

Thermoregulation of the subterranean rodent genus *Bathyergus* (Bathyergidae)

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The thermoregulation of the largest subterranean rodent, genus *Bathyergus*, comprising two species, *B. suillus* and *B. janetta*, occurring in mesic and semi-arid habitats respectively, was investigated and compared with that of other subterranean rodents. Both species display low resting metabolic rates and low body temperatures characteristic of subterranean rodents. The lower metabolism and smaller body size of *B. janetta*, may be an 'energy-saving' adaptation to its semi-arid habitat.

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Termoregulering in die grootste ondergrondse knaagdier, genus *Bathyergus*, wat uit twee spesies, *B. suillus* en *B. janetta*, bestaan, is ondersoek en met die van ander ondergrondse knaagdiere vergelyk. *B. suillus* en *B. janetta* kom onderskeidelik in gematigde en droë streke voor. Beide spesies vertoon lae rustende metaboliese tempo's en lae liggaamstemperatuur, wat kenmerkend is van ondergrondse knaagdiere. Die laer metabolisme en kleiner liggaamsgrootte van *B. janetta* mag 'n energiebesparingsaanpassing by sy droë habitat wees.

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Subterranean rodents spend their lives underground in closed burrows, rarely, if ever, coming on to the surface (Nevo 1979). The commitment of these animals to a subterranean existence is reflected in several convergent structural and functional adaptations within the subterranean taxa (Ellerman 1956; McNab 1966; Dubost 1968; Nevo 1979). For instance, they show distinctive physiological traits, such as low body temperature (T_b), low resting metabolic rate (RMR), and high conductance (C_m) (McNab 1979, for general review). Various hypotheses have been proposed to explain these unusual physiological states.

It has been suggested that the combination of low RMR, low T_b , and high C_m , reduces the possibility of overheating in burrows where evaporative cooling and convection play minor thermoregulatory roles (McNab 1966; MacMillen & Lee 1970; McNab 1979). A low RMR could represent an adaptation to hypoxia and hypercapnia (Arielli 1979; Arielli, Arielli, Heth & Nevo 1984). Finally, it has been suggested that a low resting metabolic rate may represent an energy-saving adaptation in response to the enormous energetic cost of burrowing (Vleck 1979, 1981), and limited food availability and resource patchiness (Jarvis 1978).

The task of establishing the relative roles and influences of each of the above possible physiological determinants, as well as the possible interplay between them, is very difficult. One approach is to investigate interspecific comparisons of the ecophysiological characteristics of subterranean mammals differing in body size, social status, and habitat.

This paper examines the thermoregulation of the genus *Bathyergus*, which is represented by two solitary species *B. suillus*, and *B. janetta*, occurring allopatrically in mesic and semi-arid habitats respectively, in the western Cape Province of South Africa. *B. suillus* is probably the largest extant subterranean rodent. The data obtained from this study should therefore assist the future determination and interpretation of the allometry of the metabolism of subterranean rodents.

Methods

The Namaqua dune mole rat *B. janetta* is rare, and is listed in the 'South African Red Data Book' of rare and endangered species. Its distribution is limited to the loose, calcareous sand dunes along the north-western Cape coast, from Port Nolloth to the Orange River (De Graaff 1981). This region is arid to semi-arid, with cool, moist oceanic winds and fog providing frequent relief from high temperatures and low relative humidity (Louw & Seely 1982).

Ten *B. janetta* were trapped near Oranjemund, Namibia, in December 1983. Each animal occupied its own burrow

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system (Jarvis & Lovegrove, unpubl.) contrary to the notion that this species is social (De Graaff 1981). Solitary animals were housed in 32 × 60 cm glass terraria under a continuous light at 23°C for at least two months prior to experimentation, and were fed on fresh grasses, herbaceous plants, chopped vegetables, and 'Pronutro' (Cerebos Food Corporation Ltd., Wadeville), a nutritionally-balanced cereal food. A 5–6 cm layer of dry sandy soil was placed in the bottom of the terraria every two days. The molerats regularly shifted the sand around the cages, but were unable to actually construct burrows. Of the 10 molerats, only three, one male and two females, survived. After losing weight for the first two weeks, they regained capture weights (354 g, 380 g, and 485 g) and thereafter remained in good condition prior to, and including the entire experimental period.

