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Thermoregulation in the Namib Desert Golden Mole, *Eremitalpa granti namibensis* (Chrysochloridae)

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Studies on the thermoregulatory capabilities of a small desert insectivore, *Eremitalpa granti namibensis*, have revealed unusual features including a high rate of thermal conductance, a low basal metabolic rate, a low and labile body temperature and poor ability to thermoregulate. Two factors suggested to have selected for these physiological traits are the gaseous regime of the undersand environment in which moles burrow and the need to minimize energy expenditure in an energy sparse sand dune environment.

lab study
1983 - 84

Introduction

Behavioural adaptations such as nocturnalism and burrowing habits allow many small mammals to avoid environmental extremes. The physiological abilities of such animals are more related to selected microenvironmental conditions than prevailing climate (Buffenstein, 1984; Bradley & Yousef, 1975), especially for subterranean mammals spending most of their existence in closed burrow systems where environmental fluctuation is minimal in comparison to above ground conditions (Dubost, 1968; Kennerly, 1964).

McNab (1966, 1979) concluded that subterranean mammals, although having evolved in several taxonomically diverse families, possess similar physiological characteristics including relatively low body temperatures with a tendency towards reduced thermoregulatory capacity, reduced basal metabolism and elevated thermal conductances. He concluded that these metabolic tendencies reduce overheating in an environment where evaporative and convective cooling are of little importance. Vleck (1979) and Jarvis (1978) questioned this interpretation and have suggested that low metabolic rate is an energy saving adaptation in response to limited resource availability and the high energy expenditure concomitant with burrowing. Finally, a low metabolic rate could represent an adaptation to the hypoxic and hypercapnic conditions typical of burrow atmospheres (Arieli *et al.*, 1984; Baudinette, 1972).

Given these possible physiological determinants, the metabolic and thermoregulatory capacities of the Namib golden mole *Eremitalpa granti namibensis* are of particular interest. *Eremitalpa g. namibensis* inhabits an arid sand dune environment and has diverged somewhat from the subterranean habitat typical of other African golden moles (Family Chrysochloridae). The Namib mole does not dwell in a sealed burrow system, but is nocturnally active on the dune surface searching for insect prey. Daylight hours are spent buried in loose shifting dune sand. In the present study, the bioenergetic characteristics of

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E.g. namibensis are examined to evaluate their significance as adaptations to a psammophilous habit in a thermally demanding and energy sparse environment.

Materials and methods: field studies

Body temperature determinations

Adult *E.g. namibensis* were caught by hand in the Namib dunes at Gobabeb (23°34′S, 15°30′E) and Far East (23°45′S, 15°30′E) during 1983 and 1984. Time and date of capture, depth and temperature of sand from where the animal was excavated, and location of capture (in open sand or under a vegetation clump) were noted. Body temperature (Tb) of freshly caught individuals was obtained by inserting a sheathed type 'K' thermocouple 5 mm into the cloaca. The thermocouple was attached to a Digitron 1408 themometer accurate to ±0·01°C. Each Tb measurement typically required 15 seconds handling time.

To examine the relationship between Tb and Ta one individual was placed in a 12-l bucket filled with dune sand immediately after capture. The open container was buried almost to its rim in a dune, and kept shaded during the day to prevent overheating from 38–40°C air and 50–60°C surface sand temperatures. The animal was removed from the container every 2 hours and Tb recorded along with sand temperature in the bucket where the mole had been resting. Rectal and sand temperatures were monitored for 36 h.

Microenvironmental measurements

At a site approximately 8 km from Gobabeb, surface and subsurface (30, 20 and 10 cm) sand temperatures were measured employing a data logger (Campbell CR-21) equipped with four thermistor probes accurate to 0·01°C. Thermistor probes were attached to a thermally inert rod buried vertically in the dune. The rod was located on level sand on an east-facing upper dune slope approximately 2 m distant from the nearest vegetation. An equilibration period of 4 h preceded recording. Readings were taken every hour for 24 h during a typical summer (January 1984) and winter day (July 1984).

A comparison of thermal conditions between non-vegetated and vegetated dune areas involved simultaneous measurements of sand temperatures at surface and 10 and 20-cm depths beneath a clump of perennial dune grass (*Stipagrostis sabulicola*) having a basal area of 0·75 m^2 and in an area of unvegetated sand approximately 1 m distant. Readings were taken over a 24-h period (March 1987) using the procedure described above.

Laboratory studies

Animals were maintained in the laboratory for at least 3 weeks prior to experimentation. Individuals were housed in a 60 × 30 × 30 cm glass terraria filled to a depth of 15 cm with Namib dune sand. A lamp with a red 50 watt light bulb was positioned in one corner of the tank as a heat source. Ambient temperatures approximated 25°C, and a 12-h light cycle was maintained with illumination during 0700–1900 h. Diet included *Tenebrio molitor* larvae, beetles (*Onymachris* sp.) and day-old mice (*Mus musculus*). Water was not provided since succulence was present in the diet. Moles generally maintained weights approximating capture levels (range 17–40 g, mean 24·6 g).

