

Thermoregulation and evaporative water loss in growing African giant rats *Cricetomys gambianus*

M.H. Knight

Mammal Research Institute, University of Pretoria, Pretoria

With an increase in mass, weaned giant rat pups *Cricetomys gambianus*, showed a corresponding decline in mass specific metabolism, conductance and evaporative water loss. The decline in metabolism correlates better with mass than age, while conductance correlates better with age than mass. After 77 days of age the relative importance of dry thermal conductance increased and this is attributed to the testes becoming scrotal, and acting as a thermal window. The final desertion of the nest by young is suggested to coincide with the advent of an efficient thermoregulatory capacity.

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Met 'n toename in massa vertoon gespeende reuserotkleintjies (*Cricetomys gambianus*) 'n ooreenkomstige afname in spesifieke metaboliese massa, konduktansie en waterverlies tydens verdamping. Die afname in metabolisme korreleer beter met massa as ouderdom terwyl konduktansie beter korreleer met ouderdom as massa. Sodra die kleintjies 77 dae oud is word droë termiese konduktansie belangrik en dit word hoofsaaklik toegeskryf aan die afsak van die testes in die skrotum wat dan as 'n termiese venster gebruik word. Daar word voorgestel dat die kleintjies se finale verlatting van die nes saamval met die nadering van hul doeltreffende termoregulerende kapasiteit.

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The African giant rat, *Cricetomys gambianus*, with an average adult mass of 1,4 kg is the largest murid species occurring in Africa, being confined to the moist savanna regions (Smithers 1983). They are nocturnally active, omnivorous rodents restricting their activity to areas with reasonable vegetational cover (Knight 1984). They possess cheek pouches and are noted for their avid hoarding behaviour, storing the hoarded food within the bedding material in their burrows (Ewer 1967; Ajayi 1977).

Giant rat young are altricial at birth. Their physical development has the characteristics of 'fast' developers with a lower birth mass, weaning mass and growth rate than predicted from body size relations (Knight 1984). However their overall behavioural development appears 'slow' with the final desertion of the nest being only after 95 days although weaning took place at a much earlier 28 days. It has been suggested that the selection by giant rats for moist foods, and cool deep burrows in moist environments is a result of their thermoregulatory characteristics of a close to predicted metabolic rate, a high thermal conductance and a general inability to cope with high ambient temperatures (Knight 1984). As to how these characteristics develop in growing giant rats is not known. Therefore it was decided to investigate metabolism, conductance and evaporative water loss changes in relation to physical and behavioural development in growing giant rat pups in an attempt to understand their late emergence from the nest.

Methods

Two giant rat litters, containing three and four young respectively, were noted for the day of first appearance of the fur and its pattern of emergence. Single readings of the mid-dorsal and ventral fur length were recorded with a ruler calibrated in millimetres every three or four days for the first two months, followed by weekly samples for the next two months.

The oxygen consumption ($\dot{V}O_2$) was determined from individuals of a single litter of four pups (all males) between the ages of one month ($549,03 \pm 82,50$ g) to four months ($1401,3 \pm 82,50$ g). Oxygen consumption experiments were undertaken during the day, following the open-circuit system and calculations of Decopas and Hart (1957). A 2,8 l perspex metabolic chamber was used. Beneath the perforated platform, a layer of paraffin oil was added to prevent evaporation of moisture from urine and faeces voided while the animal was in the chamber. Compressed air was dried through columns of silica gel and flowed through the chamber at a rate of 1015 ml/min. Excurrent air passed through columns

M.H. Knight

Present address: Kalahari Gemsbok National Park, Private Bag X5890, Upington, 8800 Republic of South Africa

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of silica gel before entering a Beckman OM-14 polarigraphic oxygen analyser. Output from the oxygen analyser was recorded by an analog recorder. The animals were individually tested at an ambient temperature (T_a) of 25°C. The metabolic chamber temperature was regulated to within 0,2°C of the desired temperature by submerging the chamber in a temperature regulated water bath. The temperature inside the chamber was determined with a copper-constantan thermocouple linked to a Kay-May 2013 digital thermometer. Body masses were recorded to the nearest 0,1 g. The animals were not in a post-absorptive state when experimented upon. Each animal was allowed a stabilizing period of 1,5–2,0 h at the ambient temperature of 25°C before oxygen consumption was recorded.