The Cape dune molerat, *B. suillus*, occurs in the mediterranean winter rainfall region of the western Cape, South Africa, wherever loose coastal calcereous sand dunes and sand flats are present (De Graaff 1981). De Graaff (1981) describes *B. suillus* as living in small colonies of two to five individuals, but again, Davies & Jarvis (1986) found this species to be strictly solitary. De Graaff (1981) also gives mean body masses of 750 g for males, and 500 g for females, whereas Davies & Jarvis (1986) give mean masses obtained from larger sample sizes of 933 g for males (maximum recorded: 1700 g), and 635 g for females.

In April 1984 eight *B. suillus* were trapped at various localities in the western Cape. Solitary animals were housed in 44 × 90 cm fibreglass tanks, and were kept under the same conditions and fed the same diet as *B. janetta*. Four animals, two males and two females, maintained weights (520 g, 633 g, 703 g and 800 g) throughout the experimental period, and were used to measure metabolic rate. In addition, eight metabolic measurements were obtained from a large 1004-g male before it began to lose weight and condition.

In general, molerats of the genus *Bathyergus*, particularly the rare *B. janetta*, do not adapt well to captivity and seem to require a long period of adjustment before body weights stabilize. This is a serious problem with respect to obtaining large sample sizes, which can only really be achieved at the expense of high mortality in captivity.

Oxygen consumption ($\dot{V}O_2$) was measured at ambient temperatures (T_a) of 13–34°C using a negative pressure flow-through system. The respirometer was a transparent 4,54 l cylindrical perspex chamber fitted with a plastic base-plate and 6 mm inlet and outlet ports, and was placed inside a 110 l temperature-controlled cabinet. Air was drawn through the respirometer at a constant rate of 900 and 1200 cm³min⁻¹ for *B. janetta* and *B. suillus* respectively. Airflow was monitored with a calibrated 'Rotameter 1100' flow-meter placed downstream from the respirometer, but upstream from a set of CO₂ and H₂O scrubbers. A subsample of the expired air was drawn off downstream from the gas scrubbers and analysed with an 'Applied Electrochemistry S-3A' oxygen analyser. An 'Esterline Angus P.D.2064' data logger recorded the electrical output of the analyser (equivalent to percentage oxygen), at 2-min intervals for 2–3 h. Control 'blank' readings of the percentage of atmospheric O₂ were obtained from a parallel circuit consisting of a replicate respirometer and gas scrubbers.

Animals were deprived of food for 3 h prior to measurement of metabolic rate in order to reduce the influence of specific dynamic action. Rectal temperatures were recorded with a rectal thermocouple inserted approximately 3 cm into the rectum, within 1 min of the termination of each run. The

existence of a possible endogenous diel metabolic rhythm was determined by continuous 24-h monitoring of metabolic rate of a single animal of each species, at 27°C and 28°C for *B. suillus* and *B. janetta* respectively. Readings were taken at 5-min intervals, with the mean of the five lowest readings per hour being used to plot the pattern of metabolism.

Results were analysed for individual animals, and for various groups, depending on the individual results. The mean body size of *B. janetta* was 406 g. The *B. suillus* were divided into three groups; all five animals (mean body size of 732 g), the four 520–800-g animals (mean body size of 664 g), and the three 633–800-g animals (mean body size of 712 g). The first hour of exposure was regarded as a period of adjustment. The mean of the ten lowest $\dot{V}O_2$ values after the first hour was used to calculate RMR in cm³g⁻¹h⁻¹ (STP) using the equation of Durnin & Passmore (1967). Resting metabolic rates within the thermoneutral zone (TNZ) are expressed as the means (\pm SD) for individual animals, and as the population mean (\pm SE) for the groups. Conductance below the lower limit of thermoneutrality (T_l) was calculated using the formula: $C_m = \dot{V}O_2 / (T_b - T_a)$ McNab (1980), and expressed as individual means (\pm SD), and population means (\pm SE) for the groups, in cm³g⁻¹h⁻¹°C⁻¹ (STP). Conductance was compared with the value predicted by the equation of McNab & Morrison (1963); $C_m = 1,00 M^{-0,50}$. All statistical tests are from Zar (1974).

