Micromammals from owl pellets in the Skeleton Coast Park, SWA/Namibia

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ABSTRACT

Remains of mammalian prey were extracted from pellets cast by *Asio capensis* (marsh owl) and *Tyto alba* (barn owl) at a number of sites in the Skeleton Coast Park and neighbouring Damaraland. Analysis of these remains provided information on micromammalian distribution and community structure. Evidence for population structure of *Gerbillurus paeba* and *G.* cf *setzeri* was also forthcoming.

CONTENTS

1 INTRODUCTION

Owl pellets were collected from a number of localities in the Skeleton Coast Park (SCP) and neighbouring Damaraland in Namibia during 1982 and 1983. Appendix 1 contains collectors' notes on the sites, dates of collection and owl involved, and grid references (Fig. 1). Owl pellets serve two useful purposes; they provide information not only on the diet of the owls concerned but also on the distribution and population structure of the prey species. In the present instance emphasis is placed on the latter, specifically the mammalian prey species. S.G. Braine is identifying the invertebrate prey remains and it is hoped that the avian and reptilian prey remains will be examined in due course.

Asio capensis, marsh owl, is known to have produced the pellets that were found in the Uniab River (Loc. 7) and the Ugab River (Loc. 11). No owl was seen in the vicinity of the two Hoanib River sites (Loc. 2) or at the Strathmore Tantelite Mine (Loc. 12) (see Appendix 1). However, on the basis of the pellets, it is possible that the former was *A. capensis* whereas the latter was almost certainly *Tyto alba,* barn owl. In all the other cases there is more or less secure reason to believe that the pellets were cast by *T. alba.*

2 MICROMAMMALIAN DISTRIBUTION

Figure 1 and table 1 show the distribution of micromammals in the region of the SCP, as evidence by the contents of the owl pellets. Three insectivore and nine rodent species are represented and, as might be expected, four of the latter are gerbils. *Gerbillurus paeba,* hairy-footed gerbil, and *G.* cf *setzeri,* Setzer's hairy-footed gerbil, both occur at nine of the twelve collecting localities but, with the notable exception of the Uniab River (Loc. 7), the latter species is generally

