

Daily and seasonal temperatures in the burrows of African rodent moles

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Burrow, soil surface and ambient temperatures were compared in mesic and xeric climates in tropical and sub-tropical Africa. In all the areas studied there was a similar daily pattern of change in the temperature of the soil surface and the burrow air but the magnitude of the changes and the time of day at which maximal and minimal temperatures occurred varied. In all areas, changes in burrow temperature were of a lower amplitude than those above ground. Mean monthly subsoil temperatures show that the annual amplitude of temperature fluctuation is greatest at the soil surface and diminishes with increasing depth. At depths greater than 0,6 m mean annual soil temperatures vary minimally. The depth at which this occurs is to some extent dependent upon soil type and ground cover. The mean daily burrow temperatures also show that the daily amplitude of temperature fluctuation is less with increasing depth. The subtropics show marked seasonal changes in mean burrow and above-ground temperatures whereas the available information in the literature shows that little seasonality occurs in the tropics. We suggest that this regional difference in temperature profiles may lead to the seasonality in breeding and in moulting shown by rodent moles from the subtropics and for the absence of this seasonality in rodent moles from the tropics.

Tonnel-, grondoppervlak- en lugtemperatuur word in matige en droë klimate in tropiese en subtropiese Afrika vergelyk. In al die gebiede wat bestudeer is, het 'n soortgelyke daaglikse patroon van verandering in die temperatuur van die grondoppervlak en die tonnellug voorgekom, maar die grootte van die veranderinge en die tyd van die dag wanneer maksimum- en minimum-temperatuur voorgekom het, het verskil. In al die gebiede, was die veranderinge van tonneltemperatuur van 'n laer wydte as die van bo-grondse temperatuur. Gemiddelde maandelikse ondergrondse temperatuur toon dat die jaarlikse wydte van temperatuurfluktuasie die grootste op die grondoppervlak is en verminder met toenemende diepte. By dieptes van meer as 0,6 m, varieer die gemiddelde jaarlikse grondtemperatuur minimaal. Die diepte waar dit gebeur hang, tot 'n sekere mate, van die grondtipe en gronddekking af. Die gemiddelde daaglikse tonneltemperatuur wys ook dat die daaglikse wydte van temperatuurfluktuasie minder word met toenemende diepte. Die subtropiese het merkbare seisoenale veranderinge in gemiddelde tonnel- en bo-grondse temperatuur getoon, terwyl die beskikbare inligting in die literatuur toon dat daar min seisoenaliteit in die trope voorkom. Ons stel voor dat hierdie strekverskille in temperatuurprofiel mag lei tot seisoenaliteit by teling en verharig in knaagmolle van die subtropiese en die afwesigheid van hierdie seisoenaliteit by knaagmolle van die trope.

Two families of African rodent moles (Bathyergidae and Rhizomyidae) occur south of the Sahara (Misonne 1968; De Graaff 1981). With the exception of *Tachyoryctes macrocephalus* (Yalden 1975), all live an entirely subterranean existence, in a wide variety of soil types and climates. Thus, some Bathyergidae live in soft sandy soils and others in extremely compact soils, some live in regions exhibiting large daily changes in soil surface temperature (50°C to below freezing), while other rodent moles live in more equitable climates. Similarly, the seasonal changes in mean temperature are very small in the tropics and much more marked in subtropical areas.

The burrows of all the rodent moles have a similar architecture: they consist of numerous long superficial foraging galleries (15–35 cm deep) and usually a deeper area, more protected from predators and from temperature extremes, containing a nest and a bolt-hole (Jarvis & Sale 1971; Davies & Jarvis 1986; Lovegrove & Painting 1987). In the burrow systems of *Cryptomys damarensis* we have found nests as deep as 2,5 m below ground. Dissimilarities in burrow length and complexity can be attributed to the availability of food and to the number of animals occupying a single burrow system (Jarvis & Sale 1971; Jarvis 1985; Davies & Jarvis 1986; Brett 1986).

Most rodent moles excavate their burrows by biting at the soil face with their incisors. One genus, Bathyergus,

excavates with well-clawed forefeet. All species then clear away the loosened soil with their feet and dispose of it either by filling in old sections of the burrow system or by pushing it up a side branch and through a small hole onto the surface to form a mound. With one exception, the hole to the surface is only open for a very short time; once the first few plugs of soil have been pushed up, the mole-rat pushes out subsequent plugs through the loose soil of the first plugs. *Heterocephalus glaber* is the exception in that it kicks a fine spray of soil out of an open hole. In the burrows of all genera the side branch leading to a completed mound is firmly plugged with soil. When foraging, most of the Bathyergidae remain underground. They may dig upwards from a foraging burrow to expose the roots of plants and then pull the whole plant down into the burrow, but with the exception of *T. splendens* they rarely forage from an open hole.

