

Heat production in nocturnal (*Praomys natalensis*) and diurnal (*Rhabdomys pumilio*) South African murids

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Heat production by means of oxygen consumption (Vo_2) was measured at different ambient temperatures (T_a) 6–34 °C in both species. The thermoneutral zone for both species was found to be at $T_a = 32 \pm 1$ °C. Below the lower critical point Vo_2 for the diurnal species (*R. pumilio*) was significantly higher ($p < 0,001$) than Vo_2 for the nocturnal species (*P. natalensis*). Non-shivering thermogenesis (NST) was measured as a response to an injection of noradrenaline (1,5 mg/kg s.c.) in both species and NST magnitude for *R. pumilio* was significantly higher ($p < 0,001$) when compared to *P. natalensis*. The differences in heat production are related to the difference in fur insulation and this may derive from the fact that *R. pumilio* is diurnal while *P. natalensis* is nocturnal.

S. Afr. J. Zool. 1980, 15: 91–94

Suurstofverbruik (Vo_2) van twee knaagdierspesies is bepaal by varierende omgewingstemperatuur (T_a) 6–34 °C as 'n indeks tot metaboliese hitteproduksie. Die termoneutrale grense vir beide spesies is vasgestel op $T_a = 32 \pm 1$ °C. By temperature benede die laer kritieke grenswaarde vertoon die diurniese *R. pumilio* 'n betekenisvolle Vo_2 toename ($p < 0,001$) in vergelyking met die nokturniese *P. natalensis*. Metaboliese hitte generasie (MHG) is bepaal as reaksie op 'n noradrenalin (1,5 mg/kg) onderhuidse inspuiting toegedien aan beide spesies. Die gevolglik versnelde MHG faktor wat bepaal is vir *R. pumilio* was betekenisvol ($p < 0,001$) hoër as by *P. natalensis*. Die verskil in liggaamshitte produksie waargeneem word gedeeltelik toegeskryf aan die verskil in pelsbedekking wat beskryf is vir *R. pumilio* en *P. natalensis*.

S.-Afr. Tydskr. Dierk. 1980, 15: 91–94

Heat production in rodents has been extensively studied for the past three decades and many of these studies were summarized by Hart (1971). So far the published data on heat production of indigenous South African rodents is limited. Such information can contribute to a better understanding of the distribution patterns, environmental thermal limitations, activity patterns and quantitative estimation of food requirements.

The present investigation was aimed at studying heat production by physiological means in two murid species, *Praomys natalensis* and *Rhabdomys pumilio*, which are common in South Africa (Davis 1974).

The multimammate mouse *Praomys natalensis* is a nocturnal rodent and occurs in both warm and cold mesic areas. The striped mouse *Rhabdomys pumilio*, is a diurnal species and inhabits arid and hot regions as well as cold mesic areas. Apart from the fact that this species does not exist in the eastern tropical corridor (Coetzee 1970), the two species co-exist in most habitats.

Non-shivering thermogenesis (NST) was found to be an important mechanism for heat production in small mammals such as rodents (Heldmaier 1971; Jansky 1973). It therefore seemed of interest to compare NST in both species due to the fact that one is nocturnal and the other diurnal.

Material and Methods

Individuals of both species were collected in Pretoria (Rietondale Experimental Farm) and acclimated for several weeks at an ambient temperature of 25 °C with a photoperiod of 12L:12D. The mice were kept individually in cages with sawdust bedding. Rat pellets and water were provided ad libitum. Carrots and cucumbers supplemented the diet. Mice of both sexes weighing between 25 and 54 g were used in these experiments.

Heat production was measured by means of oxygen consumption (Vo_2) at different ambient temperatures (6–34 °C) using an open flow system (Depocas & Hart, 1967), with a flow of dried air (silica gel) at a rate of 300 ml/min. Carbon dioxide was not removed from the system at any stage (Hill 1972). Oxygen concentration was measured with a Beckman E2 paramagnetic oxygen analyzer. Copper constantan thermocouples were used for measuring body (rectal) temperature (T_b) and ambient temperature (T_a). The results were recorded on an Esterline Angus recorder.

The experiments were carried out during the day in a

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Submitted 13 March 1979; accepted 4 October 1979

darkened perspex metabolic chamber (volume 800 ml). Vo_2 was recorded after 60 min, after a 2 – 3h stabilizing period, at each test. Only five readings at intervals of 3 min (that did not differ by more than 0,015% O_2) were used for calculating resting metabolic rate (RMR). All results were corrected to standard temperature and pressure (STP).

