

## Thermoregulation and energy metabolism in the lesser bushbaby, *Galago senegalensis moholi*

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Received 29 January 1988; accepted 4 October 1988

Thermoregulation and energy metabolism were studied in adult and juvenile *G. s. moholi* at ambient temperatures ranging from 6 to 35°C. In the adults, oxygen consumption decreased with increasing ambient temperature reaching minimum values of  $0,7 \pm 0,04$  (males) and  $0,9 \pm 0,04$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (females) at the lower critical temperature of 28°C. Between 28 and 35°C, the thermal neutral zone, oxygen consumption remained constant and was found to be 32% (males) and 16% (females) below the theoretical mass specific level. In the juveniles oxygen consumption also decreased with increasing temperature but reached the lowest measured value at 35°C. Oxygen consumption in this group was significantly higher than in the adults at each temperature. Body temperature remained constant over most of the temperature range, but increased significantly in the female and juvenile groups at 35°C. Evaporative water loss increased linearly with temperature in all groups. At 35°C less than 50% of the endogenous heat production was dissipated by this means. The results are discussed with reference to the age, habitat and behaviour of the animal.

Temperatuurregulering en energiemetabolisme is in volwasse en jong *G. s. moholi* ondersoek onder heersende temperature tussen 6 en 35°C. In volwasse diere het suurstofopname met stygende temperature verminder totdat 'n minimumwaarde van  $0,7 \pm 0,04$  (mannetjies) en  $0,9 \pm 0,04$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (wyfies) by 'n lae kritieke temperatuur van 28°C verkry is. Tussen 28 en 35°C, die neutrale temperatuursone, is suurstofopname teen 'n waarde laer as die teoretiese massaspesifieke waarde gehandhaaf. Suurstofopname in onvolwasse diere het ook verminder met stygende temperatuur, maar die laagste waarde is by 35°C ondervind. By dieselfde heersende temperatuur is suurstofopname van onvolwasse diere statisties hoër as dié van volwasse diere. Liggaamstemperatuur is konstant gehandhaaf, behalwe by 35°C in vroulike en onvolwasse diere. Waterveries deur verdamping het lineêr vermeerder met verhoging in temperatuur in alle groepe. By 35°C is minder as 50% van die interne hitte geproduseer deur verdamping, verloor. Resultate word met betrekking tot ouderdom, habitat en leefwyse bespreek.

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Bushbabies are primates of the sub-order Prosimii, family Galagidae, whose members are found throughout Africa in a wide range of habitats including semi-arid regions, open woodland, orchard bush, scrub and isolated thickets with grassland (Doyle & Walker 1974). The animal used in this study, *Galago senegalensis moholi*, is a sub-species found in the northern Transvaal of South Africa where it often encounters extremes of temperature (-6 to 38°C). These animals (maximum mass 300 g) are nocturnal, becoming inactive for long periods on cold nights to reduce energy expenditure (Martin & Bearder 1979). They are not obligate drinkers, an adaptation which must be of importance in affecting the distribution of the species (Doyle & Bearder 1976).

It is of interest to determine how the animal copes energetically in the extreme environmental conditions described above, these being characterized by high diurnal temperatures and relatively low nocturnal temperatures, when they are normally active. Studies on other prosimian species have revealed that they share several physiological peculiarities, namely hypometabolism, a labile body temperature, intolerance to heat and a surprising ability to withstand low ambient temperatures (Muller 1979). Considering the phylogenetic status of the group, there has been much speculation as to whether these features indicate a poor thermoregulatory

capacity or are, in fact, adaptations to the different habitats in which these animals are found.

The present study was undertaken to obtain more information on the thermoregulatory strategies of the bushbaby by measuring the physiological responses of adult and juvenile *G.s. moholi* to several ambient temperatures.

### Methods

#### Animals and maintenance

All bushbabies, *G. s. moholi*, were obtained from a colony maintained by the Primate Behaviour Research Unit at the University of the Witwatersrand. They were housed either singly in wire cages or in groups of 3 to 10 in small rooms. The temperature varied between 22 and 25°C throughout the year and they were exposed to a reversed photoperiod regime of 12L : 12D. The diet consisted of a commercial porridge containing balanced proportions of protein, carbohydrates, vitamins and minerals, supplemented with nuts, fruit and mealworms.