Metabolic determinations

Heat production or standard metabolic rate (Bligh & Johnson, 1973) was measured by recording oxygen consumption rates (VO_2) of post-absorptive moles over an ambient temperature (Ta) range of 10–40°C. Since *E.g. namibensis* is nocturnal, all measurements were made during daylight hours. The respirometer chamber was a large glass bell jar (volume 2100 cm^3), sealed with an O ring clamp system and equipped with an outlet port for extraction of air samples; a sachet of soda lime was enclosed for absorption of exhaled carbon dioxide. The chamber was placed in a dimly illuminated constant temperature cabinet controlled to ±1°C of the required Ta. After a 3-h acclimation period at each Ta (reduced to 0·5 h at stressful Tas of greater than 30°C) animals were weighed and then sealed individually in the respirometer for approximately 1 h. Prior to removing the mole from the test chamber, three 50-ml gas samples were extracted through the outlet port with a syringe. Using a static sampling system, gas samples were injected into a Beckman OM-14 paramagnetic oxygen analyzer. Before entering the oxygen analyzer, each sample was dried by passing it through a column of anhydrous silica gel. The first 10 ml of each sample cleared the 'dead space' around the silica crystals of air from the previous sample; the remaining 40 ml was then injected into the oxygen analyzer evenly over a 10-s period and any displacement from the 20·93% O_2 calibration value was used to calculate oxygen consumption. Oxygen consumption rates were expressed as $cm^3\ O_2\ g^{-1}\ h^{-1}$ after correction to standard temperature and pressure. Although the apparatus used did not allow for measurement of VO_2 in conjunction with associated activity patterns, most animals remained inactive during experimental runs. Data from individuals who showed any sign of activity or agitation were discarded. Therefore values of standard metabolic rates are, if anything, slightly overestimated. Body temperature of test animals was recorded after each VO_2 measurement. The temperature in the respirometer, although not monitored continuously during experimentation, was recorded immediately upon removal of the animal from the chamber.

In a second series of experiments, VO_2 rates of animals submerged in sand were measured. Experimental protocol was similar to that described above, except that animals were provided with 166 cm^3 of Namib dune sand during both periods of acclimatization and VO_2 measurement. Prior to extraction of gas samples, the bell jar was gently shaken for several seconds to ensure complete mixing of air.

Thermal preferenda

The temperature gradient chamber for determination of thermal preferenda of *E.g. namibensis* consisted of a circular run (10 cm width, 95 cm outer diam.) partitioned into two halves which enabled monitoring of two animals simultaneously. The floor of each half-run contained 16 copper tubes arranged in parallel fashion and covered to a depth of 4 cm with dune sand. A linear temperature gradient was maintained in each semicircular chamber by controlling the rates of hot and cold water pumped through the counter current tubing. (Hot water was supplied by a lauda circulating water bath (Model NB4); a 40-l bucket of ice water provided the cold water). Sand temperatures at the cool and warm ends of the chamber were maintained at 20°C (±1°C) and 38°C (±1°C) respectively. Animals were placed in the temperature gradient for at least 1 h prior to any body temperature determinations. After acclimatization, body temperatures of the moles were measured hourly for 24 h (during which food was not provided) and the position of the mole in the gradient recorded.

Diurnal Tb variation

Diurnal Tb variation was measured in *E.g. namibensis* housed in a windowless constant temperature room at Ta 21°C, ambient humidity (30–50% RH), and a 12-h photoperiod with light from 0700–1900 h. Animals were kept individually in 9-l plastic buckets filled nearly to capacity with Namib sand; *T. molitor* larvae were provided daily at 1700 h and any excess removed at the next feeding time. The Tb of each animal was measured on 12 occasions over a period of 2 weeks; the times of measurement were distributed uniformly throughout the day–night cycle.

Results

Field observations

Body temperatures of animals just after capture were variable and ranged from 19·2°C to 38·2°C (Fig. 1). These measurements are generally representative of animals caught between 0800 and 1000 h since later on in the day, dune surface glare and afternoon winds made it difficult to locate areas where moles were buried. Summer individuals (November–April) had a mean Tb of 29·7°C (SD ± 4·5°C) which was significantly different (Student's *t*-test; $t = 3{\cdot}98$; df $= 21{\cdot}00$; $p < 0{\cdot}001$) to a mean Tb of 22·1°C (SD ± 3·5°C) for winter individuals. A strong positive linear correlation was found between Tb and ambient sand (Ta) at depths where moles were located (Fig. 2). In 23 paired comparisons, no significant difference was observed between the two parameters (paired *t*-test; $t = 1{\cdot}4$; df $= 22{\cdot}00$; $p > 0{\cdot}05$).

A frequency distribution of depths at which moles were captured (Fig. 3) indicates few animals at depths less than 5 cm or greater than 30 cm (maximum 37 cm and minimum 5 cm). Moles excavated from beneath clumps of vegetation were at significantly (Student's

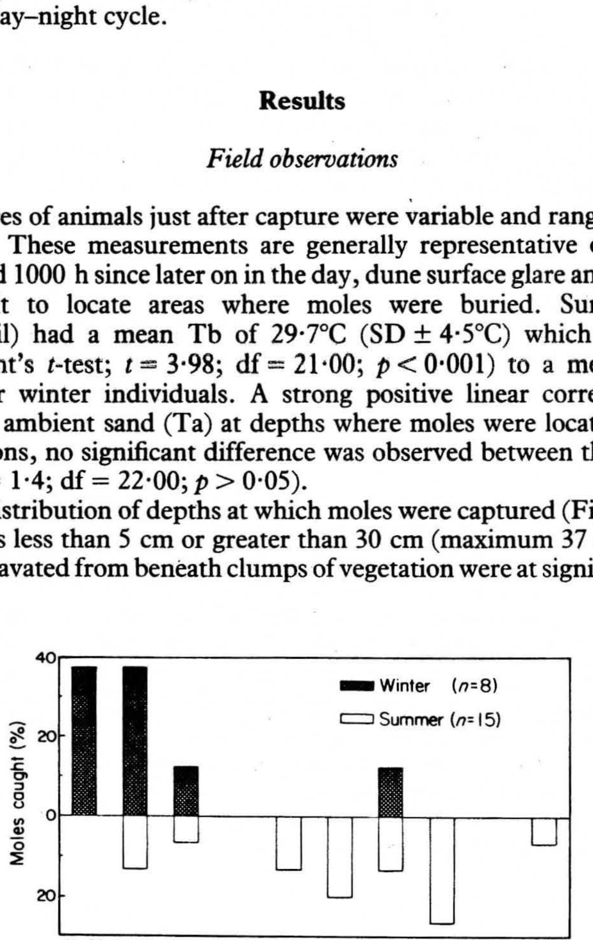

Figure 1. Body temperatures of *E.b. namibensis* recorded immediately after capture.