Thermal conductivity (C) was calculated for both species at $T_a = 30\text{ }^\circ\text{C}$ using the formula proposed by Hart (1971), making the assumption that the main avenue for heat loss under experimental conditions was through 'dry' physical parameters and not through evaporation.

Non-shivering thermogenesis was measured as the ratio between the minimal Vo_2 of anaesthetized (Sagatal, Maybaker 75 mg/kg, i.p.) mice and maximal Vo_2 due to an injection of noradrenaline (NA) (Sigma 1,5 mg/kg, s.c.) following Heldmaier (1971). Body temperature and interscapular brown adipose tissue temperature (T_{IBAT}) were measured using copper constantan thermocouples. The experiments were carried out in a metabolic chamber at $T_a = 31\text{ }^\circ\text{C}$. Vo_2 was recorded every 3 min. NA was injected only after five successive readings which differed by no more than 0,015% O_2 . Recordings were made for one hour after the NA injection. Student's t-test was used to test for significance.

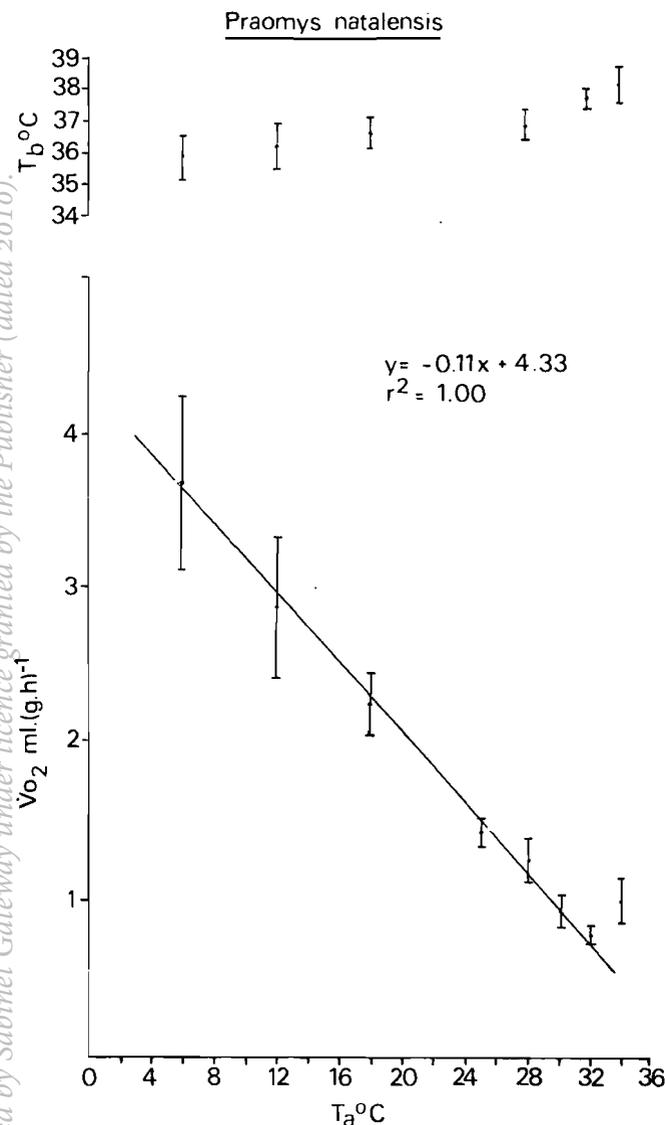


Fig. 1 Mean (\pm S.D.) oxygen consumption (Vo_2) in $ml_o_2(g.h)^{-1}$ and body temperature (T_b) of *P. natalensis* at different ambient temperatures (T_a) ($n = 6$).

Table 1 Thermal conductance (C) of *P. natalensis* and *R. pumilio* calculated from oxygen consumption at $T_a = 30\text{ }^\circ\text{C}$. The figures are mean (\pm S.D.) of six individuals. W_b – body weight

<i>Praomys natalensis</i>		<i>Rhabdomys pumilio</i>	
W_b g	C $ml_o_2(g.h.1^\circ C)^{-1}$	W_b g	C $ml_o_2(g.h.1^\circ C)^{-1}$
$41,49 \pm 8,30$	$0,121 \pm 0,010$	$39,62 \pm 9,70$	$0,166 \pm 0,017$

Results

The relationship between oxygen consumption Vo_2 and T_a as well as T_b are given in Fig. 1 for *P. natalensis* and in Fig. 2 for *R. pumilio*. Each point is the mean (\pm S.D.) of six individuals. From the Figures it is evident that the thermoneutral zone for both species is at $T_a = 32 \pm 1\text{ }^\circ\text{C}$. At ambient temperatures below the critical temperature *R. pumilio* consumed significantly more oxygen than *P. natalensis*. The increase in Vo_2 above the thermoneutral zone was accompanied by an increase in T_b in both species.

