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An investigation of the macro- and micro-environments of four *Gerbillurus* species

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G. paeba
tytonis
setzeri
vallinus

June 86
Mar 87

The micro- and macro-environments of *Gerbillurus paeba, G. setzeri, G. tytonis* and *G. vallinus* are described, as detailed information about habitat and environment are essential for an understanding of the physiological tolerances and adaptations of these arid zone inhabitants. The burrows provide a stable milieu where the animals remain inactive diurnally to avoid the harsh surface environment during the day.

INTRODUCTION

Detailed knowledge of the macro-environments of the four *Gerbillurus* species, *G. paeba paeba, G. tytonis, G. setzeri* and *G. vallinus,* is essential for an understanding of their physiological tolerances and adaptations. Seasonal and circadian temperature changes, precipitation, soil types and vegetation analysis, together with a description of each species' micro-environment should be included in such descriptions. Since the investigation of the micro-environment of *Dipodomys spectabilis* and *D. merriami* (Schmidt- Nielson *et al.* 1950) and their relation to evaporative water loss, few studies (Kay 1977) have measured the temperature and humidity conditions to which desert rodents are exposed. Bolwig (1958) examined the microclimate of small mammals of the Kalahari, including *G. paeba.* He found that the temperature in the burrows was probably about 26°C despite great diurnal variations in surface temperatures. In addition the surface humidity varied greatly compared to the near saturation levels in the burrows.

Detailed descriptions of the habits and environment of study animals are required if the biological significance of trends observed in the laboratory are to be determined meaningfully. This applies particularly to the understanding of water budgets and temperature relations of arid zone inhabitants.

The *Gerbillurus* species investigated in this study are nocturnally-active, deserticolous, fossorially-diurnal rodents. Therefore, the primary aim of this study was to measure the micro-environmental parameters of the burrow in conjunction with the surface climate, particularly at night. An assessment of the environmental conditions that the gerbils experience in a xeric macro-environment as well as in their micro-environment is fundamental for further investigation of the physiological adaptations of these animals. Secondly, a description of the various burrow structures and the degree of food caching is basic to understanding the social (Dempster 1987) and foraging behaviour (Boyer 1988) of these gerbils.

Distribution and habitat preferences

The distributions of the *Gerbillurus* species referred to in this paper are shown in Fig. 1. *Gerbillurus paeba paeba* (A. Smith 1936) is confined mainly to the arid areas from south western Angola to the Cape. Isolated populations occur in the northern Namib, northern Transvaal and in the sand dunes near Port Elizabeth (De Graaff 1981 , Smithers 1983). In the Kalahari, they are absent or scarce on the calcrete riverbanks, raised plateau, or pans where fine soil predominates but are found in the other grades of sand, particularly that of dune slopes and dune crests (Nel & Rautenbach 1975).

Gerbillurus tytonis (Bauer & Niethammer 1960) is found only on the shifting red sand dunes of the Namib Desert, South West Africa (De Graaff 1981, Smithers 1983). *Gerbillurus vallinus vallinus* (Thomas 1918) occurs from north-western Cape to the lower Orange River (Smithers 1983, Erasmus pers. comm.), particularly on the gravel flats. *Gerbillurus setzeri* (Schlitter 1973) occupies the gravel plains, generally north of the Kuiseb River (Smithers 1983), although they have been trapped south of the Kuiseb River at Cha-ré (M. Griffin, pers. comm.).

Description of the southern African arid ecosystem

The regions where the four *Gerbillurus* species studied here occur, fall within the arid zone of southern Africa and are characterised by rain-

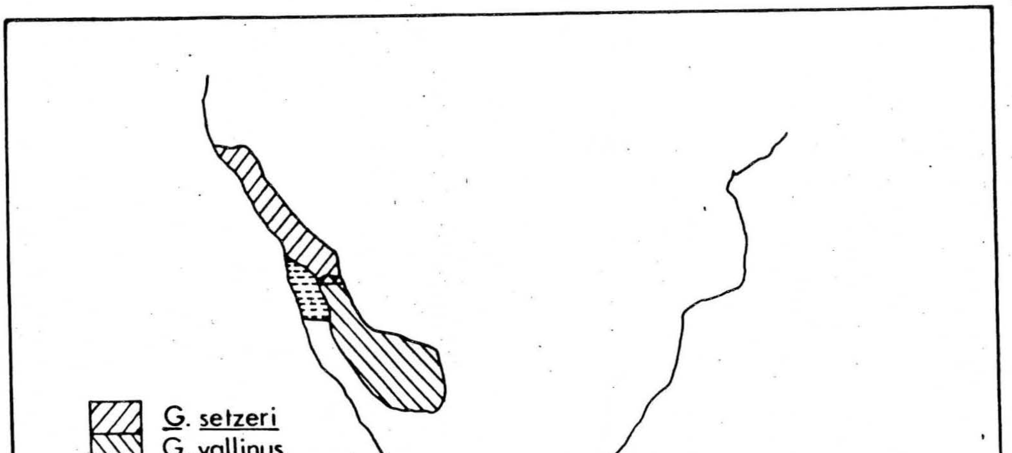


Figure 1. The distribution of *Gerbillurus* species in southern Africa.

