

Thermoregulatory capabilities of the woodland dormouse, *Graphiurus murinus*

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Received 2 July 1998; accepted after revision 3 December 1998

The woodland dormouse, *Graphiurus murinus*, in common with many other small rodents, enters torpor under conditions of food deprivation and low temperatures. Its thermoregulatory capabilities under more favourable conditions, however, have not been investigated. We measured metabolism and thermoregulation in woodland dormice acclimated to long-day length, moderate temperature and abundant food over a temperature range (T_a) of approximately 5–37°C. The thermal neutral zone for this species lay between 29 and 35°C. Estimated resting metabolic rate (RMR) within this range averaged $21.10 \pm 3.28 \text{ J g}^{-1} \text{ h}^{-1}$. Below 29°C energy expenditure increased with a decrease in T_a , with a maximum value of $90.76 \text{ J g}^{-1} \text{ h}^{-1}$ measured at 6°C. Both evaporative water loss (EWL) and thermal conductance (C) were minimal and independent of T_a between 5 and 32°C but increased above the thermal neutral zone, maximum EWL and C being $6.7 \text{ mg g}^{-1} \text{ h}^{-1}$ (79% of metabolic heat production) and $19.74 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$, respectively, at 37.3°C. Thermal conductance and RMR of *G. murinus* were approximately 48% and 30% below predicted for rodents of equivalent mass, respectively. This pattern is consistent with that suggested for warm-temperate arboreal rodents. Although body temperature (T_b) was labile and was significantly related to T_a over the temperature range investigated, dormice maintained T_b s between 34 and 38°C using typical thermoregulatory responses that included increased activity at low T_a and postural adjustments and salivating at high T_a . While not as impressive as some rodent species, under favourable conditions *G. murinus* is a competent thermoregulator and torpor in the species is facultative.

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Small mammals have a high surface area to volume ratio, which results in rapid heat exchange with the environment (Tracy 1977; Haim 1987; Schmidt-Nielsen 1990). Although fur is generally a good insulator, small size necessitates relatively short, light fur to facilitate mobility. The insulatory value of fur to small mammals is consequently relatively poor compared with larger mammals. To thermoregulate effectively, small mammals must therefore maintain high rates of metabolic heat production through shivering, non-shivering thermogenesis or increased activity if they are to maintain normal body temperature (T_b) at low ambient temperatures (T_a). Thermoregulatory capabilities of small rodents vary considerably. Some species can maintain a T_b of 38°C at T_a well below freezing (Hart 1971), whereas others, such as the pygmy mouse, *Baiomys taylori*, show extremely labile T_b , allowing it to drop sharply at low T_a (Hudson 1965). Small rodents with relatively low basal metabolic rates (BMR), such as the pocket mice *Perognathus* spp. are noticeably poorer thermoregulators and are unable to maintain a large temperature differential with the environment for any extended period (McNab 1983). Behavioural thermoregulatory mechanisms such as huddling, nesting, microhabitat selection and altered activity patterns are therefore of considerable importance to small mammals (Vogt & Lynch 1982; McDevitt & Andrews 1994).

While reducing exposure to cold stress these behavioural thermoregulatory mechanisms may not, however, be sufficient at low temperatures and many small mammals temporarily abandon homeothermy, allowing T_b to fall close to T_a . In this way they avoid the costs of maintaining normal T_b at low T_a and are able to conserve energy reserves (Vogt & Lynch 1982; Snyder & Nestler 1990). Many small mammals conse-

quently use daily torpor to reduce energy expenditure during their inactive phase when they are not actively foraging and may undergo winter hibernation (Hudson 1978; Ruf & Heldmaier 1992).

The woodland dormouse, *Graphiurus murinus*, is a small ($\approx 40\text{g}$) rodent that occurs widely throughout Africa south of the Sahara. In South Africa it inhabits mainly wooded areas of the southern, eastern and northern Cape and KwaZulu-Natal. These nocturnal mammals are swift, agile climbers and are mainly arboreal. They forage singly at night for insects and vegetable matter such as seeds (De Graaff 1981; Skinner & Smithers 1990). T_b of *G. murinus* may fluctuate with T_a , activity, and diel rhythm (Lachiver & Petter 1969). The species is able to enter spontaneous torpor and several studies have focussed on this aspect of its physiology (Ellison & Skinner 1991; Webb & Skinner 1996). These studies have shown that torpor can be induced by low T_a , and/or food restriction. Surprisingly, however, no studies have assessed the general thermoregulatory capabilities of this species under favourable nutritional conditions. The aim of this study therefore was to determine the thermoregulatory capabilities of *G. murinus* acclimated to moderate temperature (approximately 22°C), long day, and with adequate food.