Because of these digging and foraging behaviours, the burrow system of most rodent moles is essentially a sealed system. Consequently, most aspects of the microenvironment within the burrow can be expected to deviate greatly from conditions above ground.

Although the physiology of subterranean rodents, in relation to thermoregulation and metabolism, is receiving increasing attention (McNab 1966; Nevo & Shkolnik 1974; Arieli, Ar & Shkolnik 1977; Vleck 1979; Haim & Fairall 1986; Lovegrove 1986a; 1986b), little has been

published on the actual temperatures to which subterranean rodents are exposed in their burrows. With the exception of Brett (1986) and Rahm (1980), most of the measurements that have been made were either taken over a short period of time or do not reflect seasonal changes (McNab 1966; Kennerly 1964). During the course of our research on the ecology of African rodent moles, we have recorded burrow, surface and ambient temperatures from a range of habitats and often at several times of the year. These data provide basic information for future physiological studies on subterranean mammals.

Materials and Methods

Data on burrow temperatures were obtained from the following places and rodent mole burrow systems:

(i) Subtropical Africa

(a) Mesic climate: *Georchus capensis* (Bathyergidae), from Rondebosch, S.W. Cape, S. Africa (33°56'S / 18°28'E) and *Cryptomys hottentotus* from Darling (33°22'S / 15°25'E), Stellenbosch (33°56'S / 18°51'E) and Wellington (33°38'S / 18°57'E), S.W. Cape, South Africa.

(b) Xeric climate: *Cryptomys damarensis* from Dordabis (22°52'S / 17°41'E) and Otjiwarongo (20°27'S / 16°42'E) in South West Africa (Namibia) and from Twee Rivieren (26°25'S / 20°28'E) in the Kalahari Gemsbok National Park, South Africa.

(ii) Tropical Africa

(a) Mesic climate: *Tachyoryctes splendens* (Rhizomyidae), from Nairobi, Kenya (1°17'S / 36°49'E).

(b) Xeric climate: *Heterocephalus glaber* (Bathyergidae), from Archers Post and Lerata Water Hole, Northern Kenya (0°38'N / 37°40'E).

Mean monthly subsoil temperatures for mesic and xeric subtropical Africa were obtained from the South African Weather Bureau. These temperatures were taken at 08h00, 14h00 and 20h00 at depths ranging from 0,05 m to 1,20 m for 4,5 years. They were taken in locations and soil types resembling those where the burrow temperatures were recorded. Mean subsoil temperatures for the xeric tropical environment were obtained from Brett (1986).

Burrow, soil surface and ambient temperatures were monitored using either a Yellow Springs telethermometer or a Baily Batt thermister. When taking the soil surface and ambient temperatures, the tip of the thermister probe was kept out of the sun and the height above ground of the probes measuring ambient temperature was noted. Where possible, the burrow occupants were captured before temperature measurements were taken; nevertheless the probe in the burrow was routinely protected from possible damage by the rodent moles by inserting it into a hard plastic pipe with a perforated metal end that allowed a free flow of air over the sensor. Once the probe and piping were in place, the opened end of the burrow was sealed thoroughly and the system was left to equilibrate with the rest of the burrow overnight, before monitoring of burrow temperatures began. Experimentation had shown us that equilibration occurred within 1 h of the disturbance. At the end of the study period, the burrow was opened and

the distance of probe insertion into the burrow and its depth below the surface were recorded. The burrow was then opened up for a short distance to ensure that it was indeed open to the rest of the burrow. Because it was difficult to locate the deeper sections of the burrow system without completely destroying the system, the majority of burrow temperature profiles were recorded from the more superficial foraging burrows.

Results and Discussion

In all the study areas there was a similar general daily pattern of change in the temperature of the soil surface and burrow air. However, the magnitude of the changes and the precise times at which maximal and minimal temperatures occurred varied. The lowest soil surface temperatures occurred at or just before sunrise and rose steadily reaching a peak around mid-afternoon (15h00–16h00). Thereafter, the temperature dropped steeply until just after sunset and then more gradually throughout the night. Changes in burrow temperatures were of a lower amplitude than soil surface temperatures but followed a similar pattern of events which lagged behind those of the soil surface: the lowest temperatures occurred around 10h00 and 11h00 and the highest well after sunset at 20h00 to 22h00 (Figures 1 and 2). This daily reversal of heat flow was such that twice every 24 h soil surface and burrow temperatures were the same. The time of this 'double cross' (Kennerly 1964) in temperature can be seen in Figures 1 and 2.

