Bioenergetics, thermoregulation and urine analysis of squirrels of the genus *Xerus* from an arid environment

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A comparative thermoregulatory and bioenergetic study including urine analyses of two species of southern African ground squirrels from the genus *Xerus* was carried out. Both *X. princeps* (a rock dweller) and *X. inauris* (a burrow dweller) are well adapted to a hot and arid environment. Both species have low resting metabolic rates (RMR) and high conductances (C). In *X. princeps* RMR is lower and C is higher relative to *X. inauris*. Both species can increase their body temperature (T_b) in their thermoneutral zones and in ambient temperatures (T_a) above this. Salivation in both species was observed only at T_a = 38°C. At T_a = 5°C *X. princeps* increase their oxygen consumption significantly cf. *X. inauris* (p < 0.005) and regulated their T_b at 36.1 ± 0.5°C while *X. inauris* maintained T_b at 34.8 ± 0.8°C. Nonshivering thermogenesis was measured as maximal VO_2 and T_b of anaesthetized squirrels injected with noradrenaline (NA). *X. inauris* and *X. princeps* responded to NA by increasing VO_2 and T_b.

Both species show a low digestible dry matter intake as predicted for desert rodents. In both squirrels percentage moisture in faeces is low but significantly (p < 0.05) lower in *X. princeps* than in *X. inauris*. Urine analyses of hydrated squirrels showed that in *X. inauris* urea and Mg**+** concentrations were significantly higher cf. *X. princeps* (p < 0.05; p < 0.01).

Ground squirrels of the genus *Xerus* are represented in the Southern African subregion by two species: (i) The Cape ground squirrel *X. inauris* which is widely distributed in the subregion; in the Southern Savanna grasslands west of the Great Escarpment, and in the West South Arid biotic zone (De Graaff 1981; Smithers 1983), and (ii) the mountain ground squirrel *X. princeps* which occurs only in South West Africa/Namibia. This species is a typical representative of the South West Arid biotic zone and is distributed from Great Namqualand in the south up into Angola in the north, through Damaraland and the Kaokoveld (De Graaff 1981; Smithers 1983). *Xerus princeps* and *X. inauris* are sympatriic in South West Africa/Namibia throughout the areas in which *X. princeps* is distributed. *X. princeps* is a rock dweller and *X. inauris* a burrow dweller (Shortridge 1934). *X. princeps* is solitary or sometimes two individuals may dwell under the same boulder while *X. inauris* is social and up to 30 individuals can share the same burrow system (Herzig-Strachil 1978).

The aims of the present study were to compare their bioenergetics, thermoregulation and urine composition, to establish if there are any differences between the two species, as well as to compare the results with those of ground squirrels from deserts of the new world, and tree squirrels from Africa.

Materials and Methods

Seven specimens of *X. inauris* (four males and three females) and seven specimens of *X. princeps* (three males and four females) were captured in the area of Usakos, South West Africa/Namibia, in August 1984. Most *X. inauris* were caught in the river bed while *X. princeps* were captured under boulders. All squirrels were trapped during daytime.

The squirrels were acclimated for at least three weeks to an ambient temperature (T_a) of 25°C with a photoperiod of 12L:12D. The animals were kept separately in cages and were fed Pronutra powder mixed with water ad. lib. Apples and carrots were added as a source of moisture. Shredded paper was provided for bedding.

Oxygen Consumption

Oxygen consumption (VO_2) was measured for both species at different ambient temperatures between 5 - 38°C, using an open circuit system (Depocas & Hart 1957; Hill 1972). VO_2 was monitored on a Beckman OM-14 Polarigraphic oxygen analyser. A flow of air, dried over silica gel, (UniLAB), at a rate of 1000 ml/min was used. VO_2 was recorded for a period of 30 min after a 2 - 3 h stabilizing period at each temperature. The average resting metabolic rate RMR (oxygen consumption of the 30-min period) was calculated when readings did not differ by more than 0.02%. The oxygen analyser was calibrated before and after each measurement, as in Haim (1982). All results were corrected to standard conditions, (STPD).