fall of less than 250 mm per annum. The region is described by Leistner (1979), McGinnies *et al.* (1977), Robinson & Seely (1980), Lancaster *et al.* (1984) and Seely (1987) and consists of four areas. Briefly:

a) the Namib, which receives less than 125mm of rain annually. The Namib has a dry central strip with the northern boundary receiving summer rains. In the south it merges into the less extreme desert which has winter rains. This zone has a high occurence of advective fog along the coast caused by the cold Benguela current. Fog is an important alternative source of moisture, increasing the humidity along the coast. There is a steep climatic gradient from the coast inland as the average humidity decreases sharply while temperature increases rapidly. The zone 30 to 60 km inland is the most extreme climatic zone as fog and high humidity frequently occur in the morning and disappear before noon. The northern area is predominantly gravel flats with scattered sand accumulations and rocky outcrops of hills or mountains. Two major dune-fields occur in the Namib. The larger southern dunes lie between the Orange and Kuiseb Rivers while the northern dune-field extends from Torra Bay to the Curoca River in Angola. Three major types of dunes, transverse, linear and star, are common. The Namib has scanty vegetation, with the exception of the river valleys including the wide flood plain of the Kuiseb River, where riverine vegetation occurs.

(b) the Pro-Namib, which merges into the western escarpment zone, has less severe arid conditions.

(c) the Kalahari (which merges with the Namib in southern SWA/ Namibia). The northern area has neither the climate nor the vegetation of a true desert system but lacks surface water. South of 22° latitude to the Orange River the Kalahari is more truly desert. Rainfall, which occurs in summer, is low and unpredictable. The area receives on average less than 255 mm annual rainfall and experiences high temperatures and low humidities (Mills 1981). It is predominantly a sand dune system supporting small trees, bushes and grasses. Calcrete beds underlying the dunes are exposed in valleys, around pans and along riverbeds.

(d) the upper Karoo subdesert, which extends south of the Orange River. Rocky outcrops and table mountains arise abruptly from the stony to sandy plains. The area receives 125 mm to 250 mm rain per annum. Here the main precipitation is in the form of convectional showers during the summer and winter and is sufficient to support low succulent shrubs. In the eastern part of the southern African arid region rainfall variability is 25–30% and rapidly increases westwards.

METHODS

Burrow temperature and humidity

The temperatures and relative humidities of burrows were measured during field trips to South West Africa/Namibia and the northern Cape in June 1986 and March 1987. The study sites were at Gobabeb (23° 34′ S, 15° 03′ E), Rössing, (22° 24′ S, 14° 59′ E), the Swakop River near its mouth (22° 42′ S, 14° 31′ E) and Lemans Holte farm, Kenhardt (29° 38′ S, 21° 59′ E). A temperature recorder (U.N.P., Electronics Dept.), with multiple probes accurate to 1.0°C and a 24h printout, was used to monitor surface and burrow temperatures. Probes were inserted into burrows at depths greater than 200 mm from the burrow entrance. Burrow humidity was measured by using a Lovibond chemical indicator method. Lengths of rubber tubing (15 mm diameter) were used, with stoppers 50 mm from the one end. A strip of cobalt thiocyanate paper was placed at this end. A fine (2 mm) gauze mesh prevented the paper falling out or sand entering. The end containing the cobalt thiocyanate paper was positioned in burrows at depths of 200 mm or more from the soil surface, for hourly periods at random times during the day. The paper was examined immediately on removal from the burrow using a Lovibond Comparator to determine the relative-humidity. The method was tested and verified at the Gobabeb Weather Station and in the laboratory using a wet and dry bulb thermometer with precision of 5% R.H.

Burrow description

Prior to excavation the general locality, surroundings and position of burrows were noted together with the number of entrances and the compass direction that each faced. During excavation the dimensions, direction, depth and the form of the burrow were recorded and later drawn to scale. All food caches and nests were collected.

Weather data

Climatological data including the maximum and minimum daily temperatures, soil temperatures at different depths (50 mm, 100 mm, 200 mm, 300 mm, 600 mm and 1200 mm), the amount of fog and precipitation, and the percent relative humidity at set times (08h00, 14h00 and 20h00) during the day were collected from the First Order Weather Station at Gobabeb. Further meteorological information was obtained from the 'Climate of southern Africa' (Weather Bureau 1986). As temperature and rainfall separate climate poorly, Thornwaite's moisture index, based on humidity and aridity indices (Poynton 1971) (Fig. 2) was used.

RESULTS

Macro- and micro-climate

The macro-environment climatic data including the minimum and maximum temperatures, the relative humidity at 08h00, 14h00, 20h00, the amount of precipitation and/or fog, and the soil temperatures at depths of 0.05 m to 1.2 m