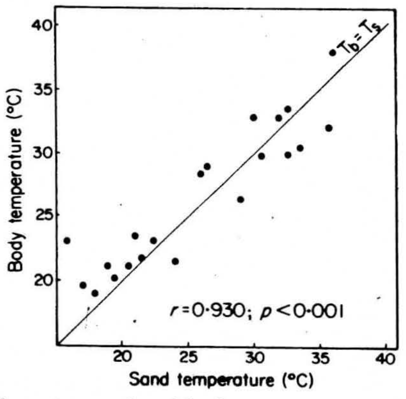

Figure 2. Relationship between sand and body temperature of freshly caught *E.g. namibensis.*

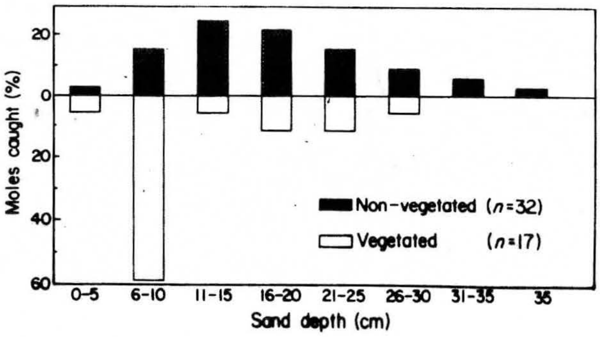

Figure 3. Subsurface depths at which *E.g. namibensis* was caught in the dunes both in vegetated and non-vegetated areas.

t-test; $t = 2{\cdot}61$; df = 47; $p < 0{\cdot}05$) shallower levels ($\bar{\chi} = 13{\cdot}06$ cm; SD ± 7·04) than those in unshaded sand ($\bar{\chi} = 19{\cdot}21$ cm; SD ± 8·25).

To establish where moles show a preference for daytime refuging, all tracks encountered in the field during a 2-week period (March 1987) were followed and their point of termination noted. Of 33 observations, only four tracks ended in open sand, while the remainder ended in vegetation clumps. This difference was highly significant (chi-squared = 18·94; df = 1; $p < 0{\cdot}001$).

Body temperatures of the specimen kept in a container of sand exposed to a natural thermally fluctuating environment ranged from 18·1°C to 31·6°C (Fig. 4). Body temperatures closely paralleled changes in sand temperatures and were on average 0·7°C (SD ± 1·6°C) higher than sand. Differences between Tb and Ta were not statistically significant (paired *t*-test; $t = 1{\cdot}93$; df = 19; $p > 0{\cdot}05$). During the period of measurement, the mole rested near to the bottom of the bucket at about 20 cm depth.

Micorenvironmental conditions

Winter and summer dune temperature profiles are given in Fig. 5. Summer surface diel temperature range was 40°C with measurements exceeding 50°C by midday. With increasing depth, thermal conditions became more moderate and stable. Mean summer temperature at 30 cm was 34°C with a daily fluctuation of 1°C. Daytime surface temperatures were always higher than subsurface temperatures with the situation reversed

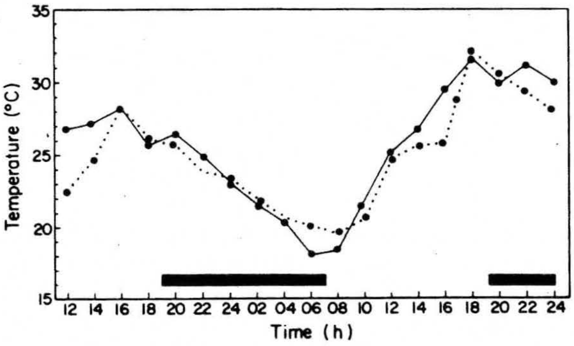

Figure 4. Daily variation of body (solid line) and sand (broken line) temperature of a single *E.g. namibensis* held captive in a plastic container submerged in a Namib dune (12–13 September 1984). Solid bars indicate night time.

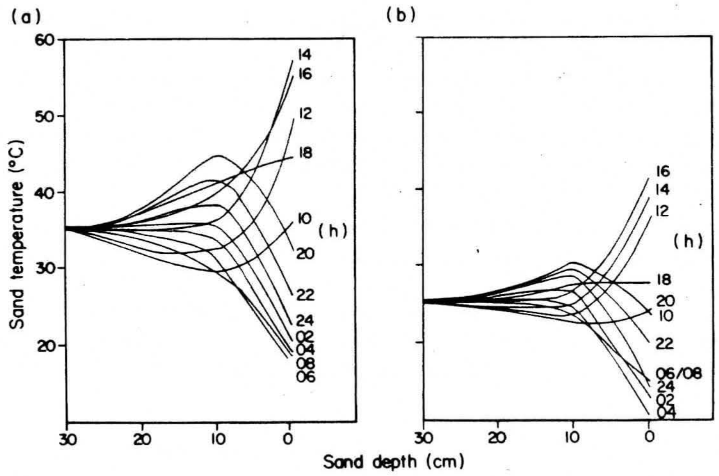

Figure 5. Temperatures of subsurface sand (0–30 cm) on a dune slope in the Namib desert during (a) summer (21–22 January 1984) and (b) winter (6–7 July 1984).

at night. In winter, maximum surface temperature was 16°C lower than in summer. Subsurface readings were approximately 8–10°C below summer measurements at corresponding depths.