Temperature

Body (rectal) temperatures (T_b) and ambient temperatures were measured using a chromel-alumel thermocouple connected to a Kane-May 2013 potentiometer. T_b was recorded...
at the end of every $\text{VO}_2$ measurement by inserting the thermocouple 3 cm into the rectum of the squirrel for a period of no longer than 1 min.

Overall thermal conductance

The overall thermal conductance (C) was calculated for both species at temperatures below their lower critical point (for $X. \text{inaurus}$ at $T_a = 26^\circ C$ and for $X. \text{princeps}$ at $T_a = 29^\circ C$) using the formula of Scholander, Hock, Waleters & Irving 1950 (in Hart 1971) ($C = \frac{M}{T_b} - T_a; M -$ metabolism).

Nonshivering thermogenesis

Nonshivering thermogenesis (NST) was measured as the maximal $\text{VO}_2$ of anaesthetized (Sagatal, Maybaker, S.A., 75 mg/kg i.p.) squirrels obtained, in response to noradrenaline (NA, Sigma, 1,5 mg/kg S.C.) injection according to Heldmaier (1971). Measurements were carried out at $T_a = 28^\circ C$ for $X. \text{inaurus}$ and at $T_a = 31^\circ C$ for $X. \text{princeps}$. $\text{VO}_2$ and $T_b$ were simultaneously measured and recordings of both parameters were made every 3 min during a period of 120 min after NA injection.

Urine analysis

Urine was collected over paraffin oil in metabolic cages, during a period of 24 h. During this period (as well as 24 h before) the squirrels were kept on a diet of freshly weighed carrots. The uneaten carrots were weighed after 24 h, and were replaced by another weighed portion of carrots. Urine volume was measured to the nearest 0,1 ml.

Sodium — Na+, potassium — K+, chloride — Cl−, and urea were determined using iono-specific electrodes in an Astra-8 (Beckman) instrument, and in the case of urea, after a treatment with urease. Calcium — Ca2+ and magnesium — Mg2+ were determined by atomic absorption spectrometry using lithium nitrate dilution. Phosphate was determined by colour development according to the method of Taussky & Shorrre (1953) and monitored on a fleacigen (ENI). Bicarbonate — HCO3−, was measured by titration as in Haim, Heth, Nevo, Gruner & Goldstein (1985).

Urine osmolarity was determined by using a 5130C vapor pressure osmometer (Wescor Inc.) and pH was measured by a Labotec pH meter.

The per cent moisture content in the faeces of both species was determined by collecting the faeces immediately after extrusion. The faeces were weighed and then dried to constant mass in an oven at 80°C.

All results are given as mean ± standard deviations. Student’s t test was used to test significant differences.

**Results**

The relationships between $\text{VO}_2$ and $T_b$ at different ambient temperatures are illustrated in Figure 1 for $X. \text{inaurus}$ and in Figure 2 for $X. \text{princeps}$. The thermoneutral zone TNZ for $X. \text{inaurus}$ lay between $T_b = 29 - 35^\circ C$ and for $X. \text{princeps}$ between 32 - 35°C. $\text{VO}_2$ in TNZ was 0,602 ± 0,08 ml O2/g h with $T_b$ between 36,8 - 39,1°C for $X. \text{inaurus}$ and 0,565 ± 0,10 ml O2/g h for $X. \text{princeps}$, with $T_b$ between 37,6 - 38,7°C. In TNZ and above it, both species became hyperthermic. $T_b$ in both species always exceeded $T_a$. Salivation in both species was observed only at $T_a = 38^\circ C$. A significant difference in thermoregulation between these two species was observed at $T_a = 5^\circ C$. $X. \text{princeps}$ showed higher $\text{VO}_2$ values (2,00 ± 0,22 ml O2/g h) and maintained its $T_b$ at 36,1 ± 0,5°C, while $X. \text{inaurus}$ had a significantly ($p < 0,005$) lower oxygen consumption (1,65 ± 0,29 ml O2/g h) and body temperature declined to 34,8 ± 0,6°C.

