Session 9 Integrating the efficiency equation

Integration of metabolism and digestion in the hyrax

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Metabolic adaptations and digestive ability were integrated to explain the ecological efficiency of the hyrax *(Procavia capensis).* Metabolic rate was shown to decrease linearly with a drop in ambient temperature, but at a lower rate than an animal of equivalent size, the guinea-pig *(Cavia porcellus).* This is achieved by lowering the body temperature with a drop in ambient temperature. Maintenance energy requirements within the thermoneutral zone are *ca* 700 kJ/day for mature and 400 kJ/day for immature hyrax and were supplied even on a poor quality laboratory diet. These factors explain the wide adaptability and competitive ability of the hyrax where its predators have been eliminated.

Metaboliese aanpassings en verteringsvermoë is geïntegreer ten einde die ekologiese effektiwiteit van die dassie *(Procavia capensis)* te verklaar. Die tempo van metabolisme het liniêr toegeneem met 'n verlaging in omgewingstemperatuur, maar teen 'n laer tempo as vir 'n dier van dieselfde grootte, die marmot *(Cavia porcellus).* Dit is moontlik deur die liggaamstemperatuur te verlaag wanneer die omgewingstemperatuur verlaag. Onderhoudsenergie vereistes binne die termoneutrale gebied is *ca.* 700 kJ/dag vir volwasse en 400 kJ/dag vir onvolwasse dassies en is aan voldoen, selfs op 'n lae gehalte laboratoriumrantsoen. Hierdie faktore verklaar die wye aanpasbaarheid en die vermoë van die dassie om mee te ding waar sy roofvyande reeds uitgewis is.

Keywords: Hyrax, temperature-regulation, digestion, metabolic rate, conservation of energy

Introduction

The hyrax *Procavia capensis* is a successful small herbivore of Africa and the Middle East that has colonized habitats as divergent as the high rainfall coastal areas of South Africa, the deserts of South West Africa and Israel and also the high mountains of South and East Africa.

Being slow moving and with few defences against predators, it has survived by colonizing rocky areas that provide shelter but also vegetation of sub-optimal quality. This study attempts to integrate metabolic adaptations and digestive ability to explain the ecological efficiency of the hyrax.

Methods

Resting metabolic rates of mature (>2 kg) and juvenile (<1,5 kg) hyrax were studied in the laboratory by measuring oxygen consumption (V_{O_2}) in an open flow system (McNairn & Fairall, 1979). In the present study animals were acclimated at 25°C which is within the thermoneutral zone (20° – 30° mature, 25° – 30° immature) and V_{O_2} was measured at 5, 10, 15 and 20°C. The ability of the hyrax to use an external energy source was investigated by measuring deep body temperature response to infra-red heating in animals acclimated at 10, 15 and 20°C. Temperature was measured telemetrically by temperature sensitive radios implanted abdominally. This method was also used to study deep body temperature during metabolic experiments.

Digestion was investigated using stomach samples of field hyrax shot during the cool dry or late winter season and the hot wet or summer season. These seasons represent the lowest and highest nutritional state of the vegetation at the study site near Brits (25°35′S, 27°44z′E).

A detailed study was performed in the laboratory using 10 adult hyrax fed two diets (5 per diet) differing in fibre and protein level (Table 1). Following adaptation to the diets

Table 1 Chemical composition and digestibility of two laboratory diets and stomach contents in two different seasons. (Means of three replicates).

	Chemical composition					
	Protein	NDF	ADF	ADL	Cellulose	Digestibility %
Diet 1	19,2	15,5	6,5	4,0	5,5	84,22
Diet 2	7,8	49,5	32,5	14,0	17,5	66,96
Hot Wet	21,0	49,5	40,5	26,0	3,0	–
Cool Dry	24,1	54,5	43,0	26,2	19,4	–

and seven days of digestibility trial the animals were sacrificed to examine the hindgut. Volatile fatty acid (VFA) composition was determined by gas chromatography and total VFA concentration was determined by steam distillation. Methane production and urinary energy was also measured to allow metabolizable energy (ME) determination. Energy of food, digesta, faeces and urine was determined with a ballistic bomb calorimeter. Total VFA production was determined according to Allo *et al.* (1973) and the energy value was calculated using the separate values for each of the respective acids. Analysis for dietary fibre was done by the method of Goering and Van Soest (1970) and for nitrogen by standard Kjeldahl determination; crude protein was calculated as N × 6,25. To obtain comparable units for digestible and metabolizable energy the metabolic rates were converted assuming a value of 20,1 kJ/1 oxygen.

