

Metabolic rates, food consumption and thermoregulation in seasonal acclimatization of the Cape porcupine *Hystrix africaeaustralis*

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Received January 2, 1990 / Accepted January 23, 1990

Summary. Metabolic rates by means of oxygen consumption ($\dot{V}O_2$) at various ambient temperatures (T_a) and food consumption as well as water intake and thermoregulation were compared between individuals of the Cape porcupine *Hystrix africaeaustralis* acclimated to $T_a=32^\circ\text{C}$ with a photoperiod of 16L:8D summer-acclimated and $T_a=10^\circ\text{C}$; 8L:16D winter-acclimated. The lower critical temperature as well as overall minimal thermal conductance were lower for the winter-acclimated porcupines when compared to summer-acclimated ones, while $\dot{V}O_2$ at the thermoneutral-zone was significantly ($P<0.001$) higher in the winter-acclimated porcupines. Dry matter intake, apparent digestible dry matter intake, gross digestible energy intake, as well as water intake, were significantly higher in the winter-acclimated porcupines. Yet, while dry matter intake increased 4 times in the winter-acclimated porcupines, apparent digestible dry matter increased only at a rate of 2.9 times. This difference is better reflected in terms of digestibility efficiency which in the winter-acclimated porcupines is only at a rate of 67.5% while in the summer-acclimated porcupines it is at a rate of 90%. From the results of this study, it is possible to assume that heat production in the winter-acclimated porcupines is partly increased by food intake. Increased heat production on the one hand, and a decrease in overall minimal thermal conductance on the other, seem to be important mechanisms in winter acclimatization of the Cape porcupine.

Key words: Metabolic rates – Thermoregulation – Digestibility – Winter acclimation – Conductance

The Cape porcupine *Hystrix africaeaustralis*, which is the largest Southern-African rodent, is widely distributed in the subregion. This species has a wide ecological tolerance (De Graaf 1981; Smithers 1983; and Skinner et al. 1984). It is a nocturnal species and may be exposed

throughout its range of distribution to very cold nights during winter, while in summer it can be active at ambient temperatures that exceed those of the winter by more than 25°C .

Seasonal acclimatization in endothermic species involves thermoregulatory mechanisms, which are reflected by increased metabolic rates, as well as decreased conductivity when exposed to low ambient temperatures. Results of several studies on seasonal acclimatization of thermoregulation and metabolic rates which have been reported, deal mainly with small rodents, of body mass less than 100 gr. (Rosenmann et al. 1975; Cygan 1985; Helmaier et al. 1986; Feist and Feist 1986).

The body mass of the Cape porcupine is 100 times and more greater than that of the smallest rodents studied. Therefore it was of great interest to study seasonal acclimatization of metabolic rates and thermoregulation of this large rodent and to compare the results with those of small rodents.

In this study, the metabolic and thermoregulatory responses of the Cape porcupine to induced seasonal changes were investigated under “Summer” ($T_a=32^\circ\text{C}$; 16L:8D) and “Winter” ($T_a=10^\circ\text{C}$; 8L:16D) conditions.

Materials and methods

Six adult (three males and three females) Cape porcupines (third generation of inestorres, captured in the Laxiton district Karroo, South Africa), were acclimated to two different ambient temperatures (T_a) and photoperiod regimes: $T_a=32^\circ\text{C}$; 16L:8D summer-acclimated and $T_a=10^\circ\text{C}$; 8L:16D winter-acclimated. Studied porcupines were acclimated to each one of these conditions for three weeks at least. For this purpose they were kept in a climatic chamber, Spech Scientific, with an average relative humidity of 60%. They were maintained two in a cage and were fed with rat pellets and given water *ad lib*.

Oxygen consumption

Oxygen consumption ($\dot{V}O_2$) was measured at ambient temperatures between 13°C and 28°C for winter-acclimated porcupines, and between 20°C and 36°C for summer-acclimated porcupines, using

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an open circuit system (Depocas and Hart 1957; Hill 1972). For $\dot{V}O_2$ measurements the porcupines were removed from the climatic chamber into a large isolated metabolic chamber (127 × 75 × 65 cm, made of two distant boards of perspex). Cooling or warming was achieved through copper coils aligned to the inner perspex board and circulating the air by a fan, which was installed on the ceiling of the chamber. The porcupine inside the metabolic chamber was kept in a cage with a metal tray under it for collection of urine and faeces. The rate of air flow through the chamber was 10 l/min.

