and *Aethomys*.

The main aspects of the ecology of the small mammals of Tumasberg (summarised in Table 9) do not generally conform to the demographic patterns of typical cricetid (*Petromyscus*), murid (*Aethomys*) and sciurid-like (*Petromys*) rodents (French et al., 1975). The numbers of litters born per female, per year, by *Petromyscus* and *Aethomys* at Tumasberg (probably one or two litters) are less than expected, as is the number of young born per litter (*Petromyscus*, 2 - 3; *Aethomys*, 2 - 5), for a "typical" cricetid (3,3 litters/year, 4 young/litter) or murid (3,3/year, 6,1/litter). The survival rate of *Aethomys* (57 % per month survive) is high for a murid whereas the survival rates for *Petromyscus* and *Petromys* are, as expected, even higher. The home ranges of the Namib species were smaller than expected, and the densities of *Aethomys* and *Petromys* were also lower than expected.

These differences in demography of the Namib Desert rodents can be attributed to the extreme xeric habitat in which they live, and the highly seasonal, low rainfall regime. The reproductive cycles of the rodents are clearly dependent upon the availability of water and plant productivity, both of which are of short duration. Hence, the number of litters which can be born per year are limited, perhaps to one or two. The low number of young born per litter, the small home ranges, and low densities reflect the low vegetation cover and annual productivity. The Namib rodents have apparently opted for a relatively stable, high-

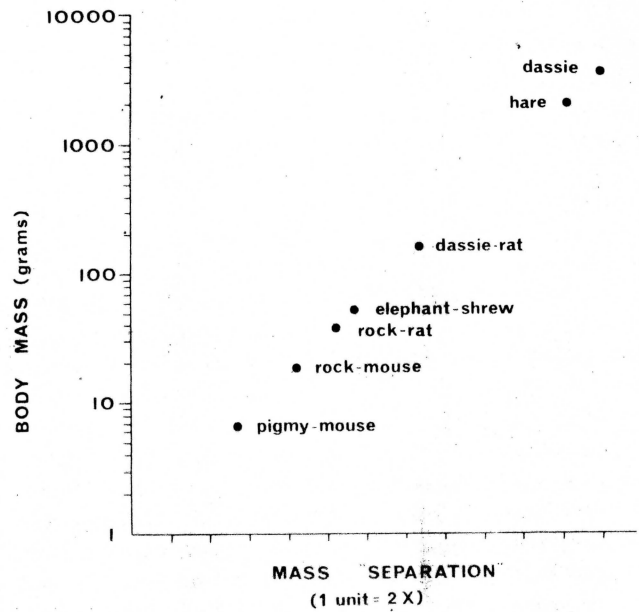


FIGURE 9: Representation of body mass distribution for Tumasberg small mammals. Ordinate is actual body mass on logarithmic scale; abscissa indicates 2 X increments in body mass, which is the approximate value conferring sufficient ecological separation in nature to minimise competition (MacArthur, 1972).

survival existence (k-selected) rather than high reproductive output and marked population fluctuations (r-selected), in response to the severity of their environment.

A further difference between the small mammal community at Tumasberg, and other desert rodent faunas, is the absence of specialised granivorous rodents in the Namib community. This might be due to the low, and sporadic, annual rainfall at Tumasberg, which

TABLE 9: Summary of demographic and ecological data for the four small mammals studied on Tumasberg.

				Reproduction			Survival		Home Range		Density	
	Mean body mass (g)	Diet	Seasonal	# lit- ters/yr.*	# per litter*	% fe- males† reprod.	Life expect. (mths)	Monthly survival rate	Area (hectare)	Max. dist. moved (m)	#/hec- tare	g/hec- tare
<i>Petromyscus</i>	18.3	omniv.	yes	1 or 2	2-3	>44 % (preg.) >90 % (v.p.)	6.6	0.9	0.27	<30-180 m	9.5	174
<i>Aethomys</i>	36.8	omniv.	yes	1 or 2	2-5	>33 % (preg.) >100 % (v.p.)	1.2	0.57	0.31	30-150 m	5.4	199
<i>Petromys</i>	155.0	omniv. Pred. grass	yes	1(?)	2-4	>25 % (preg.) >100 % (v.p.)	--	1.0	0.31	30-150 m	2.8	431
<i>Elephantulus</i>	50.7	insect.	no(?)	?	1-2	100 % (?)	--	--	>1.2	>240 m	0.4	18

* personal observations and/or Shortridge (1934)

† preg. = % females pregnant; v.p. = % females either pregnant or with perforate vagina.

could limit plant production in general, and specifically seed production. Furthermore, much of the vegetation at Tumasberg is comprised of large species such as *Euphorbia*, *Aloe* and *Commiphora* and annuals and perennials are less abundant; this could mean that a smaller proportion of the total plant productivity is diverted to seed production at Tumasberg compared to many other desert communities where annuals and perennials are more predominant. Thus, there might simply not be enough seed produced at Tumasberg to support a granivorous specialist, particularly as ants are also numerous and they are potential competitors with granivorous rodents.

The community structure and interactions of the species at Tumasberg are relatively clear. However, *Petromyscus* and *Petromus* are also common in similar-appearing rocky habitats, e.g. the Kuiseb Canyon and the numerous canyons entering the Kuiseb, but *Aethomys* and *Elephantulus* are conspicuously absent (personal observation; M. Griffin, personal communication; Stuart, 1975). No other species appear to replace *Aethomys* or *Elephantulus* in this canyon habitat (note that the distinctive "riverine" rodent community (Coetzee, 1969; Stuart, 1975) is strictly limited to the water course proper, and does not extend even to the canyon walls). A rock dormouse (*Graphiurus platyops*) was caught in Gorob Canyon in association with *Petromyscus* and *Petromus*, but this species is relatively uncommon. *Aethomys* is clearly a "generalist" rodent (both ecologically and physiologically), and its absence could be explained in any, or combinations, of the following way. *Aethomys*, as a recently invading species, might not have reached the canyon but this is unlikely as parts of the canyon are as close to Tumasberg, as Tumasberg is to some other inselbergs. *Graphiurus* might competitively exclude *Aethomys* from the canyon habitat. There may be subtle vegetation differences, or habitat differences, between Tumasberg and the canyon which are important to *Aethomys*. Perhaps the most likely explanation is that the lower rainfall regime of the canyon may exclude *Aethomys*, as it has higher water turnover rates than *Petromyscus* and *Petromus* (Withers, Louw and Henschel, in preparation). *Elephantulus*, an insectivore, might be excluded from the canyon habitats by virtue of its specialised diet. If the insect abundance was lower in the lower rainfall canyons, it, like *Aethomys*, would be excluded by *Petromyscus* and *Petromus*.

The small mammals of the Namib Desert, particularly the relict, endemic species, show remarkable ecological (and also physiological) adaptations to their extreme environment. There are clearly many further aspects pertaining to the ecology of the small mammals in rocky habitats of the Namib Desert which require investigation, as well as studies of other Namib species in different habitats such as the gravel plains and sand-dunes.

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