Results and Discussion

The hyrax has a lower metabolic rate than the standard calculated (Kleiber, 1947) value and this increase in a linear fashion with a drop in ambient temperature (T_a) (Figure 1) but at a lower rate than that of an animal of equivalent size, the guinea-pig *Cavia porcellus* (McNairn & Fairall, 1979). This efficiency is achieved by the ability of the hyrax to lower its body temperature (T_b) with a drop in T_a (Figure 1). Conductance is decreased by this strategy and is further enhanced

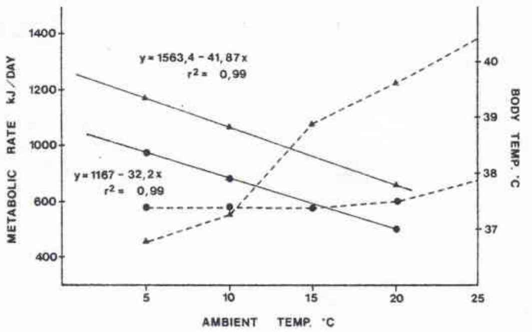

Figure 1 The effect of ambient temperature on metabolic rate (——) and deep body temperature (.....) of juvenile (●) and mature (▲) hyrax.

by postural means. This saving in energy by decreased T_b is accompanied by a torpid state which is again overcome by using an external energy source, the sun, to heat the body by the well known basking habit of this animal. This is illustrated experimentally in Figure 2 and is seen to be more effective on acclimation to lower T_a. Further conservation of energy is achieved behaviourally by the habit of huddling (Sale, 1970), the effect of which was not measured in the present study.

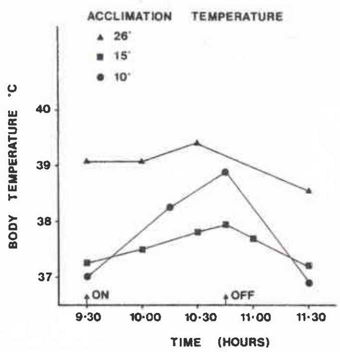

Figure 2 The effect of exposure to infra-red heating on deep body temperature of hyrax acclimated and measured at different ambient temperatures. Duration of heating indicated on time axis.

The hyrax has a wide food spectrum and their natural diet contains a large percentage of fibre (Table 1) which is fermented efficiently in the unique sacculation and dual caeca (Eloff, 1981). Metabolizable energy (ME) on the two laboratory diets differed considerably and the percentage contributed by VFA was higher on the high fibre diet (Table 2). Food intake and consequently ME on the field diets was unknown but judging from the digesta mass and VFA energy production figures given, the field values should have been nearly equivalent to those an the low fibre diet as protein digestibility varied between 50 and 70 percent and the high protein content would therefore have contributed substantially to the non VFA metabolizable energy component.

Minimal energy requirements (maintenance) within the thermoneutral zone are *ca.* 700 kJ/day for mature and 400 kJ/day for immature hyrax (Figure 1) and these amounts are supplied even on a poor quality diet in the laboratory (Table 1). From information on the field diet and its digestion it can be assumed to supply sufficient energy for maintenance. At lower T_a the metabolic rate of the laboratory hyrax increased to values above the available digestible energy on the laboratory diets. These values are however calculated on a 24-hour basis and because of their behavioural strategies the hyrax will seldom be exposed to such conditions for extended periods.

It would appear that the hyrax, through efficient metabolic adaptations coupled to a complex and efficient digestive system, is able to provide for its energy needs even under adverse nutritional conditions. This explains its wide adaptability and its competitive ability where predators have been eliminated.

Table 2 Digestive efficiency of five hyrax on two laboratory diets and available data for the natural diet in five samples in each of two different seasons.

	Mean body mass (kg)	Food intake (g)	Hindgut digesta mass (g)	Metabolizable energy (kJ/day)	VFA energy production (kJ/day)
Diet 1	3,3	52,7	171	840,0	407,5
Diet 2	2,6	55,0	282	688,6	351,5
Hot Wet	2,2	–	201	–	330,0
Cool Dry	2,8	–	275	–	404,5

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References

ALLO, A.A., OH, J.H., LONGHURST, W.H. & CONNOLLY, G.E., 1973. VFA Production in the digestive systems of deer and sheep. *J. Wildl. Mgmt* 37, 202.

ELOFF, A.K., 1981. The digestion in the hyrax *Procavia capensis*. M.Sc. thesis, University of Pretoria.

GOERING, H.K. & VAN SOEST, P.J., 1970. Forage fibre analysis. Agriculture Handbook 379, Agricultural Research Services, Washington D.C.

KLEIBER, M., 1947. Body size and metabolic rate. *Physiol Rev.* 27, 511.

McNAIRN, I.S. & FAIRALL, N., 1979. Relationship between heart rate and metabolism in hyrax *Procavia capensis* and the guinea-pig *Cavia porcellus*. *S. Afr. J. Zool.* 14, 230.

SALE, J.B., 1970. The behaviour of the resting rock hyrax in relation to its environment. *Zool. Afr.* 5, 87.