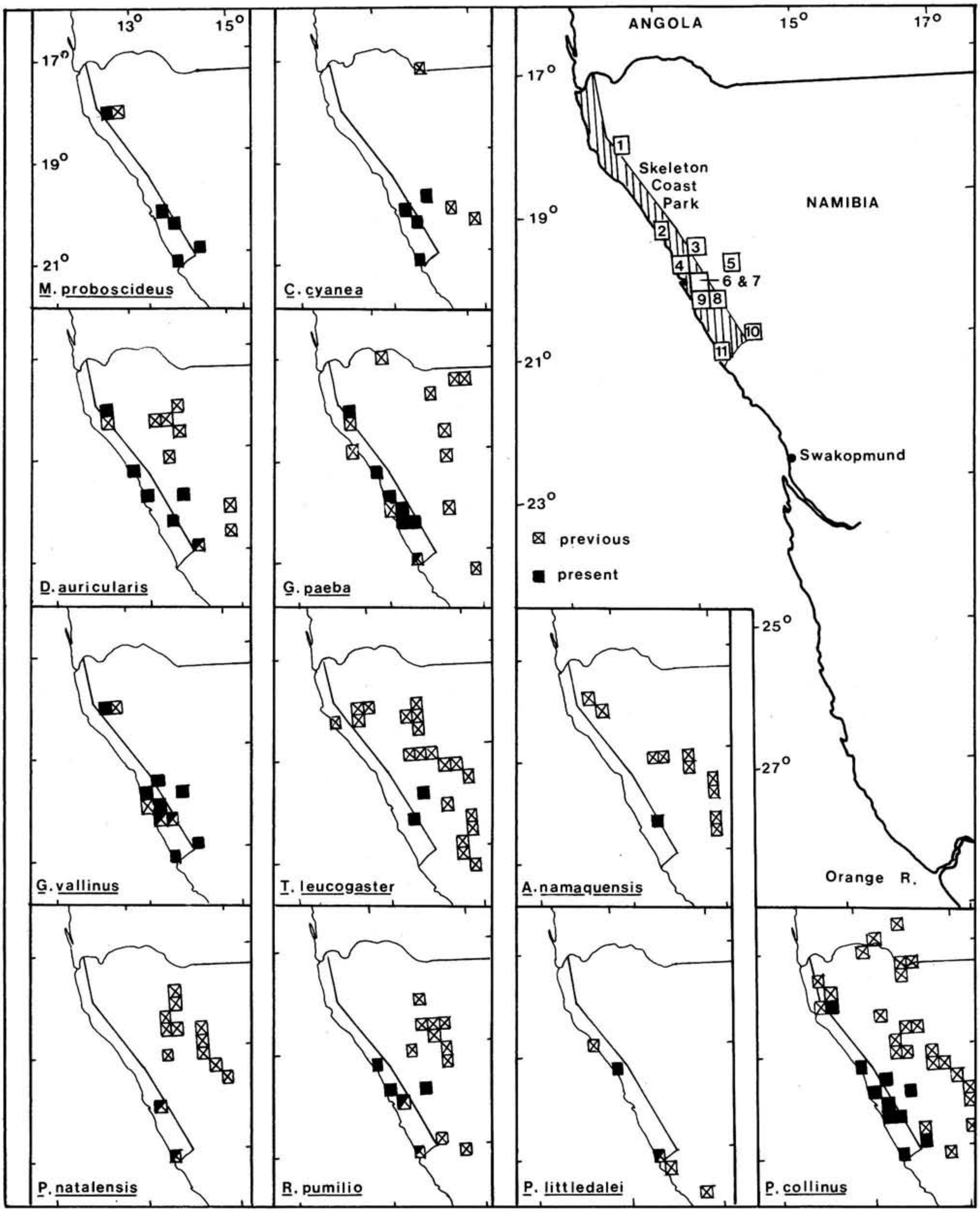

FIGURE 1: Position of collecting localities and distribution of micromammals, based on owl prey remains. Previous data from Davis 1974 and I.L. Rautenbach, pers. comm.

better represented. Here it should be noted that M. Griffin (pers. comm.) and C.G. Coetzee (ref. comm.) both state that the larger *Gerbillurus* of the area is *G. setzeri* and that, Smithers (1983) notwithstanding, *G. vallinus* does not occur north of the Swakop River. M. Griffin further states that there is a second species

TABLE 1: Minimum number of individual rodents and insectivores represented in *Tyto alba* (barn owl) and *Asio capensis* (marsh owl) pellets from various localities in and near the Skeleton Coast Park (SCP).

	Tyto alba								*A. capensis*		*Unknown*	
	1	3	4	5	6	8	9	10	7	11	2	12
INSECTIVORA												
28 *Elephantulus intufi* bushveld elephant shrew	—	—	—	?1	—	—	—	—	—	—	—	—
31 *Macroscelides proboscideus* short-eared elephant shrew	3	—	—	—	1	7	—	2	—	—	—	1
36 *Crocidura cyanea* reddish-grey musk shrew	—	—	—	1	—	2	—	—	1	3	—	—
RODENTIA												
215 *Desmodillus auricularis* short-tailed gerbil	13+?1	—	1	7	—	29	—	1	—	4	4	—
216 *Gerbillurus paeba* hairy-footed gerbil	7	—	3	—	1	1	3	—	218	11+?1	—	1
217 *Gerbillurus* cf *setzeri* Setzer's hairy-footed gerbil	125+?1	5	15	2+?2	18+?7	96+?1	1+?1	6	—	—	—	2
223 *Tatera leucogaster* bushveld gerbil	—	—	—	3	—	3	—	—	—	—	—	—
234 *Aethomys namaquensis* Namaqua rock mouse	—	—	—	—	—	4	—	—	—	—	—	—
245 *Praomys natalensis* multimammate mouse	—	—	—	—	1	—	—	—	1	43+?1	—	—
250 *Rhabdomys pumilio* striped mouse	—	—	2	5	—	—	—	—	6	1	3	—
267 *Parotomys littledalei* Littledale's whistling rat	—	—	—	—	—	—	—	—	6	1	—	—
270 *Petromyscus collinus* pygmy rock mouse	7	6	—	7	3	63	3+?1	3	—	3	—	—
	157	11	21	28	31	205	9	12	226	69	12	4

See Appendix 1 for collecting localities.
Species list is according to Swanepoel *et al.* 1980.

that is not yet distinguishable cranially from *G. setzeri*. In view of this fact, the species will here be referred to *G.* cf *setzeri*.

