Heat production and dissipation in a South African diurnal murid *Lemniscomys griselda*

A. Haim
Mammal Research Institute, University of Pretoria, Pretoria

Heat production measured as oxygen consumption (V_{O_2}) and heat dissipation calculated as the means of the overall thermal conductance were studied in a South African diurnal murid *Lemniscomys griselda*. This species maintains its body temperature (T_b) well at around 36,5 ± 1,0 °C over ambient temperatures (T_a) ranging between 5 and 34 °C. The thermoneutral zone lies between T_a = 30 – 34 °C. When exposed to temperatures below the low critical point *L. griselda* at rest conforms to Newton's law of cooling. Non-shivering thermogenesis (NST) was studied as a response to an injection of noradrenaline (sc). Following the administration of 1,5 mg noradrenaline per kg body mass to an anaesthetized animal, an increase of 329% in V_{O_2} was recorded. The distribution pattern of *L. griselda* in comparison with that of *Rhabdomys pumilio*, the more common diurnal murid species in South Africa, is discussed.

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Hitte-produksie, gemeet as suurstofverbruik (V_{O_2}) en hitte-vrystelling, bereken as die gemiddelde van die totale hitte-geleiding is in 'n Suid-Afrikaanse daglewende muis *Lemniscomys griselda* bestudeer. Hierdie spesie hou sy liggaamstemperatuur (T_b) by 36,5 ± 1,0 °C by omgewingstemperature (T_a) wat wissel tussen 5 en 34 °C. Die termoneutrale sone lê tussen T_a = 30 – 34 °C. Wanneer blootgestel aan temperature benede die lae kritiese punt, en in 'n rustoestand, voldoen *L. griselda* aan die vereistes van Newton se wet van afkoeling. Daar is gekyk na nie-bewende hitte-produksie (NST) as 'n reaksie op 'n inspuiting van noradrenalien. Na toediening van 1,5 mg noradrenalien per kg liggaamsmassa, aan 'n dier onder verdowing, is 'n toename van 329% in V_{O_2} aangeteken. Die verspreidingspatroon van *L. griselda* in vergelyking met dié van die meer algemene daglewende *Rhabodomys pumilio* word bespreek.

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A. Haim
Present address: University of Haifa, Oranim,
P.O. Kiryat-Tivon, Israel.

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The single-striped mouse *Lemniscomys griselda* (Thomas 1904) is a diurnal rodent species which occurs in bushveld habitats and forests. In South Africa this species is distributed through Natal and the Transvaal. Its distribution in the Transvaal was studied by Rautenbach (1978) and from his study it is evident that this species occurs in regions which are determined as southern savanna woodland.

Recently heat production was studied in the four-striped mouse *Rhabdomys pumilio* which, similarly to *L. griselda*, is also a diurnal rodent, but it is widely distributed in South Africa (Haim & Fourie 1980a). A careful look into the distribution patterns of these two diurnal species in South Africa (Davis 1974) shows that they are, on a broad basis, mutually exclusive. They do, however, occur in part in the same area, but then they are segregated by their habitat requirements (Smithers 1971, Rautenbach 1978).

In the light of the distribution patterns of these two diurnal species it seemed interesting to study heat production and energy demands in *L. griselda* as compared to *R. pumilio*.

Materials and Methods

Ten individuals of both sexes were collected in the Itala game reserve, Natal, during July 1980. The mean and standard deviation of body mass was 50,53 ± 6,33 g. The mice were acclimated for three weeks at an ambient temperature (T_a) of 25 °C with a photoperiod of 12L:12D. Each mouse was kept in a separate cage with sawdust bedding and fed with rat pellets. Carrots or cucumbers were added to provide succulence.

Heat production was studied by means of oxygen consumption (V_{O_2}) which was measured in an open circuit system (Depocas & Hart 1957, Hill 1972) using a Beckman OM-14 polarigraphic oxygen analyser. V_{O_2} was monitored at various ambient temperatures between 5 and 36 °C. A flow of dried air (silica gel — uniLAB) of 300 ml/min was used. The measurements were carried out on each individual during the day in a darkened perspex metabolic chamber (volume 800 ml). Resting metabolic rate RMR was calculated as in Haim & Fourie (1980a).

Body temperature (T_b) and T_a were measured using chromel-alumel thermocouples and the results were monitored on a Kane-May 2013 potentiometer. T_b was recorded at the end of V_{O_2} measurement at each ambient temperature by inserting the thermocouple approximately 2 cm into the rectum.

The overall thermal conductivity (*C*) was calculated at T_a = 25 °C, 28 °C and 30 °C using the formula of Scholander *et al.* (1950) as given by Hart (1971), assuming that the main avenue for heat loss under the experimental conditions was through 'dry' physical parameters. Calculations are valid for T_a less than the lower critical temperature T_l.

