Comparative thermoregulatory adaptations of southern African tree squirrels from four different habitats

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Energy metabolism was investigated for *Funisciurus congicus* from arid savanna in north-western Namibia, *Paraxerus cepapi cepapi* from woodland savanna in central southern Africa, *P. palliatus tongensis* from mesic eastern coastal forest and *P. p. ornatus* from evergreen subtropical forest. They are all adapted to hot regions and oxygen consumption was lower than the expected Brody-Proctor prediction. *F. congicus* had the highest thermal conductance. The two forest squirrel species showed heat stress at T_a 34°C contrary to the two savanna species. RMR for *F. congicus* was 0,85 ml O_2/g h, the same as for *P. p. tongensis* which is twice its mass, and it was 0,65 ml O_2/g h and 0,71 ml O_2/g h for *P. c. cepapi* and *P. p. ornatus* respectively. All four species maintained $T_b \leq$ 39°C at T_a from 12–32°C.

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Energiemetabolisme is in *Funisciurus congicus* van die droë savanne van noordwes-Namibië, *Paraxerus cepapi cepapi* van savannebosveld in sentraal suidelike Afrika, *P. palliatus tongensis* van die klam oostelike kuswoud en *P. p. ornatus* van immergroen subtropiese woud ondersoek. Hulle is almal aangepas by warm gebiede en suurstofverbruik was laer as wat verwag sou word van die Brody-Proctorvoorspelling. *F. congicus* het die hoogste termiese geleiding getoon. Die twee woudeekhoringspesies het tekens van hittestremming by T_a 34°C getoon in teenstelling met die twee savannespesies. RMT vir *F. congicus* was 0,85 ml O_2/g h — dieselfde as vir *P. p. tongensis* wat twee keer so swaar is. Dit was 0,65 ml O_2/g h en 0,71 ml O_2/g h vir *P. c. cepapi* en vir *P. p. ornatus* onderskeidelik. Al vier die spesies het $T_b \leq$ 39°C behou by T_a tussen 12 en 32°C.

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Africa harbours 37 species of tree squirrels (Amtmann 1966) but little is known of their biology. The only comprehensive studies are those by Emmons (1975) in Gabon and by Viljoen (1975, 1980) in South Africa. Dobroruka (1970), Rahm (1970) and Kingdon (1974) have provided additional information on the tree squirrels of East Africa.

In SWA/Namibia, Botswana and South Africa, there are four different tree squirrels from three species in four different habitats (Table 1): the Western striped squirrel, *Funisciurus congicus*, in arid savanna of north-western SWA/Namibia; the yellow-footed bush squirrel, *Paraxerus cepapi cepapi*, in woodland in north-eastern SWA/Namibia, northern and eastern Botswana and in the north of the Transvaal Province of the Republic of South Africa; the Tonga yellow-chested squirrel, *P. palliatus tongensis*, on the southern tip of the Mozambique plain in subtropical xeric to mesic coastal forests; and the Ngoye red squirrel, *P. p. ornatus*, also on the eastern seaboard, but isolated in the evergreen, moist, subtropical Ngoye forest which covers an area of 2 900 ha. The former two habitats are considerably more xeric than the latter two mesic forest habitats (Table 1).

A comparative study on the biology of these southern African tree squirrels (Viljoen 1980) revealed that the two forest subspecies *P. p. ornatus* and *P. p. tongensis* have a higher level of activity (Viljoen 1983a) and that there is more energy available in their food supply (proximate analyses of fruit and kernels) (Viljoen 1983b). To extend the study of the energetics, the oxygen consumption (total heat production) and the thermal conductance (insulation) of the four squirrels were investigated in the present study.

Although metabolism of ground squirrels in temperate regions has been studied (Hart 1971; Hudson & Deavers 1973; Chappell & Bartholomew 1981; Ward & Armitage 1981) only a few investigations concern oxygen consumption levels of the tree squirrels *Sciurus carolinensis, S. aberti* and *Tamiasciurus hudsonicus* (Irving, Krog & Monson 1955; Bolls & Perfect 1972; Wunder & Morrison 1974; Golightly & Ohmart 1978; Innes & Lavigne 1979; Pauls 1981).