Cooler thermal conditions beneath a clump of *S. sabulicola* compared to those in unshaded sand (Fig. 6) illustrate clearly the buffering effect of vegetative cover; maximum surface temperatures were 11°C lower with plant cover, while at a depth of 10 cm the average temperature (29·4°C) was 4·7°C less than unshaded sand (34·1°C). Mean shaded and unshaded temperatures at 20 cm depths were 29·1°C and 33·9°C respectively.

Metabolic determinations

For moles out of sand, a basal metabolic rate of $0{\cdot}52\ \mathrm{cm^3\ O_2\ g^{-1}\ h^{-1}}$ (SD $\pm$ 0·09) was measured at Ta = 31°C (Fig. 7). Below the thermoneutral point at 31°C, the increase in VO_2 with reduced air temperature was non-linear with the rate of change in VO_2 being less at Ta = 15°C than at Ta = 22°C and 26°C. Below 15°C, heat production declined rapidly and showed no increase relative to that at Ta = 31°C.

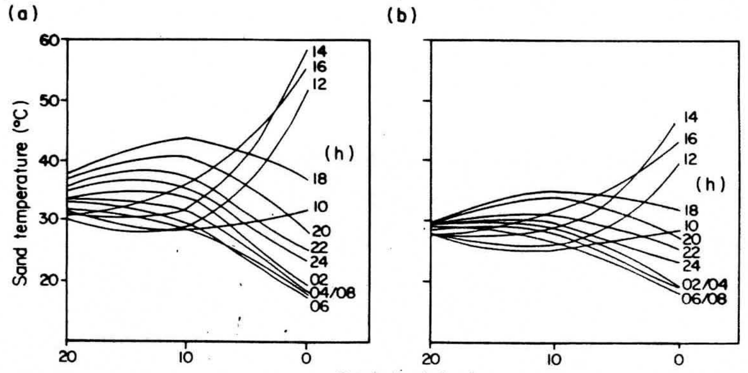

Figure 6. Temperatures of subsurface sand (0–20 cm) in open sand (a) and beneath a clump of *S. sabulicola* (b) on a dune slope in the Namib desert during 19–20 March 1987.

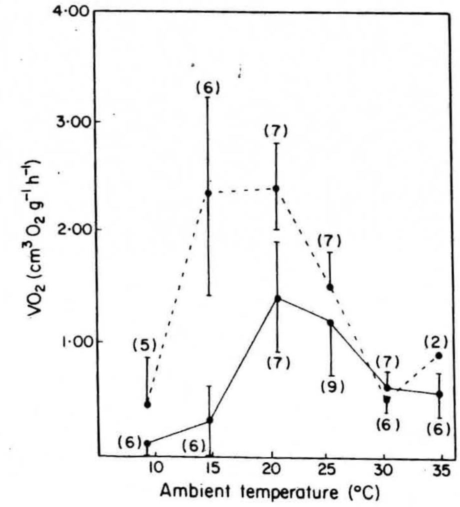

Figure 7. Oxygen consumption of *E.g. namibensis* in (solid line) and out (broken line) of sand at different ambient temperatures. Results expressed as mean (±S.D.). Number in parentheses indicates sample size.

For moles in sand, a thermoneutral zone rather than point was evident. Thermoneutrality was estimated to lie between Ta 31–36°C, since no statistical difference was observed between VO_2 at these temperatures ($t = 0{\cdot}46$; $\mathrm{df} = 11$; $p > 0{\cdot}05$). The average resting metabolic rate in thermoneutrality was 0·59 (S.D. ± 0·2) $\mathrm{cm}^3\ O_2\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}$ which was not significantly different from the basal out of sand metabolism ($t = 0.69$; $\mathrm{df} = 17$; $p > 0{\cdot}05$). Below thermoneutrality, changes in VO_2 followed a similar pattern to that recorded previously except that rates of metabolism were significantly less than those out of sand at Tas below 25°C (Student's *t*-test: $p < 0{\cdot}01$ at 22°C, $p < 0{\cdot}001$ at 15°C, $p < 0{\cdot}05$ at 9°C) and moles were unable to sustain elevated VO_2s at Tas below 20°C.

Body temperatures were extremely labile (range 10·9–37·7°C) and varied directly with Ta (Fig. 8). The slope of the regression of Tb on Ta for moles in sand differed significantly from that out of sand ($t = 2{\cdot}12$; $\mathrm{df} = 70$; $p < 0{\cdot}05$) showing that the rate of decline in Tb with decreasing Ta was greater for moles in sand. Body temperatures out of sand were significantly higher than those in sand over the Ta range 31–15°C (Student's *t*-test; $p < 0{\cdot}01$ at 31 and 15°C, $p < 0{\cdot}02$ at 26°C, $p < 0{\cdot}001$ at 22°C). Fatalities from heat exposure occurred at 36°C out of sand but only at 40°C in sand. At these stressful temperatures, the bare feet and nose became bright pink due to peripheral vasodilation, while the throat and chest regions became wet as a result of salivation.

Based on field and laboratory observations, a temperature ethogram for *E.g. namibensis* is given in Table 1. At Tbs as low as 26°C, moles are fully alert and capable of normal coordinated movement. Below 26°C, alertness and coordination began to decline until at Tbs below 15°C, moles are completely unresponsive and make no attempt to dig when placed in sand. Metabolic and behavioural responses at Tbs below 10°C were not investigated.

Thermal conductance

Physical laws of heat exchange (*i.e.* Newton's Law of Cooling) state that the temperature of a body at equilibrium is determined by the rate of heat exchange, the difference between body and ambient temperature, and the thermal conductance, *i.e.* for an animal, $HB = C(Tb - Ta)$ where HP is the rate of heat production and C is thermal conductance.

