Metabolism and Thermoregulation in the Cape Porcupine, *Hystrix africaeaustralis*

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Abstract

Oxygen consumption ($\dot{V}_{O_2}$) and body temperature (T_b) were measured at various ambient temperatures (T_a) between 13° and 39° C in individuals of the Cape porcupine (Hystrix africaeaustralis), acclimated to T_a = 25° C at a controlled photoperiod of 12L:12D. $\dot{V}_{O_2}$ of this species in the thermoneutral zone (T_a = 24°–27° C) is only 57% of the $\dot{V}_{O_2}$ of an 11.1 ± 0.7 kg mammal as predicted by Kleiber. T_b was well regulated up to T_a = 30° C. Hyperthermia was observed at T_a above 30° C. T_b regulation was accompanied by an increase in overall thermal conductance and respiratory frequency rate. Overall minimal thermal conductance calculated at lower critical point T_a = 24° C is higher than predicted by Bradley and Deavers. Apparently digestible dry-matter intake and gross digestible energy intake are relatively low and correlate with the low $\dot{V}_{O_2}$ values recorded for this species. Water intake in this species is significantly lower than that of the crested porcupine (H. indica) under similar conditions. Low metabolic rates on the one hand and high overall thermal conductance on the other appear to be important physiological adaptations for this large, burrowing, nocturnal rodent, which has a wide ecological tolerance.

Introduction

Cape porcupines, *Hystrix africaeaustralis*, are large (12–18 kg) nocturnal hystricomorph rodents that reside in habitats ranging from tropical forests to deserts throughout southern Africa. They live in extended family groups in shelters and breed in caves, rock crevices, modified aardvark burrows, and/or burrows that they dig themselves. Porcupines usually forage alone and feed on the bulbs, tubers, and bark of a variety of plants, several of which are known to be poisonous to man and/or domestic animals (De Graaff 1981; Smithers 1983).

Extensive research has been carried out on the Cape porcupine including

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the reproductive and population biology (Van Aarde 1985*a*, 1985*b*, 1987) and digestion (Van Jaarsveld 1983; Van Jaarsveld and Knight-Eloff 1984). However, no information is available on their metabolism and energy requirements, although these aspects have been reported by Alkon et al. (1986) and Sever (1986/1987) for the related Indian porcupine, *H. indica.*

The present study was designed to investigate the bioenergetics and thermoregulatory abilities of captive Cape porcupines as part of an ongoing project on the ecology and physiology of these animals.

Material and Methods

Six adult porcupines (three males, three females) bred in captivity (third-generation offspring of free-ranging adults trapped in the semiarid Karoo, South Africa) were acclimated for 3 wk to an ambient temperature (T_a) of 25°C and a photoperiod of 12L:12D. Relative humidity within the climate room (Speck Scientific) averaged 60%. The porcupines were housed in pairs in separate cages within the room and fed daily on commercial pellets (Antelope Cubes, Epol [Pty] Ltd., Vereenigin, South Africa). Drinking water was freely available. All measurements were carried out from August to November 1986.

Oxygen Consumption

We measured oxygen consumption ($\dot{V}_{O_2}$) at various T_a's between 13° and 39°C, using an open flow system (Depocas and Hart 1957; Hill 1972). For this purpose the selected animal was moved from the climate room to a large custom-built metabolic chamber (127 × 75 × 65 cm), consisting of two layers of Perspex with 4 cm of insulation between the layers. Temperature was controlled by pumping hot or cold water from a bath into copper pipes that densely surrounded the inner layer of Perspex of the chamber. A fan was installed in the ceiling of the chamber. Within the metabolic chamber the porcupine was kept in a wire-mesh cage, and under the cage was a metal tray in which urine and feces were collected. Dried air (silica gel: Holpro) was pumped at a rate of 10 L/min through the metabolic chamber. Each porcupine was kept in the chamber for a period of 3 h. We recorded $\dot{V}_{O_2}$ at 3-min intervals for at least 60 min using an Amtek S-3A/II (Applied Electrochemistry) oxygen analyzer. Five consecutive readings that did not differ by more than 0.01% were used to calculate resting metabolic rate (RMR). O_2 concentration in the metabolic chamber did not drop lower than 19.95%. The oxygen analyzer was calibrated before and after each group of

recordings. All $\dot{V}o_2$ measurements were carried out during the light phase and were corrected to STPD.