Material and Methods

Considering the seasonal and geographic differences that occur in energy metabolism, it is important to conduct comparisons between different species during the same season and in animals having the same thermal history (Hart 1971). The experimental squirrels (four adults of each of the four different squirrels) are diurnal and had all been kept in outdoor cages in Pretoria in the same conditions for two years prior to the oxygen consumption measurements. The experi-

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Table 1 Habitat description of four tree squirrel species (Data from Viljoen 1980)

Species and adult mass Mean (g) and S.D.	Colour	Habitat description and tree (dbh $\geq$ 2,5 cm) density according to Viljoen (1980)	Mean temperature range in habitat (°C)	Mean rainfall (mm)
Funisciurus congicus 112,3 (*n*=20) ± 7,0	White ventrum, face & legs; light brown dorsum, & cream side-stripe.	Arid, open savanna (Sun system, Tinley 1975). Tree density 0,05/m^2	14,3–27,4; frost occurs	100–400
Paraxerus c. cepapi 223,6 (*n* = 69) ± 16,0	White ventrum, face & legs; ligth brown speckled dorsum.	Open woodland/savanna (Sun system, Tinley 1975). Tree density 0,04/m^2	10,2–17,4; frost occurs	100–1024
P. palliatus tongensis 206,0 (*n* = 48) ± 18,6	Orange ventrum, face & legs; brown speckled dorsum.	(Shade system, Tinley 1975) xeric and mesic dense coastal and dune forests (deciduous). Tree density 0,16/m^2	7,9–11,5 frost-free	628–1466
P. p. ornatus 366,6 (*n* = 98) ± 21,5	Red ventrum face & legs; almost black dorsum.	Moist, 'evergreen', (Shade system Tinley 1975) montane forest. Tree density 0,29/m^2	9,7–10,6 frost-free	1315–1868

ments were carried out in July soon after the winter solstice when daylength is reasonably constant. Minimum and maximum ambient temperatures averaged 8,0°C and 20,7°C respectively during the experiment. Test individuals were kept for 1½–2 h at ambient temperatures (T_a) 12; 18; 25 and 30°C, but only for 1 h at $T_a > 34$°C to reduce possible heat stress. Squirrels were caught in wire mesh traps, weighed in a bag and transferred to the perspex metabolic chamber which was covered to minimize stress and thus enable minimal V_{O_2} readings. All measurements were made in daytime. Oxygen consumption (V_{O_2}) was then measured at each temperature on a Beckman Model E2 paramagnetic oxygen analyser as in Depocas & Hart (1957) and Hill (1972) in an open flow respirometer (4 118 ml) through which dry air passed at a rate of 600 ml/min. The squirrel crouched on a base plate underneath which silica gel was placed to dry the air in the respirometer. This was necessary as the squirrels urinated copiously and became wet. A copper constantan thermocouple inserted in a protective perspex tube (squirrels chew the copper) measured temperature in the chamber. Measurements were taken every 3 min for a period lasting 15 to 30 min depending on the variability of the reading. Only the lowest V_{O_2} readings were taken (ranging from seven readings on some individuals to 19 readings on others), thus representing minimum activity. All results were corrected to STPD.

Body temperatures (T_b) were measured immediately after the metabolic measurements had been completed by means of a copper constantan thermocouple which was inserted for 30 mm in the rectum (monitored on a Kane-May 2 013 potentiometer) and the squirrel was then reweighed. Each individual was tested only once per day and then rested for two days before retesting at a different temperature.

Thermal conductance (TC) can be regarded as being at a minimum at the lower end of the thermoneutral zone and equals the slope of the graph (V_{O_2} against T_a assuming that heat loss is through 'dry' physical parameters (McNab 1970, 1980). However, measurements of TC here include the evaporative component and must therefore be termed 'wet' conductance. Therefore, the regression fits do not extrapolate to T_b where V_{O_2} = 0 (Figure 1); and TC was calculated at all tested ambient temperatures, according to Hart's (1971) equation:

$$TC = \frac{M}{T_b - T_a}$$

where M = metabolic rate (ml O_2/g h), T_b = body temperature and T_a = ambient temperature (°C). To estimate minimal conductance, the mean conductance from data below the region of thermoneutrality was calculated (McNab 1980).