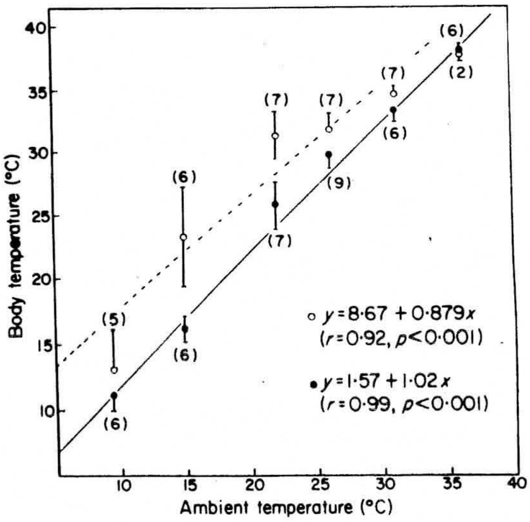

Figure 8. The relation of body to ambient temperature in *E.g. namibensis* during measurements of oxygen consumption. Results expressed as mean (solid circles in sand, open circles out of sand) and S.D. Numbers in parentheses indicate sample size.

The value C is most accurately calculated as $VO_2/(Tb - Ta)$ (McNab, 1980*a*) and such values for *E.g. namibensis* over the various experimental conditions are summarized in Table 2 (measurements include heat loss through evaporation and thus are 'wet conductances'). Both in and out of sand, C varied widely at different Tas due to variable Tb. McNab (1980*a*) has pointed out that in endotherms that regulate body temperature poorly, decrease in C with decrease in Tb and VO_2 is presumably due to a reduced heart rate rather than as a result of an active reduction in conductance *per se*. Thus, when examining differences in C between animals in and out of sand, it seemed inappropriate to make comparisons at Tas with significant discrepancies between VO_2 measurements. For these reasons, comparisons of C were restricted to Tas of 26–31°C. Under such conditions, conductances in sand were found to be significantly higher ($t = 3{\cdot}37$; df = 27; $p < 0{\cdot}01$).

Thermal preferenda

During temperature selection experiments, moles spent most of the time buried in the sand sleeping. Approximately 20% of the time was spent sandswimming or running

Table 1. *Temperature ethogram for* E.g. namibensis *based on field and laboratory observations*

Tb (°C)	Characteristics, behaviour
10–14	Stiff, motionless, completely unresponsive, breathing undetectable.
15–19	Slow and very sluggish movements. Will attempt to dig into sand, capable of vocalization. Weak shivering.
20–25	Moves slowly, movements slightly uncoordinated. Able to dig into sand. Shivers strongly when resting.
26–29	'Normal' movements. Shivers strongly when resting.
30–38	Extremely active. No shivering.
38 +	Salivation, fatality.

Table 2. *Comparison of thermal conductance (C: $cm^3\ O_2\ g^{-1}\ h^{-1}\ °C^{-1}$) for* E.g. namibensis *in and out of sand at different ambient temperatures. Values are mean ± S.D. (N)*

	C	
Ta (°C)	In sand	Out of sand
9	0·04 ± 0·02 (6)	0·08 ± 0·05 (5)
14	0·33 ± 0·39 (6)	0·27 ± 0·07 (6)
22	0·38 ± 0·11 (7)	0·27 ± 0·08 (7)
26	0·45 ± 0·20 (9)	0·30 ± 0·09 (7)
31	0·42 ± 0·16 (7)	0·17 ± 0·06 (6)
36	0·52 ± 0·19 (6)	0·44 ± 0·01 (2)

vigorously on the surface. Four of five animals tested usually selected sand temperatures between 31 and 38°C for resting (Fig. 9). A fifth individual showed a preference for the cooler parts of the thermal gradient and exhibited Tbs of 30·5–19·3°C (Fig. 10) with a mean Tb of 22·1°C (S.D. ± 2·5°C). In contrast, moles favouring warm conditions

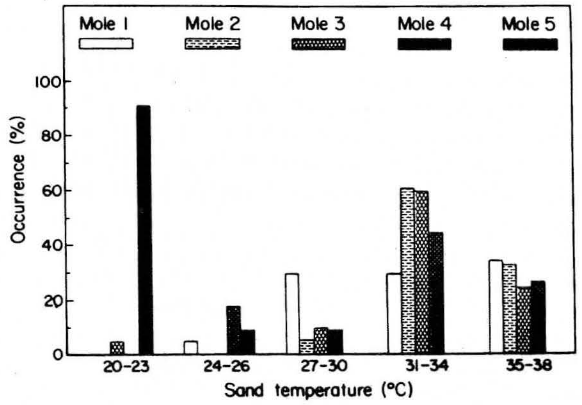

Figure 9. Temperature selection in resting *E.g. namibensis* placed in a thermal gradient for 24 h. Relative frequencies of location of moles in gradient calculated from observations at 1-h intervals.

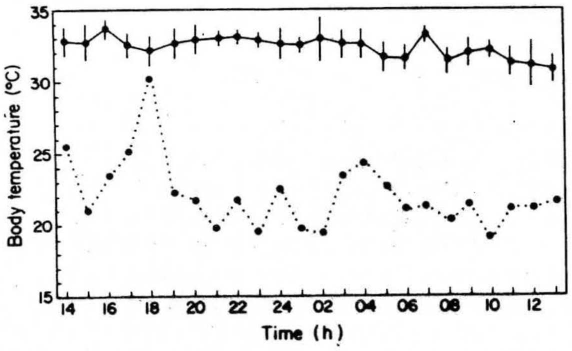

Figure 10. Body temperatures of *E.g. namibensis* during 24 h in a 20–38°C thermal gradient. Means ±S.D. given for moles 1–4 (solid line), mole 5 (broken line).

maintained high and relatively stable Tbs. No significant difference was observed between measurements for these four individuals ($F = 1{\cdot}62$: $df = 3{\cdot}92$; $p > 0{\cdot}05$) with mean Tbs between 30·8 and 30·3°C and averaging 32·4°C (S.D. ± 1·2°C). This value of 32·4°C corresponded closely to the Tb of 33·2°C measured in the lower zone of thermoneutrality for moles submerged in sand (Fig. 8) and is considered to be a 'preferred' temperature.