Evaporative water loss (EWL) (from pulmocutaneous evaporation) into dry air was collected in a pre-weighed column of silica gel, which was later re-weighed to the nearest 0,1 mg. If the animals became active during the collection period the results were discarded. For the resting metabolic rate (RMR) determinations, oxygen consumption values were recorded every 3 min until the lowest five consecutive readings were obtained. All oxygen consumption results were corrected to standard temperature and pressure (STP). Body temperatures (T_b) were determined at the termination of an oxygen consumption run by inserting a thermocouple (connected to a Kay-May digital thermometer) 4 cm into the rectum. Thermal conductance (C) was calculated by the relationship

$$C = \frac{MR}{T_b - T_a}$$

where MR = oxygen consumption in ml O_2 (g.h.)⁻¹ (Hart 1971). Experiments were undertaken between March and June 1983.

All data where more than one sample was utilized are presented as means (\bar{x}) with standard error (SE). Regression equations were calculated by the method of least squares (Cass 1973). Siegel (1956) was followed for the determinations of Kendall rank correlation coefficients and the Mann-Whitney U test.

Results

The fur first appeared on day nine and had a fluffy appearance. It grew rapidly on both the dorsal (0,53 mm/day) and ventral (0,47 mm/day) surfaces reaching its longest length of $15,3 \pm 0,3$ mm dorsally and $13,6 \pm 0,5$ mm ventrally after 38 days (Figure 1). Between day 38 and 52, the dorsal ($t = 2,6$; $d.f. = 10$; $P < 0,05$) and ventral fur ($U = 0,00$; $P < 0,01$) decreased significantly in length with the emergence of the bristly, thicker adult pelage. On day 43 the adult fur appeared on the ventral side, and moved to cover the dorsum, apart from the head and shoulders by day 52. This remaining patch was finally covered by day 86. The dorsal fur reached its longest length of 25,7 mm by day 94 with an average growth rate of 0,4 mm/day, while the ventral fur reached $17,8 \pm 1,3$ mm after 129 days with an average growth rate of 0,1 mm/day. Thereafter the fur length declined to $22,3 \pm 0,9$ mm dorsally and $15,3 \pm 0,9$ mm ventrally by day 229.

With an increase in body mass (M_b) in weaned growing giant rats, there was a curvilinear decrease in oxygen consumption described by the equation:

$$y = 39,02 M_b^{-0,55}, r^2 = 0,72 (n = 21),$$

where M_b is measured in g (Figure 2). Giant rats, 55 days old ($M_b = 548,0 \pm 30,6$ g) had an average minimal oxygen consumption rate of $1,24 \pm 0,08$ ml O_2 (g.h.)⁻¹ which declined to $0,71 \pm 0,05$ ml O_2 (g.h.)⁻¹ in 132-day-old rats ($M_b = 1401,1 \pm 36,9$ g).

Kendall's rank correlation (Siegel 1956) was performed to assess the relative importance of age and mass as factors influencing metabolic rate after weaning. Table 1 indicates that both mass and age were negatively correlated with metabolic rate, however the former shows a slightly stronger correlation. The higher partial correlation value between metabolism and mass emphasizes the stronger influence of body mass as opposed to age in this stage of development.