Three groups of animals were used: adult males ( $n = 8$ , mean mass 185 g), adult females ( $n = 10$ , mean mass 158 g) and male juveniles ( $n = 8$ , mean mass 90 g). Only the adults were post-absorptive when used and the females were in the anoestrous state. All measurements were taken during the activity period of the bushbabies.

## Measurements

Oxygen consumption ( $\dot{V}O_2$ ) was determined in an open flow system according to the method of Depocas & Hart (1957) with a Servomex OA272  $O_2$  analyser (Servomex, Sussex) and carbon dioxide production ( $\dot{V}CO_2$ ) with a Cavitron PM20 series  $CO_2$  monitor (Anarad Inc., Santa Barbara). Pre-dried air was drawn through the chamber which housed the animal (volume 2 l) at a constant rate of 280 ml/min, monitored using a calibrated flowmeter.

Ambient temperature ( $T_a$ ) within the chamber was kept constant within  $1,0^\circ C$  of the desired level (measured using a Digitec type 5810 HT series thermistor) by immersing the chamber in a darkened metal water bath at various temperatures.

Temperatures were varied between 6 and  $35^\circ C$ . No experiments were conducted above  $35^\circ C$  for fear of hyperthermia developing in the animals.

A habituation period of 2 h preceded data collection for each animal.  $\dot{V}O_2$  and  $\dot{V}CO_2$ , corrected to STP, were averaged from recordings taken at intervals of 30 s during the subsequent 30-min period. Ambient temperature choice was random and at most one experiment per day was conducted per animal. Immediately after removing the bushbabies from the chamber, rectal temperature ( $T_b$ ) was measured at a depth of 4 cm using a Digitec thermistor.

Evaporative water loss (EWL) was measured by passing the out-flowing air through two previously weighed U-tubes placed in series, the first containing silica gel and the second, anhydrous calcium chloride. The change in mass of the tubes was attributed to water loss from the animal through the skin and respiratory surfaces. To minimize the effect of urine and faeces on the determination of EWL values, liquid paraffin was placed into the bottom of the chamber below the grid on which the animal was standing.

## Statistical treatment

Two-way analysis of variance (SAS, 1982) was used to test the effect of  $T_a$  on  $\dot{V}O_2$ ,  $T_b$  and EWL and inter-group differences in these variables at each  $T_a$ . Results are reported as means  $\pm$  S.E. Linear regression was done using the method of least squares.

## Results

### Oxygen consumption

The relationship between  $\dot{V}O_2$  and  $T_a$  is shown in Figure 1. In the adults  $\dot{V}O_2$  decreased steadily with increasing  $T_a$  from 6 to  $28^\circ C$  ( $p < 0,05$ ) following the regression lines:

Males:  $Y(\text{ml } O_2 \text{ g}^{-1} \text{ h}^{-1}) = 2,75 - 0,08T_a$  ( $r = -0,99$ )

Females:  $Y(\text{ml } O_2 \text{ g}^{-1} \text{ h}^{-1}) = 2,95 - 0,07T_a$  ( $r = -0,99$ ).

The values for males and females were significantly different at all temperatures ( $p < 0,05$ ).

Minimum values of  $0,7 \pm 0,04 \text{ ml } O_2 \text{ g}^{-1} \text{ h}^{-1}$  in the males and  $0,9 \pm 0,04 \text{ ml } O_2 \text{ g}^{-1} \text{ h}^{-1}$  in the females were reached at the lower critical temperature of  $28^\circ C$  and remained at these values between 28 and  $35^\circ C$ . Within this TNZ, mean  $\dot{V}O_2$  was below the theoretical mass-