Desmodillus auricularis, short-tailed gerbil, was found at half the localities, with the highest number occurring at Bessiefontein (Loc. 8). *Tatera leucogaster,* bushveld gerbil, was restricted to Bessiefontein and Gobabis Spring (Loc. 5), both of which are inland sites. Of the remaining species, *Petromyscus collinus,* pygmy rock mouse, was recovered from most localities and represented a particularly high proportion of the mammalian prey fauna at Bessiefontein. *Macroscelides proboscideus,* short-tailed elephant shrew, and *Rhabdomys pumilio,* striped mouse, were found at just under half the localities and the remainder of the species occurred infrequently.

The present evidence has, in most cases, added to the known distribution of the species concerned. This is, however, most likely to be due more to the pattern of collecting than to any unexpected occurrences. This is suggested by the fact that there is consolidation rather than extension of the known ranges, as can be seen particularly in the case of *Petromyscus collinus.* The recovery of *Macroscelides proboscideus* and *Gerbillurus* cf *setzeri* from 1812Ab also confirms the northward limit of these species; *Desmodillus auricularis* and *Crocidura cyanea* are shown to occur rather closer to the coast than has previously been recorded.

The very high proportion of *Praomys natalensis,* multimammate mouse, at the Ugab River sites (Loc. 11) is noteworthy. Coetzee (1969: 32) has recorded the occurrence of this species in the well-vegetated parts of some river beds north of the Swakop. This is confirmed here by the recovery of single specimens from the Uniab River (Loc. 7) and its tributary the Obob (Loc. 6). In the Ugab samples, however, this species constitutes 63.7 % of the mammalian prey. There are possibly two main reasons for this somewhat unexpected situation. In the first place, the Ugab is one of four rivers in the region that flow, albeit seasonally, from the interior of Namibia (Coetzee 1969: 23), thus providing a dispersal route. The distinguishing feature of the lower Ugab River is the presence of a human settlement (the main gate of the SCP) and, moreover, evidence for past human settlement. This latter is attested by the remains of whale-bone huts close to the mouth of the Ugab (Kinahan & Kinahan 1984). *P. natalensis* are semi-commensal and it seems likley that their large numbers can be attributed to their association with human settlement. In this context it would be interesting to look for evidence of *P. natalensis* in the Huab River which also has its source in the interior but where there is no human settlement.

Since *Asio capensis* is approximately the same size as *Tyto alba* it is unlikely that any differences in prey items would be due to the capabilities of the two species. It could be argued reasonably that where such differences do exist they will be caused largely by real differences in the proportions of prey species in the landscape. One has, however, to bear in mind the possibility that different species of owl may exhibit preferences in their choice of prey and that ease of capture, or maximum return for energy expenditure, will affect their actions. Even with this in mind it would seem that, although both species of *Gerbillurus* may occur in any area, only one of them will be numerous, or preyed upon extensively by owls. Moreover, it is almost certainly fortuitous in terms of the raptor that in both of the collections ascribed to *A. capensis* the dominant, indeed the only, gerbil present is *G. paeba*. This is, however, a point that needs more observations before this can be stated with certainty.

3 EVIDENCE FOR COMMUNITY STRUCTURE

The main reason for collecting owl pellets was their potential as comparative material. The contents of accumulated owl pellets found in archaeological and palaeontological sites can be interpreted to provide information on past climates (Avery 1982). However, in order to do this it is necessary to have controls against which the fossil data can be assessed. This is the rationale behind examining the micromammalian prey remains in isolation. Clearly, in a modern ecological study one would include all the prey items. For comparison with the fossil material this holistic approach would be inappropriate because the fossil micromammalian fauna is used alone.

It is to be expected that a harsh (extreme and/or unpredictable) environment will be expressed in terms of low Shannon indices of general diversity (H) and, specifically, a high degree of dominance (c) by one or a few species, and by a low species richness (S) (Krebs 1978). These expectations are fully realised by the collections examined. Table 2 shows the diversity indices calculated for grouped samples based on bones from *Tyto alba* pellets from various areas in South Africa compared with the present samples from Namibia. It is noticeable that in Namibia the Goabis (Loc. 5) sample, although small, exhibits a different structure from that of the other samples. The reason for this is that Goabis is the only locality that lies within the 100 mm isohyet as well as being at a rather higher altitude than the other sites. If the Damaraland samples (Locs 3, 8 and 10, with or without 5) are grouped they have a general diversity index that is very similar to that for the SCP samples. The fact that the SCP samples were collected from in or near river beds probably explains this; it is to be expected that the diversity index for the desert proper would be much lower than either of these figures. It is of some interest to note that the lowest diversity index among the South African samples given here is that for the west coast. The collection was made just south of Lamberts Bay in an area of loose sand, open vegetation and relatively low rainfall, and the diversity would have been even lower had there not been a vlei and a hamlet in the vicinity.