Materials and methods

Ten woodland dormice (7 females and 3 males) were captured using Sherman live traps in the Alexandria Forest (33° 43'S, 26° 22'E) and at Fort Fordyce (32° 31'S, 26° 30'E) between November 1994 and February 1995. Captured animals were housed individually in rat cages in a long-day rodent room (14L:10D, light hours 06:00–20:00). Ambient room temperature was maintained at approximately 22°C. Animals were

provided with nest boxes and nesting material and were fed a diet of rat pellets, sunflower seeds and millet. Fresh-sliced apple and mealworms were provided approximately once a week and water was available *ad libitum*. Animals were weighed weekly to monitor general body condition. Rectal T_b s were also measured on a regular basis to determine normal T_b under these acclimation conditions.

An initial series of nine 24 h measurements of metabolism were made as described below to establish diel patterns of activity. During these runs animals were provided with food (sunflower seeds and rat pellets) in excess of daily requirements, water, and an open-ended plastic shelter in which to sleep but which provided no insulation. These runs established that *G. murinus* was mainly nocturnal as previously reported (Skinner & Smithers 1990; Webb & Skinner 1996) so subsequent experiments were conducted during daylight hours.

Oxygen consumption (V_{O_2}) and evaporative water loss (EWL) were measured simultaneously using open-flow respirometry at T_a s between 5 and 37.5°C. Several individuals showed clear signs of heat stress above 37°C so animals were not exposed to higher temperatures. Animals were weighed to 0.01g prior to each experiment and initial body temperatures measured rectally using a 36 gauge copper-constantan thermocouple attached to a SORTEK BAT-12 thermometer. Animals were then sealed into a rectangular, perspex metabolic chamber (3.5L) inside a darkened, constant temperature cabinet. A shuttered, perspex viewing window enabled animal behaviour to be observed during the experiment and a modified passive infra-red sensor placed in the metabolic chamber detected activity, which facilitated selection of metabolism during non-active periods. No food, water, or shelter was provided during these measurements.

Air from an upstream pump was dried and scrubbed of CO_2 in tubes of Carbosorb, and silica gel, respectively, before entering the metabolic chamber. Inlet flow rate was monitored using an Aalborg mass flow meter (GFM-1700) and was regulated between 400 and 800 ml min^{-1} , depending on chamber temperature. Air exiting the chamber was immediately passed through a pre-weighed silica gel tube (to measure EWL) before a sub-sample was drawn off by an Applied Electrochemistry R-1 flow controller. The sub-sample was drawn through an Applied Electrochemistry CD-3A CO_2 analyser and a tube of Carbosorb/silica gel before entering an Applied Electrochemistry S-3A/1 O_2 analyser. Flow rate, percentage O_2 and CO_2 , chamber temperature and activity were recorded directly onto a microcomputer at 20 s intervals for approximately 3.5 h using Datacan V data acquisition software (Sable Systems Inc, Salt Lake City). O_2 and CO_2 concentrations in ambient air were assumed to be 20.95% O_2 and 0.00%, respectively, and were checked before and after each experimental run. Any drift in these values was corrected using the Datacan drift-correction procedure. Metabolic rates were calculated from the lowest stable period of metabolism of at least 10 min without activity using equation (4a) of Withers (1977). On removal from the chamber a second rectal T_b was taken and the animal was re-weighed. Average mass was used when calculating mass-specific metabolic rate which was subsequently converted to $J g^{-1} h^{-1}$ assuming 1ml $O_2 = 20.083J$.

EWL was measured by calculating the change in mass of the pre-weighed silica gel tube placed immediately downstream of the chamber. EWL values were discarded if the animal urinated during measurement. Dry conductance values were calculated using the equation

$$C_{dry} = (MHP - EHL)/(T_b - T_a)$$

where MHP is the metabolic heat production, EHL is the heat equivalent of evaporative water loss, T_b is rectal body temperature and T_a is ambient temperature (McNab 1980).

Results

Metabolic rate

Mass specific metabolic rate in *Graphiurus murinus* was lowest and independent of T_a ($r = 0.03$, $P = 0.85$) between approximately 30–35°C and this was assumed to be the thermal neutral zone. The mean lower critical temperature (T_{lc}), calculated by plotting individual regressions of metabolic rate against T_a , averaged $29.0 \pm 2.2^\circ C$. Mean metabolic rate within the thermal neutral zone averaged $21.10 \pm 3.28 J g^{-1} h^{-1}$ for 10 individuals of mean mass $38.43 \pm 5.14 g$ (Figure 1). Because *G. murinus* is nocturnal it was assumed that they last fed during the night. Experimental animals were, however, not specifically deprived of food prior to experimental runs and therefore may not have been post-absorptive. A mean respiratory quotient (RQ) of 0.77 ± 0.05 between 5.1 and 37.5°C tends to support this. Measurements within the thermal neutral zone should consequently be regarded as resting metabolic rates (RMR) rather than BMR.