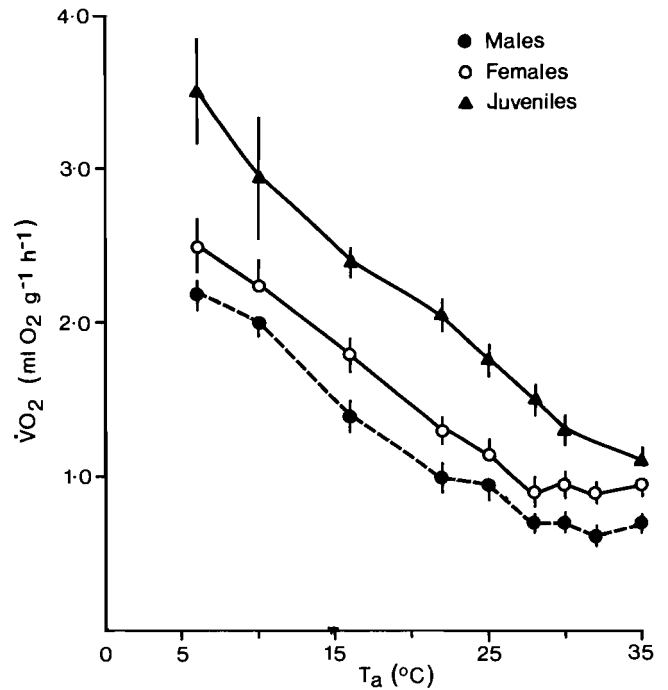


Figure 1 Effect of ambient temperature on oxygen consumption in males, females and juveniles.

specific level according to the equation  $\dot{V}O_2 = 3,8M^{-0,25}$  (Kleiber 1961). The respiratory exchange ratio ( $\dot{V}CO_2/\dot{V}O_2$ ) remained constant over most of the temperature range ( $1,0 \pm 0,04 - 1,1 \pm 0,03$  in the males,  $1,0 \pm 0,05 - 1,0 \pm 0,03$  in the females and  $0,9 \pm 0,07 - 1,0 \pm 0,05$  in the juveniles). Only in the males did  $\dot{V}CO_2$  increase at temperatures above  $28^\circ C$  resulting in a significant rise in the respiratory exchange ratio ( $p < 0,05$ ) to  $1,1 \pm 0,03$ .

Table 1 shows values for minimum thermal conductance (TC) below thermoneutrality calculated by three different methods:

1. From individual  $\dot{V}O_2$  measurements using the formula  $\dot{V}O_2 (T_b - T_a)^{-1}$
2. From the slope of the graph relating  $\dot{V}O_2$  with  $T_a$ , using McNab's (1980) correction factor
3. From the equation  $TC = 1,02W^{-0,505}$  (Herreid & Kessel 1967).

Corrected thermal conductance values were similar to mean values (calculated as in Method 1) and also to theoretical values predicted from mass using the equation in Method 3. From the lower critical temperature conductance increased significantly ( $p < 0,05$ ) with increasing  $T_a$  reaching maxima of 0,23 (males), 0,25 (females), and  $0,35 \text{ ml } O_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ C^{-1}$  (juveniles) at  $35^\circ C$ . The juveniles showed a similar response to that of the adults, with  $\dot{V}O_2$  decreasing significantly ( $p < 0,05$ ) as  $T_a$  increased from 6 to  $35^\circ C$ :

$Y(\text{ml } O_2 \text{ g}^{-1} \text{ h}^{-1}) = 3,92 - 0,09T_a$  ( $r = -0,99$ ).

$\dot{V}O_2$  was significantly higher than in the adults at each temperature and reached a minimum at  $35^\circ C$  (Figure 1).  $\dot{V}O_2$  was significantly higher at  $30^\circ C$  than at  $35^\circ C$  suggesting that the lower critical temperature may lie

**Table 1** Minimum thermal conductance, mean body temperature and mean maximum evaporative water loss in males, females and juveniles

	Males	Females	Juveniles
1. Mean min TC (ml O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0,07	0,084	0,112
2. Corrected slope (ml O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0,06	0,087	
3. Predicted min TC (ml O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0,073	0,079	0,105
Mean Tb ± S.E (°C)	37,9 ± 0,2	37,8 ± 0,2	37,0 ± 0,2
Mean max EWL ± S.E. (ml H <sub>2</sub> O kg <sup>-1</sup> h <sup>-1</sup> )	2,15 ± 0,14	2,31 ± 0,27	3,72 ± 0,53

1. Calculated from the formula  $\dot{V}O_2 (T_b - T_a)^{-1}$
2. Calculated using McNab's (1980) correction factor
3. Taken from Herreid & Kessel (1967).