Overall thermal conductance — C calculated for $X. \text{inaurus}$ ($M_0 = 542,3 ± 52,1$ g) at $T_a = 26^\circ C$ was 0,071 ± 0,003 ml O2/g h 1°C while for $X. \text{princeps}$ ($M_0 = 602,3 ± 98,1$ g), the calculated C at $T_a = 29^\circ C$ was 0,084 ± 0,005 ml O2/g h 1°C. In $X. \text{princeps}$ values were 15,9% greater than in $X. \text{inaurus}$.

The values of NST for both species are given in Table 1. Both species showed a high response to NA injection by increasing $\text{VO}_2$ which was accompanied by an increase in $T_b$.

The urine analyses for both species are summarized in Table 2. Urea and magnesium concentrations were significantly higher in the urine of $X. \text{inaurus}$ when compared with $X. \text{princeps}$ ($p < 0,05; p < 0,01$). All the other values were
Table 1 Nonshivering thermogenesis (NST) measured as the maximal oxygen consumption (VO$_2$ max) obtained as a response to a noradrenaline (NA — 1.5 mg/kg S.C.) injection into an anaesthetized squirrel. VO$_2$ max — maximal body temperature measured as a response to NA. VO$_2$ min and T$_{min}$ — minimal values measured in anaesthetized squirrels. VO$_2$max/VO$_2$ min — NST capacity, $\Delta$T$_{b}$ — the rate of increase in T$_b$ from T$_{min}$ to T$_{max}$, M$_b$ — body mass. The figures are mean ($\pm$ S.D.) of six individuals.

<table>
<thead>
<tr>
<th></th>
<th>X. inauris</th>
<th>X. princeps</th>
</tr>
</thead>
<tbody>
<tr>
<td>M$_b$ (g)</td>
<td>515,3 ± 63,3</td>
<td>627,0 ± 91,5</td>
</tr>
<tr>
<td>VO$_2$max ml O$_2$/g h</td>
<td>1,99 ± 0,28</td>
<td>1,66 ± 0,46</td>
</tr>
<tr>
<td>VO$_2$min ml O$_2$/g h</td>
<td>0,43 ± 0,06</td>
<td>0,37 ± 0,05</td>
</tr>
<tr>
<td>T$_{max}$ °C</td>
<td>39,3 ± 1,8</td>
<td>37,3 ± 1,6</td>
</tr>
<tr>
<td>T$_{min}$ °C</td>
<td>32,8 ± 0,8</td>
<td>33,2 ± 1,8</td>
</tr>
<tr>
<td>VO$_2$max/VO$_2$ min</td>
<td>4,8 ± 1,2</td>
<td>4,6 ± 1,4</td>
</tr>
<tr>
<td>$\Delta$T$_b$ °C</td>
<td>6,5 ± 1,1</td>
<td>4,1 ± 0,6</td>
</tr>
</tbody>
</table>

Table 2 Comparison of several variables in the urine of two ground squirrel species from the genus Xerus. 24 h water intake, when kept on a diet of carrots was 69,04 ± 26,22 ml/1000 g for X. inauris and 57,83 ± 24,42 ml/1000 g for X. princeps. All figures are mean ($\pm$ S.D.) of seven individuals ($p < 0.05$; $p < 0.01$) statistically indistinguishable. Dry matter intake (carrots) was 8,266 ± 3,43 g/1000 g day for X. inauris and 6,696 ± 3,42 g/1000 g day for X. princeps which did not differ significantly from one another.