The average body temperature of $36,7 \pm 0,23$ °C showed no significant ($t = 0,61$; $d.f. = 6$; $P > 0,05$) change with an increase in body mass (Figure 2). Total thermal conductance (C) also showed a curvilinear decrease with an

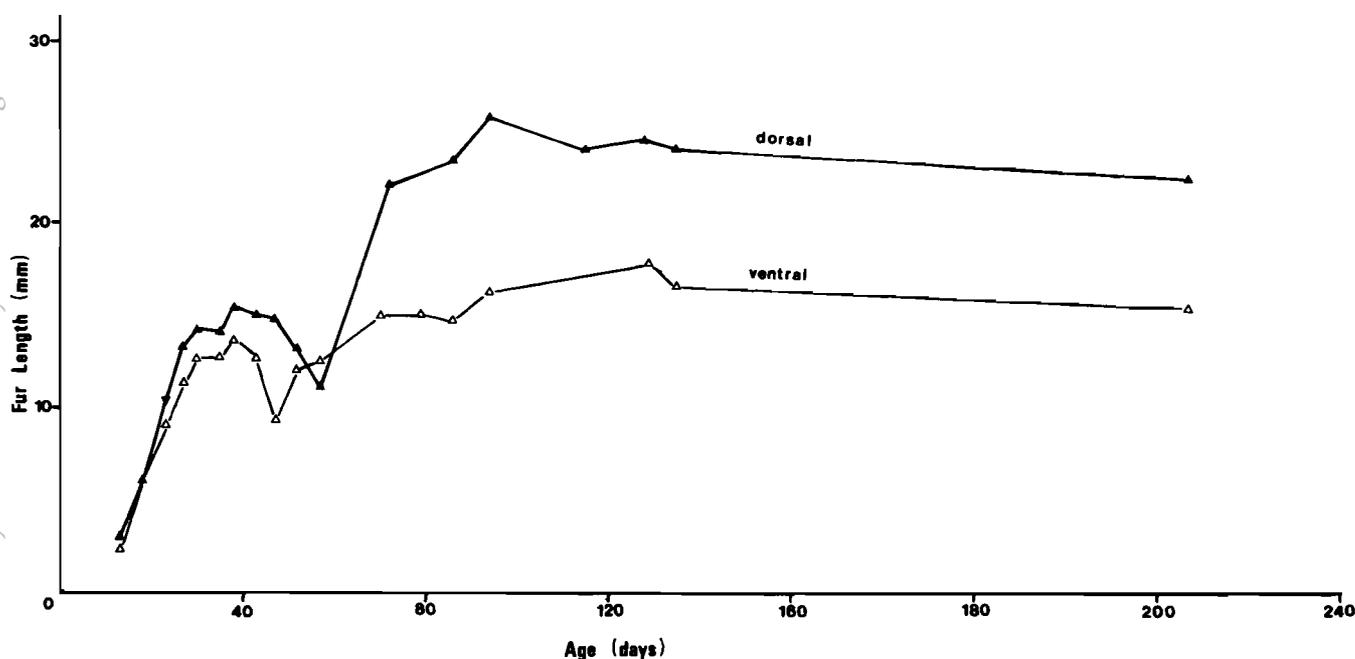


Figure 1 Growth curves of dorsal and ventral fur lengths of giant rats ($N = 7$).