Details of the mean, maximum and minimum temperatures for the air, soil surface and burrow are given in Table 1 as is the information on the burrow depths at which the temperatures were recorded, the study site and soil type. In the subtropical mesic climate of the S.W. Cape, *Georchus capensis* and *Cryptomys hottentotus* occur sympatrically (De Graaff 1981; Lovegrove & Jarvis 1986) and there is a significant overlap in mean foraging burrow depths and in soil types (Lovegrove & Jarvis 1986). For this reason we have felt justified in combining the data from these two species (Figure 1).

Many of the temperatures obtained in our study come from foraging burrows and therefore represent the extremes in the temperatures to which the rodent moles are exposed. Apart from the temperatures obtained from one deeper *Cryptomys damarensis* burrow, the more equitable temperatures found in the deeper nest and bolt-hole areas were not measured. The greatest range in annual and daily subsoil temperatures occur within the first 0,3 m of soil (Figure 3). However, even within this top 30 cm of soil the mean annual temperature change with depth is only 0,01°C cm⁻¹ in the mesic subtropics and 0,075°C cm⁻¹ in the xeric subtropics. It was impracticable to measure all burrow temperatures at the same depth below ground, however, all except three were at depths of between 11,5 and 26 cm, a depth range of 14,5 cm (Table 1). From the above figures on temperature change with depth, 14,5 cm represents a mean annual temperature change of not more than 1,1°C. From this and also from seasonal data obtained from burrows at the same depth (Figure 3), we would suggest that the seasonal differences

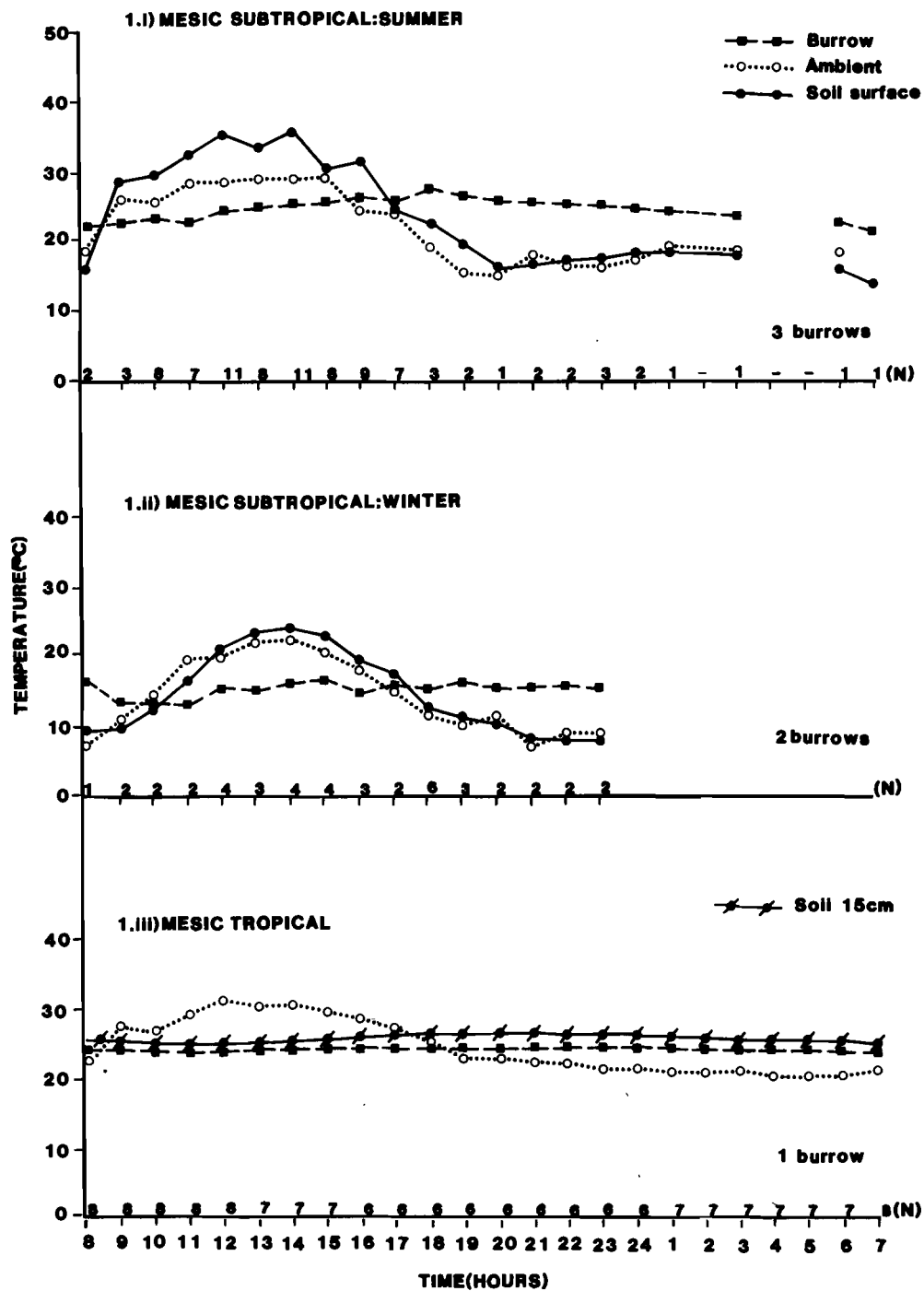


Figure 1 Daily changes in mean ambient, soil surface and burrow temperatures in mesic areas. Details of the time of year, the study areas and the positions of the probes are given in Table 1.