Diurnal variation in Tb

Diurnal changes in Tb at constant low Ta are shown in Fig. 11. Although there was considerable variation in Tb between the four individuals at every sampling time, a clearly marked daily rhythm in Tb was evident. During the period of darkness, Tbs were considerably lower and less variable than during daylight hours, and generally remained within 1 or 2°C of ambient temperature. Body temperatures were highest between midday and early evening.

Discussion

Primitive or specialised

The lability of VO_2 and Tb in *E.g. namibensis* has previously been shown for the mesic dwelling, but closely related, Cape golden mole *Chrysochloris asiatica* (Withers, 1978) and the Hottentot golden mole *Amblysomus hottentotus* (Kuyper, 1985). Although body temperatures of these two species are somewhat dependent on Ta, they usually choose to maintain a Tb greater than 30°C at ambient temperatures as low as 5°C. Data from the present study indicate that ambient temperatures below 15°C are completely beyond the regulatory capacity of *E.g. namibensis*.

Withers (1978) maintained that the poor thermoregulatory abilities of golden moles is attributable to their evolutionary status as 'primitive mammals' with low metabolic rates representing an intermediate stage between other eutherian mammals (high energy turnover) and reptiles (low energy turnover). However, McNab (1978, 1980*b*) argued convincingly that poor temperature regulation of certain mammalian groups is in fact adaptive and related to environmental factors as opposed to being a phylogenetic legacy.

An examination of the metabolic characteristic of the three chrysochlorid species studied to date (Table 3) favours the arguments of McNab (1978). The higher than expected thermal conductances, together with low Tbs (and in the case of *E.g. namibensis* and *C. asiatica*, lower than expected basal metabolic rates (BMR)) are physiological traits

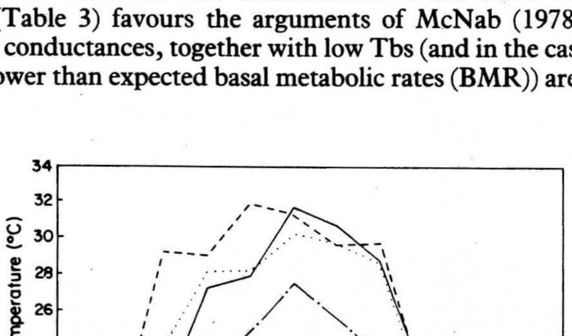

Figure 11. Variation in body temperatures of four *E.g. namibensis* in a constant sand temperature of ±21°C. Sampling times are given along bottom axis. Solid bar indicates period of darkness.

Table 3. *Basal metabolic rates (BMR: $cm^3\ O_2\ g^{-1}\ h^{-1}$), thermal conductances (C: $cm^3\ O_2\ g^{-1}\ h^{-1}\ °C^{-1}$) and body temperatures (Tb: °C of three species of golden moles*

Species	Mass (g)	BMR	% Expected[2]	C[3]	% Expected[4]	Tb[5]	Source
Eremitalpa granti namibensis[1]	26·1	0·52	22	0·30	158	34·7	This study
Amblysomus hottentotus	69·8	1·37	103	0·15	120	33·5	Kuyper, 1979, 1985
Chlorotalpa asiatica	36·0	1·20	62	0·25	151	35·0	Withers, 1978

[1] Values given for animals out of sand.

[2] Expected BMR calculated from BMR = $15{\cdot}67W^{-0{\cdot}582}$ based on values for 26 species of insectivores (Hayssen & Lacy, 1985).

[3] Minimum wet conductance estimated below thermoneutrality at Ta 25°C for *E.g. namibensis* and *C. asiatica* and 20°C for *A. hottentotus*.

[4] Expected C calculated from C = $0{\cdot}760W^{-0{\cdot}426}$ based on values for 180 mammalian species (Bradley & Deavers, 1980).

[5] Body temperature at lower limit of thermoneutrality.

characteristic of many other advanced and highly specialised subterranean taxa (Bradley *et al.*, 1974; Haim & Fairall, 1986; McNab, 1966, 1979; Nevo, 1979) and are believed to have evolved as a result of similar selection pressures concomitant with the subterranean milieu.

The very low basal metabolic rate of *E.g. namibensis* greatly exaggerates the trend found in most subterranean mammals, but seems consistent with the findings of Lovegrove (1986), that aridity related factors are instrumental in selecting for lower metabolic rates in desert species. Specifically which physical or ecological determinant of the Namib dune environment is favouring the unusual physiological traits of *E.g. namibensis* requires an evaluation of existing hypotheses concerning the energetics of subterranean mammals.

Thermal stress hypothesis

Burrows of subterranean mammals are usually near saturation with water vapour (Dubost, 1968; Kennerly, 1964). Under such circumstances, evaporative cooling is unlikely to be of much importance. McNab (1979) proposed that low metabolic rate, high thermal conductance and low body temperature are important mechanisms to prevent overheating in warm humid burrow systems where the potential for evaporative and convective cooling is reduced. Thus in very warm environments, such as those occupied by the naked mole rat, *Heterocephalus glaber* (McNab, 1965), prevention of thermal stress requires such a radical combination of small size, high thermal conductance and low metabolism, that poor thermoregulatory abilities and labile body temperature result.