Body Temperature

Body (rectal) temperature (T_b), was measured at the end of each $\dot{V}o_2$ measurement with a chromel-alumel thermocouple connected to a 52 K/J Fluke thermometer, which was inserted approximately 3 cm into the rectum for about 30 s. To facilitate this we moved the porcupine from the metabolic chamber into a custom-built cage ($70 \times 29 \times 49$ cm) within which it could be restrained.

Respiratory Frequency

Respiratory frequency was measured at the end of each $\dot{V}o_2$ recording before the porcupine was removed from the metabolic chamber. Three consecutive measurements of 1 min each were taken with a stopwatch.

Overall Thermal Conductance

We calculated thermal conductance (C) at $21°$, $24°$ (lower critical temperature), $27°$ (upper critical temperature), and at $30°C$, using the formula of Scholander et al., as given by Hart (1971): $C = (M/T_b - T_a)$, where M = metabolic rate, T_b = body temperature, and T_a = ambient temperature.

Food Consumption and Gross Digestible Energy Intake

Food consumption over a 5-d period, measured as apparent digestible dry-matter intake (DDMI), was calculated as the difference between the mass of dry food consumed and the mass of dry feces excreted daily. For this purpose individuals were kept within the temperature room in wire-mesh cages ($101 \times 75 \times 65$ cm) below which a stainless-steel tray was set at a slope, a tray in which feces accumulated and from which urine ran off through a funnel into a jar containing paraffin. A known mass of pellets dried at $70°C$ and a measured volume of fresh water were provided every day in metal containers. The volume of water left over was measured and removed every day, while the remaining pellets were dried in an oven and then weighed. Porcupines were weighed at the onset and at the end of the 5-d experimental period. Feces were removed daily from the tray and dried in an oven at $70°C$ to a constant mass.

We calculated gross digestible energy intake from the energy values of the pellets and feces determined using a DDS CP 400 bomb calorimeter.
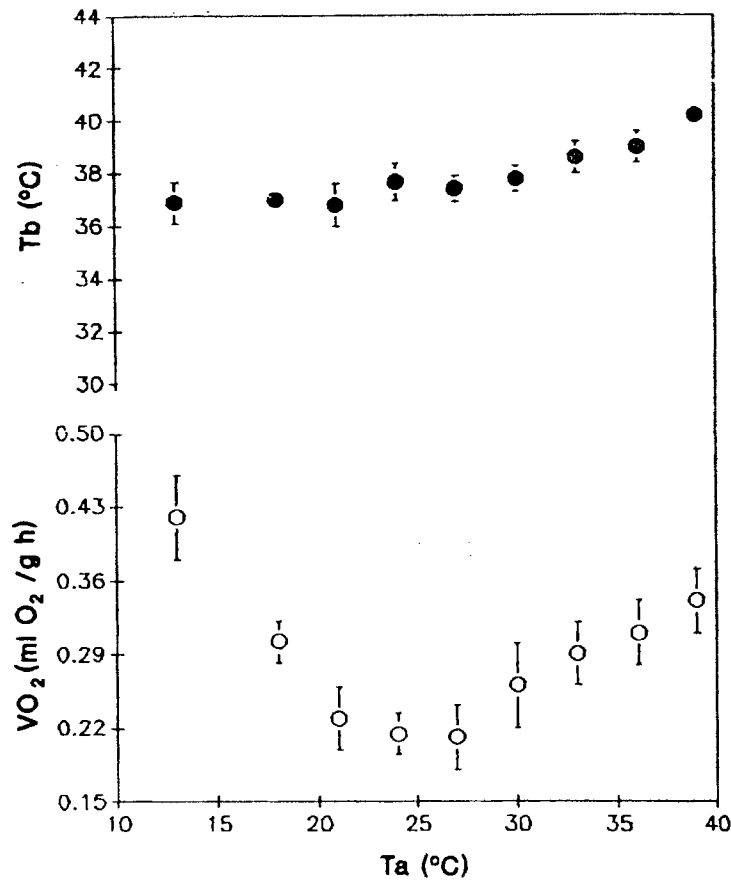
Fig. 1. Oxygen consumption ($\dot{V}o_2$ mL $O_2/g \cdot$ h) and T_b (° C) of the Cape porcupine Hystrix africaeausralis at different T_a's (° C). Porcupines were acclimated to $T_a = 25°$ C at a controlled photoperiod of 12L:12D. All results are given as $\overline{X} \pm SD$ of n = 6.