in the burrow temperatures we recorded are real and not due to variations in the depths at which the measurements were made. Missone (1959) showed that in the Arizona desert the change in subsoil temperatures with depth was far more dramatic than our data indicates in the subtropical mesic and xeric environments of Africa. Burrows in the Arizona desert extend to depths in excess of 50 cm, this may well be due, in part, to the more extreme seasonal temperatures which prevail in this region.

Mesic regions

The mean burrow temperatures and temperature profiles from the mesic subtropics and mesic tropics differed in a number of ways.

(a) The daily fluctuation in burrow temperatures in the mesic subtropics was greater (2,9–3,4°C in winter and 6,8°C in summer, Table 1a) than that in the mesic tropics (1,6°C, Table 1b).

(b) The seasonal variation in mean burrow temperature in the subtropics was 13,9°C (26,1°C in summer, 12,2°C

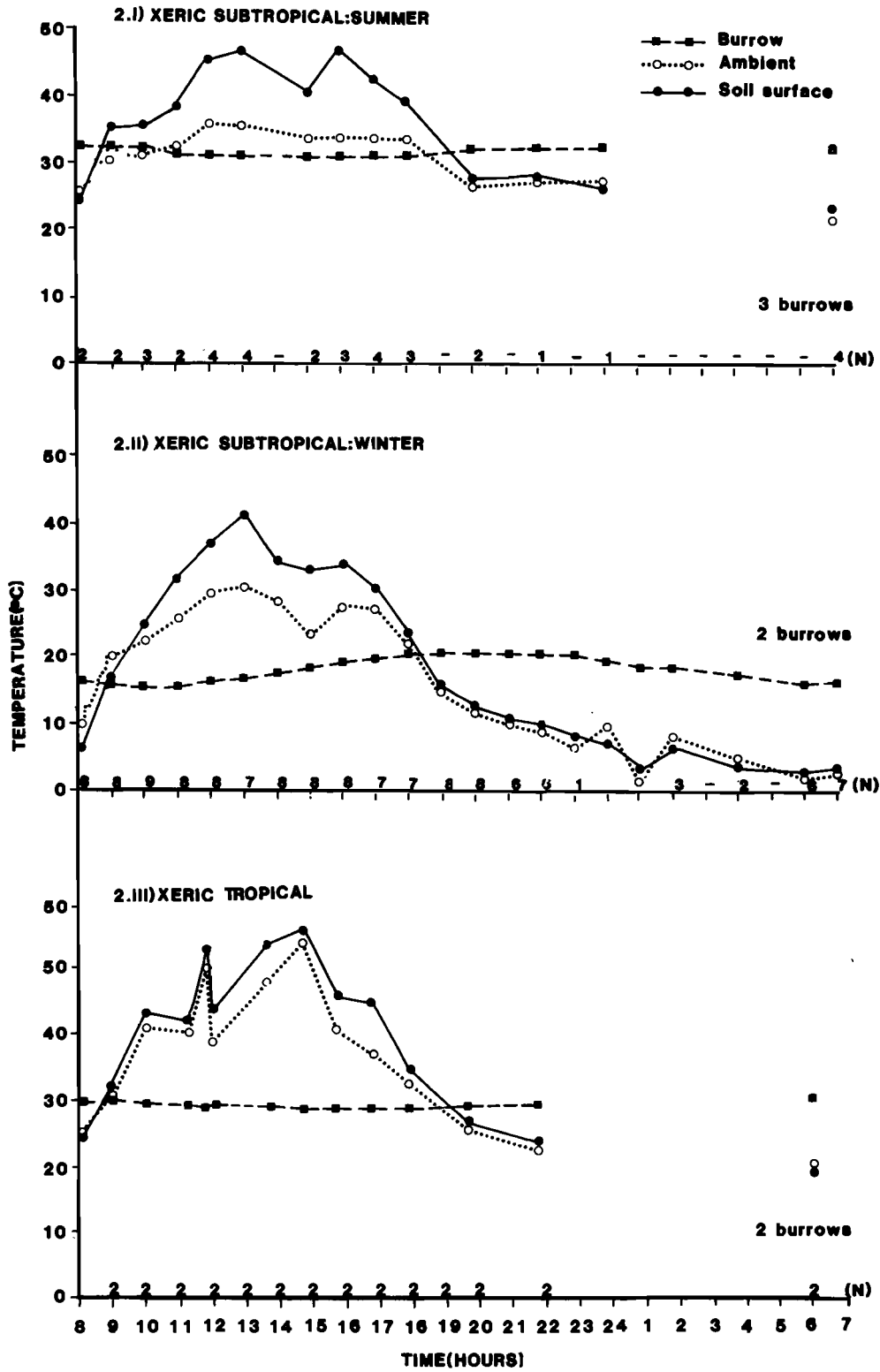


Figure 2 Daily changes in mean ambient, soil surface and burrow temperatures in xeric areas. Details of the time of year, the study areas and the positions of the probes are given in Table 1.

in winter, Table 1a). Although we have no data on seasonal variation in mean burrow temperatures from the tropics, Rahm (1980) found only a 3°C change in the burrow temperature of *T. splendens* from Zaire (21°C in the wet season, 18°C in the dry), which again suggests that the degree of seasonal variation is greatest in the subtropics.

The mean cross-over times in the subtropics changed