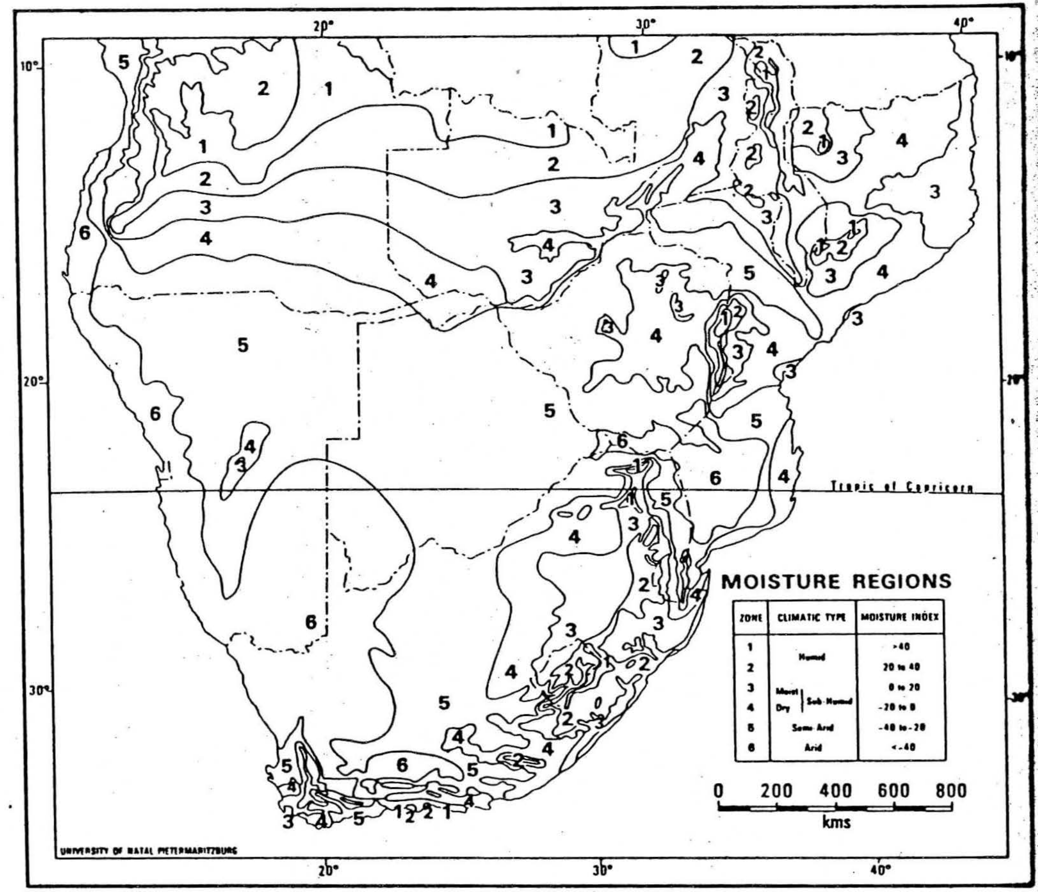


Figure 2. Moisture regions after Poyton (1972).

for the months when field work was done at Gobabeb are shown in Table 1. Analysis of variance for each parameter was applied to determine any difference between means among months. June 1986 had significantly lower minimum and maximum temperatures ($P < 0.05$) compared to March 1987. The relative humidity at 08h00 was significantly higher for June ($P < 0.05$) than March. However, at 14h00 and 20h00 there were no significant differences between months. During June the soil temperature at different depths was also significantly different ($P < 0.05$).

Figures 3 to 6 show the change in burrow temperature with time compared to surface temperatures. Burrow temperatures fluctuated little compared to the large surface temperature variation.

Table 2 gives the mean burrow temperature and the ranges of burrow and sand surface temperatures for each species. The burrow temperatures of the four species were not significantly different (Anova, $P < 0.05$). The range in surface temperatures was greater for the gravel plain species, *G. vallinus* and *G. setzeri*.

The relative-humidity measurements of burrows, at various times during the day, are shown in Figure 7. The humidity of burrows was significantly higher in the early morning and was affected by the presence of fog or cloudy conditions.

Thornwaite's moisture index values for the major areas where the hairy-footed gerbils occur are <-40 (zone 6) and -40 to -20 (zone 5) (Poynton 1971). The limits of the major 5 and 6 zones are similar to the distribution limits of the more widely distributed *G. paeba paeba* (Figs 1 and 2). However, the distribution is further limited by the requirement of sandy soils.

Table 1. Climatic data collected (mean and range) at the Gobabeb weather station for the periods when field work were done there.

		Nov '85	June '86	March '87
Monthly Temperature (°C)	Maximum	32.9 (22.7–43.6)	28.0 (18.9–35.9)	33.0 (28.3–38.1)
	Minimum	13.8 (08.3–25.0)	11.9 (06.8–19.1)	15.2 (09.1–22.8)
Relative Humidity (%)	08h00	75.0 (47.0–97.0)	52.6 (15.0–97.0)	73.7 (28.0–100)
	14h00	28.6 (11.0–43.0)	24.6 (07.0–69.0)	27.3 (14.0–41.0)
	20h00	39.2 (19.0–66.0)	43.8 (11.0–98.0)	32.4 (10.0–54.0)
Fog (litres)	Total	3.26	2.45	1.85
Soil Temperatures at various depths (°C)	50 mm	21.25 (15.4–31.0)	11.06 (06.1–17.9)	19.79 (16.2–27.0)
	100 mm	24.29 (19.8–30.6)	17.41 (14.2–21.1)	25.58 (21.9–31.2)
	200 mm	28.99 (25.3–35.2)	21.25 (19.5–24.0)	29.86 (27.3–33.4)
	300 mm	30.02 (27.3–33.7)	22.87 (21.8–25.3)	31.10 (29.1–33.8)
	600 mm	28.60 (27.0–30.4)	24.88 (20.7–26.9)	30.58 (29.8–31.7)
	1200 mm	27.90 (27.3–29.0)	26.64 (25.9–29.0)	30.03 (29.7–30.5)

Table 2. Surface and burrow temperatures of four *Gerbillurus* species during March 1987.