All results are given as mean values and followed by 1 SD of the mean. Student's t-test was used to test the level of significance of differences.

Results

The thermoneutral zone of the Cape porcupine, with a mean body mass of 11.1 kg, acclimated to $T_a = 25°$C and 12L:12D, lies between 24° and 27°C (fig. 1). Mean $\dot{V}o_2$ within this zone (RMR) was 0.209 ± 0.02 mL $O_2/g \cdot$ h, and mean T_b was 37.6°C at $T_a = 24°$C and 37.3°C at 28°C. Between the lower critical temperature (24°C) and 13°C $\dot{V}o_2$ increased at 0.0168 mL $O_2/g \cdot$ h · °C (fig. 1). At T_a's above the upper critical point ($T_a = 28°$C), $\dot{V}o_2$ increased at a rate of 0.0009 mL $O_2/g \cdot$ h · °C.

Body temperature was well regulated up to a T_a of 30°C, and at higher

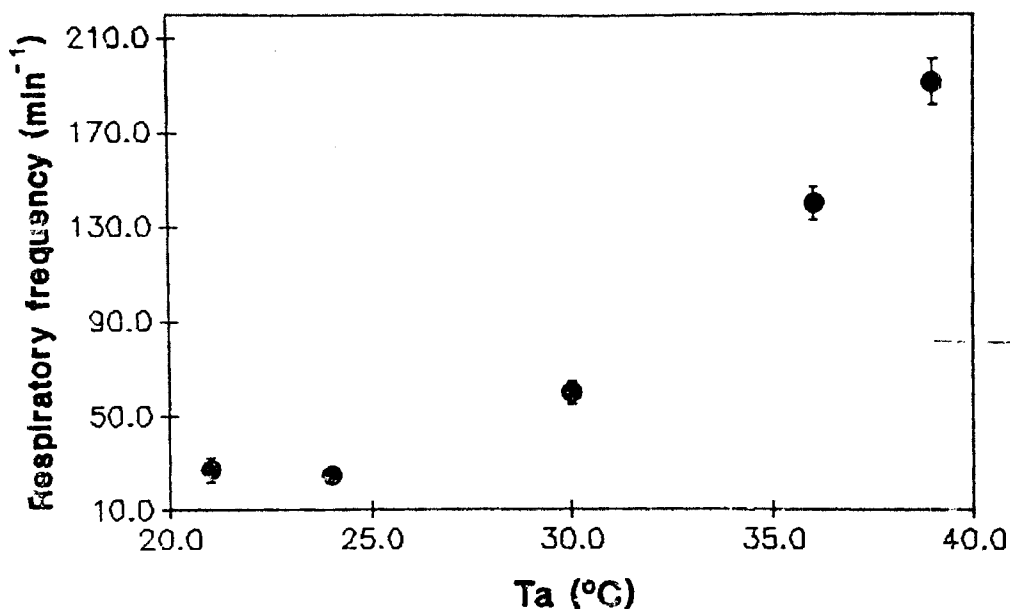*Fig. 2. Respiratory frequency of the Cape porcupine* Hystrix africaeausralis *(breaths/min), as a function of* T$_a$ *(° C). Porcupines were acclimated to* T$_a$ = *25° C with a photoperiod of 12L:12D. All results are given as* $\overline{X}$ ± *SD of* n = *6.*

temperatures hyperthermia occurred (fig. 1). Respiratory frequency also increased with an increase in T$_a$ (fig. 2). We noticed that, at T$_a$'s above 30°C, the porcupines were wet when removed from the metabolic chamber, while at a T$_a$ of 39°C all studied porcupines urinated in the metabolic chamber.

Overall C was significantly higher (P < 0.005) at T$_a$ = 27°C than at 24°C and T$_a$'s below it (table 1).