Student's t test (between the means of the V_{O_2} measurements of the four tested individuals of each species) was used to test for significant difference between measurements in the thermoneutral zone.

Results

As the difference between V_{O_2} at 32 and 34°C was significant in all four species, and the minimum V_{O_2} [resting metabolic rate (RMR)] was measured at 34°C ± 1,0°C, the thermoneutral zone must be at $T_a = 34$°C ± 1°C. Therefore, $T_a = 12$, $T_a = 18$, $T_a = 25$ and $T_a = 30$, were used in the calculation of the regression fit of T_a on V_{O_2} (Figure 1).

RMR for *F. congicus* was 0,85 ml O_2/g h, the same as for *P. p. tongensis* which is twice the mass. In *P. c. cepapi* and *P. p. ornatus* the RMR was 0,65 ml O_2/g h and 0,71 ml O_2/g h respectively. However, in both the two mesic and the two xeric squirrels, the smaller species (*P. p. tongensis* and *F. congicus* respectively) had the higher RMR.

The increment in V_{O_2} between 34 and 36°C was greater in the two mesic species ($P < 0,005$ in *P. p. tongensis*; $P < 0,01$ in *P. p. ornatus*) than in the two xeric species ($P < 0,05$ in *P. c. cepapi* and NS in *F. congicus*). This increment in V_{O_2} is 19% in *P. p. tongensis*, 28% in *P. p. ornatus* (mesic squirrels with less tolerance for the higher T_a s), 6,59% in *F. congicus* and 15,58% in *P. c. cepapi*. However, in *F. congicus*, a steeper slope to the regression (Figure 1) indicates a higher conductance in this species (Table 2). The mean TC was calculated (Table 3) but the value at $T_a = 25$°C was found to correspond closely to the fitted values of the regression curve and was therefore taken as the TC of the particular species. *F. congicus* had a higher conductance (0,1158 ml O_2/g h °C) than the *Paraxerus* spp.

Body temperature of the different species did not differ much (Table 2), all four species maintaining $T_b \leq 39$°C at T_a from 12 to 32°C (*F. congicus* 38,88°C ± 0,13; *P.c. cepapi*
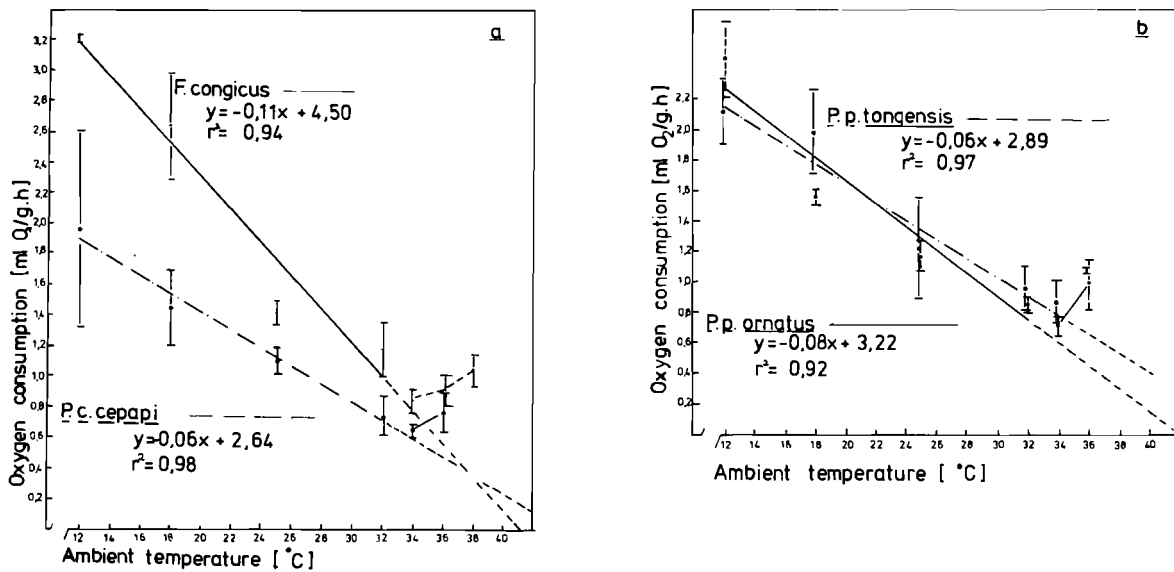
Figure 1 Oxygen consumption (ml O_2/g h) of four southern African tree squirrels at ambient temperatures 12; 18; 25; 32; 34 and 36°C. (a) Arid, 'open habitat' squirrels, *F. congicus* and *P. c. cepapi*, (b) Moist forest squirrels, *P. p. tongensis* and *P. p. ornatus*.