Relative humidities of between 46 and 25% have been reported at depths of 10 cm in Namib sand dunes (Robinson & Seely, 1980; Seely & Mitchell, 1987), but these values are representative of conditions in relatively dry, highly mobile sand on a dune slipface. Within the confined microenvironment of a mole resting submerged in sand, accumulation of respiratory water vapour may result in near saturation levels. In such a situation, evaporative heat loss may be of little importance. Indeed, heat dissipation by evaporative water loss does not appear to be very effective in *E.g. namibensis,* since even salivating was insufficient to prevent hyperthermia at temperatures above thermoneutrality. Cooling is further hindered by absence of sparsely haired extremities other than the small naked feet and nose. Out of sand, *E.g. namibensis* were not able to tolerate ambient temperatures greater than 35°C, which is several degrees below the 38–40°C typical for small mammals (Hudson & Rummel, 1966; Lee, 1963; McNab & Morrison, 1963), but similar to the 34–36°C range reported for *C. asiatica* (Withers, 1978), *A. hottentotus* (Kuyper, 1979), and other species of subterranean mammals (McNab, 1966).

Thermal conductance, as a measure of the ease of heat transfer from an animal, seldom reflects a constant physiological property but is dependent on environmental variables as well (Tracy, 1971). Thus when submerged in sand, the physical properties of this substrate (high conductivity and high specific heat; Stolzy & Jury, 1982) enhance heat transfer in *E.g. namibensis.* Since higher rates of thermal conductance were not compensated by higher rates of heat production, moles in sand exhibited lower body temperatures than moles out of sand at similar ambient temperatures. The resulting smaller temperature differential (Tb–Ta) effectively extended the thermal tolerance of *E.g. namibensis* to environmental temperatures between 39 and 40°C.

Summer temperatures in the superficial sand layers rise above 40°C, but moles can easily avoid these extremes by burrowing to deeper levels. Mean depths at which moles were excavated in unshaded sand (±19 cm) correspond to summer temperatures averaging 34–35°C measured in the present study to the somewhat lower 32°C reported by Robinson & Seely (1980). These temperatures lie well within the zone of thermoneutrality measured for *E.g. namibensis* in sand. Favourable thermal conditions exist at even shallower depths (± 13 cm) underneath plants. Moles may favour refuge under vegetative cover to minimize required depth for avoidance of stressful temperatures. Furthermore nocturnality allows avoidance of high temperatures when emerged on the sand surface.

For the above reasons, we believe that avoidance of thermal stress is not the main factor favouring lowered metabolic rates and high thermal conductance in *E.g. namibensis,* since it is unlikely that moles are exposed to unfavourable temperatures under natural circumstances. Furthermore, tolerance of *E.g. namibensis* to high temperatures is a consequence of the physical properties of sand. Out of sand, Namib moles show no better ability to cope with stressful temperatures than other chrysochlorid species.

Adaptations to hypoxia and hypercapnia

The primary means of gas exchange in the plugged burrow systems of subterranean mammals is by diffusion through soil (Boggs *et al.*, 1984). Often diffusion is not sufficient to prevent large gradients of respiratory gas build-up, resulting in high CO_2 and low O_2 concentrations (Arieli, 1979; Schaefer & Sadlier, 1979). Low metabolic rates in subterranean mammals may serve to reduce total oxygen demand during hypoxia and decrease dependency upon high diffusion rates through soil (Baudinette, 1972; McNab, 1966; Nevo, 1979).

Compared to other soils, dune sand has a large percentage of total pore space composed of macropores (usually filled with gases) as opposed to micropores (which generally contain water). This permits a faster exchange of water and gases, hence better aeration (Foth & Turk, 1972; Robinson & Seely, 1980). Thus it is unlikely that *E.g. namibensis* is subject to conditions of hypoxia and hypercapnia any more severe than those found in subterranean burrow systems. In support of this conclusion, Arieli *et al.* (1984) found that conditions of hypoxia and hypercapnia in the burrows of the mole rat *Spalax ehrenbergi* decrease with increasing aridity due to a combination of low rainfall and lighter, sandy soils.

Nonetheless, the Namib mole is precluded access to the large gaseous reservoir of a burrow system because of the soft shifting nature of the sand in which it lives. Although good aeration properties of dry dune sand may prevent the development of low O_2 and high CO_2 tensions *per se,* the amount of oxygen available to the mole is limited by the physical constraint of withdrawing sufficient interstitial air from between sandgrains. The very low metabolic rate of *E.g. namibensis* is thus viewed as an adaptation to decrease gaseous exchange where the absolute amount of available air is limited by diffusion rates through sand.

This conclusion is supported by the experimental evidence of the present study. Although the relationship between VO_2 and ambient temperatures for moles in sand was qualitatively similar to that for moles out of sand, metabolic heat production was significantly reduced in sand at ambient temperatures below 25°C. This indicates that the problem of extracting sufficient quantities of air from within sand limits the extent to which metabolic heat production can be increased at low ambient temperatures. Indeed, in sand at temperatures below 20°C, *E.g. namibensis* completely abandons any attempt to thermoregulate. However, field measurements indicate that sand temperatures much below 20°C lie outside of those normally experienced by Namib moles.

Out of sand, *E.g. namibensis* were unable to sustain elevated levels of metabolism below 15°C. Since moles are nocturnally active on the dune surface all year round, air and sand surface temperatures below 15°C may be encountered during winter (Lancaster *et al.*, 1984). However moles usually restrict winter foraging activities to the warm early evening, while in summer they forage throughout the night (unpublished observations).