Species	burrow No.	Temperature (°C) burrow $\bar{x}$	SE	surface range	Locality
G. tytonis	1	30.7	1.7	13.1–33.0	Red dunes Gobabeb
	2	31.1	1.2		
G. paeba	1	24.4	2.2	15.8–28.4	Riverbed Swakopmund
	2	22.9	0.3		
G. vallinus	1	26.4	0.8	13.6–39.6	Gravel plains Kenhardt
	2	26.5	0.8		
G. setzeri	1	27.6	1.20	10.0–>40	Gravel plains Gobabeb
	2	26.7	1.64		
	3	28.4	0.92		
	4	28.2	0.30		
	5	29.4	1.09	11.4–38.9	Gravel plains Rossing
	6	27.5	2.87		

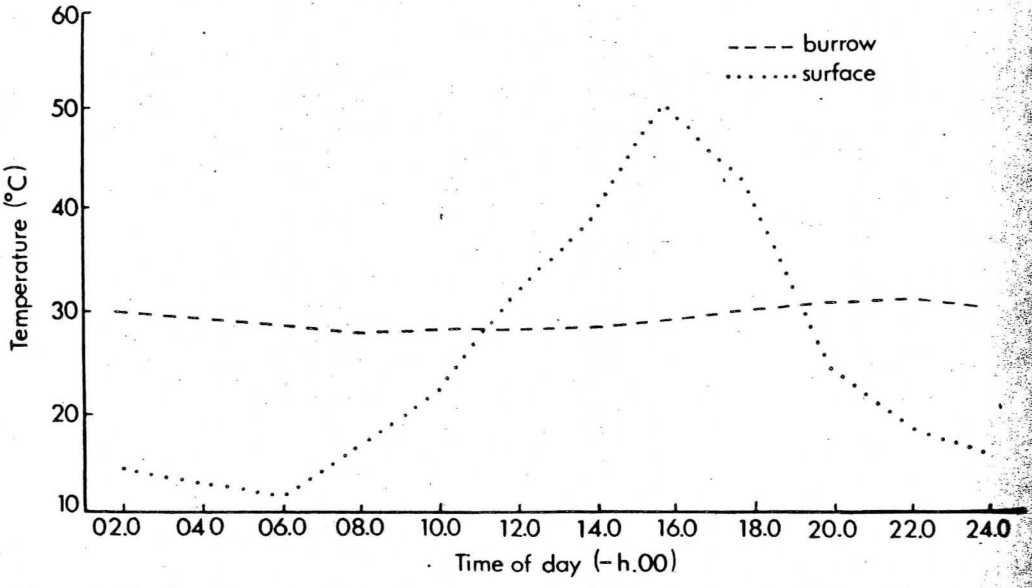


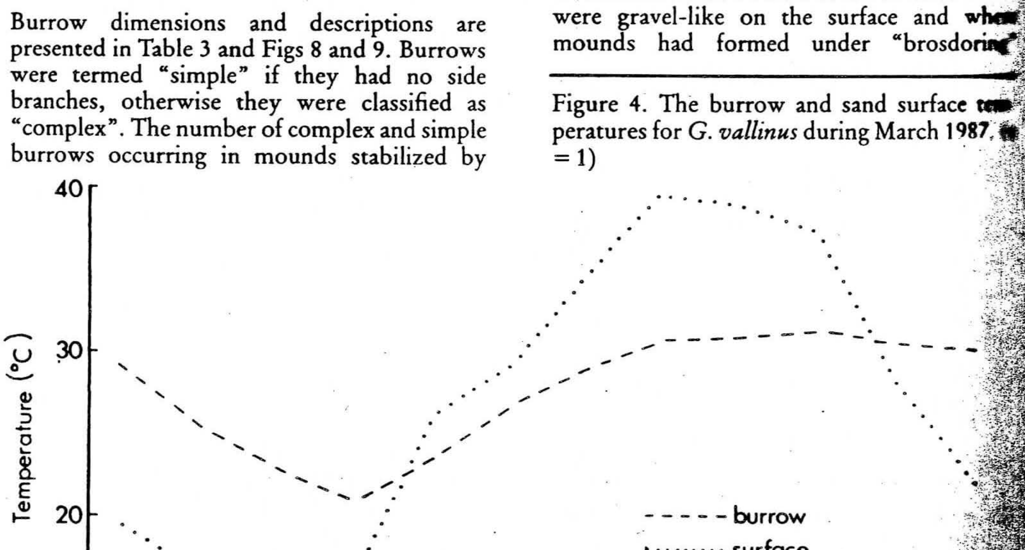
Figure 3. The burrow and sand surface temperatures for *G. setzeri* during March 1987. (n = 1)

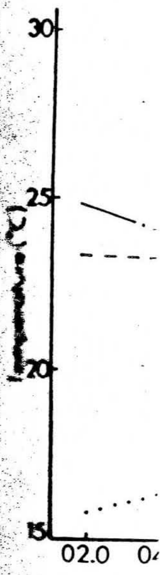
Burrow description

Burrow dimensions and descriptions are presented in Table 3 and Figs 8 and 9. Burrows were termed "simple" if they had no side branches, otherwise they were classified as "complex". The number of complex and simple burrows occurring in mounds stabilized by vegetation is shown in Table 4. The tunnel diameter of each burrow was fairly uniform but some areas of the tunnels were slightly enlarged.