TABLE 2: Aspects of micromammalian community structure reflected by grouped samples of owl prey remains.

Locality	N	S	H	c	e
SCP	519	9	1.390	0.336	0.633
Damaraland	256	10	1.419	0.318	0.616
Damaraland (excl. Goabis)	228	8	1.270	0.354	0.611
Goabis	28	7	1.756	0.191	0.902
West coast	162	14	1.606	0.336	0.609
Cedarberg Mts	991	21	2.240	0.159	0.736
Southwest coast	1360	24	2.715	0.079	0.854
South coast	542	15	1.729	0.319	0.639
Swartberg Mts	2053	24	2.467	0.115	0.776
East coast	327	13	2.086	0.150	0.813

N number of individuals
S number of species
H Shannon index of general diversity — $(P_i \log_e P_i)$
c index of dominance — $(n_i/N)^2 = p^2i$
e index of equitability $H/\log_e S$

The south coast sample, from Wilderness, is almost certainly anomalous, reflecting the apparent preference of the owls for *Otomys irroratus,* the vlei rat which is apparently abundant in this region, rather than the reality of the situation. It is, however, instructive to compare this situation with that at the Uniab River (Loc. 7). Here it is possible that the extremely low H (0.179) is due either to a preference for, or a plague of, *Gerbillurus paeba* (see below), or to the fact that the owls were eating relatively large quantities of birds, lizards and insects, none of which is taken into account in the calculation. Both samples make it clear that such biases may cause a range of diversity indices for a given area or type of environment. Context will, however, generally expose an anomaly and, moreover, if the anomalous results from different areas are compared they are likely to be quite as distinct as are the general results. These latter show that H for the other South African samples is considerably higher than those for the SCP and Damaraland; they indicate clearly the range that may be expected. In most cases dominance and equitability vary inversely, as would be expected, but it is evident that the correlation is not complete. A detailed study may therefore benefit from the separate examination of various aspects of diversity.

4 POPULATION STRUCTURE

There are three samples that are sufficiently large to allow an attempt at analysis of population structure. Two present populations of *Gerbillurus* cf *setzeri* (from Sechomib River Loc. 1 and Bessiefontein Loc. 8) and the third a population of *Gerbillurus paeba* (from Uniab River Loc. 7). The Sechomib site is some 250 km and 3° north of the other two sites which lie in relatively close proximity (see Fig. 1). This makes it possible to compare the effects on population structure of differences not only in species but also in location. As in the case of the analysis of community structure the reason for basing population analyses directly on owl pellet data is to allow comparison with material from archaeological sites. Rather than suggesting that owls provide an accurate census of the prey population, the analysis constitutes an exercise in assessing the accuracy of such data for environmental interpretation on a relative basis.

