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THE IMPORTANCE OF MICROHABITAT IN THERMOREGULATION AND THERMAL CONDUCTANCE IN TWO NAMIB RODENTS—A CREVICE DWELLER, *AETHOMYS NAMAQUENSIS*, AND A BURROW DWELLER, *GERBILLURUS PAEBA*

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Abstract—1. Thermoregulatory measurements of two Namib rodents; *Gerbillurus paeba*, a burrow dweller, and *Aethomys namaquensis*, a crevice dweller were compared. Both were similar to other small arid-adapted rodents in that basal metabolic rates were reduced, thermoneutral zones narrow and evaporative water losses low. Rates of conductance and thermal lability, however, at ambient temperatures (T_a) below the thermoneutral zone, were significantly different ($P \leqslant 0.01$).

2. The rock rat *A. namaquensis*, living in a microclimate characterized by a large diel range and low humidities, compensates for a reduced basal metabolic rate by having a low rate of conductance. In this way it maintains precise thermoregulatory control. *G. paeba*, on the other hand, living in a thermally-stable milieu, does not control body temperature precisely. This animal instead utilizes a high rate of conductance to remove metabolic heat produced within the body. This would be advantageous to an animal living in a plugged burrow where the high humidities encountered impede the rate of evaporative cooling.

3. The energetic responses of both species, above the thermoneutral zone, appear to reflect very closely the environmental conditions which occur in the microhabitat that they rest in during the day. *G. paeba* shows less tolerance to temperature fluctuations than *A. namaquensis*, but shows more marked increases in short-term cooling mechanisms at high T_as.

4. Despite the increased use of evaporative cooling through salivation and panting in addition to pulmocutaneous evaporation, exposure to T_as above 38°C is rapidly lethal to *G. paeba*.

Key Word Index—Thermoregulation; thermal conductance; metabolic rate; evaporative water loss; crevice dweller; burrow dweller; *Aethomys namaquensis*; *Gerbillurus paeba*; Namib; desert.

INTRODUCTION

Interspersed amongst the characteristic red sand dunes of the Namib desert are gravel plains and numerous rocky outcrops called Kopjies or inselbergs (Logan, 1960). *Aethomys namaquensis*, the rock rat, is the predominant rodent on the rocky outcrops of the eastern side of the desert (Coetzee, 1969). Unlike most rodents in the Namib, the rock rat does not excavate burrows but rather utilizes rock crevices as a shelter from predation and intense solar radiation, leaving this sanctuary after dark to forage (Roberts, 1951).

Gerbillurus paeba, the pigmy gerbil, is the most abundant gerbil on the lower slopes and in the troughs of the sand dunes. Here, it excavates simple burrows, measuring approx. 30–40 mm in diameter and 2.5 m in length, to depths of approx. 20 cm (De Graaff and Nel, 1965). The entrance of the burrow is plugged with sand during the day, so providing not only a shelter from predators and radiation but also a microhabitat, where changes in light, temperature and humidity, like that of gophers, are negligible (Kennerly, 1964; McNab, 1966).

Whilst literature on thermoregulation in rodents is generally abundant [see Hart (1971) and McNab (1983) for reviews], there is a dearth of information concerning African rodents. Furthermore, whilst energetics of fossorial and semi-fossorial rodents have received much attention (Hart, 1971; Bradley and Yousef, 1972; McNab, 1979a), a comparison of the effects of microhabitat on thermoregulation and associated parameters has not been previously examined.

This paper attempts to examine whether there are significant differences in thermoregulation that may be attributed to the open crevice microhabitat of *A. namaquensis* and the sheltered burrow microhabitat of *G. paeba*.

MATERIALS AND METHODS

Animals were trapped in the Namib Park near Tumasberg (23°29′S, 15°32′E), and near Gobabeb (23°34′S, 15°03′E). The climate of these areas has been described by Schulze and McGee (1978).