Cost of burrowing and habitat productivity

The 'energy limitation hypothesis' of Vleck (1979, 1981) proposed that the high cost : benefit ratio of burrowing and the resulting premium on energy conservation (especially in habitats of low productivity), is the primary factor selecting for low metabolic rates and small size in subterranean mammals.

The patchy and sparse distribution of prey resources in the Namib dunes has already been shown to have important implications for the foraging behaviour of the Namib mole (Fielden *et al.*, *in press*). The unusual physiological traits of this small dune insectivore may likewise be linked to minimization of energy expenditure in response to scarce and widely dispersed food resources.

A metabolic rate that is 22% of that expected would considerably reduce overall requirements of moles, and in conjunction with high rates of thermal conductance and small size, open the way to low cost behavioural thermoregulation. Low metabolism and high thermal conductance in *H. glaber* are believed to be similarly involved (Jarvis, 1978). Namib moles exposed to a thermal gradient usually selected temperatures corresponding to those of their thermoneutral zone, thus enabling maintenance of high body temperatures with a minimum of energy expenditure. Measurements of summer sand temperatures indicate that physiologically optimal temperatures (30–36°C) are accessible day and night within the sand column at moderate depths. Thus it is possible at certain times of the year for *E.g. namibensis* to utilize behavioural thermoregulation. When temperatures are lower or higher than preferred, moles can passively offload or gain heat by simply moving to depths which have favourable thermal conditions. Considering the close relationship found between sand and body temperature in wild caught moles, it is significant that individuals caught in summer generally exhibited body temperatures close to their preferred levels.

However, during winter, temperatures within the sand column may lie below the lower limit of thermoneutrality for moles during most of the day. Because of the small size and high rates of thermal conductance of *E.g. namibensis,* especially in sand, maintenance of only moderately high body temperatures requires a considerable increase in metabolic expenditure. Since the high energy demands associated with thermoregulation often augment the problems inherent in energy-sparse environments, natural selection will repeatedly favour the establishment of temporal patterns of energy utilization such as torpor, which allows animals to reduce their energy expenditure and thus total demands for energy and water (Bartholomew, 1972; Lindstedt, 1980).

Maintenance of a low and labile Tb is qualitatively different from true torpor where body temperature is closely regulated during periods of activity and rapidly decreases to almost ambient during periods of reduced metabolism (Hudson, 1973; Hudson & Bartholomew, 1964). Most small mammals which use torpor do so in response to food shortage and/or cold and maintain relatively precise homeothermy at all other times (Hudson, 1973). In contrast, *E.g. namibensis,* even when normally active had body temperatures as low as 27°C. This ability allows *E.g. namibensis* an increased activity range without the necessity for high energy expenditure to maintain a typical eutherian level of body temperature. A criterion distinguishing torpor from hypothermia is the ability of the animal to warm up by means of endogenous heat production (Hayden & Lindberg, 1970). Moles maintained in the laboratory at constant low temperature (±22°C) were able to rewarm spontaneously to body temperatures as high as 10°C above ambient, with arousal invariably occurring near to midday, and elevated temperatures being maintained till late evening. This daily cycle of rewarming seems consistent with the concept of a circadian clock (Nicoll, 1986) and qualitatively similar to the diurnal torpor employed routinely in the presence of adequate food in other small mammals including small insectivorous marsupials (Dawson & Wolfers, 1978; Geiser, 1986; Morton & Lee, 1978), shrews (Frey & Vogel, 1978), rodents (Hill, 1975) and bats (Lyman, 1970). The indication of a circadian rhythm involving torpor in *E.g. namibensis* begs the answer of its possible role under natural conditions.

The diel variation in body temperature in the laboratory independent of ambient was qualitatively similar to the rise and fall of body temperature of a mole kept in a bucket of sand exposed to the natural thermal fluctuations of the dune environment. In the laboratory, elevation of body temperature was achieved by internal heat production, whereas in the bucket buried in a dune, rewarming was facilitated by an external heat source. In both situations moles had elevated body temperatures to coincide with the start of nocturnal activity. It is suggested that during winter, when favourable sand temperatures are not always accessible, moles employ a daily cycle of torpor attuned to the daily warming and cooling pattern of the undersand environment. Field evidence lends support to this supposition.

In contrast to summer, winter caught moles, excavated during mid-morning, exhibited low body temperatures (<25°C) reflecting the cool conditions in the sand column at this time. With the heating of the dune surface later in the day, movement to shallower parts of the sand column would enable moles to employ passive means to elevate body temperatures for nocturnal foraging periods. However, Robinson & Seely (1980) report considerably cooler thermal conditions in winter (Ta = 22·9°C at 20 cm deep) than those measured in this study. Under these circumstances, moles would have to place increased reliance on internal heat production for elevation of body temperatures to levels sufficiently high to enable evening activity.

Summary

The unusual metabolic traits of *E.b. namibensis* greatly exaggerate physiological trends found in most other subterranean mammals, including other chrysochlorids. The extremely low metabolic rate and resulting thermolability of *E.g. namibensis* are not viewed as a manifestation of a primitive phylogeny but rather as adaptations to fossoriality in an energy sparse and arid sand dune environment. Tolerance of stressful temperatures is affected primarily by behavioural rather than physiological means, i.e. nocturnal activity and selection of favourable microclimates within the sand column. For these reasons, largely non-thermoregulatory determinants are suggested as selecting for the physiological traits of *E.g. namibensis*. A low metabolic rate is of advantage in an undersand environment where gaseous exchange is limited. Furthermore, a low metabolic rate reduces energy expenditure, and together with high thermal conductance and small size, enables the utilization of low cost behavioural thermoregulation. Employment of diurnal torpor may be an additional energy conserving mechanism associated with seasonal changes in the thermal regime of the undersand environment.

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