Apparent DDMI was 7.48 ± 1.11 g/kg · d, and gross digestible energy intake was 144.8 ± 17.1 kJ/kg · d. Dry-matter digestibility was 87.0% ± 2.3%, and water intake under the conditions of acclimation was 40.7 ± 4.3 mL H$_2$O/kg · d.

Discussion

In their wide distribution throughout southern Africa, Cape porcupines experience a variety of climatic conditions. Animals in the Karoo, on the one hand, face a dry, cold winter during which they are exposed to relatively low T$_a$'s during their nocturnal bouts of activity. On the other hand, during summer nocturnal T$_a$'s can be much higher (25°C and above).

The present study shows that Cape porcupines acclimated to 25°C can

TABLE 1

Overall thermal conductance (C) of six Cape porcupines

T_a (°C)	m_b (kg)	C (mL O_2/g · h · °C)
15	11.6 ± .7	.016 ± .001
18	11.5 ± .9	.017 ± .002
21	11.5 ± .9	.016 ± .002
24	11.1 ± .7	.018 ± .001
27	11.2 ± .8	.023 ± .002*
30	11.1 ± .7	.032 ± .005**

Note. Values for C calculated using the formula C = MR/T_b − T_a (MR = metabolic rate as measured by oxygen consumption) at T_a's 13°, 18°, 21°, 24°, 27°, and 30°C. m_b = body mass. All values are $\bar{X}$ ± SD; n = 6.
* P < 0.005 when compared with C at T_a = 24°C.
** P < 0.005 when compared with C at T_a = 27°C.

regulate their T_b's at T_a's between 13° and 30°C. At higher T_a's (31°–39°C) an increase in metabolic rate occurred, and porcupines became hyperthermic at 39°C. However, in their natural environment in the Karoo it may be assumed that porcupines are not exposed to T_a's above 30°C since they are nocturnal.

Metabolic rates measured through $\dot{V}o_2$ in the Indian crested porcupine during spring (0.312 mL O_2/g · h; Sever 1986/1987) are higher than those recorded for the Cape porcupine in the thermoneutral zone. $\dot{V}o_2$, furthermore, is 43% lower than the value expected from Kleiber's equation (Kleiber 1961). Low metabolic rates recorded in several desert rodents (see Hudson and Wang 1969; Hart 1971; Yousef and Johnson 1975; Yousef 1980; Lovegrove 1986; Haim 1987; McNab 1988) may be a useful adaptation because they minimize the need for water and food, which are usually in short supply in arid environments.

The relatively low metabolic rate and high C recorded for porcupines (table 1), which are in agreement with those recorded for other fossorial rodents, may aid in preventing overheating during burrowing (see McNab 1966). Overall minimal C measured at the lower critical point in porcupines (0.018 ± 0.001 mL O_2/g · h · °C) was 29% higher than the value expected from Bradley and Deavers's equation, C = 0.760$W^{-0.426}$ (Bradley and Deavers 1980), and this may aid in reducing heat storage during spells of high activity.

At high T_a's it seems that porcupines dissipate heat by evaporative water loss. Above the upper critical point, overall minimal C (table 1) and respiratory frequency (fig. 2) increase significantly. The increase in these parameters is accompanied by an increase in $\dot{V}O_2$. Although regulation of T_b is achieved by loss of water, in typical desert rodents under equal conditions an increase in T_b is used, a mechanism that conserves water (Haim 1984, 1987).

The daily DDMI rate of 7.48 ± 1.11 g/kg · d and gross digestible energy intake of 144.8 ± 17.7 kJ/kg · d obtained in the present study is similar to that recorded for the crested porcupine kept on 40% of ad lib. diet (8.13 g/ kg · d and 72.3 ± 38.2 kJ/kg · d; Alkon et al. 1986). Digestibility in Cape porcupines under our experimental conditions (87.0% ± 2.33%) is higher than that of the crested porcupine (68.3% ± 15.9%; Alkon et al. 1986) but very close to the rate (83.04% ± 2.52%) reported by Van Jaarsveld (1983) for Cape porcupines kept on high protein diet. Dry-matter intake reported by Van Jaarsveld (1983) for the Cape porcupine (35.12 g/kg · d) is higher than that reported by us, possibly because of the different conditions to which animals were acclimated. Daily water intake for the Cape porcupine (40.7 ± 4.3 mL H_2O/kg · d) was significantly lower than that of crested porcupines on a 40% ad lib. diet during summer, but similar to that of crested porcupines kept on 60% of ad lib. diet during winter (Alkon et al. 1986).