Results

For the individuals of both species there was no marked difference in metabolic rate between the normal light and dark hours. Typically, the 24-h period was characterized by 1–2-h periods of relatively constant metabolic rate when the molerats were involved in grooming, feeding, resting and coprophagous behaviour, interspersed by shorter 20–30-min periods of elevated metabolic rates associated with scratch-digging behaviour and the gnawing of the inside of the respirometer. The lack of a marked endogenous diel metabolic pattern in *Bathyergus* is consistent with observations in other subterranean rodents (Vaughan & Hansen 1961; Gettinger 1975; Andersen & MacMahon 1981). I assumed that I could ignore diel endogenous fluctuations in metabolic rate.

The body temperature of *B. suillus* remained stable at T_a between 13–27°C (Figure 1b). The mean T_b of the 664-g group in this temperature range was 35,3 \pm 0,1°C (Table 1). The 1004-g molerat had a lower T_b of 34,8 \pm 0,4°C (Table 1). Above 27°C, T_b increased to approximately 38°C at a T_a of 34°C, the highest temperature to which *B. suillus* was exposed. The mean body temperature of *B. janetta* between 24–27°C was 34,7 \pm 0,3°C, and was stable (Figure 2b). However, below 24°C the mean body temperature, 34,8 \pm 0,8°C, was significantly more variable ($p < 0,05$; one-tailed F test) (Figure 2b). The mean T_b at T_a between 16–27°C was 34,7 \pm 0,3°C (Table 1), which was significantly lower than that of the 664-g *B. suillus* group ($p < 0,05$; Student's t test). Above 27°C, T_b increased to approximately 39°C at a T_a of 35°C.

The 664-g group of *B. suillus* had a resting metabolic rate of 0,48 \pm 0,02 cm³g⁻¹h⁻¹ (Table 1) within a thermoneutral zone of 25–31°C (Figure 1a). The 1004-g molerat had a RMR of 0,32 \pm 0,02 cm³g⁻¹h⁻¹ (Table 1), which was significantly lower than the population mean for the 664-g group ($p < 0,05$; Student's t test). Below T_l to a T_a of 13°C, there was a significant linear increase in metabolism with decreasing T_a in all *B. suillus* ($p < 0,05$; least-squares fit) (Table 2). The smallest molerat showed the greatest metabolic increase below T_l ; $\dot{V}O_2 = -0,050 T_a + 1,698$