Before measurements began, the animals were kept for a stabilizing period of at least three hours in the metabolic cage. $\dot{V}O_2$ was recorded for a minimum of 60 min, using an Amtek S-3A/II (Applied Electrochemistry) oxygen analyzer. Five consecutive readings of 3 min intervals, which did not differ by more than 0.01%, were used for calculating resting metabolic rate (RMR). The oxygen analyzer was calibrated before and after recording each animal. All $\dot{V}O_2$ measurements were carried out during the light phase and all results were corrected to standard temperature and pressure dry (STPD).

Body temperature

Body (rectal) temperature (T_b), was measured using a chromel-alumel thermocouple connected to a 52/K/J Fluke thermometer. The thermocouple was inserted into the rectum of the porcupine for a period of 30 seconds during which T_b was recorded. For this purpose the porcupine was removed from the metabolic chamber into a special cage (70 × 29 × 49 cm). On both sides of the narrow part of the cage, there were sliding doors from which the porcupine could enter or leave the cage. The ceiling of the cage could be pushed downwards, while the floor was made from net. The animal was forced to the entrance and the ceiling pressed down. The thermocouple could thus be inserted into the porcupine's rectum through a mesh in the net.

Overall minimal thermal conductance

Overall minimal thermal conductance (C) was calculated for porcupines of the two groups at their lower critical temperature, using the formula of Scholander, as given by Hart (1971): $C = M / (T_b - T_a)$; (M , metabolism = $\dot{V}O_2$). For the summer-acclimated group C, was calculated at $T_a = 32^\circ\text{C}$, while for the winter-acclimated group at $T_a = 24^\circ\text{C}$.

Food and water consumption

Food consumption in both groups of porcupines was measured as apparent digestible dry matter intake (DDMI), calculated from the difference between total dry food consumed and dry faeces outlet. The porcupines were kept in special cages (101 × 75 × 65 cm) made of metal net. Having an underneath tray, the urine was run-off through a funnel to a jar and was collected under paraffin oil.

Measurements of summer-acclimated porcupines were carried out during November, December 1986 and January 1987, while for winter-acclimated ones they were carried out during July and August 1987. All results are given as mean \pm SD. Student's T-test was used for statistical analyses.

Results

Winter-acclimation caused an increase in metabolic rates as evidenced by the oxygen (Fig. 1) and food consumption (Table 2), when compared to summer-acclimated

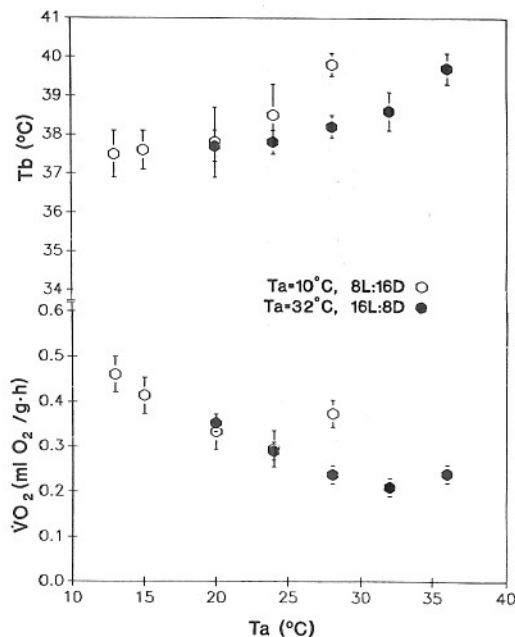


Fig. 1. Oxygen consumption ($\dot{V}O_2$ mlO₂/g.h. and body temperature (T_b °C) of winter-acclimated ($T_a = 10^\circ\text{C}$, 8L:16D - open circles) and summer-acclimated ($T_a = 32^\circ\text{C}$; 16L:8D - Closed circles) porcupines *Hystrix africaeanstralis* at different ambient temperatures. All results are given as mean \pm S.D. of $n = 6$