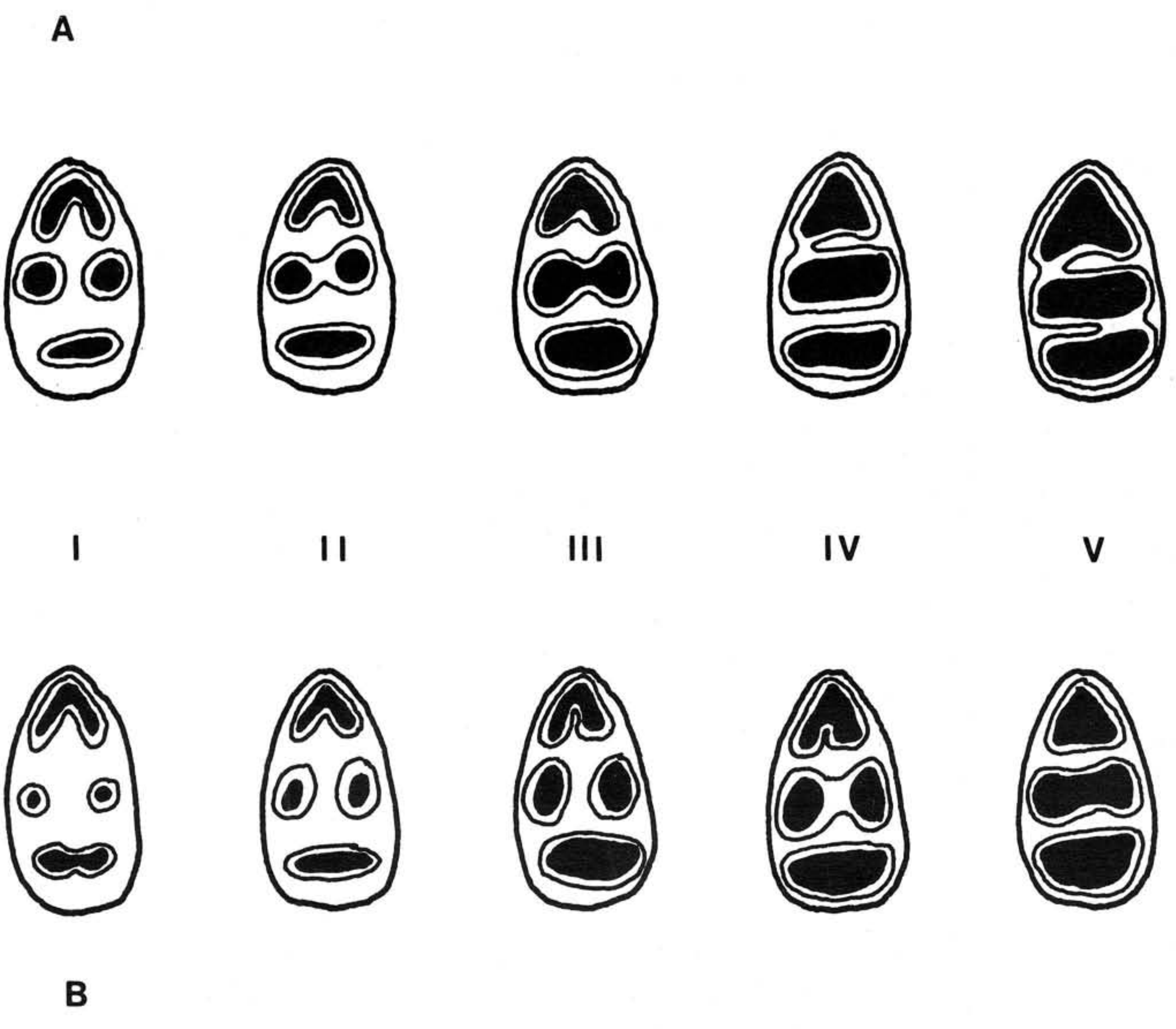

FIGURE 2: Age classes of *Gerbillurus paeba* (A) and *G. cf setzeri* (B), based on wear patterns of the lower first right molar.

In the absence of information on the age determination of *Gerbillurus,* or indeed their longevity, age classes were established on the basis of wear patterns of the lower first molar. Five categories were determined which were slightly different in the two species owing to minor differences in tooth morphology (Fig. 2). Table 4 shows the results of the analysis of the samples. In each case only the right lower first molars were examined in order to eliminate any possible duplication. (In some cases the lower right first molars could not be found which explains why the numbers of specimens given in Table 1 do not agree with those in Table 3.)

The results of the contingency tests (Table 4) show that in general there is a significant difference in the structure of the three samples. However, when pairs of samples were tested it became clear that the northern sample was significantly different from both of the southern samples which did not differ from each other. The Sechomib sample differs in that the youngest age class is much less well represented than it is in the other samples. At both the Uniab and Bessiefontein the owls were almost certainly taking advantage of a population explosion, as was suggested above. This explosion was presumably encouraged by the abnormally high rainfall experienced in the area during 1982 (R. Loutit, pers. comm.). It will be important to determine the nature of the population structure in years of lower rainfall, if indeed there are sufficient gerbils present to attract the owls to the area. It could be postulated that the pattern will be closer to that found at Sechomib since it may be that this pattern represents a more stable population. The differences between Sechomib and the more southerly sites may be seasonal since the former was collected some seven months after that from the Uniab (collection date of the Bessiefontein material was not given). However, the work of Nel & Rautenbach (1975) indicates that fluctuations in populations of *G. paeba* are independent of the time of the year. In Botswana the same species was recorded as breeding throughout the year (Smithers 1971). It seems much more likely that the *Gerbillurus* populations are responding to a change in the environment, in this case variation in the food supply caused by fluctuations in the rainfall.