For 2 months prior to the experiment, 15 *G. paeba* and 15 *A. namaquensis* were kept individually in cages floored with fine sand and containing a nest box. These cages were placed in an air-conditioned room with a 12L:12D photoperiod at a temperature of 20–26°C and an r.h. of 44–50%. The rodents were fed an *ad libitum* diet of mixed bird seed. Water was provided in the form of fresh vegetables. During this period body mass was regularly monitored to the nearest 0.01 g.

The effect of ambient temperature (T_a) on body temperature (T_b), O$_2$ consumption ($\dot{V}_{O_2}$) and evaporative water loss (EWL) were all monitored during daylight hours when the rodents are normally inactive.

Body temperature (T_b)

T_b was monitored by inserting a Cu–constantan thermocouple approx. 2 cm into the rectum. The rodents were given 4 h to become thermally equilibrated before T_a was recorded. At T_as above 40°C, this equilibration period was reduced to 2.5 h.

O_2 consumption ($\dot{V}_{O_2}$)

$\dot{V}_{O_2}$ and EWL were measured simultaneously over T_as of 12–41°C in 15 gerbils and 15 rock rats, using an open-flow system (as described in Buffenstein and Jarvis, 1984). Air flowed through the Perspex respiratory chamber at 200 $cm^3.min^{-1}$ and then over an r.h. probe (Vaisala humicap HM1-14) before being dried over silica gel and fed into an O_2 analyser (S-3A, O_2 analyser, N-37 O_2 sensor, Applied Electrochemistry Inc.). The O_2 analyser, thermocouples and r.h. probe were connected to a data-logger (Esterline Angus P.D. 2064) which was programmed to record at 5-min intervals.

At each new T_a the animal was allowed to equilibrate for 1 h. Thereafter, $\dot{V}_{O_2}$ was monitored for at least 3 h. At each T_a, the lowest six readings for each animal, corrected to STP were used in calculating the post-absorptive resting minimal metabolic rate. Rectal temperatures (T_{re}) were taken immediately after each run.

Evaporative water loss (EWL)

The change in r.h. between the air leaving the experimental chamber and the control was used to determine the EWL using the equation:

$$\mathrm{EWL} = \frac{\mathrm{CTA.RH}.F.60}{1000.100.M}, \tag{1}$$

where EWL is water loss ($mgH_2O.g^{-1}.h^{-1}$), CTA is the mass of water in saturated air at the T_a, ($g.cm^{-3}$), RH is the change in r.h. caused by the animal (%), F is the flow rate ($cm^3.min^{-1}$) and M is the mass of the mouse (g).

So as to avoid damage to the O_2 sensor, no mineral oil was placed beneath the mesh in the respiratory chamber. During the experimental run, the chamber was frequently examined through a viewing port in the outer temperature control chamber. If the rodent had roused and urinated, the run was interrupted, the apparatus cleaned and dried and left to equilibrate for 20 min. As most rodents urinated on handling, prior to being placed in the chamber, such interruptions were infrequent.

Respiratory frequency (RF)

RF (breaths.min^{-1}) was monitored whilst measuring $\dot{V}_{O_2}$. It was calculated from the mean of 10 counts of the number of breaths taken in 30 s.

Dry thermal conductance (Cd)

Cd was calculated according to Dawson and Schmidt-Nielsen (1966):

$$\mathrm{Cd} = \frac{\mathrm{HP} - \mathrm{EHL}}{T.S}, \tag{2}$$

where Cd is dry thermal conductance ($J.cm^{-2}.°C^{-1}.h^{-1}$), HP is metabolic heat production ($J.h^{-1}$) assuming 1 cm^3 O_2 is equal to 20.1 J, EHL is evaporative heat loss ($J.h^{-1}$) assuming 1 mg water is equal to 2.34 J, T is the temperature difference between T_b and T_a (°C), and S is surface area of a mouse (cm^2) where $S = 10 \times$ animal $\mathrm{mass}^{0.67}$ (g).