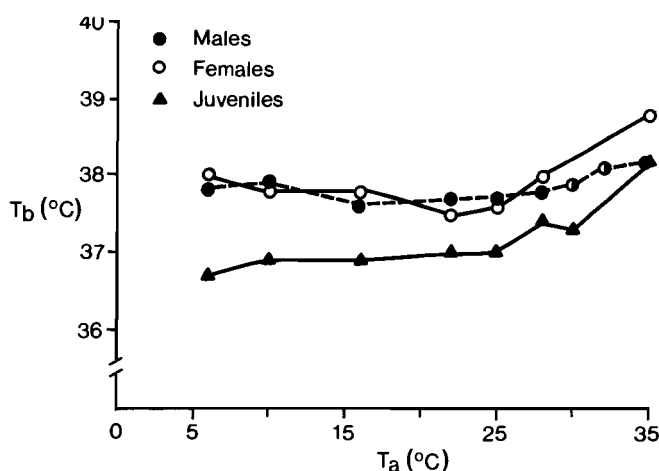
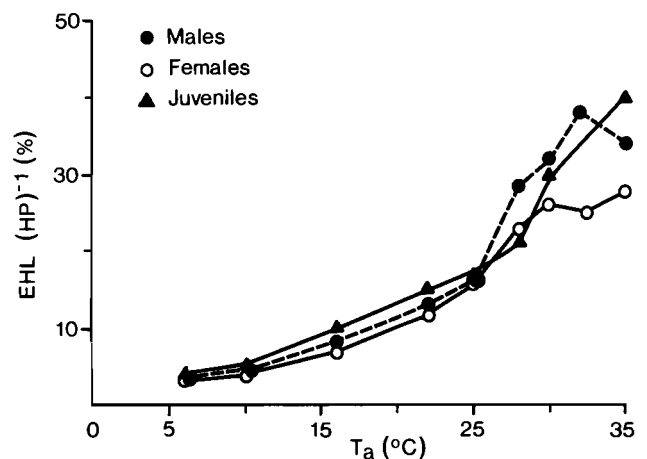
either somewhere between these temperatures or even above 35°C. The calculated values for TC were also significantly higher than in the adults ( $p < 0,05$ ) and the minimum value at 30°C was slightly above that obtained from the  $\dot{V}O_2$  regression but agreed with the theoretical mass-specific level (Table 1).

### Body temperature

In the males, rectal temperature remained stable at the resting level over the entire temperature range ( $38,7 \pm 0,25^\circ\text{C}$  at 6°C to  $38,2 \pm 0,29^\circ\text{C}$  at 35°C). In the female group Tb was constant between 6°C ( $38,0 \pm 0,53^\circ\text{C}$ ) and 32°C ( $38,1 \pm 0,36^\circ\text{C}$ ) but increased significantly ( $p < 0,05$ ) to  $38,8 \pm 0,54^\circ\text{C}$  at 35°C. Tb was maintained at a significantly lower level in the juveniles ( $p < 0,05$ ) than in the adults ranging from  $36,6 \pm 0,62^\circ\text{C}$  at 6°C to  $37,3 \pm 0,41^\circ\text{C}$  at 32°C. At 35°C, Tb increased significantly ( $p < 0,05$ ) to  $38,2 \pm 0,32^\circ\text{C}$  (Figure 2).

### Evaporative water loss

EWL increased with Ta in all groups reaching a maximum within the TNZ. The regression lines for males, females and juveniles respectively are:

**Figure 2** Effect of ambient temperature on body temperature in males, females and juveniles.**Figure 3** Effect of ambient temperature on evaporative heat loss as a percentage of heat production in males, females and juveniles.

$$Y(\text{ml H}_2\text{O kg}^{-1} \text{ h}^{-1}) = 0,03 \pm 0,06T_a \quad (r = -0,97)$$

$$Y(\text{ml H}_2\text{O kg}^{-1} \text{ h}^{-1}) = 0,20 \pm 0,06T_a \quad (r = -0,99)$$

$$Y(\text{ml H}_2\text{O kg}^{-1} \text{ h}^{-1}) = 0,56 \pm 0,09T_a \quad (r = -0,99)$$

and showed significant correlation ( $p < 0,05$ ) in all groups.

Figure 3 shows the relationship between Ta and evaporative heat loss as a % of heat production (EHL/HP × 100). Values of 2,34 J/mg H<sub>2</sub>O and 20,1 J/ml O<sub>2</sub> were used in converting EWL and  $\dot{V}O_2$  to thermal units (as in Buffenstein & Jarvis 1985):

$$\text{EWL} \times 2,34 / (\dot{V}O_2 \times 20,1) = \text{EHL/HP}$$

The ratio, EHL/HP × 100, which is a measure of the effectiveness of evaporative cooling, increased significantly ( $p < 0,05$ ) with Ta in each group reaching maximum values of 33,8; 28,3 and 40,0% for males, females and juveniles respectively.