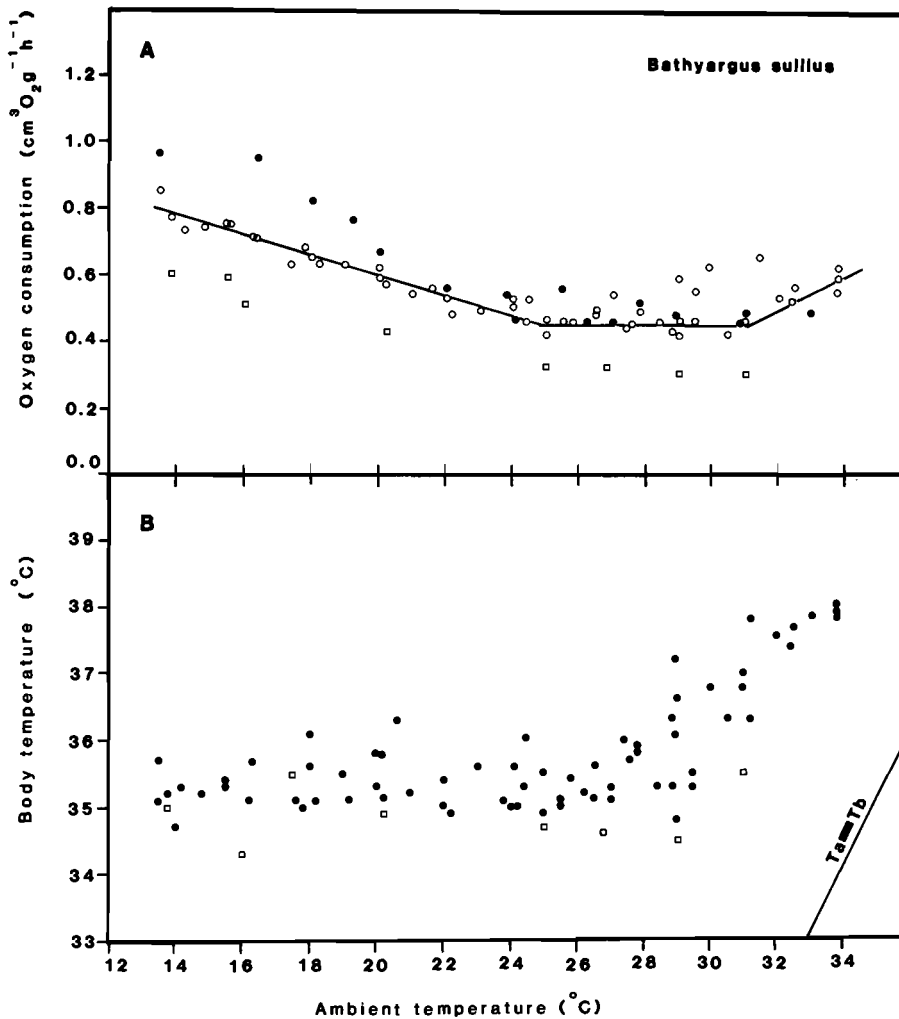


Figure 1 The Cape dune mole rat *Bathyergus suillus*. (A) Oxygen consumption as a function of ambient temperature. Symbols represent three size groups; three mole rats with a mean body mass of 712 g (circles), a single 520-g animal (dots), and a single 1004-g animal (squares). The horizontal line represents the mean resting metabolic rate of the 712-g and 520-g groups. The line below the lower limit of thermoneutrality represents the regression of the 712-g data. (B) Body temperature as a function of ambient temperature. The 712-g and 520-g groups are pooled (dots), and the squares represent the 1004-g animal.

Table 1 Mean body sizes, resting metabolic rates (at thermoneutrality), body temperatures, and conductances (below the lower limit of thermoneutrality), of five *B. suillus*, and three *B. janetta*; population means and standard errors of various size groups are also given

Species	Animal number	Body mass (g)	RMR $\text{cm}^3 \text{g}^{-1} \text{h}^{-1}$ (n)	SD	T_b °C (n)	SD	C_m $\text{cm}^3 \text{g}^{-1} \text{h}^{-1} \text{°C}^{-1}$ (n)	SD
<i>B. suillus</i>	2	520	0,51 (7)	0,05	35,4 (10)	0,3	0,045 (7)	0,003
<i>B. suillus</i>	1	633	0,45 (6)	0,01	35,2 (9)	0,3	0,039 (7)	0,003
<i>B. suillus</i>	3	703	0,52 (7)	0,07	35,3 (10)	0,3	0,037 (6)	0,002
<i>B. suillus</i>	5	800	0,46 (7)	0,03	35,5 (6)	0,3	0,038 (9)	0,001
<i>B. suillus</i>	6	1004	0,32 (3)	0,02	34,8 (6)	0,4	0,029 (4)	0,001
<i>B. suillus</i>	1,3,5	712	0,48	0,02	35,3	0,2	0,038	0,001
<i>B. suillus</i>	1-3,5	664	0,48	0,04	35,3	0,1	0,040	0,003
<i>B. janetta</i>	1	485	0,50 (7)	0,05	34,9 (9)	0,6	0,066 (9)	0,001
<i>B. janetta</i>	2	354	0,57 (6)	0,08	34,9 (12)	0,6	0,070 (12)	0,001
<i>B. janetta</i>	4	380	0,54 (6)	0,08	34,4 (8)	0,5	0,069 (8)	0,001
<i>B. janetta</i>	1,2,4	406	0,54	0,03	34,7	0,3	0,069	0,003