Minimal "wet" conductance (Cm)

Cm, i.e. including EWL, is calculated using the equation of McNab (1980):

$$\mathrm{Cm} = \frac{\dot{V}_{O_2}}{T_b - T_a}, \tag{3}$$

where Cm is the rate of minimal conductance ($cm^3O_2.g^{-1}.°C^{-1}.h^{-1}$) and $\dot{V}_{O_2}$ is the rate of O_2 consumption ($cm^3O_2.g^{-1}.h^{-1}$).

Cm was also calculated from the slope of the graph relating $\dot{V}_{O_2}$ with T_a, below the region of thermoneutrality, using McNab's (1980) correction factor.

All values are presented as means and standard errors. Zar (1974) was consulted in calculating the linear regressions and the relevant t-tests used. A probability of less than 0.05 was taken as the level of significance.

RESULTS

Body temperature (T_b)

Within the T_a range from 10–33°C, mean T_b in *A. namaquensis* remains fairly constant (Table 1). *G. paeba* on the other hand was more thermolabile. T_b was independent of T_a between 25.5 and 34°C, and was similar to that exhibited by *A. namaquensis*. Below 25.5°C, T_b was dependent on T_a and can be described by the equation

$$y = 29.08 + 0.30x, \quad r = 0.99\ (n = 6), \tag{4}$$

where y = mean T_b and x = mean T_a. Above T_as of 34°C T_b increased with increasing T_a in both species (Fig. 1). Although the mean rate of increase in *G. paeba* [$y = 11.32 + 0.76x$, $r = 0.99$, $(n = 4)$] appears to be greater than that of *A. namaquensis* [$y = 15.76 + 0.64x$, $r = 0.99$, $(n = 4)$] it was not significantly different ($P \geqslant 0.10$).

O_2 consumption ($\dot{V}_{O_2}$)

A. namaquensis. $\dot{V}_{O_2}$ of *A. namaquensis* was minimal (0.89 ± 0.04 $cm^3O_2.g^{-1}.h^{-1}$) between T_a = 31.6°C and T_a = 34.2°C, so indicating a fairly small thermal neutral zone. A regression line (as shown by the line AB in Fig. 2a), fitted by the method of least squares to the data below those in the thermoneutral zone, is described by the equation

$$y = 2.780 - 0.060x, \quad r = 0.85\ (n = 49). \tag{5}$$

where [for equations (5)–(8)] $y = \dot{V}_{O_2}$ ($cm^3O_2.g^{-1}.h^{-1}$) and x = temperature (°C). This line

Table 1. Comparison of some aspects of thermoregulation in a crevice dweller, *A. namaquensis*, and a burrow dweller, *G. paeba*

	A. namaquensis	*G. paeba*
Mass (g)	48.37 ± 11.64	31.13 ± 5.28
T_a range in which T_b is independent (°C)	10.0–33.0	25.0–34.0
T_{NZ} (°C)	31.6–34.2	33.3–35.6
Independent T_b (°C)	36.4 ± 0.81	36.64 ± 0.86
BMR ($ml\,O_2.g^{-1}.h^{-1}$)	0.89 ± 0.13	0.89 ± 0.20
EWL ($ml\,H_2O.ml\,O_2^{-1}$)	0.90 ± 0.45	0.93 ± 0.29
Cm.10^{-1} ($cm^3\,O_2.g^{-1}.h^{-1}.°C^{-1}$)	0.98 ± 0.29	1.56 ± 0.30
Cd.10^{-1} at $T_a < 30°C$ ($J.cm^2.h^{-1}.°C^{-1}$)	0.16 ± 0.05	0.31 ± 0.07
Cd.10^{-1} at $T_a = 38°C$ ($J.cm^2.h^{-1}.°C^{-1}$)	1.13 ± 0.30	0.85 ± 0.45