<table>
<thead>
<tr>
<th></th>
<th>X. inauris</th>
<th>X. princeps</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass (g)</td>
<td>523,8 ± 50,7</td>
<td>612,4 ± 94,8</td>
</tr>
<tr>
<td>Urine volume ml/1000 g W$_b$</td>
<td>71,4 ± 16,6</td>
<td>66,4 ± 10,2</td>
</tr>
<tr>
<td>pH</td>
<td>6,70 ± 0,15</td>
<td>7,04 ± 0,75</td>
</tr>
<tr>
<td>Osmolality mmol/liter</td>
<td>431,6 ± 80,4</td>
<td>403,4 ± 43,0</td>
</tr>
<tr>
<td>Urea mmol/liter</td>
<td>231,0 ± 58,9</td>
<td>152,7 ± 52,9</td>
</tr>
<tr>
<td>HCO$_3$ meq/liter</td>
<td>16,6 ± 6,4</td>
<td>18,9 ± 11,1</td>
</tr>
<tr>
<td>Cl$^-$ meq/liter</td>
<td>33,7 ± 20,5</td>
<td>22,3 ± 7,4</td>
</tr>
<tr>
<td>Phosphate mmol/liter</td>
<td>2,57 ± 1,30</td>
<td>2,57 ± 0,62</td>
</tr>
<tr>
<td>K$^+$ mmol/liter</td>
<td>78,1 ± 19,9</td>
<td>99,0 ± 36,3</td>
</tr>
<tr>
<td>Na$^+$ mmol/liter</td>
<td>32,4 ± 23,4</td>
<td>17,1 ± 8,9</td>
</tr>
<tr>
<td>Ca$^{2+}$ mmol/liter</td>
<td>0,91 ± 0,40</td>
<td>0,84 ± 0,20</td>
</tr>
<tr>
<td>Mg$^{2+}$ mmol/liter</td>
<td>3,01 ± 0,50</td>
<td>2,08 ± 0,50</td>
</tr>
</tbody>
</table>

Discussion

The two species of the genus Xerus were captured during daytime around Usakos. The strictly diurnal activity of X. inauris was noted by Herzig-Strachil (1978). Individuals of X. princeps were captured in rocky areas under rocks as well as along river beds (gravel). In one case an individual of X. princeps was captured in an opening of a burrow and 200 m away in another burrow X. inauris was captured. From our studied individuals X. inauris was never captured under a rock. Roberts (1951) states that X. princeps can inhabit plains as well as rocky areas and our capture data support this idea.


Both species of ground squirrels showed a low VO$_2$ in relation to their body mass, according to Kleiber's (1961) equation. X. princeps and X. inauris had VO$_2$ values which were 20% and 21% less than predicted for rodents of 608 g and 528 g body mass respectively. A low basal metabolism was recorded from desert and semi-desert species of new world ground squirrels and this was shown to be an adaptation to tolerance of high temperatures (Hudson & Deavers 1973).

In a recent study (Vijioen 1985) on thermoregulation of Southern African tree squirrels, all four species had RMR values below those predicted from Brody's (1945) equation (VO$_2$ = 3,8W$^{0.75}$, W — body mass). These low values were interpreted as an adaptation to a warm climate. Furthermore, the two xeric species, Paraxerus cepapi from woodland savanna in Central Southern Africa, and Funisciurus congicus from arid savanna habitats in north-western Namibia, were further below the predicted values (Brody-Proctor equation) for their body mass (34% and 26% respectively).

In both species of Xerus, the thermoneutral zone is high, yet the lower critical point for X. princeps ($T_a$ = 32°C) is higher than for X. inauris ($T_a$ = 29°C). High values for lower critical points are recorded from several rodent species from extreme arid areas: Acomys russsatus (Haim & Borut 1981), Gerbillus nanus (Haim 1984), Seketamyus calurus (Haim & Borut 1986). The difference in the lower critical point between the two species may indicate that the rock-dwelling X. princeps is better adapted to high temperatures than the burrow-dwelling X. inauris. Both species at $T_a$ = 35°C become hyperthermic, $T_B$ = 38,7 ± 0,3°C for X. princeps and $T_B$ = 39,1 ± 0,6 for X. inauris.

It was assumed by Goyal, Ghosh & Prakash (1982) that a relatively high $T_B$ may help to reduce evaporative water loss. In a comparative study of ground squirrel thermoregulation, Hudson et al. (1972) discovered that the most tolerant species to high ambient temperatures was Citellus tereicicus which inhabits hot deserts and can withstand ambient temperatures up to 46°C with a $T_B$ of only 41,2°C. They also noted that the appearance of thermal distress varied in conformity with the habitat of the species.

In the southern African tree squirrels from arid habitats, F. congicus and P. cepapi, a resistance to high ambient temperatures was noted and at $T_a$ = 38°C; $T_B$ was only 39,8 ± 0,3 and 39,7 ± 0,35 respectively (Vijioen 1985).