Non-shivering thermogenesis NST was measured at T_a = 30 °C using the method of Heldmaier (1971). Noradrenaline (L – noradrenaline – bitartarat 1:1, Merck), 1,5 mg/kg was injected s.c. into anaesthetized mice (Sagatal, Maybaker, 75 mg/kg, i.p.), after five successive V_{O_2} readings which differed by no more than 0,015‰. The magnitude of NST was calculated as the ratio between minimal V_{O_2} measured in an anaesthetized individual and maximal V_{O_2} values due to noradrenaline injection. T_b and interscapular brown adipose tissue temperature (T_{IBAT}) were measured simultaneously with V_{O_2}. Recordings were made for 120 minutes after noradrenaline injection. All results are given as mean and standard deviations of six individuals. Student's t-test was used to test for significant differences.

Results

V_{O_2} and T_b of *L. griselda* at different ambient temperatures are given in Fig. 1. The thermoneutral zone lies between 30 and 34 °C. Mean V_{O_2} in the thermoneutral zone is 1,213 ± 0,023 mlO$_2$/g.h. and mean T_b is 36,88 ± 0,22 °C. An increase in V_{O_2} and a significant ($P < 0,001$) increase in T_b were observed at T_a = 36°C which is above the thermoneutral zone. The line describing metabolic rate (V_{O_2}) against T_a, extrapolates to M = 0 at T_a = 36,3 °C.

A significant ($P < 0,02$) increase in overall thermal conductance is observed at T_a = 30 °C when compared to the value at T_a = 25 °C. An increase is also observed when compared to the value at T_a = 28 °C (Table 1).

Table 1 Overall thermal conductance (*C*) of *L. griselda* calculated from oxygen consumption at ambient temperature T_a = 25;28 and 30 °C. The figures are mean (± SD) of six individuals. W_b – body mass. ($C = M/T_b - T_a$)

T_a °C	W_b (g)	mlO$_2$/g.h. 1 °C
25	46,43 ± 3,13	0,1417 ± 0,009
28	46,75 ± 3,14	0,1567 ± 0,019
30	47,51 ± 3,51	0,1728 ± 0,019

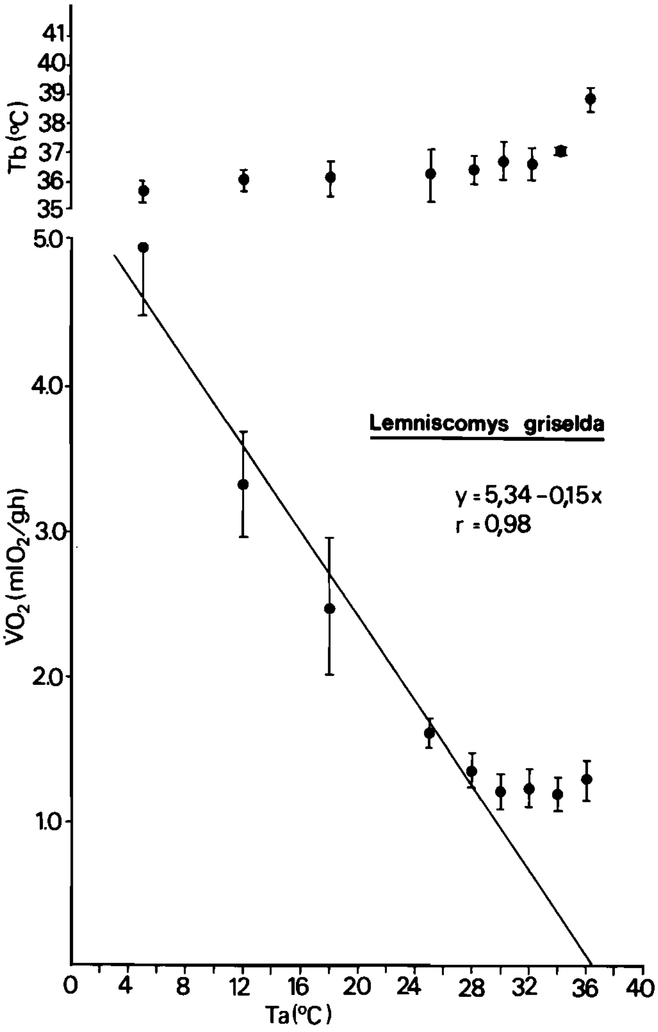

Fig. 1 Mean (± SD) oxygen consumption (V_{O_2}) in mlO$_2$(g.h.)$^{-1}$ and body temperature (T_b) of *L. griselda* at different ambient temperatures (T_a). (n = 6).

The mean minimal value of V_{O_2} measured following the injection of Sagatal was 0,847 ± 0,086 mlO$_2$/g.h. in all anaesthetized mice. A drop of 4 – 6 °C in T_b was also observed in such mice. The mean maximal V_{O_2} measured after noradrenaline injection (NST-magnitude) was 3,29 times higher than the V_{O_2} measured in anaesthetized mice. The maximal values for V_{O_2}, T_b and T_{IBAT} as a response to noradrenaline injection are given in Table 2.