G. vallinus burrows were found in areas which were gravel-like on the surface and where mounds had formed under "brosdoring"

Figure 4. The burrow and sand surface temperatures for *G. vallinus* during March 1987. (n = 1)





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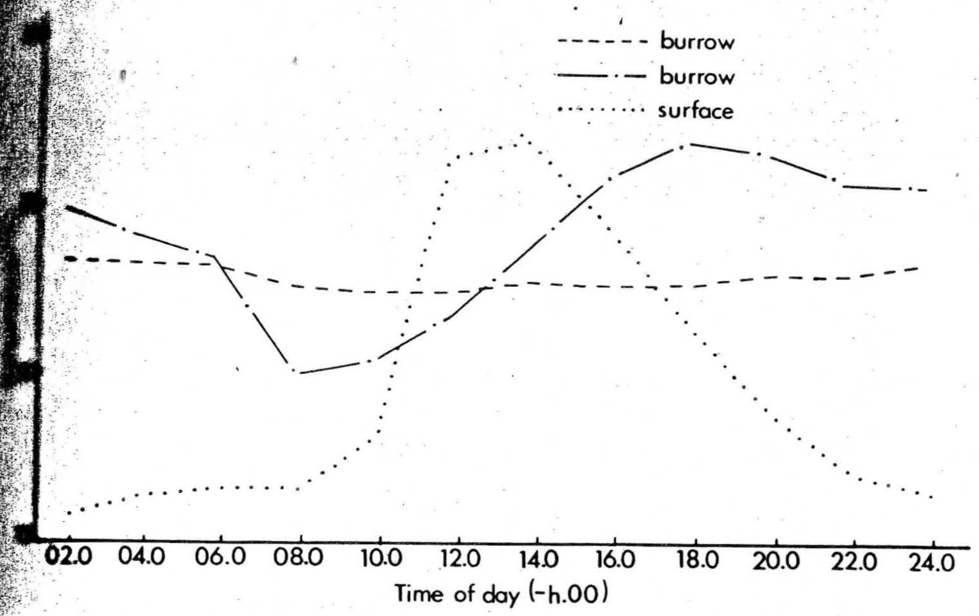

Figure 5. The burrow and sand surface temperatures for *G. p. paeba* during March 1987. (n = 2)

bushes, *Phaeoptilum spinosum*. The burrows of *G. setzeri* occurred in dry river washes where the surface soil was loose and gravelly, although subsurface soil was compact and fine. [illegible]-six percent of *G. tytonis* burrows occurred in sand mounds that were always stabilized by vegetation, either *Trianthema hereroensis* or *Stipagrostis sabulicola*.

The identity of the inhabitants of burrows was presumed from trapping results. *G. tytonis*, *G. setzeri* and *G. paeba paeba* were the only species caught in the areas where their respective burrows were excavated. *Macroscelides proboscideus* and *G. p. paeba* were trapped in the vicinity of *G. vallinus* burrows.

Simple burrows constituted 82% of all *G. paeba paeba* burrows and had a single entrance leading to a blind-ending tube which was occasionally broadened, forming a cavern-like area. Complex burrows constituted 56%, 90% and 75% for *G. tytonis*, *G. setzeri* and *G. vallinus*, respectively. *G. setzeri* and *G. vallinus* burrows had more side branches in complex burrows than *G. tytonis*, while simple burrows of these species had a number of bends. *G. setzeri* had burrows with the greatest total length and the greatest number of burrow entrances (see Fig. 8).

Food caches and nests

The nest materials and food items found in the *Gerbillurus* burrows are shown in Table 5. Two burrows of *G. paeba* had large quantities of the fruits of *Zygophyllum stapffi* stored in them. One cache was moist and smelt of urine. Food caches consisting of seeds and grass stored in a specific chamber-like area of the burrow were rare (< 5% for all species). However, the burrows had chewed grass, bracts, and insect remains scattered along the entire length of the burrow. Nests were also rare (< 1% for burrows of all species).

DISCUSSION

The behavioural avoidance of extreme diel temperatures and low humidities through nocturnalism and burrowing is common among small desert rodents (Purohit 1964, Ghobrial & Nour 1975, Gordon 1977). The major physiological implications of this mode of life are the minimization of water loss and the avoidance of temperature stress. Temperature and humidity fluctuate less and provide conditions more amenable to life processes beneath the sand surface than above it (Robinson & Seely 1980). The preferred and tolerated microclimatic variables are limiting within a macro-environment.

The *Gerbillurus* species occur in arid desert climates as described by Shultze and McGee (1978). *G. tytonis* and *G. setzeri* occur in hot,

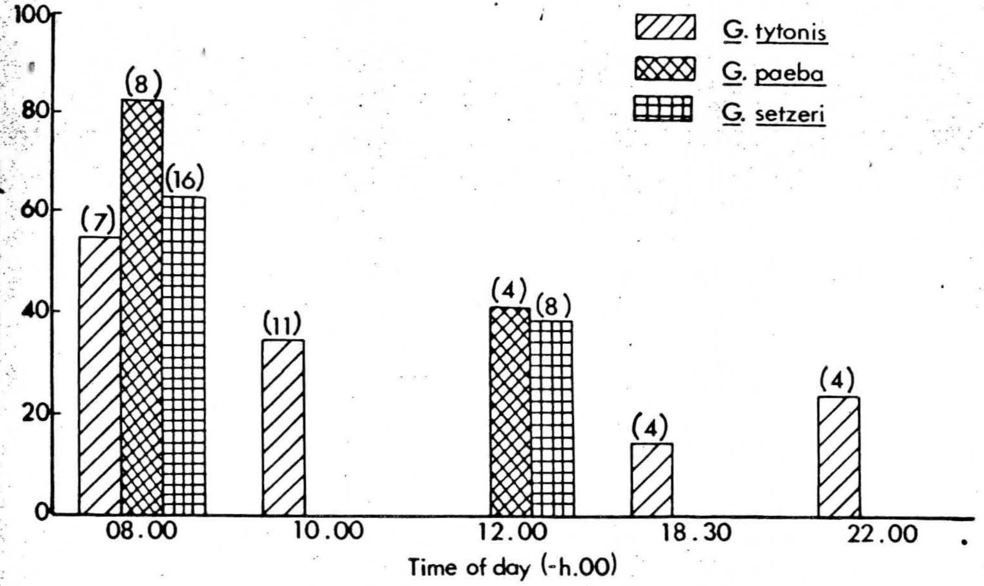

Figure 7. The humidities of *Gerbillurus* burrows at different times of the day (n value in parentheses).

was affected by the presence of fog or dew. The relative humidity of the macro-environment as measured at Gobabeb (Table 1) showed a similar trend (Lancaster *et al.* 1984).