seasonally [08h00 and 17h00 in summer, Figure 1(i); 10h00 and 17h30 in winter, Figure 1(ii) while those in the tropics showed less change (08h00 and 18h00 in the wet season, 07h00 and 18h00 in the dry, Rahm 1980).

Xeric regions

Here there was again a marked difference in the burrow

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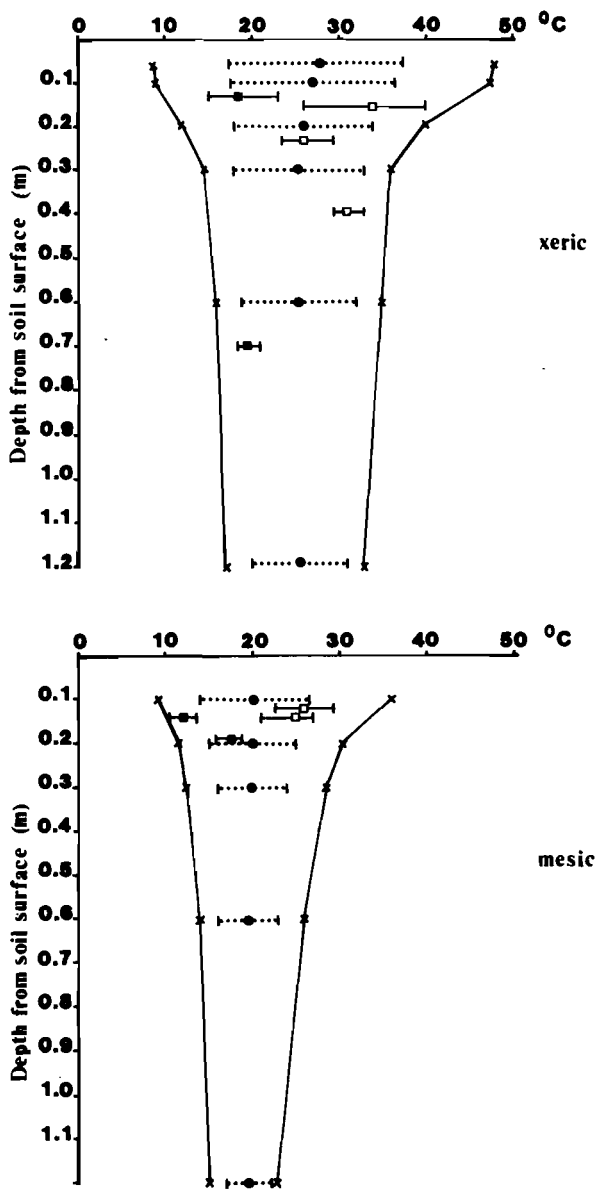


Figure 3 Annual subsoil and burrow temperature profiles for a mesic and xeric environment.

Annual range of sub-soil temperatures.

Minimum Maximum

—●— Mean annual sub-soil temperature and standard deviation from mean. —□— Mean daily burrow temperature and range for summer. —■— Mean daily burrow temperature and range for winter.

temperature profiles between the sub-tropics and tropics.

(a) The mean daily temperature fluctuation of *Cryptomys damarensis* burrows in the subtropics was 3,4°C in summer and 13,8°C in winter (Table 1c), while that of *Heterocephalus glaber* burrows in the tropics was very small, only fluctuating by 1 to 1,5°C (Table 1d). The difference in the summer burrow temperatures between the tropics and subtropics was unexpected because the soil

surface temperatures in the two areas are very similar (Table 1c, 1d; Figures 2i, ii, iii). The vegetation cover in the two areas was comparable as were burrow depths but there were obvious differences in the type and degree of compaction of the soil. *Cryptomys damarensis* occurred in wind-blown Kalahari sands where the top 25 to 30 cm of sand was soft and loose during the dry summer season, whereas the soil where *H. glaber* occurred was fine-grained very compact and extremely hard when dry.