Table 2 Maximal non-shivering thermogenesis NST in *L. griselda*, expressed as the ratio between maximal V_{O_2} after noradrenaline injection — V_{O_2}NA and RMR of anaesthetized individual — V_{O_2}min T_b °C maximal body temperature measured in the rectum. T_{IBAT} °C — temperature measured in interscapular brown adipose tissue

V_{O_2}min	V_{O_2}NA/ V_{O_2}min	Before — NA		After — NA	
mlO$_2$(g.h.)$^{-1}$		T_b °C	T_{IBAT} °C	T_b °C	T_{IBAT} °C
0,847±0,086	3,29±0,66	31,94±0,5	30,90±0,62	39,23±0,48	39,70±0,35

Discussion

From the results of this study it can be seen that individuals of *L. griselda* acclimated at T_a = 25 °C with a photo-period of 12L:12D maintained their body temperature (T_b) at about 36,5 ± 1,0 °C in ambient temperatures (T_a) between 5 and 34 °C. At T_a = 36 °C a significant ($P < 0{,}001$) increase in T_b is observed and mice become hyperthermic (Fig. 1).

RMR measured as V_{O_2} in the thermoneutral zone (Fig. 1) is 9,8% less than expected (for mice with a body mass of 47,5 g) from Kleiber's equation (Kleiber 1961) as modified for rodents by Hart (1971). This difference is not significant and it seems that mice of this species have a 'normal' metabolism. An increase in V_{O_2} is observed at T_a = 36 °C which is above the thermoneutral zone and this increase correlates with the increase in T_b (Fig. 1).

The curve of V_{O_2} against T_a extrapolates to M = 0 at T_a = 36,3 °C. Therefore, according to McNab (1970, 1980) the slope of the curve of V_{O_2} against T_a below the lower critical temperature (T_l) is equal to conductance and *L. griselda* conforms to Newton's law of cooling. From the calculated values of conductance it can be seen that the value of *C* increases with the increase of T_a from 25 °C to 28 °C and to 30 °C.

Evaporative water-loss was not considered, yet calculation of *C* (using the same methods of calculation) shows a marked increase ($C = 0{,}259 \pm 0{,}043$ mlO$_2$/g.h. 1 °C) in this value. It seems that due to this increase in heat dissipation, body temperature remains low. However, the values for *C* of *L. griselda* are 0,15 mlO$_2$/g.h. 1 °C (Fig. 1) and 0,1567 ± 0,019 mlO$_2$/g.h. 1 °C at T_a = 28 °C (Table 1). These values do not differ from *R. pumilio* measured under the same experimental conditions (Haim & Fourie 1980a).

T_l calculated according to Newton's law ($T_l = T_b - \mathrm{RMR}/C$) is 30 °C and this value is in agreement with the results in Fig. 1.

The importance of NST in heat production of rodents and other small mammals has been emphasized in many studies, most of which were summarized by Jansky (1973). In *R. pumilio* a high NST magnitude (V_{O_2}NE/V_{O_2} min = 516%) was found (Haim & Fourie 1980b). The values for *L. griselda* are much lower (Table 2) although there is an increase of T_b and T_{IBAT}, similar to that found in *R. pumilio*. Another point of importance is that *R. pumilio* showed maximum response to noradrenaline after no more than 60 min following the injection of noradrenaline. In *L. griselda*, however, a maximum response was obtained only after 90 min or more.

The lower values of NST as recorded in *L. griselda* may be related to the fact that in its natural habitat it is not exposed to low ambient temperatures to the extent *R. pumilio* experiences. When exposed to cold, *L. griselda* seems to depend on changes in either conductance or muscular thermogenesis (shivering or motor activity), or a combination of the two factors as well as NST.

Differences in thermogenesis may explain the difference in the distribution pattern of *L. griselda* and *R. pumilio*, both diurnal murids of a similar body size. In a recent study on heat production in *R. pumilio* it was found that the metabolic rate is 47% lower than expected (Haim & Fourie 1980a). *R. pumilio* inhabits hot and arid regions as well as cold and mesic ones. The difference in RMR between the two species is significant ($P < 0{,}001$). From this study and the previous one on *R. pumilio* (Haim & Fourie 1980a) it may be assumed that *R. pumilio* adapts more readily to different ecological conditions. Due to its low metabolism and its low energy requirements, it can survive in more arid areas where food is scarce in winter, winter being the dry season in large areas of South Africa. Indeed, in dry parts of the Transvaal (grasslands) *R. pumilio* is very common, while *L. griselda* is restricted to woodlands or bushveld (Rautenbach 1978).

It is important to point out the fact that both species are omnivores (Perrin & Curtis 1980). However, in East Africa, Field (1975) found that the diet of *L. striatus* contains termites in the wet season but it can feed also on grass, leaves and stems as well as utilizing seeds.

The absence of *R. pumilio* from the tropical corridor was mentioned by Coetzee (1970). It is tempting to speculate that *R. pumilio* does not exist in this region while *L. griselda* is common to it, due to exclusion by *L. griselda*, of *R. pumilio* from the woodlands. A further ecological study may support this idea.

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