Thermal conductivity for mice of both species, calculated at $T_a = 30\text{ }^\circ\text{C}$, is given in Table 1. The difference in thermal conductivity between the two species is highly significant ($p < 0,001$) and *R. pumilio* has the higher thermal conductance. In each species, individuals with a low body mass have high conductance values, when compared to individuals with a high body mass.

The magnitude of (NST) is given for both species in Table 2. The ability of *R. pumilio* acclimated at $T_a = 25\text{ }^\circ\text{C}$ (12L:12D) to produce heat by means of NST is significantly ($p < 0,001$) higher than that of *P. natalensis*. The increase of Vo_2 in both species was accompanied by an increase in T_b and T_{IBAT} .

Discussion

Oxygen consumption (Vo_2) for both species at the thermoneutral zone ($T_a = 32 \pm 1\text{ }^\circ\text{C}$), a mean (\pm S.D.) of $0,79 \pm 0,07\text{ ml } O_2/g.h.$ for *P. natalensis* and $0,81 \pm 0,90\text{ ml } O_2/g.h.$ for *R. pumilio* (Figs. 1 & 2), is 47% lower than that expected from Kleiber's equation (Kleiber 1961), which gives a value of $1,5\text{ ml/g.h.}$ for mice with a mass of 40 g. Such low values of Vo_2 may point to the fact that both species are well adapted to hot environments, while the main difference in their biology is that *R. pumilio* is diurnal and *P. natalensis* is nocturnal. Low Vo_2 values were found in the golden spiny mouse *Acomys russatus*, which is a diurnal rodent inhabiting extreme arid, hot areas in the Rift Valley of Israel (Shkolnik & Borut 1969).

Hudson and Wang (1969), Hart (1971) and Yousef and Johnson (1975) all state that low values of Vo_2 are characteristic of rodents from hot desert habitats. Such an attribute may aid in reducing evaporation through the respiratory tract as well as reducing energy requirements. This would seem in the case of both investigated species to be a good adaptation for winter, which is the dry period.

The significantly high levels of Vo_2 in temperatures below the lower critical point in *R. pumilio* when compared to *P. natalensis* shown by the difference in the slope of Figs. 1

Table 2 Maximal NST in *P. natalensis* and *R. pumilio* expressed as the ratio between mean (\pm S.D.) maximal Vo_2 after noradrenaline injection (NA) – Vo_2 NA and the mean (\pm S.D.) RMR of each anaesthetized individual before the injection – Vo_2 Min., T_b °C – Mean (\pm S.D.) body temperature measured in the rectum. T_{IBAT} °C – Mean (\pm S.D.) temperature measured in interscapular brown adipose tissue

	Vo_2 Min	Vo_2 NA	Before — NA		After — NA	
	$mlo_2(g.h.)^{-1}$	Vo_2 Min	T_b °C	T_{IBAT} °C	T_b °C	T_{IBAT} °C
<i>P. natalensis</i>	0,794 \pm 0,05	2,74 \pm 0,60	35,05 \pm 0,45	35,00 \pm 0,30	38,30 \pm 0,52	39,08 \pm 0,86
<i>R. pumilio</i>	0,722 \pm 0,06	5,16 \pm 0,21	34,56 \pm 0,50	34,48 \pm 0,45	38,80 \pm 0,43	40,50 \pm 0,51

and 2, point to differences in thermal conductivity between the two species. The difference in conductance (Table 1) conforms with the difference in insulation. The fur of *P. natalensis* is much thicker and longer than that of *R. pumilio* (Keogh 1974). The poor insulation and dark skin pigmentation of *R. pumilio* seem to be a good adaptation for a diurnal rodent, which can both dissipate and again heat easily, thus reducing energy requirements.

Food consumption measurements of both species (unpub. data) show that under experimental conditions at $T_a = 25$ °C (12L:12D) *R. pumilio* consumes more food per gram body mass when compared to *P. natalensis*. For *R.*

pumilio with a mass of 29,7 g food consumption was 0,13 g (gWb day) $^{-1}$ while for *P. natalensis* with a mass of 28,5 g the consumption rate was 0,087 g (gWb day) $^{-1}$. It therefore appears that increased metabolism and the fact that *R. pumilio* is diurnal may compensate for its poor insulation.