($r^2 = 0,942$), whereas the largest *B. suillus* had the lowest; $\dot{V}O_2 = -0,025T_a + 0,936$ ($r^2 = 0,952$) (Table 2). There was no significant difference between the regression coefficients of the three intermediately sized mole rats comprising the 712-g

group ($p < 0,05$; comparison of slopes). The pooled data for this group showed the best fit of the groups, given by the equation $\dot{V}O_2 = -0,029 + 1,182T_a$ ($p < 0,05$; $r^2 = 0,931$, least-squares fit) (Table 2, Figure 1a). The regression coef-

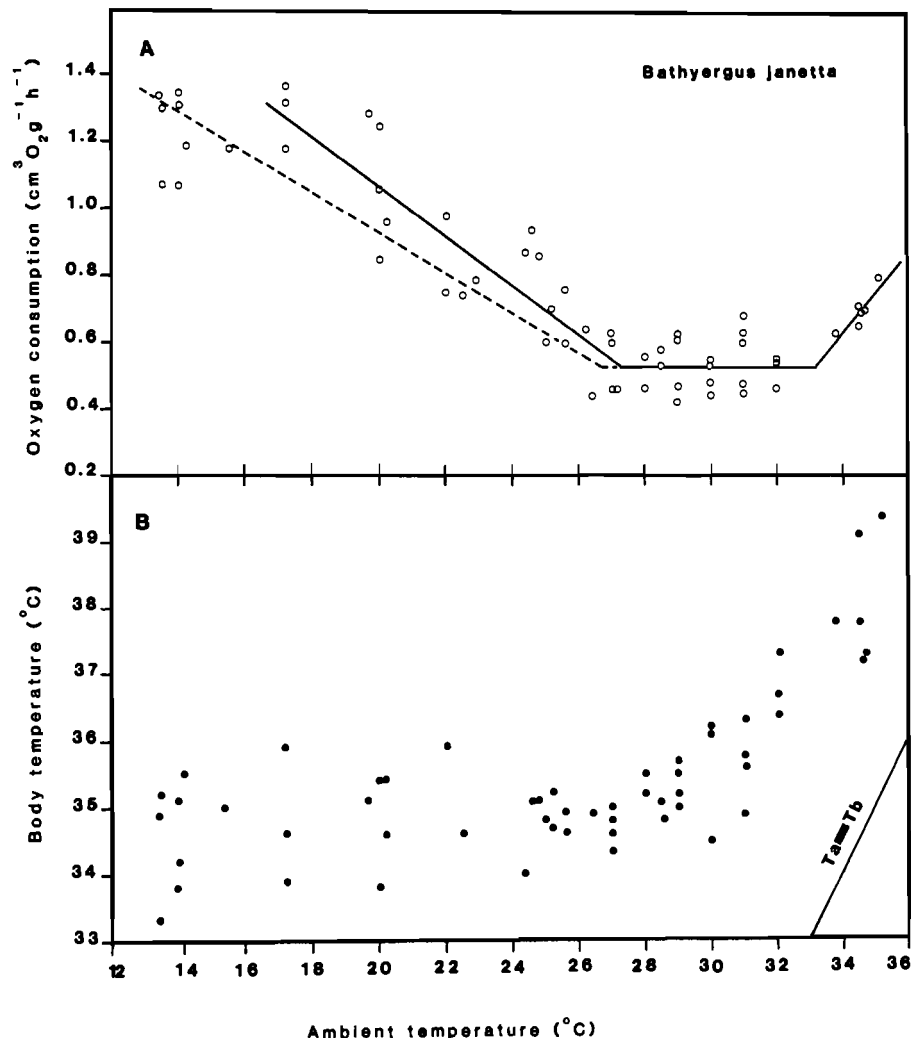


Figure 2 The Namaqua dune mole rat. (A) Oxygen consumption as a function of ambient temperature. The horizontal line represents the mean resting metabolic rate. The lines below the lower limit of thermoneutrality represent the regression of all $\dot{V}O_2$ and ambient temperature (broken line), as well as $\dot{V}O_2$ as a function of ambient temperatures down to 16°C (solid line). (B) Body temperature as a function of ambient temperature.