The soil surface to burrow temperature gradient was steeper in the soft sands (1,02°C cm⁻¹) than in compact soils (0,74°C cm⁻¹) for *C. damarensis* and 0,1°C cm⁻¹ in *H. glaber*. *Heterocephalus glaber* was thus exposed to a much more equitable temperature regime than that of *C. damarensis*. This difference in the burrow temperatures in the two xeric areas is also illustrated in Table 1c and d where the mean daily fluctuation in burrow temperature is expressed as a percentage of the daily temperature fluctuation on the soil surface; that of *H. glaber* burrows was between 2,7 and 3,3% of the surface, whereas that of *C. damarensis* ranged between 10 and 32%.

Our field observations indicate that on hot days the temperatures in the foraging burrows of *C. damarensis* may come close to lethal levels. Indeed in one instance an animal captured at mid-day died in under 30 min (the time interval between trap checks). The live-trap in which it was confined was shaded and well ventilated and was buried at the depth of the foraging burrow. In *C. damarensis* burrows (Table 1c) the mean maximum burrow temperature and the daily fluctuation decrease with depth. It is possible that *C. damarensis* retreat into deeper sections of their burrow to escape extreme temperatures in the foraging burrows. This may be the reason why *C. damarensis* have the most extensive network of very deep (1–2 m) burrows, of all the rodent mole burrows so far excavated by us. In two partially excavated *C. damarensis* burrow systems we found several deep burrows radiating out from the nest area for distances of 5 m or more before they rose and linked up with the shallower foraging burrows.

(b) Seasonally there was a 13°C mean temperature differential in *C. damarensis* foraging burrows (31,0°C in summer, 18,6°C in winter, Table 1c). We have no data on seasonal changes in the temperature of *H. glaber* burrows but Brett (1986) showed that, at depths greater than 30 cm, the soil temperature in the habitat of *H. glaber* varied little daily or seasonally from a mean of 27,5°C. Knoch & Schultze (cited by Schultze & McGee 1978) also mention that seasonal changes in ambient temperature are much less marked in tropical Africa than in other parts of Africa.

(c) The cross-over times from the xeric subtropics again showed seasonality (08h30 and 19h30 in summer, Figure 2i; 09h00 and 18h00 in winter: Figure 2ii). We have no seasonal data for *H. glaber* but would suggest from data given by Brett (1986) and Rahm (1980) that the mean cross-over times of 08h00 and 19h00 (Figure 2iii) would vary very little throughout the year.

In conclusion our data have shown that, as would be expected, the burrow temperatures were far more uniform than were the temperatures above ground. We

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Table 1 Details of the time of year and the localities at which the temperatures were measured, the position of the probes, mean, maximal and minimal temperatures and the species of mole-rats whose burrows were measured