It is of some interest to note that, on the basis of the present evidence, *Gerbillurus paeba* appears to have a rather different mortality rate from *G.* cf *setzeri* (Table

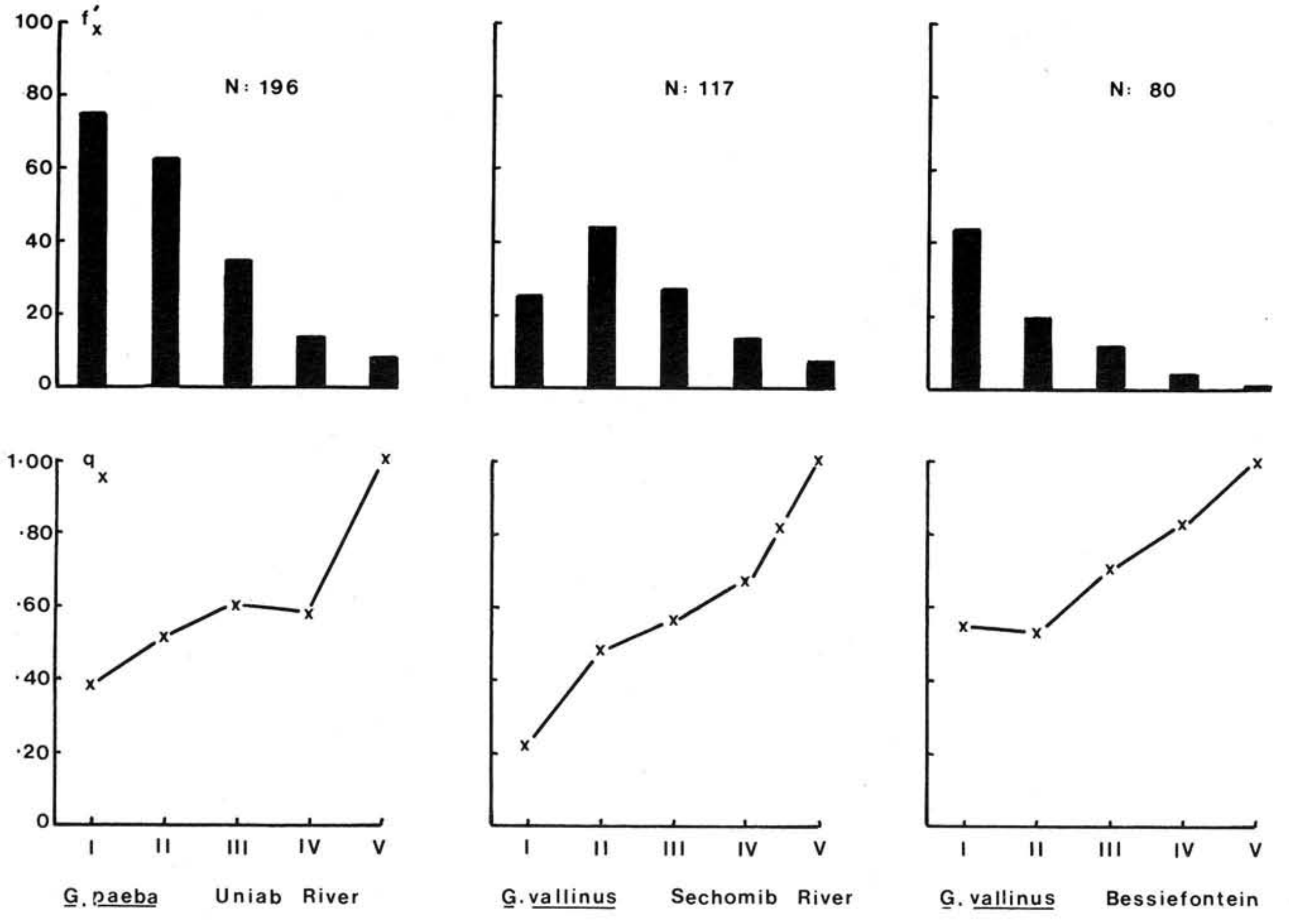

FIGURE 3: Frequency of ages at death (f'_x) and mortality rate (q_x) in three populations of *Gerbillurus,* based on owl prey remains.