### Discussion

The minimum oxygen consumption (between 28 and 35°C) for males is in agreement with the data of Dobler (1982) who found basal metabolic rate in these animals ( $0,77 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) to be 76% of the value predicted from Kleiber's formula ( $\dot{V}O_2 = 3,8M^{-0,25}$ ). In the present

study, means of  $0,7 \pm 0,04 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (males) and  $0,9 \pm 0,04 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (females) represent reductions to 68% and 84% respectively.

The allometric relationship between basal metabolic rate and body mass has recently been reviewed by Hayssen & Lacy (1985). These authors emphasize the inadequacy of the Kleiber formula in describing this relationship since it was based on a very small and unrepresentative subset of mammals. Their revised allometric equation based on data collected from 248 eutherian species resulted in a line with slope significantly different from that of Kleiber's line. Lower predicted BMRs were obtained in this study using the Hayssen & Lacy equation and this results in reductions to 77% (males) and 92% (females) of predicted values.

The depressed level of heat production in *G. s. moholi* is similar to that found in its larger relative *G. crassicaudatus* (Table 2), but in other Lorisiidae basal metabolic rate is reduced to a greater extent compared to predicted values (Table 2). In addition, body temperature is generally lower than in mammals of similar size and follows a marked circadian rhythm (Muller 1979). These features, and phenomena such as lethargic states (characteristics of certain Malagasy lemurs), have long been considered indicative of an inadequate thermoregulatory system reflecting the primitive state of the group. However, there is much evidence to suggest that the level of basal metabolism and body temperature regulation of an animal are closely related to the degree of thermal stability and food availability of its environment, rather than phylogenetic status (Muller 1985). For instance, the majority of tropical mammals exhibit hypometabolism and a certain degree of lability in body temperature (Muller 1979). The results obtained for body temperature in this study confirm the statement by Dobler (1976) that, within the Lorisiidae, the galagos attain the highest degree of homeothermy. Body temperature in *G. s. moholi* was maintained at a constant level over most of the temperature range and regulated at a higher level than that recorded for other prosimians. The greater bushbaby, *G. crassicaudatus*, responds in a similar

manner except that temperatures above 28°C lead to a marked increase in body temperature (Muller & Jaksche 1980). In the slow loris and potto rectal temperature was highly variable, several degrees lower than in guinea pigs, cats and rabbits and showed a distinct correlation to the activity pattern of the animal (Hildwein & Goffart 1975; Muller 1979).

The ability of bushbabies to maintain body temperature at low ambient temperatures, while other Lorisiidae do not, may be due to a large increase in heat production and to their dense fur which offers excellent insulation. In addition, postural adjustments and peripheral vasoconstriction (although not observed) probably serve to maintain thermal conductance at a minimum value below thermoneutrality. When exposed to low ambient temperatures, many hypometabolic animals reduce conductance by allowing certain peripheral parts of the body to cool while retaining a homeothermic core. This strategy leads to a considerable saving of energy and is thought to occur in the slow loris (Muller 1979) and the greater bushbaby (Muller & Jaksche 1980) at low temperatures. The constant minimum conductance in adult bushbabies at all temperatures below thermoneutrality suggests that these animals remained strictly homeothermic over this range.

Although evaporative water loss increased linearly with ambient temperature, values expressed as a percentage of heat production indicate that evaporative cooling is not an effective means of dissipating excess heat in these animals. (Maximum values at 35°C were 34% for males, 28% for females and 40% for juveniles). This limited ability to lower the endogenous heat load through evaporation appears to be characteristic of many prosimian species. The greater bushbaby, for example, can eliminate only 1/3 at 33°C and 2/3 at 38°C of the internal heat load by evaporation (Muller & Jaksche 1980). These estimates are similar for the potto (Hildwein & Goffart 1975) and the slow loris (Muller 1979). It has thus been suggested that these animals were not forced to develop highly efficient mechanisms of evaporative cooling during evolution mainly owing to their nocturnal behaviour. Higher primates rely, to a large extent, on sweating to enhance evaporative cooling but in prosimians sweat glands are not thought to play a major role in thermoregulation (Hiley 1976). These primates rather promote heat loss by increasing respiratory frequency (Hildwein & Goffart 1975) and this may have caused the significant increase in respiratory exchange ratio found in the male group within the thermal neutral zone. Because bushbabies are found in areas where water resources are limited, using evaporative cooling as a long-term thermoregulatory mechanism would be disadvantageous to them. It may, however, act as a short-term emergency mechanism at very high temperatures should body temperature reach lethal levels.