Species from which burrow temperature taken	Locality	Soil type	Season & month	Position of probe	Probe depth/height (cm)	Temperature measurements					Daily temp. range (a) °C	(a) as % of mean soil surf. range		
						Mean °C	N	SD	Max. °C	Min. °C				
(a) Mesic sub-tropics														
<i>Georychus capensis</i>	Rondebosch	Compact clay	Summer	Burrow	11,5	26,1	20	2,19	29,7	22,9	6,8	19,5		
	Cape Town		January	Soil surface		33,6	20	13,1	50,0	15,2			34,8	
			Ambient	10,0	26,2	20	6,0	33,0	18,0	15,0				
<i>Georychus capensis</i>	Rondebosch	Compact clay	Winter	Burrow	14,0	12,2	35	1,08	13,8	10,2	3,4	24,0		
	Cape Town		July	Soil surface		12,3	35	5,04	20,0	5,2			14,8	
			Ambient	10,0	12,5	35	4,95	22,0	5,0	17,0				
<i>Cryptomys hottentotus</i>	Wellington	Compact clay	Late summer,	Burrow	14,0	25,1	64	2,04	27,8	21,0	6,8	24,0		
	Cape		April	Soil surface		25,1	64	8,2	40,5	13,0			27,5	
			Ambient	10,0	22,2	64	5,8	32,0	11,8	20,2				
<i>Cryptomys hottentotus</i>	Darling	Compact sand/clay	Winter	Burrow	20,0	17,5	50	0,98	18,8	15,9	2,9	17,0		
	Cape		May	Soil surface		15,8	50	4,5	26,6	9,7			16,9	
			Ambient	10,0	15,9	50	5,3	26,8	7,4	19,4				
(b) Mesic tropics														
<i>Tachyoryctes splendens</i>	Nairobi	Moderately compact soils	Dry	Burrow	20,0	24,3	166	1,76	25,1	23,5	1,6			
	Kenya		October	Soil	15,0	25,9	166	0,69	27,2	24,5			2,7	
				Soil	30,0	25,6	166	0,38	26,0	25,0			1,0	
				Ambient	10,0	24,7	166	3,95	33,0	18,5			14,5	
(c) Xeric sub-tropics														
<i>Cryptomys damarensis</i>	Dordabis	Wind-blown Kalahari sands	Winter	Burrow	13,0	18,6	78	2,73	22,8	15,0	7,8	18,0		
	Namibia		August	Burrow (deep)	70,0	19,3		0,59	20,9	18,8			2,1	4,0
				Soil surface		21,2	78	12,46	43,8	1,5			42,3	
				Ambient	10,0	19,8	78	11,37	34,5	0,0			34,5	
<i>Cryptomys damarensis</i>	Twee	Wind-blown Kalahari sands	Summer	Burrow	38,0	31,9	38	1,03	33,0	29,9	3,4	10,0		
	Rivieren		February	Soil surface		37,5	38	9,75	51,0	18,4			32,6	
	S. Africa			Ambient	10,0	31,2	38	5,52	39,6	18,9			20,7	
<i>Cryptomys damarensis</i>	Otjiworongo	Fine-grained compact mud	Summer	Burrow	14,5	34,8	6	4,9	40,0	26,2	13,8	32,0		
	Namibia		January	Soil surface		45,6	6	15,3	63,0	21,0			42,0	
				Soil	14,0	31,0	6	3,06	34,5	26,3			8,2	
				Ambient	10,0	38,0	6	10,7	54,0	22,0			32,0	
<i>Cryptomys damarensis</i>	Otjiworongo	Fine to med. grain Kalahari sands	Summer	Burrow	23,5	26,1	11	1,08	29,6	23,6	6,0	13,0		
	Namibia		January	Soil surface		43,9	11	13,4	63,0	16,5			46,5	
				Soil	17,5	26,0	11	1,47	28,6	23,6			5,0	
				Soil	23,0	30,4	11	2,38	34,6	27,0			7,6	
				Ambient	10,0	29,9	11	6,54	36,7	14,0			22,7	
(d) Xeric tropics														
<i>Heterocephalus glaber</i>	Lerate,	Very Hard soils	Dry	Burrow	31,0	29,6	16	0,36	30,0	29,0	1,0	2,7		
	N. Kenya		August	Soil surface		38,2	16	11,53	56,0	19,0			37,0	
				Ambient	10,0	27,6	16	4,48	35,0	19,0			16,0	
<i>Heterocephalus glaber</i>	Archers	Very hard soils	Dry,	Burrow	26,0	31,1	12	0,62	32,0	30,5	1,5	3,3		
	Post, N. Kenya		Late July	Soil surface		33,8	12	12,4	63,0	18,0			45,0	
				Soil	26,0	30,8	12	0,73	32,0	30,0			2,0	
				Ambient	10,0	31,5	12	9,8	53,0	18,5			34,5	

suggest that the extent to which the burrow temperatures, at the same depth, varied depended on the characteristics of the soil as well as on the magnitude of the seasonal variation in daylength, which affected the mean soil and ambient temperatures. In both the mesic and xeric

subtropics there were marked seasonal differences in mean burrow temperature while there was little seasonality in burrow temperatures in the tropics.

This presence or absence of seasonality in burrow temperature may be an important factor in determining

whether there is seasonality in physiological processes, such as reproduction and the replacement of the pelage of rodent moles. Thus the two tropical rodent moles for which reproductive patterns are known, breed throughout the year (*H. glaber* and *T. splendens*, Jarvis 1969, 1981; Rahm 1980), whereas the following subtropical Bathyergidae are known to breed seasonally (*Bathyergus suillus*, *B. janetta*, *G. capensis*, *C. hottentotus*, Jarvis 1969; Van der Horst 1970; Taylor, Jarvis, Crowe & Davies 1985; Bennett & Jarvis 1988; Bennett in prep; Jarvis in prep). *Georychus capensis*, *C. hottentotus* and *C. damarensis* also have a seasonal moult (Bennett unpub. data) whereas *T. splendens* showed no seasonality in moult (Jarvis, unpub. data). In *G. capensis* and *C. hottentotus* this moult coincides with the summer-autumn interface and is accompanied by substantial (10%) loss in body mass. Kennerly (1964) suggested that moult in *Geomys* was linked to temperature change in the burrow. It is therefore possible that seasonal changes in burrow temperature provide important cues triggering the onset of breeding and moulting in subterranean rodents living in subtropical regions.