Table 2 Statistics of the linear regressions of metabolic rate as a function of ambient temperature below 25°C and 27°C, for *B. suillus* and *B. janetta* respectively; regressions were calculated on data from individual animals, as well as from data pooled for various groups

Species	Animal number	Sample size	Regression coeff.	SE	Y intercept	SE	Correlation coeff. (r^2)	p slope = 0
<i>B. suillus</i>	2	8	-0,050	0,005	1,698	0,017	0,942	< 0,05
<i>B. suillus</i>	1	8	-0,029	0,004	1,188	0,014	0,903	< 0,05
<i>B. suillus</i>	3	8	-0,031	0,002	1,194	0,008	0,969	< 0,05
<i>B. suillus</i>	5	11	-0,027	0,002	1,152	0,006	0,972	< 0,05
<i>B. suillus</i>	6	5	-0,025	0,003	0,936	0,013	0,952	< 0,05
<i>B. suillus</i>	1-3,5,6	40	-0,030	0,004	1,195	0,014	0,617	< 0,05
<i>B. suillus</i>	1-3,5	35	-0,033	0,003	1,287	0,011	0,787	< 0,05
<i>B. suillus</i>	1,3,5	27	-0,029	0,002	1,182	0,006	0,931	< 0,05
<i>B. janetta</i>	1	10	-0,056	0,013	2,060	0,059	0,710	< 0,05
<i>B. janetta</i>	2	14	-0,052	0,006	2,066	0,031	0,846	< 0,05
<i>B. janetta</i>	4	9	-0,051	0,010	1,988	0,052	0,772	< 0,05
<i>B. janetta</i>	1,2,4	33	-0,053	0,005	2,050	0,025	0,773	< 0,05

coefficients of the 520-g and 1004-g animals were significantly greater and lower respectively, than that of the 712-g group ($p < 0,05$, comparison of slopes).

B. janetta had a TNZ from 27,5–33,2°C, and a RMR of $0,54 \pm 0,03 \text{ cm}^3 \text{ g}^{-1} \text{ h}^{-1}$ within this range (Figure 2a, Table 1). All three *B. janetta* showed a significant linear

increase in metabolic rate below T_i ($p < 0,05$; least-squares fit). There was no significant difference between individual regression coefficients ($p < 0,05$; comparison of slopes). The regression of the pooled data for the group is given by the equation $\dot{V}O_2 = -0,053 + 2,050T_a$ ($p < 0,05$; $r^2 = 0,773$; least-squares fit) (broken line in Figure 2a, Table 2). The regression coefficient for this group was significantly greater than that of the 712-g group of *B. suillus* ($p < 0,05$; comparison of slopes).

An interesting observation of the metabolic increase below T_i for the *B. janetta* group, is that it decreases at T_a below 16°C (Figure 2a). A sign-test, significant at the 1% level, showed that all eight data points below 16°C, fall below the values predicted by the equation of the regression of $\dot{V}O_2$ and T_a between 16–27,5°C ($\dot{V}O_2 = -0,075T_a + 2,566$; $p < 0,05$; $r^2 = 0,800$; least-squares fit, solid line in Figure 2a). The regression coefficient of this curve was significantly greater than that for the curve relating $\dot{V}O_2$ to all T_a below T_i ($p < 0,05$; comparison of slopes).

Conductance in *B. suillus* ranged from $0,045 \pm 0,003 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$ for the 520-g molerat, to $0,029 \pm 0,001 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$ for the 1004-g animal (Table 1). The mean conductance for the 712-g group was $0,038 \pm 0,001 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$ (Table 1). The conductances of the 520-g and 1004-g molerats were significantly greater and lower respectively, than the mean conductance of the 712-g group ($p < 0,05$; Student's *t* test). The mean conductance over all T_a below T_i of the *B. janetta* group, was $0,069 \pm 0,003 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$ (Table 1), which was significantly greater than the mean conductance of the 712-g group of *B. suillus* ($p < 0,05$; Student's *t* test). The highest mean group estimate of C_m was $0,072 \pm 0,003 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$ between 16–27,5°C. The mean group conductance below 16°C, $0,060 \pm 0,007 \text{ cm}^3\text{g}^{-1}\text{h}^{-1}\text{°C}^{-1}$, was significantly lower than the mean group conductance between 16–27,5°C ($p < 0,05$; Student's *t* test).