A highly saturated environment would minimize evaporative water loss if cooling was necessary and so conserve water. The gerbil burrows are dry during the day but as burrow temperatures are not extreme, the animals do not have to employ costly evaporative cooling mechanisms. Respiratory water loss would depend on the efficiency of the nasal counter-current system (Gordon 1977).

Schmidt-Nielson *et al.* (1950) found the ventilation of burrow systems increased dryness. Vogel and Bretz (1972) predicted that a multi-entrance, unplugged burrow system should have a fairly rapid circulation rate reducing the possibility of hypoxia and hypercapnia. Unlike the findings of Louw (1972) and Buffenstein (1984), but similar to those of Ascaray (1986), gerbil burrow entrances were open, allowing ventilation but also a decrease in the relative humidity of the burrows.

The dimensions and complexity of the various burrow systems of the respective *Gerbillurus* species (Table 2) may be related to the degree of compactness of the soil, the stabilizing effect of vegetation, the size of the animal and the social system. The burrow systems of the gregarious *Tatera robusta* on the sandy Serengeti plains (Sentzoa 1984) are similar to the burrow system of the social *G. setzeri*. *Tatera robusta* also prefer sandy areas where the fine subsurface sand is compact. Kenagy (1973) found that the friability of soil, particularly at shallow depths, determined the burrow pattern of the *Dipodomys* species. *G. vallinus* burrows are generally in the soil that has accumulated and is stabilized beneath shrubs. Previous studies on *G. paeba* burrows indicate that they occur singly (Nel 1975), are simple in structure (De Graaff & Nel 1975) and close to vegetation (Seely 1977). Ascaray (1984) found that *G. p. exilis* burrows were either simple or complex. Laycock (1975) found that the main entrance of these burrows extended down for 200 mm at an angle of 45° to a smaller chamber from which other exits and the main tunnel lead off. However, the locality that Laycock (1975) studied indicates that the animals were probably *G. tytonis*. In this study, burrows that showed this pattern belonged to *G. tytonis*.

Large concentrated food caches were rare but many had plant material or the remains of insects scattered along their length (Table 5). Larder hoarding (Robinson & Brodie 1982) gives protection while feeding and is a reserve when food is scarce. Scatter hoarding (Robinson & Brodie 1982) of food at different sites within

Table 3. Burrow descriptions of four species of *Gerbillurus* at several localities.

Species	No. of Entrances		Burrow diameter (mm)			Total length (m)			Average depth (mm)			Maximum depth (mm)			Type of burrow
	$\bar{X}$	(n)	$\bar{X}$	(n)	SE	$\bar{X}$	(n)	SE	$\bar{X}$	(n)	SE	$\bar{X}$	(n)	SE	
G. paeba Swakopmund	1.0	(9)	60	(8)	18	0.41	(8)	0.28	302	(9)	151	393	(9)	298	simple (82%)
	1.0	(2)	38	(2)	04	1.66	(2)	0.76	365	(2)	304	875	(2)	884	complex (18%)
	1.0	(11)	56	(10)	18	0.66	(10)	0.63	313	(11)	168	480	(11)	440	both types
G. tytonis Gobabeb	1.0	(8)	56	(7)	18	0.61	(8)	0.42	282	(5)	245	316	(8)	254	simple (44%)
	2.0	(9)	54	(7)	07	1.37	(10)	0.79	288	(9)	120	436	(10)	204	complex (56%)
	1.5	(17)	55	(14)	13	1.03	(18)	0.74	286	(14)	165	383	(18)	229	both types
G. setzeri Rössing	1.0	(1)	100	(1)	—	1.20	(1)	—	320	(1)	—	450	(1)	—	simple (10%)
	1.9	(9)	66	(8)	18	2.17	(9)	1.92	277	(9)	128	372	(9)	137	complex (90%)
	1.8	(10)	69	(9)	20	2.08	(10)	1.83	281	(10)	122	380	(10)	131	both types
G. vallinus Kenhardt	1.0	(1)	60	(1)	—	0.40	(1)	—	150	(1)	—	150	(1)	—	simple (25%)
	4.3	(3)	60	(1)	—	1.80	(3)	1.06	235	(2)	92	267	(3)	115	complex (75%)
	3.5	(4)	60	(2)	—	1.45	(4)	1.11	207	(3)	81	238	(4)	111	both types
G. setzeri Gobabeb	1.0	(3)	58.3	(3)	0.76	77.0	(3)	43.86				365.0	(3)	106.1	simple (33%)
	1.8	(6)	55.8	(6)	058	213.83	(6)	163.25	392	(5)	55.6	506.0	(6)	56.8	complex (66%)
	1.67	(9)	56.7	(9)	0.61	168.3	(9)	147.6	392	(1)	49.8	465.7	(9)	93.6	both types