animals. Minimal resting metabolic rate for winter-acclimated porcupines, (Body mass of 11.4 ± 1.1 Kg.) was 0.294 ± 0.02 mlO₂/g.h. with a lower critical point (T_{lc}) 24°C . At $T_a = 28^\circ\text{C}$ winter-acclimated porcupines were in hyperthermia and T_b rose up to $39.8 \pm 0.2^\circ\text{C}$. Minimal resting metabolic rates for summer-acclimated porcupines (body mass of 10.7 ± 1.0 Kg.) was only 0.190 ± 0.021 mlO₂/g.h. but at T_{lc} of 32°C . Under such acclimation conditions hyperthermia was observed at $T_a = 36^\circ\text{C}$ ($T_b = 39.2 \pm 0.4$).

All induced summer-acclimated porcupines, molted into summer short fur and lost their thick coat.

Overall minimal thermal conductance was significantly ($P < 0.001$) higher in the summer-acclimated porcupines compared with the winter-acclimated group (Table 1).

Dry matter intake (D.M.I) and apparent digestible dry matter intake (D.D.M.I), as well as gross digestible energy intake (G.D.E.I) values, were higher in winter-acclimated group when compared with summer-acclimated group (Table 2). But digestibility (the ratio be-

Table 1. The effect of "seasonal acclimatization" on overall minimal thermal conductance-C. Body mass- W_b . All results are mean (\pm S.D.) of 6 individuals

	C ml O ₂ /g.h · 1° C	W_b Kg
$T_a = 32^\circ\text{C}$ 16L:8D	0.028 ± 0.003	10.7 ± 1.0
$T_a = 10^\circ\text{C}$ 8L:16D	0.019 ± 0.001	11.4 ± 1.1

Table 2. The effect of "seasonal acclimatization" on food and water consumption and on gross digestible energy intake in the cape porcupine *Hystrix africaeaustralis*: DDMI – Digestible dry matter intake, DMI – Dry matter intake, % Digestibility – (DDMI/DMI) × 100, H₂O intake – Water intake, W_b – body mass. The figures are mean (±S.D.) of six individuals

	$T_a = 32^\circ \text{C}$ 16L:8D	$T_a = 10^\circ \text{C}$ 8L:16D
D.D.M.I. g/Kg.day.	5.13 ± 2.1	15.2 ± 2.0
D.M.I. F/Kg.day.	5.7 ± 2.2	22.5 ± 1.9
% Digestibility	90 ± 1.7	67.5 ± 2.6
G.D.E.I. Kj/Kg.day.	90.2 ± 27.3	252.0 ± 28.8
H ₂ O intake ml/Kg.day.	52.7 ± 5.8	97.1 ± 7.3
W _b Kg.	10.9 ± 1.3	11.1 ± 0.7

tween D.D.M.I and D.M.I expressed in percent) was found to be much higher in the summer-acclimated porcupines when compared with the winter-acclimated (Table 2). Water intake of winter-acclimated porcupines was almost twice the water intake of summer-acclimated (Table 2). Body mass did not differ significantly between porcupines of the two groups acclimated.

Discussion

When exposed to low ambient temperatures and to long scotophase, homeothermic mammals increase heat production. In mammals of the size of a porcupine – shivering thermogenesis is expected to be the main source for initial heat production. During the period of winter acclimatization, overall minimal thermal conductance will decrease by increasing insulation, (Hart 1956; Jansky 1973; Webster 1974; Heldmaier et al. 1986). On the other hand, when exposed to high ambient temperatures and short scotophase, homeothermic mammals will decrease heat production and increase heat dissipation by increasing overall minimal thermal conductance.

The porcupine *Hystrix africaeaustralis* is a large burrowing nocturnal rodent and in winter it may experience very cold nights for a long period of activity, in many parts throughout its distribution in Southern-Africa, while during summer it will be active for a shorter period at much warmer conditions.