Discussion

Overall, the various statistics for the 712-g group of *B. suillus*, are probably the most representative of the species. This group showed the least mass-specific variation in RMR, conductance and body temperature, over all ambient temperatures.

The fact that the body temperature of *B. janetta* was variable below 24°C, and that the metabolic increment decreased at ambient temperatures below 16°C, suggests that *B. janetta* does not thermoregulate as effectively as *B. suillus* over the same temperature range. Although the results for *B. janetta* suggest that this molerat was able to reduce conductance below 16°C, the fact that in a few instances body temperatures fell below 34°C at ambient temperatures below 14°C, might suggest that this species is incapable of producing sufficient metabolic heat to compensate for heat loss below 14°C. It is not known whether *B. janetta* enters torpor at ambient temperatures lower than 14°C.

The resting metabolic rates of both species are lower than expected for rodents (Hayssen & Lacey 1985), being 83% (664-g group) of expected for *B. suillus*, and 79% of expected for *B. janetta*. The resting metabolic rate of *B. janetta* is not as low as that measured in smaller arid-adapted subterranean rodents, such as *Heterocephalus glaber* (39 g) (McNab 1979), *Thomomys umbrinus* (85 g) (Bradley, Miller & Yousef 1974), *Heliophobius argentocinereus* (88 g) (McNab 1966) and *Spalax ehrenbergi* (2n = 60 chromosome species) (121 g) (Nevo & Shkolnik 1974). These smaller subterranean rodents appear to be more flexible in adapting to thermal stresses (McNab

1979), and the energetic demands of a subterranean existence (Vleck 1979, 1981; Jarvis 1978; Lovegrove 1986), by manipulating metabolic rate, body temperature and conductance.

The eusocial naked molerat *Heterocephalus glaber* (Jarvis 1981), which inhabits semi-arid regions of Kenya, is completely hairless and virtually incapable of thermoregulation, having the highest conductance (242% of expected), and the lowest resting metabolic rate (43% of that predicted by Hayssen & Lacey 1985) and body temperature (32,1°C) of any eutherian (McNab 1979; Withers & Jarvis 1980). *B. suillus* on the other hand, may represent the largest size that a completely subterranean rodent can attain while maintaining a 'precise' thermoregulatory ability over a wide range of ambient temperatures.

Exactly which physical or ecological factors select for low metabolic rates, low body temperatures and body size in subterranean rodents, is not clearly understood. The fact that *B. janetta* is smaller than *B. suillus*, does not necessarily suggest that an adaptation to warm burrows or thermal stress (McNab 1979) is the only factor selecting for body size. The conductance of *B. janetta* (125% of expected) is higher than that of *B. suillus* (103% of expected; 712-g group), lending some support for the 'overheating' hypothesis. However, the low RMR and smaller body size of *B. janetta* may also represent 'energy-saving' adaptations. From the RMRs and body sizes of these two species, it can be calculated that the daily energetic expenditure of *B. janetta* is approximately 30% lower than that of *B. suillus*, despite its higher mass-specific RMR. Assuming that the semi-arid habitat of *B. janetta* has a lower productivity than that of *B. suillus*, it is possible that constraints involved in foraging for low abundance, poor quality food resources, have optimally selected for a low RMR and small body size in this molerat.

The interspecific differences in metabolic rate, conductance, and body size of the bathyergids, may represent a compromise between the energetic constraints of foraging in soils differing in hardness and resource parameters, and the energetic constraints imposed by different thermal regimes. It is important to establish the relative habitat-specific roles that these two factors play in the inclusive fitness of the various bathyergids. This will enable a better understanding of not only the eco-physiology of the bathyergids, but also of the adaptive significance of their various social systems.

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