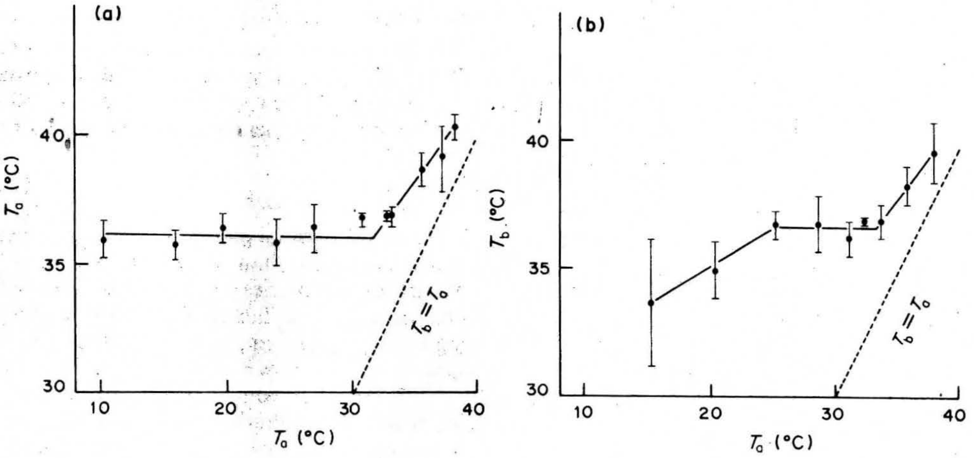

Fig. 1. Effects of T_a on T_b in (a) *A. namaquensis* and (b) *G. paeba*.

(5) intercepts the ordinate at 3.14 times the basic metabolic rate (BMR).

At T_as above the thermoneutral zone, $\dot{V}_{O_2}$ increased linearly (as shown by the line CD). These increases may be described by the equation

$$y = -7.345 + 0.241x, \quad r = 0.65\,(n = 23). \quad (6)$$

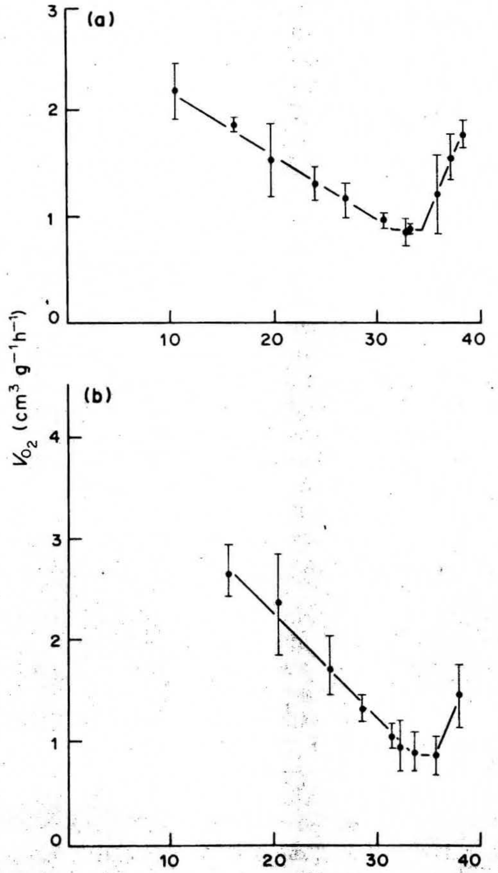

Fig. 2. Effects of T_a on $\dot{V}_{O_2}$ in (a) *A. namaquensis* and (b) *G. paeba*.