Below the T_{lc} metabolic rate increased as T_a decreased, the relationship being described by the equation Metabolic rate = $91.97 - 2.44T_a$ ($r = -0.87$) for all animals combined. Animals at about 6°C and below were noticeably more active than at 10°C and above.

Above 35°C two distinct groups of dormice could be identified. The first group maintained metabolic rate close to RMR (mean = $20.99 \pm 0.89 J g^{-1} h^{-1}$, $n = 4$ individuals) despite the increased T_a , whereas the second group showed a significantly elevated metabolic rate (mean = $28.02 \pm 1.25 J g^{-1} h^{-1}$, $n = 4$ individuals; $t = 9.127$, $P < 0.001$).

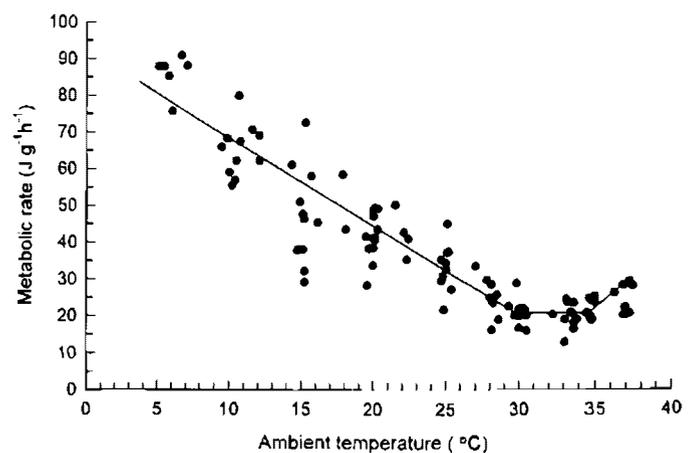


Figure 1 Metabolic rate of *Graphiurus murinus* in relation to temperature

Body temperature

Mean setpoint T_b (Lovegrove, Heldmaier & Ruf 1991), calculated from the intercept of the regression line relating metabolism to T_a with the x-axis for each individual, averaged $36.0 \pm 1.3^\circ\text{C}$ but T_b s ranged from 30.9 to 39.8°C . Several individuals showed T_b s significantly lower by about $2\text{--}3^\circ\text{C}$ ($P_s < 0.05$) than other animals measured at the same T_a . These low T_b s were not restricted to specific individuals and the animals were immediately responsive when handled suggesting that they were not partially torpid. There were also no significant differences in mass, metabolism, or conductance of these animals when compared to other individuals at the same T_a ($P_s > 0.25$) and differences were independent of the sex of the animals. It was consequently assumed that these low T_b s resulted because the rectal probe did not penetrate sufficiently far to record a proper T_b and they were not subsequently used. Overall, T_b was significantly related to T_a over the entire range of ambient temperatures ($r = 0.64$, $P < 0.001$; Figure 2).

Mean T_b of animals acclimated to 22°C under long day conditions in the rodent room was $35.4 \pm 1.3^\circ\text{C}$ and ranged from $32.0\text{--}37.5^\circ\text{C}$.

Evaporative water loss

Between 5.8 and 32.3°C water loss was independent of T_a ($r = 0.123$, $P = 0.316$) and averaged $2.53 \pm 0.66 \text{ mg g}^{-1} \text{ h}^{-1}$ (Figure 3). Above 33.0°C water loss increased markedly and was described by $\text{EWL} = -20.9 + 0.71T_a$ ($r = 0.77$, $P < 0.001$). The highest rate of EWL measured was $6.7 \text{ mg g}^{-1} \text{ h}^{-1}$ at 37.2°C , which represented 79% of the metabolic heat production in this specific individual.

Conductance

Mean minimum wet conductance, estimated from the slope of the regression line relating individual metabolism to T_a , averaged $2.46 \pm 0.35 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Dry conductance was minimum and independent of T_a between 5.8 and 32.3°C ($r = 0.023$, $P = 0.862$), and averaged $2.64 \pm 0.49 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ (Figure 4). Above T_a of 33.0°C conductance increased markedly and was significantly related to T_a ($r = 0.67$, $P = 0.001$). The highest measured conductance was $19.74 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at 37.3°C .