Table 2 Mean body temperatures and S.D. of four tree squirrel species at ambient temperatures from 12°C to 38°C ($n = 4$)

Species	Ambient temperature range						
	12°C	18°C	25°C	32°C	34°C	36°C	38°C
Funisciurus congicus	39,85± 0,06	38,86± 1,21	38,93± 0,04	38,70± 0,42	39,75± 0,78	39,38± 0,73	39,83± 0,28
Paraxerus cepapi cepapi	39,27± 0,55	38,71± 0,56	– [a]	38,44± 0,77	39,45± 0,07	39,70± 0,07	39,70± 0,35
Paraxerus palliatus tongensis	37,55± 0,45	38,70± 0,35	39,28± 0,98	39,17± 0,29	39,85± 0,21	40,06± 0,55	– [b]
P. p. ornatus	– [a]	38,67± 0,25	38,95± 0,07	38,85± 1,29	39,85± 0,78	39,93± 0,25	– [b]

[a] Thermocouple broke. [b] *Paraxerus palliatus tongensis*, and *P. p. ornatus* not measured at 38°C as they already showed severe reactions to heat stress at 36°C

Table 3 Aspects of energy metabolism in four tree squirrel species (TC = Thermal conductance; RMR = resting metabolic rate)

Species (see Table 1 for mass and habitat)	Mean observed RMR in July at 34°C (ml O_2/g h) ± S.D.	Brody-Proctor expected RMR (ml O_2/g h Hart 1971)	% that observed RMR is lower than expected	TC (ml O_2/gh °C)							
				T_a=12°C	T_a=18°C	T_a=25°C	Mean TC 12/18/25°C ± S.D.	T_a=32°C	T_a=34°C	T_a=36°C	TC according to slope of regression fit
Funisciurus congicus	0,87±0,09	1,17	26	0,1193	0,1268	0,1158	0,1206± 0,0056	0,1761	0,1500	0,2676	0,11
Paraxerus cepapi	0,65±0,04	0,98	34	0,0725	0,0705	0,0816	0,0749± 0,0059	0,1156	0,1182	0,2026	0,06
P. palliatus tongensis	0,87±0,12	1,00	13	0,0828	0,0908	0,0853	0,0863± 0,0041	0,1333	0,1500	0,2634	0,06
P. p. ornatus	0,72±0,06	0,87	18	–	0,0758	0,0836	0,0797± 0,0055	0,1232	0,1214	0,2564	0,08

38,80°C ± 0,46; *P. p. tongensis* 38,70°C ± 0,78; *P.p. ornatus* 38,87°C ± 0,15). The two xeric species still maintained T_b at only a slightly higher level up to $T_a = 38°C$ (*F. congicus* 39,67°C ± 0,23); *P. c. cepapi* 39,67°C ± 0,15) but in the

two mesic species at $T_a = 34°C$, T_b was elevated to 40,0°C ± 0,14 in *P. p. tongensis* and to 39,9°C ± 0 in *P. p. ornatus*, and evaporative cooling (sweating) set in. Thus the two mesic species show a tendency to elevate T_b sooner and more rapidly

than the two xeric species. Little or no salivation occurred in *P. c. cepapi* and *F. congicus* although one individual of the latter species did salivate slightly at $T_a = 38°C$. Pronounced salivation spread over the face with the paws occurred in the two mesic species at $T_a = 36°C$ and therefore they were not subjected to higher air temperatures.