G. paeba. $\dot{V}_{O_2}$ decreased with increasing T_a in the temperature range 15–30°C (Fig. 2b). This decrease in $\dot{V}_{O_2}$ (as shown by the line AB in Fig. 2b) is described by the equation

$$y = 4.363 - 0.104x, \quad r = 0.84\,(n = 36). \quad (7)$$

At T_as > 35°C, $\dot{V}_{O_2}$ increased linearly (line CD, Fig. 2b) and may be described by the equation

$$y = -7.688 + 0.241x, \quad r = 0.75\,(n = 15). \quad (8)$$

There was a fair amount of individual variability in $\dot{V}_{O_2}$ between 32 and 36°C and for this reason the zone of thermoneutrality was not easily defined. The mean $\dot{V}_{O_2}$ in this range was 0.886 ± 0.200 cm^{3}O$_2$.g^{-1}.h^{-1}; $n = 24$). Using the two equations describing $\dot{V}_{O_2}$, this value corresponds to T_as of 33.25 and 35.64°C. It is possible that the thermoneutral zone was smaller than this range and was not accurately detected as no measurements were made at that particular temperature. Nevertheless, the measured BMR value was 62% of that predicted by mass from Kleiber's (1975) equation.

BMR values (expressed as a percentage of that predicted by mass) for *A. namaquensis* (67.55 ± 8.33, $n = 10$) did not differ significantly ($P \geqslant 0.10$) from *G. paeba*, $\dot{V}_{O_2}$s at temperatures greater than the thermoneutral zone were also not significantly different ($P \geqslant 0.10$) in the two species. However, at temperatures below the thermoneutral zone, the slopes of the two equations (5, 7) were significantly different ($P \leqslant 0.01$).

Respiratory frequency (RF)

RF shows similar trends to that of $\dot{V}_{O_2}$. Below 24°C, RF was proportional to T_a in both species (Fig. 3). RFs at 25°C were not significantly different. However, at 38°C RF in *G. paeba* was significantly greater ($P \leqslant 0.05$), than that exhibited by *A. namaquensis*.

Evaporative water loss (EWL)

The patterns of EWL below the region of thermoneutrality (Table 1) in both species were similar ($P \geqslant 0.10$). Above 33°C EWL increased considerably and individual variation was marked (Fig. 4). Both

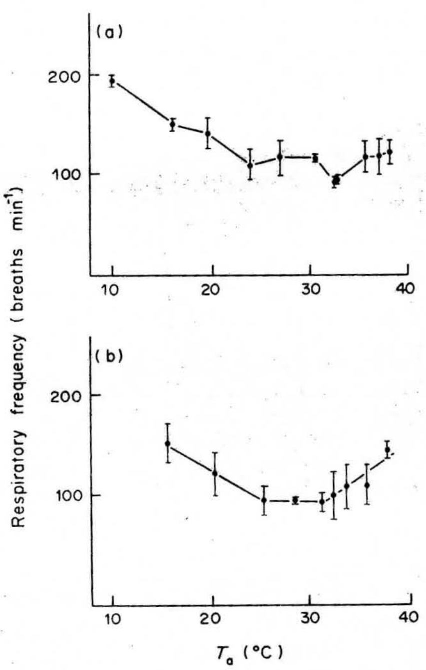

Fig. 3. Changes in RF in (a) *A. namaquensis* and (b) *G. paeba* with changes in T_a.

species behaviourally increased evaporation by licking their bodies. Despite the fact that licking of fur was more pronounced in *A. namaquensis* than *G. paeba*, the latter dissipated more heat through evaporative cooling ($P \leqslant 0.001$), primarily through "insensible perspiration". At the highest T_as measured, EWL accounted for 40.1% of the total heat produced in *G. paeba*, whereas it only accounted for 25.5% of the heat produced in *A. namaquensis*.

Minimal conductance (Cm)

Cm values for both species were fairly constant below thermoneutrality. Mean Cm for *G. paeba* between 20–30°C was significantly different to that in *A. namaquensis* ($P \leqslant 0.001$).