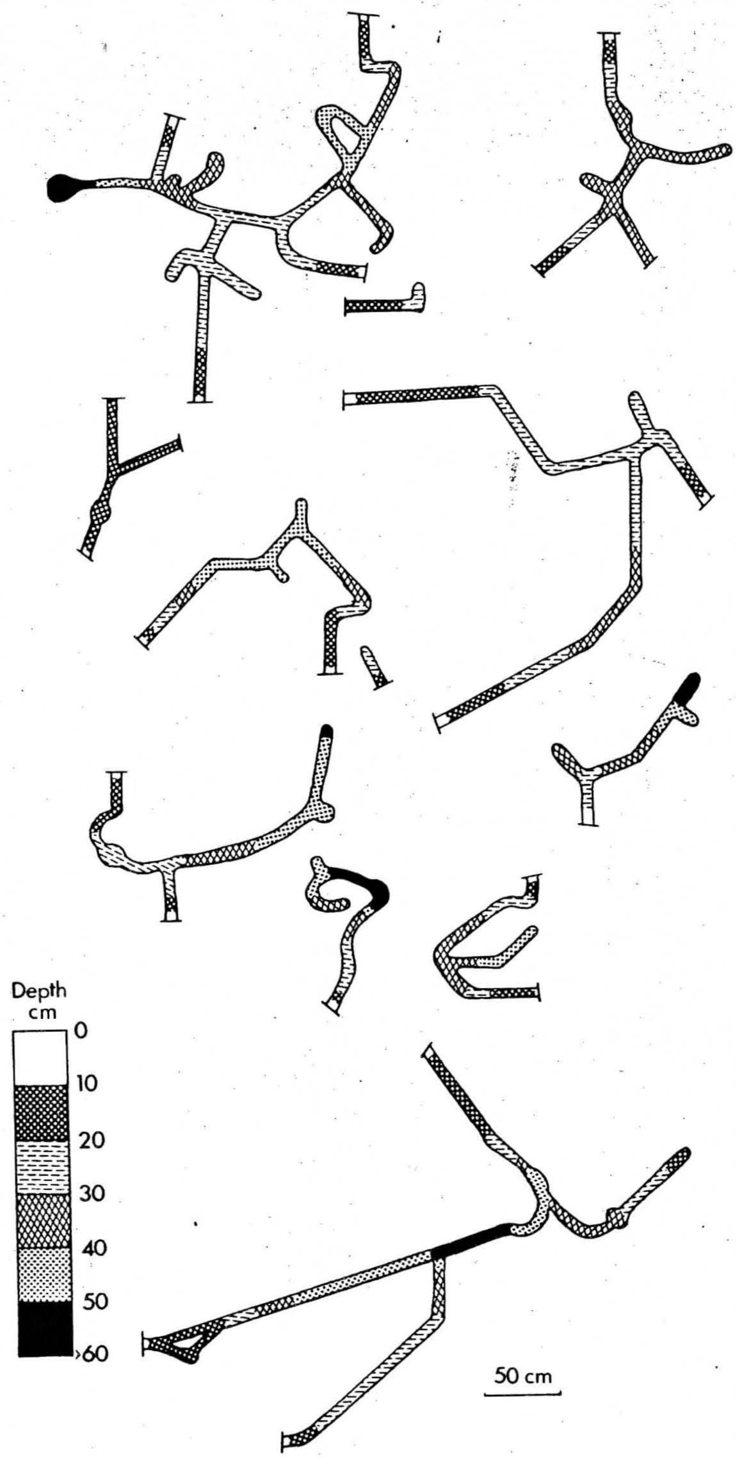

Figure 8. The burrow structures of *G. setzeri*.