TABLE 3: Dynamic life tables for three populations of *Gerbillurus* based on owl prey remains from the Skeleton Coast Park.

G. paeba (Uniab River)

Age class	f'_x	d_x	l_x	q_x
I	75	0.38	1.00	0.38
II	63	0.32	0.62	0.52
III	35	0.18	0.30	0.60
IV	14	0.07	0.12	0.58
V	9	0.05	0.05	1.00
N = 196				

G cf *setzeri* (Sechomib River)

Age class	f'_x	d_x	l_x	q_x
I	25	0.21	1.00	0.21
II	44	0.38	0.79	0.48
III	27	0.23	0.41	0.56
IV	14	0.12	0.18	0.67
V	7	0.06	0.06	1.00
N = 117				

G. cf *setzeri* (Bessiefontein)

Age class	f'_x	d_x	l_x	q_x
I	44	0.55	1.00	0.55
II	19	0.24	0.45	0.53
III	12	0.15	0.21	0.71
IV	4	0.05	0.06	0.83
V	1	0.01	0.01	1.00
N = 80				

f'_x — frequency of ages at death
d_x — probability of dying
l_x — survivorship
q_x — mortality rate

TABLE 4: Results of contingency tests of the probability of the null hypothesis that the samples were drawn from populations of indistinguishable structure. Values of P less than 0.05 are taken to show that the null hypothesis is untrue.

G. paeba Loc. 7 *G.* cf *setzeri* Loc. 1 *G.* cf *setzeri* Loc. 8	x^2 25.4735: df 8: P .01>.001
G. paeba Loc. 7 *G.* cf *setzeri* Loc. 1	x^2 10.3779: df 4: P .05>.02
G. paeba Loc. 7 *G.* cf *setzeri* Loc. 8	x^2 7.4605: df 4: P. 1
G. cf *setzeri* Loc. 1 *G.* cf *setzeri* Loc. 8	^{2} 24.9067: df 4: P .01>.001

df — degrees of freedom

3; Fig. 3). This is in spite of the fact that the structure of the two *G.* cf *setzeri* samples is different. In *G. paeba* the mortality rate of the three central age classes is relatively stable between 0.50 and 0.60, whereas in *G.* cf *setzeri* there is a more or less steady increase in the rate from the youngest to the oldest age class. More samples will show whether or not this pattern persists; if it does the information could be useful for palaeoenvironmental interpretation. Changes in patterns of mortality rate may arguably result from changing fitness to the environment in which the species is living (Avery 1984) and it is therefore essential to know the pattern for the species when it is well-adapted.

5 CONCLUSIONS

The potential of owl pellets for providing information on modern micromammals, as well as comparative data for palaeoecology, has already been established (Avery 1977, 1982). The value of the present data lies not so much in confirming this potential as in providing information on a different area and different species. Previous studies have largely concerned the temperate regions of the Cape Province of South Africa (Avery 1982). The characterisation of community structure in a harsh environment is particularly useful for palaeoecological controls. It provides some evidence of the possible range of Shannon diversity indices that may be expected, as well as a possible model for more xeric environments elsewhere in the past. The population data of the *Gerbillurus* spp. form part of a bank of such information for future use. Being able to check the differences between sibling species as well as the same species in different environments is an added bonus. In terms of modern studies the present data provide information for a region in which little work has hitherto been conducted on the micromammals.

It is clear, however, that the present report provides only preliminary information. In general, data need collecting over a number of years in order to assess the extent of the variation present. This is true of any area but it is particularly important in deserts and semi-deserts which are characterised by exceptionally unpredictable and extreme conditions. It is anticipated, therefore, that only in a few years may it become possible to begin answering some of the questions raised by this study.

6 ACKNOWLEDGEMENTS

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Appendix 1: Gazetteer of collecting localities, with collectors' notes.