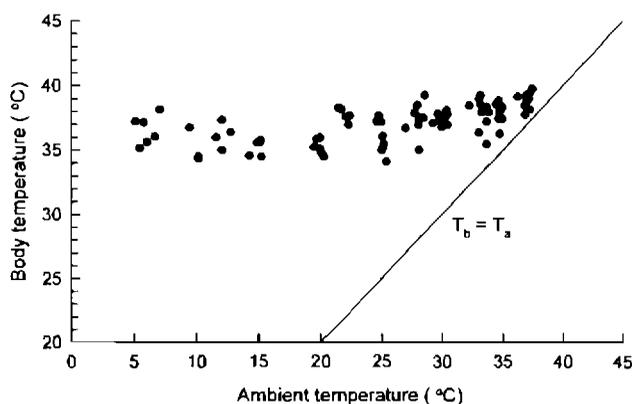


Figure 2 Body temperature of *Graphiurus murinus* in relation to temperature. The solid line represents the line of equality

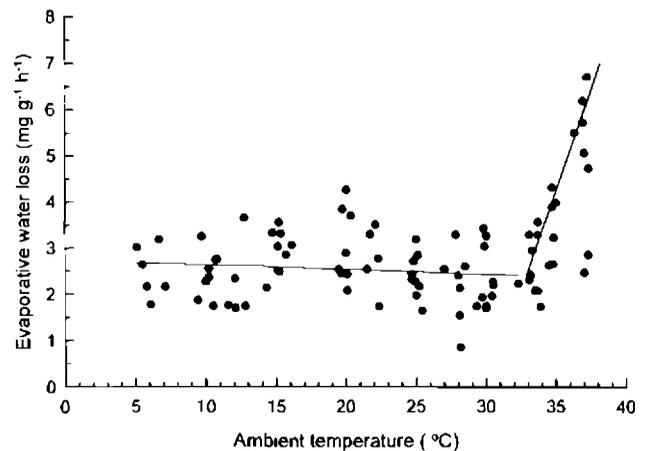


Figure 3 Evaporative water loss of *Graphiurus murinus* in relation to temperature

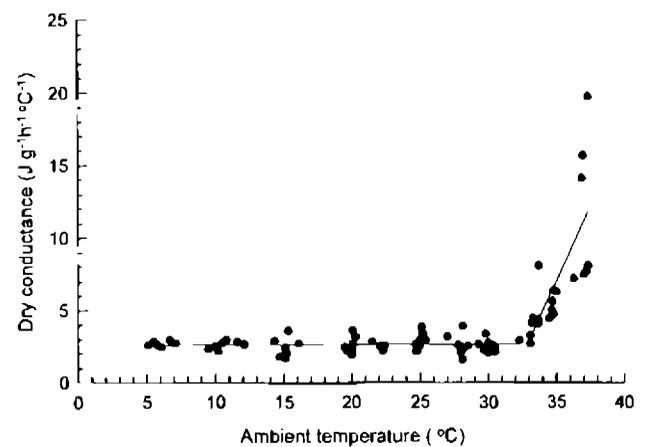


Figure 4 Thermal conductance of *Graphiurus murinus* in relation to temperature

Discussion

Thermal conductance of *G. murinus* was 48% less than expected for rodents of equivalent mass (Aschoff 1982) and their RMR ($21.10 \text{ J g}^{-1} \text{ h}^{-1}$) was approximately 30% below predicted levels for rodents of equivalent size ($\text{BMR} = 29.9 \text{ J g}^{-1} \text{ h}^{-1}$), as estimated from the allometric equation of Hayssen & Lacy (1985). Lovegrove, Heldmaier & Knight (1991) reported low thermal conductances and low resting metabolic rates for the arboreal tree rat, *Thallomys paedulus*, and the Namaqua rock mouse, *Aethomys namaquensis*, and suggested that such features are characteristic of arboreal and desert rodents from warm-temperate regions, which are exposed to large daily fluctuations in T_a . They argued that low conductances are required to maintain T_b at the lowest T_a s experienced at night whereas low resting metabolic rates are required to avoid hyperthermia that might occur at high T_a s as a consequence of the low conductances. *G. murinus* has a wide distribution in southern Africa which, to a large extent, overlaps that of *T. paedulus* and *A. namaquensis* and the pattern of low RMR and conductance observed in *G. murinus* is

thus consistent with that predicted by Lovegrove *et al.* (1991).