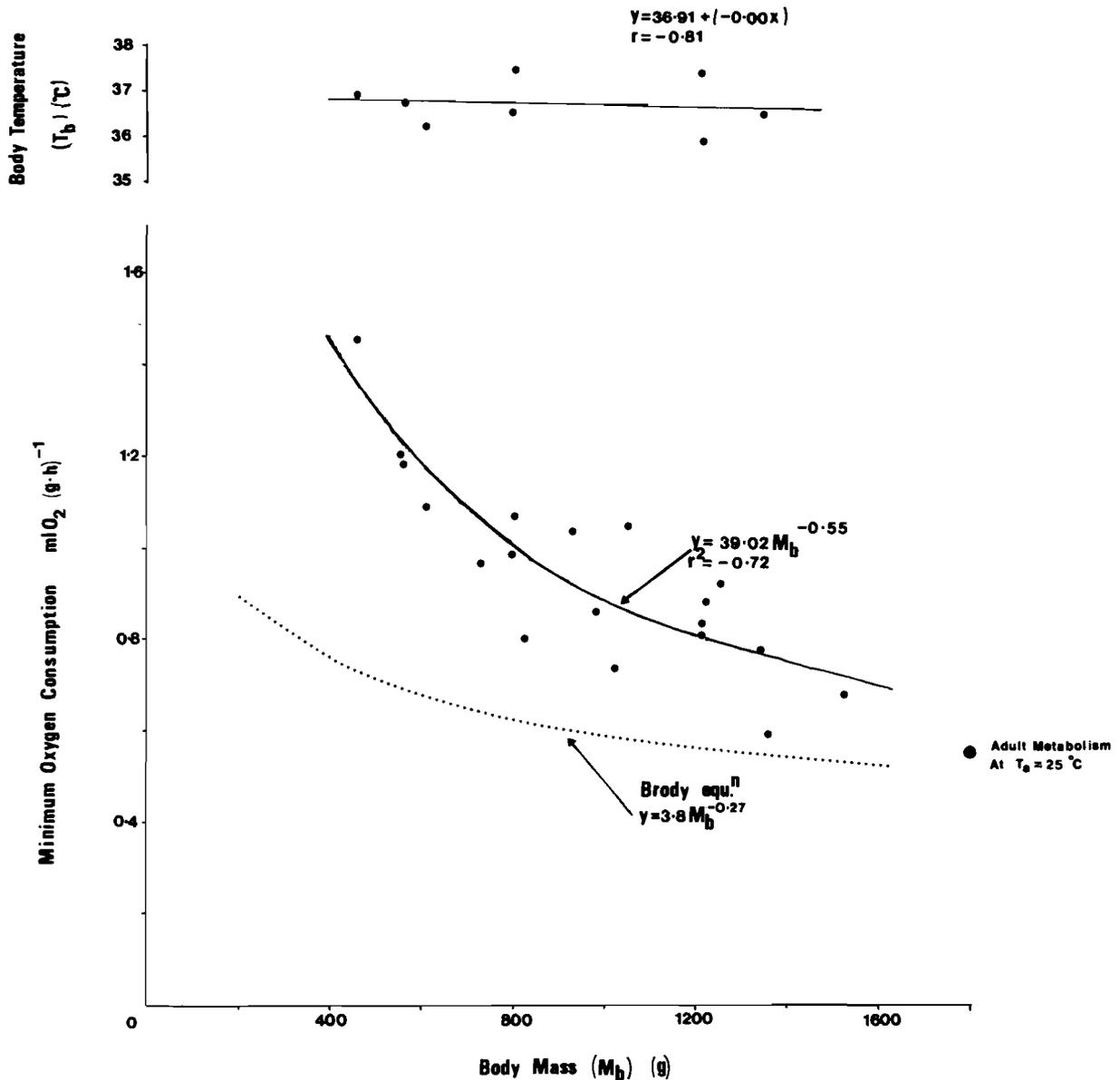


Figure 2 Minimum oxygen consumption and body temperature of growing giant rats at an ambient temperature of 25°C (N = 4).

Table 1 Kendall's rank correlation (τ) and partial rank correlation coefficients for oxygen consumption, mass and age in weaned young giant rats

Mass	N	Oxygen consumption (ml O ₂ (g.h.) ⁻¹) with mass (g)		Oxygen consumption (ml O ₂ (g.h.) ⁻¹) with age (days)	
		τ	Partial	τ	Partial
500 g	21	-0,68 ^a	-0,42	-0,58 ^a	-0,01

^aP < 0,01

Table 2 Kendall's rank correlation (τ) and partial rank correlation coefficients for thermal conductance, mass and age in weaned young giant rats

Mass	N	Thermal conductance (ml O ₂ (g.h. °C) ⁻¹) with mass (g)		Thermal conductance (ml O ₂ (g.h. °C) ⁻¹) with age (days)	
		τ	Partial	τ	Partial
500 g	15	0,75 ^a	-0,11	0,89 ^a	0,74

^aP < 0,01

increase in body mass as described by the equation:

$$y = 3,35 \times M_b^{-0,55}, r^2 = 0,73 (n = 21).$$

Table 2 indicates that both mass and age showed strong negative correlations with conductance, yet age had a higher partial correlation than mass with conductance.