Cold acclimated rodents depend on NST for heat production, while in warm acclimated rodents when exposed to cold, muscle shivering is the main source of heat production (Jansky 1973). At very low temperatures (-40 °C), NST and shivering are used for thermoregulation (Jansky & Hart 1963).

The advantages of NST for small mammals was emphasized by Webster (1974). Due to NST a great amount of heat can be produced in a very short time (minutes) without interfering with muscular function in small mammals.

A definite dependence on NST when exposed to a cold environment was found in a cold resistant population of a diurnal murid, *Acomys russatus* (Haim & Borut 1976; Borut, Haim & Castel 1978). Individuals of this population showed a strong response to noradrenaline and increased oxygen consumption 5,8 times over the RMR, even when acclimated to $T_a = 28$ °C (12L:12D).

The results of the present study indicate that *R. pumilio* has a higher NST capacity than *P. natalensis*. The difference in NST magnitude may be due to the fact that *R. pumilio* must depend on a rapid increase in heat production in order to maintain T_b when exposed to cold, while *P. natalensis* can depend on its insulation to a certain extent. The great dependence of *R. pumilio* on NST may be caused by its poor insulation and resulting high thermal conductivity.

On the other hand, the differences in the distribution patterns between these two species in South Africa cannot be explained by the results of the present study. *Rhabdomys pumilio* occurs in both hot arid regions (such as the Kalahari and Namib deserts) as well as in cooler and more mesic areas, while *Praomys natalensis* does not exist in arid areas. The fact that *P. natalensis* is nocturnal means that it can evade the hot hours of the day. There is no difference between the thermoregulatory abilities at the thermoneutral zone and even above it in the two species. Therefore, it would seem that moisture is the critical factor and a comparative study of their water metabolism might explain differences in their distribution patterns.

Acknowledgements

We thank Messrs R.D. Carr and A. Seabrook for assistance. This study was supported by a postdoctoral CSIR fellowship to A.S. Haim.

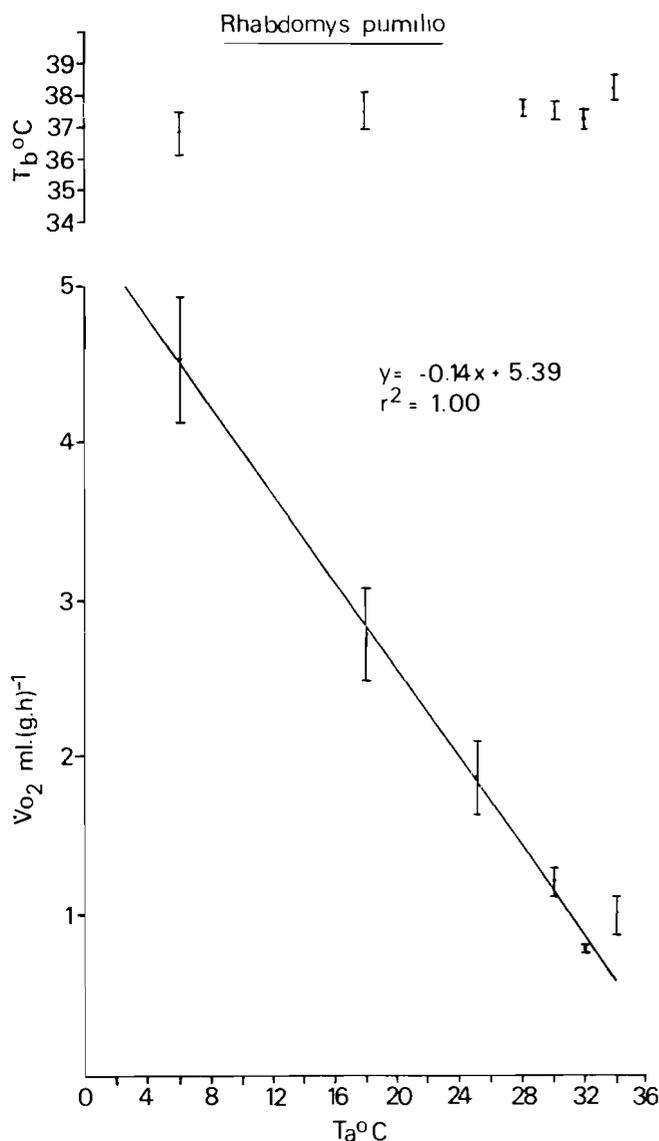


Fig. 2 Mean (\pm S.D.) oxygen consumption (Vo_2) in $mlo_2(g.h.)^{-1}$ and body temperature of *R. pumilio* at different ambient temperatures. ($n = 6$).

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