Cm values were also estimated from the slope of the equation relating $\dot{V}_{O_2}$ and T_a below the region of thermoneutrality using McNab's (1980) correction factor:

$$\mathrm{Cm} = \mathrm{Cf}\,(0.06\ \copyright T + 1.00), \qquad (9)$$

where Cm is the minimal conductance (cm^{3}O$_2$.g^{-1}.°C^{-1}·h^{-1}), Cf the fitted conductance from the slope of the line and $\copyright T$ is the over-estimation of T_b from the intercept on the abcissa. The Cm value for *A. namaquensis* estimated this way (0.096) was similar to the mean Cm value (0.098) calculated. There was however a larger discrepancy between that estimated (0.144) and that obtained (0.156) for *G. paeba*. This discrepancy may by explained by the more labile T_bs found in this gerbil and their effect on the rates of conductance. McNab (1980) suggested that in rodents that do not precisely maintain T_b, Cm derived from the slope of the line relating $\dot{V}_{O_2}$ to T_a will be an underestimate, and less accurate than that obtained from individual measurements, and this proved to be true for *G. paeba*.

Dry conductance (Cd)

Below thermoneutrality, at temperatures less than 30°C, Cd in both species was fairly constant but significantly different ($P \leqslant 0.002$). Above 30°C thermal conductance increased in both species (Table 1, Fig. 5).

Behavioural responses

During the resting phase, *A. namaquensis* was more easily disturbed than *G. paeba*. However, if not disturbed both species would remain inactive for long periods of time so facilitating measurements of resting rates. At low temperatures both species adopted spheripsoid postures and shivering was also observed.

Both species responded to increases in temperature beyond 30°C by altering their posture, so increasing their exposed surface area. As T_a increased further, both species were observed to pant and salivate. *A. namaquensis* licked most of its body until the fur appeared wet and matted, whereas *G. paeba* did not do this to the same extent but did exhibit more pronounced panting. *G. paeba* became very restless at

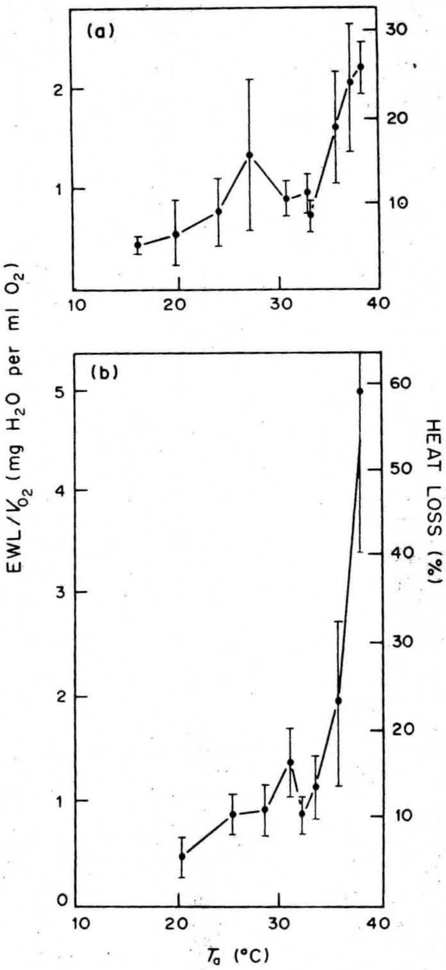

Fig. 4. The effect of T_a on (i) (left-hand ordinate) the ratios of EWL to simultaneous $\dot{V}_{O_2}$ and (ii) (right-hand ordinate) EHL as a percentage of HP in (a) *A. namaquensis* and (b) *G. paeba*. Values of 2.34 J.mg^{-1} H$_2$O and 20.1 J.cm^{-3} O$_2$ were used to convert EWL and $\dot{V}_{O_2}$ to thermal units.