$T_{b,s}$ of *G. murinus* were quite variable and ranged from 34.0 to 39.3°C between $T_{a,s}$ of 35 and 5°C even after unusually low $T_{b,s}$ had been excluded. Similarly, Lachiver & Petter (1969) reported $T_{b,s}$ to be between about 33–38°C. If 36.0°C is accepted as being the 'setpoint' T_b for the species, a number of individuals were hypothermic below the T_{lc} despite the decrease in conductance to a minimum and the increase in metabolic heat production. Even T_b of individuals maintained at 22°C in the rodent room were quite variable and ranged from 32.0–37.5°C. Labile $T_{b,s}$ are characteristic of many small rodents, which tend to regulate T_b within a range rather than at an absolute value (Hudson 1965; Chew, Lindberg & Hayden 1967; Hart 1971; Downs & Perrin 1990; Lovegrove & Raman 1998). Maintaining a more flexible T_b may allow small mammals to reduce energy expenditure during cold exposure thereby conserving resources (Vogt & Lynch 1982). Heat production at about 6 and 10°C in the present study were similar to that previously reported for the species at similar $T_{a,s}$ (Ellison & Skinner 1991; Webb & Skinner 1996) and were about four times RMR. Despite this and the generally labile and low $T_{b,s}$, there was a marked increase in activity of individuals at 6°C when compared to higher temperatures suggesting that shivering (and possibly non-shivering thermogenesis) was insufficient to maintain T_b at low T_a and that individuals rely on increased activity to elevate metabolic heat production. Similar behavioural thermoregulation at low temperature has been observed in a number of rodents (Sealander 1953, Hart 1971) and in shrews (Brown, Hunter & Baxter 1997). The White-footed Mouse, *Peromyscus leucopus*, for example, utilises a wide range of heat generating behaviours including grooming, running and shivering when provided with adequate food and water and are able to maintain normal T_b down to -30°C. In contrast, individuals deprived of food and water become hypothermic at T_a below -1°C (Sealander 1953).

Both *G. ocularis* (Channing 1984) and *G. murinus* (Ellison & Skinner 1991) readily enter torpor and *G. ocularis* is known to hibernate (B.G. Lovegrove pers. comm.) suggesting that *G. murinus* may also be capable of hibernation. To date, the little work that has been done on the thermal physiology of South African Graphiurinae has focussed on this aspect of their thermal physiology. These studies have shown that *G. murinus* enters torpor when acclimated to low temperatures and/or deprived of food, or in response to sudden decreases in temperature. Some summer-acclimated individuals even enter spontaneous torpor when food is available and temperatures are moderate (Webb & Skinner 1996). None of the individuals in the present study were found to be torpid under acclimation conditions with available food despite the inclusion in their diet of unsaturated fatty acids (sunflower seeds), which are known to enhance torpor in small rodents and marsupials (Geiser & Kenagy 1987; 1993). Notwithstanding its low RMR, *G. murinus* is clearly quite capable of maintaining T_b within its normal range when conditions are favourable.

Although *G. murinus* has a distribution that extends into hot, arid areas, individuals used in this study were not particularly tolerant of high temperatures and showed several signs of heat stress above about 36°C. These included postural adjust-

ments such as lying prostrate or belly-up with legs spread apart. Salivation and licking, which promotes evaporative cooling, were also observed in some individuals. Two contrasting groups of animals could, however, be distinguished above the thermal neutral zone. One group showed no increase in metabolic rate above 35°C and had $T_{b,s}$ averaging 38.9°C. Although not statistically significant, there was a trend for this group to have lower thermal conductances than the other group, lower rates of EWL and, although they lay inactive and spread out, they did not salivate. The second group had mean $T_{b,s}$ the same as the first but had significantly elevated metabolic rates and tended to have higher conductances, higher rates of EWL and to salivate and lick their fur as well as lying spread out on the floor of the chamber. These differences were independent of the sex of the animals and since they were all acclimated to the same conditions this suggests the possibility of intraspecific differences in the tolerance of *G. murinus* to higher temperatures. Differences in thermal physiology of animals from different populations exposed to different environmental conditions have been reported in several studies (see, for example, Mason 1974; Garland & Adolph 1991 and references therein; Haim, Plaut & Zobedat 1996; Corp, Gorman & Speakman 1997; Brown, Everitt & Baxter, in press). *Graphiurus murinus* used in the present study were collected from two different localities. Alexandria Forest is coastal with an elevation of about 200 m, whereas Fort Fordyce lies inland at an altitude of about 1200 m and is generally cooler than Alexandria Forest. While it is tempting to speculate that the individuals from Fort Fordyce comprise the group that appear less tolerant of high temperatures, the animals were collected by a third party who did not differentiate between individuals from the two localities so these differences remain, for the moment, unresolved.

Acknowledgements

We thank Dr Rehema White for collecting the animals for us. The study was supported by a grant to CRB from the Foundation for Research Development.

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