Marsh, Louw & Berry (1977) noted that X. inauris is well adapted to hot and arid areas and can withstand high ambient temperatures. They also mention that the tail is used as a parasol to reduce heat load by creating shade for the squirrel. Bennett, Huey, John-Adler & Nagy (1984) however, claim that despite the behavioural and morphological adjustments of the parasol tail in X. inauris it can not replace the thermoregulatory difficulties in their hot and arid habitat.

The marked difference in response to cold between X. inauris and X. princeps is illustrated in Figures 1 and 2. X. inauris increased VO$_2$ above RMR only 2,8 times while X. princeps increased VO$_2$ 3,7 times above RMR at $T_a$ = 5°C. This difference in VO$_2$ between the two species is significant ($p < 0,005$). In conformity with VO$_2$, a significant difference ($p < 0,005$) was recorded in $T_B$. This difference could have resulted from different rates of conductivity or differences in heat production. Conductance in both species is high yet in
X. princeps it is higher than in X. inaurus, which may be important for a rock dweller in hot and arid areas. High conductance is a great advantage in heat dissipation and water conservation (Haim & Faurie 1980; Haim & Borut 1981; Haim 1984). On the other hand, when exposed to low ambient temperatures a rapid increase in heat production is of great importance for the squirrel to compensate for heat loss.

Webster (1974) emphasized the advantage of heat production by means of NST for small mammals. In this process a great amount of heat is generated in a short period without the involvement of muscle contraction. Cold acclimated rodents depend on NST for heat production when exposed to lower ambient temperatures (Jansky 1973). This mechanism is body mass dependent (Heldmaier 1971, 1972). Results from this study show that both species when anaesthetized responded to NA injection by increasing VO2 and Tb (Table 1) although they were not cold acclimated. In X. inaurus VO2max (maximal VO2 owing to NA injection) is 20% higher when compared to X. princeps whose body mass is 21% higher than that of X. inaurus. Yet at Ta = 5°C X. princeps increased heat production significantly (p < 0.005) more than X. inaurus. This difference may be due to shivering thermogenesis and this parameter was not measured.

Under conditions of water shortage, reduction of faecal water loss is advantageous to an animal. Katz (1973) showed that in desert rodents water content of faeces is less than in the white rat Rattus norvegicus when given water ad libitum but faecal water content is even lower when they are deprived of water. Ward & Armitage (1981) compared the water budgets of mesic and xeric populations of the yellow-bellied marmot (Marmota flaviventris). They report a 40 – 55% faecal water content in the two populations when water is given ad libitum. They also note that when water was limited, faecal water loss further decreased by 72% for the mesic population and 65% for the xeric population to reduce water content to about 15%. In the present study, where the squirrels were kept on a diet of Pronutro powder mixed with water, fresh apples and carrots ad lib., a low faecal water content was nevertheless recorded for both species. The value of 14,21 ± 4.2% recorded for X. inaurus is significantly (p < 0.05) lower than 21.97 ± 4.6% recorded for X. princeps. Both species occur sympatrically in an arid area and the difference may be due to X. princeps being a rock dweller while X. inaurus inhabits burrows.

Aspects of renal physiology in X. inaurus were studied by Marsh et al. (1978). In their study they compared the urine collected from the urine bladder of squirrels shot in the dry season with that collected from squirrels shot in the wet season. The results from our study fall within their range for squirrels shot in the wet season.

There is a significant difference (p < 0.05) in the urinary urea concentration between the two species, values being higher for X. inaurus (Table 2). In desert rodents urinary urea concentration is much higher than in rodents from mesic habitats, and urea has a pronounced effect on the urea-concentrating capacity of rodents Pfeiffer (1970). A parallel increase in urinary urea and urinary osmolality was reported in Mus musculus following water restriction (Haines, Ciskowski & Harms 1973). In the present study the interpretation of the difference in urine concentration is complicated as the squirrels had enough water in their diet and the difference in urine osmolality is not significant. Differences in Mg ** concentration may emerge from a difference in absorption of Mg ** in the intestine. A similar phenomenon was found in the rabbit and rat by Cheeke & Amberg (1973). They explained the difference in urine Mg ** concentration by a differential intestinal absorption of Mg **.

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**References**