The results of our study explain to some extent how porcupines, with their low metabolic rate (lower than expected for body mass), can cope with conditions prevailing in semiarid and even arid environments. Their low metabolic rates and ability to dissipate heat by high C may be important physiological adaptations for a big burrowing mammal. Their high digestive efficiency and relatively low water intake may also be important adaptations to arid environments.

Acknowledgments

Literature Cited

ALKON, P. U., A. A. DEGEN, A. COHEN, and H. POLLAK. 1986. Seasonal energy requirements and water intake of Indian crested porcupines (*Hystrix indica*) in captivity. J. Mammal. 67:333–342.

BRADLEY, S. R., and D. R. DEAVERS. 1980. A re-examination of the relationship between thermal conductance and body weight in mammals. Comp. Biochem. Physiol. 65A:465–476.

DE GRAAFF, G. 1981. The rodents of Southern-Africa. Butterworths, Pretoria. 267 pp.

DEPOCAS, F., and J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurements of oxygen consumption of animals in open circuit system and in short lag, closed circuit apparatus. J. Appl. Physiol. 20:388–392.

HAIM, A. 1984. Adaptive variations in heat production within gerbils (genus Gerbillus) from different habitats. Oecologia 61:49–52.

———. 1987. Metabolism and thermoregulation in rodents: are these adaptations to habitat and food quality? S. Afr. J. Sci. 83:639–642.

HART, J. S. 1971. Rodents. Pages 1–149 in G. C. WHITTOW, ed. Comparative physiology of thermoregulation. Vol. 2. Academic, New York.

HILL, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

HUDSON, J. W., and L. C. H. WANG. 1969. Thyroid function in desert ground squirrels. Pages 17–33 in C. C. HOFF and M. L. RIEDESEL, eds. Physiological systems in semiarid environments. New Mexico Press, Albuquerque.

KLEIBER, M. 1961. The fire of life. Wiley, New York.

LOVEGROVE, B. G. 1986. The metabolism of social subterranean rodents: adaptation to aridity. Oecologia 69:551–555.

McNAB, B. K. 1966. The metabolism of fossorial rodents: a study of convergence. Ecology 47:712–733.

———. 1988. Complications inherent in scaling the basal rate of metabolism in mammals. Q. Rev. Biol. 63:25–54.

SEVER, Z. 1986/1987. Water and energy economies of captive porcupines and their implications under natural conditions. Isr. J. Zool. 34:97–98.

SMITHERS, R. H. N. 1983. The mammals of the Southern-African subregion. University of Pretoria, Pretoria. 736 pp.

VAN AARDE, R. J. 1985a. Age determination of the Cape porcupine, Hystrix africaeaustralis. S. Afr. J. Zool. 20:232–236.

———. 1985b. Reproduction in captive female Cape porcupines (Hystrix africaeaustralis). J. Reprod. Fertil. 75:577–582.

———. 1987. Reproduction in the Cape porcupine Hystrix africaeaustralis: an ecological perspective. S. Afr. J. Sci. 83:605–607.

VAN JAARSVELD, A. S. 1983. Aspects of the digestion in the Cape porcupine. S. Afr. J. Anim. Sci. 13:31–33.

VAN JAARSVELD, A. S., and A. K. KNIGHT-ELOFF. 1984. Digestion in the Cape porcupine (Hystrix africaeaustralis). S. Afr. J. Zool. 19:109–112.

YOUSEF, M. K. 1980. Responses of small animals to heat stress and exercise. Pages 91–119 in S. M. HORVATH and K. M. YOUSEF, eds. Environmental physiology, aging, heat, and altitude. Elsevier, New York.

YOUSEF, M. K., and H. D. JOHNSON. 1975. Thyroid activity in desert rodents: a mechanism for lower metabolic rate. Am. J. Physiol. 229:727–731.