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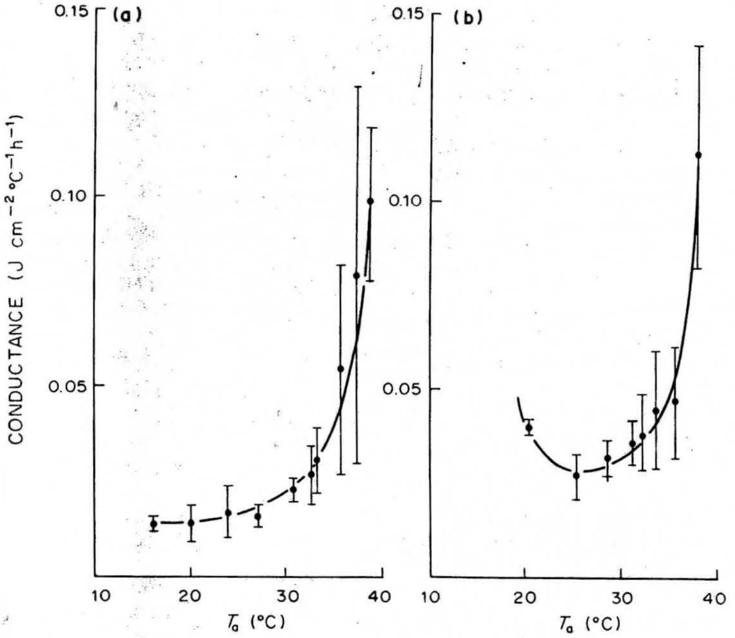

Fig. 5. Sensible thermal conductance of (a) *A. namaquensis* and (b) *G. paeba* at various T_as.

high T_a and spent long periods in frantic activity trying to escape from the chamber. These rodents succumbed rapidly (within 1.5 h) to a T_a of 38°C. *A. namaquensis*, on the other hand, appeared to be more tolerant of increased T_as. It was less restless, lying prostrate for long periods and no fatalities occurred over the same temperature range, despite the fact that these rodents remained in the chamber for considerably longer periods (4 h).

DISCUSSION

Despite the fact that *A. namaquensis* is a recent invader (Meester, 1965) of the extremely arid Namib desert, both this species and *G. paeba* (a long-term resident) appear to be well adapted to the desert and conform to trends found in most arid-adapted rodents (Hart, 1971); Borut and Shkolnik, 1974; McNab, 1979b), having narrow thermoneutral zones, low rates of EWL and reduced BMRs. These reduced rates are adaptive features in response to the limited resources in these harsh environments (Bradley *et al.*, 1974).

Recorded T_b for *A. namaquensis*, over the experimental T_as of 10–33°C, fell within the range expected for typical eutherian mammals (Schmidt-Nielsen, 1975). This thermostability shown by *A. namaquensis* implies that it has a thermoregulatory capacity adequate to meet changes in T_a. Even when resting, in its natural milieu, it is exposed to large diel temperature variations (±12°C, personal observation; and Withers, 1979) and it is therefore advantageous to maintain its independence of T_a.

G. paeba on the other hand, lives in a fairly deep burrow where T_a is relatively constant (30 ± 1.0°C, personal observation). In this study it did not show precise thermoregulatory control. At $T_a\text{s} < 24°\text{C}$, T_b was directly proportional to T_a. Nel and Rautenbach (1977) reported similar T_b variability for this species.

Differences in thermoregulatory control may be explained by the large differences in conductance between the two species ($P \leqslant 0.001$).

Cm below thermoneutrality was relatively constant in both species. In *G. paeba*, Cm deviated by 7.27% from the predicted rate (Aschoff, 1981). This small difference indicates that *G. paeba* is as efficient as expected in its employment of physical thermoregulation and so conforms to the trends of conductance rates in most burrow dwellers. High Cm is advantageous in the burrow context, for it limits heat storage. This reduces the chances of thermal death in an atmosphere characterized by high humidities which preclude the efficient use of evaporative cooling.

Cm values for *A. namaquensis* were significantly lower than those of *G. paeba*. Its Cm deviated markedly (−26.8%) from that expected from Aschoff's (1981) allometric equation, suggesting that its powers of insulation are better than expected. This would be highly advantageous for a rodent living in a rock crevice where temperatures are neither as stable nor as insulated from environmental changes as those in a plugged burrow. A low Cm under these circumstances is adaptive in that it reduces the rate of heat loss (and hence additional energy requirements for chemical thermoregulation) at low T_as, whilst also limiting the rate of physical heat gain at temperatures within the thermoneutral zone.