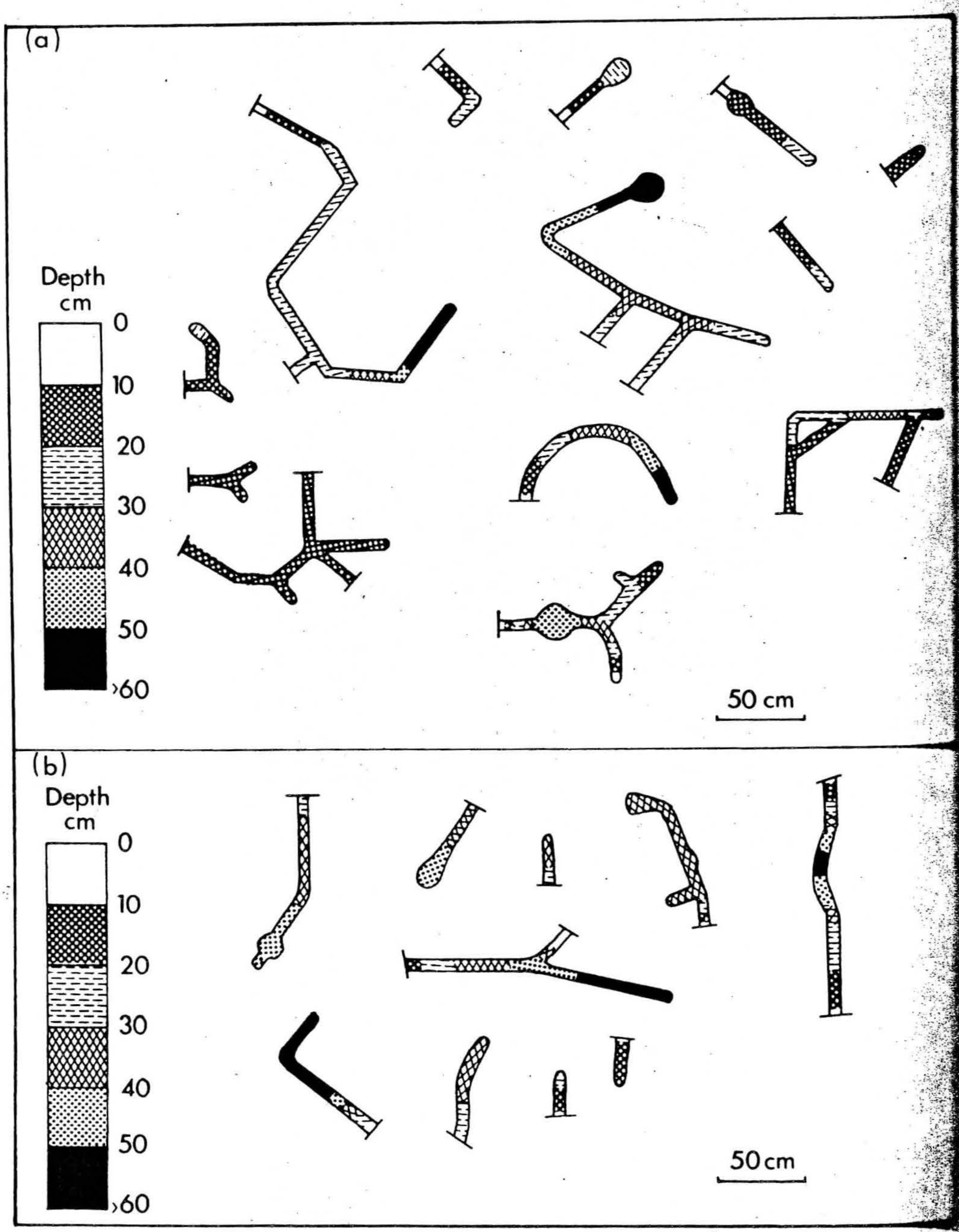

Figure 9. The burrows of (a.) *G. tytonis* and (b.) *G. p. paeba*

the range makes the animals less dependant on one main cache, reduces time and effort to move food to a cache but requires mobility within a home range. The hairy-footed have been observed to scatter-hoard in the oratory (Dempster & Perrin in prep.) A (1986) found discarded seed heads and fragments in the burrows of *G. paeba* Hoarding of food was common amo

Table 4. The number of simple and complex burrows occurring in mounds occupied by four *Gerbillurus* species.

Species	burrow types		
	simple	complex	both
G. tytonnis	87.5	50.0	66.6
G. paeba	55.5	0.00	45.4
G. setzeri	0.00	33.0	30.0
G. vallinus	0.00	100.0	75.0

paeba exilis (Ascaray 1986) and all other *Gerbillurus* species (Dempster & Perrin in prep.). In the Karoo, seed capsules of the Mesembryanthemaceae, *Psilocaulon* and *Aridaria* were taken into the burrows by gerbils where the seeds were removed and the empty capsules pushed back outside leaving tell-tale garbage piles (Dean & Dean, pers. comm.). Stored food would be particularly useful to an animal if food resources fluctuated greatly. Of the gerbils being studied, the gravel-plain species, *G. setzeri* had the greatest amount of stored food in their burrows. Boyer (pers. comm.) has collected nests of both *G. tytonis* and *G. paeba* in burrows but in this study only one nest was found in a *G. paeba paeba* burrow.

CONCLUSION

Gerbils, like heteromyids (Kenagy 1973), enjoy a mesic habitat within a harsh xeric environment. The burrow micro-environment of the four *Gerbillurus* species appears relatively stable and provides shelter from the high daytime temperatures. The effects of heat and aridity are indirect, affecting the temporal and spatial availability of food directly. However, the animals are exposed to low temperatures when active on the surface at night. Changes in the activity patterns of the gerbils when exposed to various photoperiods, temperatures and humidity regimes, need to be determined in the laboratory and the field.

ACKNOWLEDGEMENTS

D. Boyer of SWA/Namibia Nature Conservation, Gobabeb, H. Erasmus of the Cape Dept. of Nature Conservation, E. Dempster, L.J. Fielden, O. Wirminghaus and R. Nanni are particularly thanked for their assistance with fieldwork. W.R.J. Dean of the University of Cape Town, Prof. Jan Nel of the University of Stellenbosch and Dr. M.K. Seely of DERU, Gobabeb, are thanked for their correspondence. The Directorate of Nature Conservation, SWA/Namibia,

Table 5. Plant and animal material found in *Gerbillurus* burrows.

Species	Locality	Contents
G. paeba	Swakopmund	*Zygophyllum stapffi* fruit heads & seeds, Twigs and chewed grass, Faeces,
	Gobabeb	Chewed grass, Hard ball of insect remains.
G. tytonis	Gobabeb	*Acanthosicyos horrida* seed husks, *Acacia erioloba* seeds, chewed bits of grass, Gemsbok faece – larval case, Various tenebrionid beetles including exoskeleton remains, roots, *Stipagrostis leutescens* stems & seed heads.
G. setzeri	Rössing	*Tetragonia reduplicata* leaves, flower-heads & dry fruit, *Blepharis grossa* seeds, bracts, twigs & husks, *Acacia reficiens* leaves, twigs & seed pods, Chewed grass pieces of similar length, Insect elytras, Tenebrionid beetles, Sheaths of bulbs.
G. vallinus	Kenhardt	Insect exoskeleton, Spider, Monocotyledon leaves, Seeds.

The number of burrows excavated were 11, 17, 10 and 4 for *G. p. paeba, G. tytonis, G. setzeri* and *G. vallinus* respectively.

Material found was very unpredictable and items shown above occurred in only one or two of the burrows excavated.

kindly gave permission to work in the Namib-Naukluft Park. The University of Natal and the FRD of the C.S.I.R. of South Africa provided financial support.

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Manuscript received October 1988; accepted June 1989.

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