Muller (1979) points out that prosimians in general are not well equipped to cope with high ambient temperatures, even though they live in a tropical environment. In the potto, slow loris and the greater bushbaby, for example, exposure to temperatures of 35°C and above

**Table 2** Values for the thermal neutral zone and basal metabolic rate calculated as a % expected using the formula  $M = 3,8 M^{-0,25}$  (Kleiber 1961), where  $M$  = metabolic rate ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ )

Species	TNZ	BMR as %		Reference
		Expected		
<i>G. crassicaudatus</i>	25-31	71		Muller & Jaksche (1980)
<i>G. s. senegalensis</i>	28-34	72		Dobler (1982)
<i>G. demidovii</i>	30-35	80		LeMaho <i>et al.</i> (1981)
<i>P. potto</i>	25-29	55		Hildwein & Goffart (1975)
<i>N. coucang</i>	25-33	40		Muller (1979)
<i>C. medius</i>	-	80		LeMaho <i>et al.</i> (1981)
<i>G. s. moholi</i>	28-35	76		Dobler (1982)
<i>G. s. moholi</i> (M)	28-35	64-70		This study
<i>G. s. moholi</i> (F)	28-35	80-90		This study

leads to profuse salivation, fur wetting, postural adjustments and an ultimate increase in body temperature. In the present study the females displayed a significantly increased body temperature at 35°C, possibly owing to their considerable restlessness at this temperature. Although this doesn't yet indicate hyperthermia, it is possible that exposure to higher temperatures may have led to hyperthermia in both groups. Salivation and fur-wetting were observed in several adults at 35°C when removed from the chamber.

The only figures available on oxygen consumption in juvenile *G. s. moholi* come from studies by Dobler (1976, 1982) on thermoregulation in this species. He found that at an ambient temperature of 30°C there was a steady decrease in minimum oxygen consumption from the 5th day (2,9 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) to the 140th day (0,7 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>). This was attributed to a gradual increase in body mass and thermal insulation, both of which would tend to decrease the rate of heat transfer from the animal to the environment. Oxygen consumption in the juveniles at 30°C (1,34 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) was slightly higher than the value predicted from mass (1,23 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) suggesting that it does not lie within the thermal neutral zone. As  $\dot{V}O_2$  continued to decrease from 6 to 35°C, no lower critical temperature is evident and it cannot be certain that oxygen consumption at 35°C represents the minimum juvenile rate.

The significantly higher oxygen consumption in juveniles compared to adults is possibly due to the growth process which requires energy over and above that utilized for normal maintenance, activity and thermoregulation. In addition, owing to their smaller surface area to volume ratio, thermal conductance is greater in the juveniles, especially at low temperatures and this may have been the reason for the lower Tb measured in this group. The maintenance of body temperature therefore requires a higher level of metabolic heat production than in animals of larger size. However, one cannot exclude the possibility that specific dynamic action may have been a contributory factor since the juveniles were not post-absorptive.

The response of the juveniles to a temperature rise from 30 to 35°C is interesting: a significant decrease in oxygen consumption accompanied by a significant rise in body temperature. The decrease in  $\dot{V}O_2$  may be attributed to its lying within the thermal neutral zone but the reason for the increase in body temperature is not clear since no movement was observed in this group during measurement. It may suggest an inability at this age to thermoregulate efficiently in this temperature range.

Finally, the concept that a low basal metabolism is a phylogenetically primitive feature does not seem to be supported by the observations discussed. Rather, hypometabolism can be seen as an adaptation favoured by natural selection owing to its energy saving quality. The bushbaby is adequately suited to its environment: during the day, ambient temperatures are usually within the thermal neutral zone or above and hyperthermia can be prevented by retreating to the shade of trees,

reducing metabolic heat production to a minimum value and remaining inactive. At night they emerge to feed, relying on the high insulative properties of their fur and increased endogenous heat production to maintain body temperature at a level compatible with their activities.

### Acknowledgement

The financial support of the University and help from the personnel of the Primate Behaviour Research Group of the University of the Witwatersrand are gratefully acknowledged. The experiments were cleared by the A.E.C. of the University.

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