The ratio of the percentage expected metabolism and the percentage expected Cm is a measure of the temperature differential between a homeotherm and the environment at the lower limit of thermoneutrality. This ratio may be used as an indicator of the ability to maintain homeothermy (Bradley and Yousef, 1975). A ratio of approx. 1, as shown by

A. namaquensis (0.96), is indicative of well-developed endothermy. This confirms that *A. namaquensis* has balanced its low BMR with high insulative properties (low conductance) to meet the demands of its environment.

G. paeba did not precisely maintain homeothermy. Considering that *G. paeba* is nocturnal, this labile T_b seems strange, for the animal would have to contend with low T_as at night. Perhaps exercise at night is important in maintaining an elevated T_b. In the confines of the thermally-stable milieu *G. paeba* normally encounters when resting however, high Cm and low BMRs, in conjunction with the high burrow temperatures, are adequate in maintaining endothermy. This degree of homeothermy as indicated by an *F*-ratio of 0.67, whilst enough for its needs in the warm burrow context, is however, insufficient for maintaining T_b at low T_as. Non-precise temperature regulation, when considered in conjunction with a BMR 57% of the predicted minimum required for maintenance of endothermy (McNab, 1983), suggests that *G. paeba* employs torpor.

A. namaquensis was less sensitive to extreme temperature fluctuations than *G. paeba*. This finding is suggested by the fact that no deaths occurred in *A. namaquensis* at the highest temperatures monitored, whereas 3 gerbils died within 1.5 h of exposure to this T_a. At T_as between the thermoneutral zone and 38°C, T_b increased with increasing T_a in both species. This hyperthermia, when converted to absolute quantities of heat stored using the specific heat capacity of mammalian tissue of $3.5\ \mathrm{J.g^{-1}.°C^{-1}}$ (Mount, 1979), would save $0.264\ \mathrm{cm^3\ H_2O}$, in *A. namaquensis* and $0.139\ \mathrm{cm^3\ H_2O.h^{-1}}$ in *G. paeba* at a T_a of 37.5°C. *A. namaquensis* weighs 1.5 times as much as *G. paeba*. Proportionately greater tolerance to hyperthermia is therefore expected in view of its larger "heat sink". *A. namaquensis*, however, stores more than 1.5 times as much heat, confirming that it is in fact more tolerant of hyperthermia than *G. paeba*.

Despite tolerance to hyperthermia, however, both species resorted to short-term emergency evaporative cooling and increased conductance as a physiological defence mechanism against extreme heat. Small body size precludes the use of evaporative cooling alone as a homeostatic mechanism because of the relationship between surface area, heat load and transpiration (Mares *et al.*, 1977). *A. namaquensis* was more parsimonious in EWL ($P \leqslant 0.001$) than *G. paeba*, dissipating 64% of that used by *G. paeba* in cooling at the highest temperatures monitored. Both *G. paeba* and *A. namaquensis* substantially increased EWL by salivation and panting. Panting, as reflected by the substantial increase in RF, was more pronounced in *G. paeba*. In the confines of a plugged burrow, however, the high rates of EWL shown in the laboratory may be markedly reduced as EWL is impeded by high ambient humidities.

Above thermoneutrality, rate of heat loss was enhanced by increased conductance. This was facilitated by physiological, morphological and behavioural means. At high temperatures, *A. namaquensis* was observed grooming its fur so as to mat it. By incorporating all the above-mentioned means, this species was able to increase its Cd to three times the thermoneutral zone value and so overcome the morphological and physiological properties it possesses for normally maintaining low rates of conductance. Greater tolerance to high T_as is interpreted as a physiological adaptation related to the conditions it frequently encounters in its milieu during the day.

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