Indeed, under the experimental conditions, the results of this study show that the Cape porcupine can respond to seasonal climatic changes. Changes in seasonal energy requirements and water intake were reported for the Indian crested porcupine *Hystrix indica* (Alkon et al. 1986). Their study shows seasonal fluctuations in body mass. The cape porcupine did not show such fluctuations under the experimental conditions used. In the group of winter-acclimated Cape porcupines, a significant increase in oxygen consumption ($\dot{V}O_2$), D.M.I, D.D.M.I and G.D.E.I (Fig. 1, Table 2)

was noted. Alkon et al. (1986) state that there were no seasonal differences in these parameters in *H. indica*. Water intake in *H. indica*, was significantly higher in summer than in winter (Alkon et al. 1986). While in the present study, winter-acclimated *H. africaeaustralis* increased almost twice their water intake when compared to the summer-acclimated group (Table 2). This result of increased water intake in this group, is in agreement with the increased metabolic demands.

The $\dot{V}O_2$ values measured at thermoneutral zone (RMR) for porcupines of both groups is lower than the predicted value for their body mass, calculated from Kleiber's equation (Kleiber 1961). Yet, the $\dot{V}O_2$ values measured for the winter-acclimated porcupines were 81% of the expected, while for the summer-acclimated porcupines they were only 50%.

Overall minimal thermal conductance is higher in the porcupine in relation to the values predicted from body mass, calculated from the Bradley and Deavers equation (Bradley and Deavers 1980). In the summer-acclimated group, C is 92% higher than expected while in the winter-acclimated group it is only 36% higher. The high values of C can be interpreted as an adaptation for burrowing in such a large rodent. The increase in this parameter in the summer-acclimated group however, correlates well with the fact that in this group there was a massive loss of fur.

Low metabolic rates on the one hand and high overall thermal conductance on the other, seem to be important adaptations for the porcupine – a large burrowing rodent which inhabits mesic, semi-arid and even arid areas. Yet the porcupine as a nocturnal species faces very cold nights during activity in winter. Insulation, plays a significant role in improving thermoregulation in mammals of the size of the porcupine (Hart 1956). The results of this study indeed show a decrease in overall minimal thermal conductance in the winter-acclimated group, when compared to the summer-acclimated group.

Although conductance decreased in winter-acclimated porcupines, the measured values are 36% higher than expected for a mammal with a body mass of 11.1 Kg (Bradley and Deavers 1980). The porcupine as a nocturnal mammal, spends the warmer hours of the day, even during winter, in the burrow. The relatively high conductance can result from the increased metabolism when it is active.

In nonhibernating cold acclimated mammals, an elevated metabolic rate is noted due to a marked increase in sympathetic activity (Himms-Hagen 1967; Jansky 1973). Such an increase in sympathetic activity was also noted in long scotophase acclimated rats (Haim et al. 1983). Therefore the increase in heat production in the winter-acclimated group could be the result of an increase in the sympathetic activity.

The digestibility efficiency of the two acclimated groups differed markedly. The winter-acclimated group under our experimental conditions, increased D.M.I 4 times when compared with the summer-acclimated group, while D.D.M.I increased only 2.9 times (Table 2). This raises the question whether the increase in the food

intake is related to thermogenesis, as the winter-acclimated porcupines did not increase their body mass significantly, when compared to the summer-acclimated group, although they increased D.M.I.

The results of this study support the idea of Rotwell and Stock (1979), that food intake increases as a response to cold exposure, and therefore it contributes to thermogenesis. Since rat pellets as well as water were offered *ad lib*, the significant increase in water intake could be explained as a result of the high increase of D.M.I. The type of diet, rat pellets, which is relatively a high protein diet can also contribute to the increase in heat production as was shown in the sheep (Webster, 1981).

From the results of this study it may be concluded that metabolic rates and thermoregulation in the Cape porcupine are associated with seasonal acclimatization. In winter, heat production increases while heat dissipation decreases. The increase in heat production is partly achieved by an increase in D.M.I which causes a decrease in digestibility efficiency.

Acknowledgements. We thank Prof. Uri Katz for his most helpful and critical remarks on the manuscript. We also thank Messrs. Martin Haupt, Edward O'Neill and Donald Skinner for their technical assistance. This research was supported by a grant from the Council for Scientific and Industrial Research.

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