The decrease in evaporative water loss (EWL) with an increase in mass was at an overall higher rate in comparison to total conductance (C) as seen in the equation:

$$y = 2271,95 M_b^{-1,36}, r^2 = 0,79 (n = 15) \text{ (Figure 3).}$$

However, with an increase in mass the percentage evaporative heat loss did not decrease steadily, but declined suddenly in young greater than 77 days old (Table 3). Young less than 77 days old had an average evaporative water loss of 4,2%, which differed significantly ($t = 2,65; d.f. = 13; P < 0,01$) from that of the older individuals which averaged 2,2%.

Discussion

With an increase in mass in weaned giant rats a corresponding decrease in mass specific metabolism, conductance and evaporative water loss was recorded.

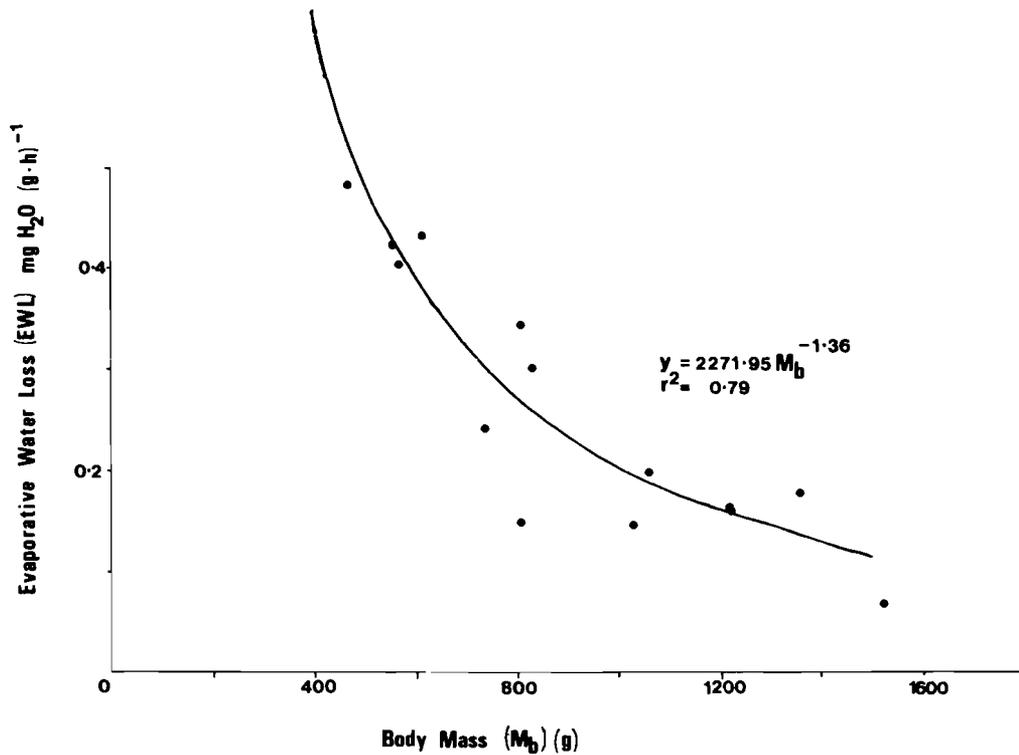


Figure 3 Evaporative water loss (EWL) of growing giant rats at an ambient temperature of 25°C ($N = 4$).