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References

- ARIELI, R., AR, A. & SHKOLNIK, A. 1977. Metabolic responses of a fossorial rodent (*Spalax ehrenbergi*) to simulated burrow conditions. *Physiol. Zool.*, 50: 61–75.
- BENNETT, N. C. & JARVIS, J.U.M. 1988. The reproductive biology of the Cape mole-rat (*Georychus capensis*) Rodentia, Bathyergidae. *J. Zool., Lond.* 214: 95–106.
- BRETT, R. A. 1986. The ecology and behaviour of the naked mole-rat (*Heterocephalus glaber* Ruppell) (Rodentia: Bathyergidae). Ph.D. thesis, University of London.
- DAVIES, K.C. & JARVIS, J.U.M. 1986. The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the South Western Cape, South Africa. *J. Zool., Lond (A)* 209: 125–147.
- DE GRAAFF, G. 1981. The rodents of southern Africa. Butterworth, Johannesburg.
- HAIM, A & FAIRALL, N. 1986. Physiological adaptations to the subterranean environment by the mole-rat *Cryptomys hottentotus*. *Cimbabasia* 8(6): 49–53.
- JARVIS, J.U.M. 1969. The breeding season and litter size of African mole-rats. *J. Reprod. Fert., Suppl.* 6: 237–248.
- JARVIS, J.U.M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* 212: 571–573.
- JARVIS, J.U.M., 1985. Ecological studies on *Heterocephalus glaber*, the naked mole-rat, in Kenya. *Nat. geogr. Res Repts. 1979 Projects.* 20: 429–437.
- JARVIS, J.U.M. & SALE, J.B. 1971. Burrowing and burrow patterns of East African mole rats. *J. Zool., Lond.* 163: 451–479.
- KENNERLY, T.E. 1964. Microenvironmental conditions in the pocket gopher burrow. *Texas J. Sci.* 16: 395–441.
- KNOCH, K. & SCHULTZE, A. 1957. Niederschlag Temperaturen und Schwüle in Afrika. World atlas of endemic diseases Vol 2. Heidelberger Akademie der Wissenschaften, Heidelberg.
- LOVEGROVE, B.G. 1986a. The metabolism of social subterranean rodents: adaptation to aridity. *Oecologia* 69: 551–555.
- LOVEGROVE, B.G. 1986b. Thermoregulation of the subterranean rodent genus *Bathyergus*. *S. Afr. J. Zool.* 21: 283–288.
- LOVEGROVE, B.G. & JARVIS, J.U.M. 1986. Coevolution between mole-rats (Bathyergidae) and a geophyte, *Micranthus* (Iridaceae). *Cimbabasia A* 8: 79–85.
- LOVEGROVE, B.G. & PAINTING, S. 1987. Variations in the foraging behaviour and burrow structures of the Damara mole-rat (*Cryptomys damarensis*) in the Kalahari Gemsbok National Park. *Koedoe* 30: 149–163.
- McNAB, B.K. 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology* 47: 712–733.
- MISONNE, X. 1959. Analyse zoogéographique des mammifères de l'Iran. Bruxelles. Inst. Royal des Sci. Nat. de Belgique, Memoires 2me ser. 59: 157 pp.
- MISONNE, X. 1968. Rodentia: Main Text. In: Mammals of Africa: An identification manual. (Eds) Meester, J. & Setzer, H.W. Part 6: 1–39. Smithsonian Inst. Press, Washington.
- NEVO, E. & SHKOLNIK, A. 1974. Adaptive metabolic variation of chromosome forms in mole-rats, *Spalax*. *Experientia* 30: 724–726.
- RAHM, U. 1980. Die afrikanische Wurzelratte *Tachyoryctes*. A. Ziemsen Verlag, Wittenberg Lutherstadt.
- SCHULZE, R.E. & MCGEE, O.S. 1978. Climatic indices and classifications in relation to the biogeography of Southern Africa. In: Biogeography and ecology of Southern Africa, (ed) Werger, M.J.A., pp 19–52. Junk, The Hague.
- TAYLOR, P.J., JARVIS, J.U.M., CROWE, T.M. & DAVIES, K.C. 1985. Age determination in the Cape mole-rat, *Georychus capensis*. *S. Afr. J. Zool.* 20: 261–267.
- VAN DER HORST, G. 1970. Seasonal effects on the anatomy and histology of the reproductive tract of the male rodent mole *Bathyergus suillus* (Schreber). M.Sc. thesis, University of Stellenbosch.
- VLECK, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol. Zool.* 52: 122–136.
- YALDEN, D.W. 1975. Some observations on the giant mole-rat *Tachyoryctes macrocephalus* (Ruppell, 1842) (Mammalia: Rhizomyidae) of Ethiopia. *Monitore zool. ital. (NS) (Suppl.)* 6(15): 275–303.