1. Barn owl pellets collected July 1983 ± 8 km SW of Orupembe in Sechomib River by S.G. Braine. (1812Ba: 18°14'S 12°32'E)

2a. Hoanib River, due E of dunefield at Auses in rocky outcrops. No sitings of owls. Collected 24 January 1983 by R. Loutit. (1912 Bd: 19°26'S 12°46'E)

2b. Hoanib floodplain, S side at krantz due E of dunes. Owl species unknown. Collected by R. Loutit on 24 January 1983. (1912Bd)

3. Hunkab River 12—13 km W of Hunkab spring in Damaraland, ie ± 3 km E of SCP boundary. Recovered from krantz on S bank. Sitings of owls nil, but barn owls seen here in August 1982 by B.D. Loutit & M.K. Seely. Collected 25 January 1983 by R. Loutit and S.G. Braine. (1913Cb: 19°36'S 13°16'E)

4. River due S of Kharu-Gaiseb River, 4 km, due E of dunefield ie 20 km E of sea. First located August 1982 by S.G. Braine; collected 28 January 1983 by S.G. Braine. Barn owl sited on evening of 28 January 1983 near locality; also recorded here by B.D. Loutit and M.K. Seely in July/August 1982. (1913Cc: approx. 19°55'S 13°11'E)

5. Goabis spring on Uniab River, grid reference 1913Dd, Damaraland. Collected 31 March 1983. *Tyto alba.* (19°55'S 13°50'E)

6a. Obob River ± 5 km inside SCP from eastern boundary in Obob River. Recovered from below krantz near spring. Barn owl recorded here on 12 January 1983 by R. Loutit and J. Paterson. Collected on 28 January 1983 by S.G. Braine and R. Loutit. (2013Ab: 20°01'S 13°24'E)

6b. Obob River 6 km SW of first locality at spring area. Collected by R. Loutit on 28 January 1983. Thought to be barn owl. (2013Ab: 20°04'S 13°24'E)

7a. Uniab R. delta on *Scirpus* hummocks in vicinity of hyaena den, ± 10 km inland. Collected on 8 December 1982 by G. Avery, D.M. Avery and R. Loutit. (2013Ab: 20°10'S 13°16'E)

7b. Uniab R. delta in *Scirpus* 0.6 km due W of old hyaena den. Collected by R. Loutit on 21 January 1983. (2013Ab: 20°19'S 10°16'E)

8. Bessiefontein, about 14 km E of the Springbokwater gate of the SCP. Barn owl. Collected by J. Paterson. (2013Bd: 20°19'S 13°45'E)

9. Koichab River, in canyon ± 20 km (? inland). Suspected barn owl but no positive sitings of any owl species. Collected on 27 January 1983 by R. Loutit. (2013Ad: 20°26'S 13°26'E)

10a. Gai-As, Damaraland. Grid reference 2014Cc. Collected on 4 December 1982. (20°46'S 14°01'E)

10b. Gai-As, 10 km east. Loose material, thought to be from owl pellets, collected on 19 November 1982 by K.P. Erb. (2014C: 20°46'S 14°07'E)

11a. Ugab River, 1.5 km W of road in dense *Sporobolus* grass and *Scirpus,* on S bank above watercourse near reeds. Marsh owl flushed. Collected by R. Loutit on 23 January 1982. (2113Ba: 21°09'S 13°39'E)

11b. Ugab River mouth. Marsh owl pellets collected by R. Loutit on 7 January 1983. (2113Ba: 21°14'S 13°36'E)

11c. Ugab River in vicinity of nest site. Marsh owl pellets collected in March 1983. (2113Ba)

11d. Ugab River. Marsh owl pellets collected on 9 April 1983. (2113Ba)

11e. Ugab River, 250 m E of nest. Marsh owl pellets collected on 8 May 1983 by R. Loutit. (2113Ba)

11f. Ugab River, saltzputz, grid reference 2113Bb. *Tyto alba.* Collected on 26 May 1983. (21°05'S 13°26'E)

11g. Ugab River, roost sites of subadult and adult birds ± 90—100 m from nest. Marsh owl pellets collected by R. Loutit on 4 June 1983. (2113Ba)

11h. Ugab River, in main river bed ± 250 m NW of nest site. Marsh owl pellets collected on 17 June 1983. (2113Ba)

12. Strathmore Tantelite Mine, 1 km W of mine and ± 10 km S of Ugabmond. Collected by S.G. Braine on 21 January 1982. (2113Ba: 21°13'S 13°42'E)