Table 3 Metabolism, conductance, evaporative energy and percentage energy loss values of growing giant rats ($N = 4$)

Age (days)	Body mass (g)	Total conductance $J (g h ^\circ C)^{-1}$	Metabolism $J (g h)^{-1}$	Evaporative energy (EWL) $J (g h)^{-1}$	Evaporative heat loss ^a (%)
55	611,8	1,88	21,89	1,04	4,8
55	553,1	2,08	24,22	1,01	4,2
56	565,7	2,04	23,73	0,96	4,1
56	465,5	2,53	29,46	1,16	3,9
77	800,8	1,69	19,73	0,83	4,2
77	829,4	1,38	16,06	0,82	5,1
78	734,0	1,66	19,32	0,58	3,0
91	804,1	1,83	21,33	0,36	1,7
92	1026,1	1,27	14,77	0,35	2,4
113	1058,2	1,58	18,39	0,33	1,8
114	1059,9	1,80	21,00	0,48	2,3
115	1219,0	1,43	16,68	0,38	2,3
115	1219,3	1,38	16,12	0,38	2,4
131	1361,2	1,02	11,84	0,42	3,6
133	1521,4	1,26	13,51	0,17	1,3

^aEvaporative heat loss = $EWL / \dot{V}O_2 \times 100$. Values of 2,4 J mg^{-1} H_2O and 20,1 J ml^{-1} O_2 were used to convert EWL and $\dot{V}O_2$ to thermal units.

Metabolism showed a decline at the power of $-0,55$ of body mass, similar to what McClure & Randolph (1980) found for the cotton rat, *Sigmodon hispidus*. In addition, mass appears to have had stronger influence upon metabolism in weaned giant rats, similar to what they noted for the cotton rat and wood rat *Neotoma floridana*. An extrapolation of the metabolism curve corresponds closely to the resting metabolic rate found in adult giant rats acclimated at 24°C and tested at the same ambient temperature (Figure 2).

Conductance also declined with a similar power ($-0,55$) to that found for metabolism and closely corresponds to the general power value of $-0,51$ for conductance determined by Aschoff (1981) for a wide range of mammalian species.

However, contrary to that found for metabolism, age appears to have a greater influence upon conductance than mass as McClure & Porter (1983) also demonstrated in the cotton rat. This is probably due to further development of fur properties such as thickness, length and hair diameter and better vasomotor control of core and skin temperatures. In adult cotton rats all these properties proved important while in nestlings only fur depth was found to be important. The faster growth rate of the fluffy juvenile fur prior to the development of the adult fur in the giant rat may be indicative of a selection for greater fur depth in neonates to improve insulation and reduce heat loss. While the slower growth rate of the adult fur probably results from increased importance of the other fur

properties and better vasomotor control.

The delayed development of the adult fur on the shoulder and head may result from increased insulation from a thicker skin or subcutaneous fat, particularly on the shoulder and neck, a region noted for brown fat deposits in young mammals (Gordon, Bartholomew, Grinnell, Jorgensen & White 1977).

The decrease in EWL with an increase in mass would be expected with a decrease in mass specific metabolism. However, the relative decline that EWL constituted of total heat loss from moulting of the juvenile fur was not constant but rather dropped suddenly after 77 days. The sudden decline corresponds with three behavioural and physical developments, being the desertion of the mother, the attainment of adult pelage on the entire body and the testes becoming scrotal (Knight 1984). The descended testes would probably account for the sudden increase in dry thermal conductance as it was noted in adult males that their exceptionally large testes descended into the hairless scrotums and became inundated with blood vessels at ambient temperatures above 28°C (Knight unpublished data). In addition, by day 77 the large hairless tail (which was 72% of adult tail length) would also play an important role in increasing dry thermal conductance.

In the field only two young giant rats were captured during a total of 411 trap nights over two years and these animals were estimated to be between 60 and 98 days old. The sparsity of juveniles suggests they are either extremely cautious or do not leave the nest until a later stage of development. In captivity the first foraging journeys by the young were noted between 43 and 52 days (which corresponds to the youngest rat caught) while they finally desert the nest after 86 days (Ewer 1967; Knight 1984). Interestingly the juveniles caught in the field had their adult fur almost fully developed. It therefore appears that the first exploratory movements out of the burrow by young giant rats probably coincides with the development of relatively efficient thermoregulation, yet by the time they finally desert the nest, thermoregulation would be even more refined with metabolism, conductance

and EWL being about 68, 36 and 57% greater, respectively, than adult values.

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