Discussion

McNab (1970) states that tropical mammals with a low RMR and high TC, can tolerate the resulting lower T_b s by living in environments characterized by thermal stability. Apart from a lower T_b, lower RMR also appears to be a related adaptation to hot, dry conditions (Hart 1971).

The T_b as well as RMR and TC of each of the four squirrels indicate adaptedness to warm, dry climate with the two xeric species being better adapted.

The mean body temperatures of all four squirrels were lower than those of the temperate *Sciurus aberti* and *S.a. kaibabensis* (38,5 − 42,7°C, $\bar{x} = 40,7°C$, Patton, Radcliff & Rodgers 1976; and 35−41,4°C, $\bar{x} = 39,0°C$, Golightly & Ohmart 1978), red squirrels *Tamiasciurus hudsonicus* (Pauls 1979, 35,9 − 41,4°C; and Morrison 1962, in Hart 1971, $T_b > 40°C$) and flying squirrels *Glaucomys volans* (Neuman 1967, in Hart 1971). All of the latter species occur in the Nearctic region and can withstand very low ambient temperatures, e.g. *T. hudsonicus*, a diurnal non-hibernator of the subarctic region, is active on the surface at temperatures down to −32°C. Only when $T_a > 34°C$ did T_b of the two forest squirrels exceed 40°C, and in the two xeric squirrels T_b did not reach 40°C even when $T_a = 38°C$. Body temperatures of the four squirrels did not differ significantly, but in the two xeric species body temperatures showed less increment when ambient temperature exceeded 34°C, thus indicating a better adaptation to extreme heat.

The equation $V_{O_2} = 3,8 \; W^{0.75} \; ml \; O_2/h$ was used in Table 3 to predict V_{O_2} (Schmidt-Nielsen 1975). Generally higher levels than those predicted by this equation are found among the temperate rodents, (*Sciurus aberti* $V_{O_2} = 104\%$ of predicted value, Golightly & Ohmart 1978; *S. carolinensis* $V_{O_2} = 114\%$ of predicted value, Bolls & Perfect 1972; *T. hudsonicus* $V_{O_2} = 180\%$ of predicted value, Irving *et al.* 1955). Pauls (1981) found an RMR of 1,12 ml O_2/g h and a TC of 0,062 ml O_2/g h °C in summer and 0,052 ml O_2/g h °C in winter-acclimatized red squirrels, *T. hudsonicus*. He ascribes the difference from the results of Irving *et al.* (1955) to a difference in techniques. *T. hudsonicus* has a higher RMR and lower TC than squirrels of a similar mass *(P. p. tongensis* and *P. c. cepapi)* of the present study. All four species in the present study had RMR values below the expected (Table 3), indicating their adaptation generally to warm climate. However, the two xeric species, *P. c. cepapi* and *F. congicus* were further below the predicted Brody-Proctor values for their weight (34% and 26% respectively) than were the two mesic squirrels (18°C and 13°C) (Table 3).

When comparing the two mesic species, the smaller of the two, *P. p. tongensis*, had higher values both of TC and RMR but this latter value was only 13% below the predicted, whereas that of *P. p. ornatus* in the slightly cooler habitat, was 18% below the predicted.

The species which now lives and probably evolved in the hottest and most arid conditions *F. congicus*, is the smallest and has an RMR 26% below the weight-expected, Brody-Proctor prediction and the highest TC (0,1158 ml/g h °C), and can thus rid itself of heat easily, having also a greater

surface area in relation to body volume and a sparse hair cover. Furthermore, this species has evolved distinct thermoregulatory behaviour patterns such as the carrying of the tail, which is longer relative to total length than in the *Paraxerus* spp. (Viljoen 1980), over and in contact with the back, thus also throwing a patch of shade over the head and presenting the white ventral surface to the sun's rays (Viljoen 1978). This habit is similar to that of the ground squirrel, *Xerus inauris* (Marsh, Louw & Berry 1978) which also occurs in hot, open regions and has been shown theoretically to reduce incoming radiation (Joules) by 30% in Abert's squirrels (*Sciurus aberti*) which have a much higher reflectance from the white ventral surface of the tail than from the grey dorsal body (Golightly & Ohmart 1978). Muchlinski & Shump (1979) found a similar role to protect the body from excess T_a in *T. hudsonicus* and *S. niger*. *F. congicus* also periodically flick the tail which could contribute to convective cooling as suggested by Chappell & Bartholomew (1981) for *Ammospermophilus leucurus*.

P. c. cepapi is also well-adapted to conserve energy, with a comparatively low RMR (34% below predicted value) and low TC. *P. c. cepapi* weighs approximately the same as *P. p. tongensis* which has a slightly higher TC but V_{O_2} only 13% below the expected value. In an environment where resources are only seasonally abundant (harsh, dry winter) and also clumped to a large extent (Viljoen 1975, 1980), it would be essential for *P. c. cepapi* to conserve energy through a lower metabolic rate. Analyses of fruits indicated that there probably is less energy in the food supply of *P. c. cepapi* (Viljoen 1980) than that of the forest squirrels. The TC of *P. c. cepapi* is not nearly as high as that of *F. congicus*, but *P. c. cepapi* possibly thermoregulates by pulmonary evaporative cooling. The three *Paraxerus* spp. also have sudoriferous glands on the footsoles (Viljoen 1980) for further evaporative cooling (*Funisciurus* not investigated).

All four species are relatively inactive at the hottest time of the day (unpublished observations) thus reducing metabolic heat load. Golightly & Ohmart (1978) found that in *T. hudsonicus*, T_b decreased considerably when the animal was motionless after a bout of activity. The two mesic squirrel species from the forested habitats reacted to heat stress at lower T_a s, and of these two, *P. p. ornatus* from the cooler habitat, noticeably more so. In captivity on warm days, they would also lie with limbs spread out laterally on the cement or branches, frequently after urinating on the surface. The increased T_b when $T_a > 34°C$ in the two mesic species and the concomitantly greater increment in V_{O_2}, necessitates evaporative cooling in the form of pronounced salivation, which is an emergency regulation for a limited period to reduce the gradient between T_b and T_a. It also occurs in *S. aberti* at $T_a > 36°C$ (Golightly & Ohmart 1978) and in the spermophilous group of squirrels (Hart 1971). The fur of the two mesic species is more dense and longer, especially in *P. p. ornatus*, and affords them the chance to conserve energy in the cooler microclimate where they cannot readily bask to regain energy.

The two xeric species inhabit areas with a wider temperature range (down to −7°C in certain areas), whereas the mesic species live in an essentially frost-free region where temperature changes are further buffered by the forest (Table 1). The xeric species have adapted by commencing activity later, and on cold mornings they bask for prolonged periods in their open habitats, (Viljoen 1975, 1978). Golightly & Ohmart (1978) found that such basking does substantially raise T_b

in temperature-monitored Abert's squirrels. They calculated that a basking Abert's squirrel would intercept ± 18,4 kJ/h. Furthermore, the two xeric species have a closely knit group structure and nest-huddled together (contact species) (Viljoen 1975, 1978). Huddling in flying squirrels, *Glaucomys*, reduced thermoregulatory energy by 33% (Neuman 1967 in Hart 1971). In the coldest months the population of *P. c. cepapi* (Viljoen 1975) was still at a maximum and group size averaged five. On the other hand the forest species have a less cohesive group system and often nest singly (Viljoen 1980). In captivity the xeric species also show more diligent nesting behaviour than the mesic species (Viljoen 1980). A nest of cotton can reduce V_{O_2} by an amount equivalent to raising the air temperature by about 15°C in *Spermophilus tereticaudus* (Hudson 1964). *F. congicus* is the only one of these squirrel species to build dreys (Viljoen 1978). This could present them with a cooler nest or could have evolved in a habitat where holes in trees are at a premium.

Acknowledgements

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