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Summer torpor in African woodland dormice *Graphiurus murinus* (Myoxidae: Graphiurinae)

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Abstract We determined the effect of food availability (presence/absence) and ambient temperature (25/10 °C) on daily energy expenditure and the use of activity and torpor in summer-acclimated captive *Graphiurus murinus*. Daily energy expenditure declined logarithmically with duration of food deprivation at a mean rate of 11 and 31% per day at 25 and 10 °C, respectively. The incidence of torpor in the presence of food at 25 °C was low (one in seven individuals) and increased on a single day's exposure to 10 °C and with duration of food deprivation. Use of torpor was highest during the day, varied between individuals, and torpor bouts of greater than 24 h duration were not noted. With food deprivation, individuals at 25 °C initially responded by reducing activity but remained euthermic while the same individuals at 10 °C responded by increasing their use of torpor during the light period; this difference in response probably reflects a difference in the relative energetic benefits of torpor at different temperatures.

Key words Torpor · Daily energy expenditure · Food deprivation · African dormice, *Graphiurus*

Abbreviations *BM* body mass · *DEE* daily energy expenditure · *RQ* respiratory quotient · *SMR* standard metabolic rate · T_a ambient temperature · T_b rectal temperature · $\dot{V}O_2$ oxygen consumption

Introduction

Many small mammals use controlled hypothermia as a mechanism for maintaining energy balance or minimising the rate of depletion of body energy reserves under conditions of high thermoregulatory demand and/or low food availability [reviews: Lyman (1982), Geiser (1994), Geiser and Ruf (1995)]. Two distinct patterns of hypothermia can generally be distinguished; daily torpor and hibernation (Geiser and Ruf 1995). Daily torpor is represented by short (up to 22 h) torpor bouts where defended minimum T_b and minimum $\dot{V}O_2$ are both comparatively high, while hibernation is represented by long (at least 96 h) torpor bouts where defended minimum T_b and minimum $\dot{V}O_2$ are both comparatively low (Geiser and Ruf 1995). In most species utilising controlled hypothermia there is often a seasonal distinction between the two categories of torpor with hibernation being associated with winter conditions and daily torpor associated with non-winter conditions.

The dormice (Myoxidae) are subdivided into two subfamilies; the Glirinae of the palaearctic and Africa north of the Sahara, and the Graphiurinae of Africa south of the Sahara (Holden 1993). The Glirinae of northern Europe are renowned as users of torpor both on an extended basis during hibernation in winter (Nevo and Amir 1964; Jaeger and Hemmer 1980) and on a daily basis as a response to a reduction in the quality or quantity of food in summer (Montoya et al. 1979; Rothwell and Stock 1986). However, studies of the use of torpor in the Graphiurinae are limited and confined to *Graphiurus murinus*, the most widespread species, with a distribution extending from southern South Africa northwards to Guinea Bissau and Kenya (Skinner and Smithers 1991). Winter-acclimated *G. murinus* from South Africa readily entered deep and prolonged (>24 h) torpor (i.e. hibernation) when exposed to cold (Ellison and Skinner 1991) and were able

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to arouse from such torpor without external assistance. However, the same species from Cameroun could not be induced to use torpor on cold exposure (Eisentraut 1962). In summer, *G. murinus* from central Africa could be induced to use daily torpor by food deprivation or exposure to cold (Lachiver and Petter 1969). However, the extent to which such hypothermia was controlled is not clear as T_b was not always defended at the comparatively high levels generally associated with daily torpor (Geiser and Ruf 1995), and once body temperature fell below 14–15 °C individuals were apparently unable to arouse without external heating (Lachiver and Petter 1969). Our intention in the present study was to further our understanding of the use of torpor by summer-acclimated *G. murinus* from a population where hibernation is known to be at least physiologically possible (Ellison and Skinner 1991).

Materials and methods

Study animals

G. murinus were live-trapped during late summer in indigenous subtropical evergreen forest at Magoebaskloof in the NE Transvaal, South Africa (29°59' E 23°51' S). Trapped individuals were transported to Pretoria where they were maintained in individual cages with food (commercial rat diet supplemented with apple and sunflower seeds) and water ad libitum. The cages were kept in a controlled-climate room under simulated summer conditions (25 °C, 14L:10D) for at least 6 weeks prior to experimentation.

The effect of low ambient temperature (T_a) and food deprivation on oxygen consumption ($\dot{V}O_2$) and the use of activity and torpor

Resting $\dot{V}O_2$ of seven *G. murinus* (mean BM 24.9 g, SD = 3.9) was determined using open-flow respirometry while euthermic at both 25 and 10 °C. Individuals were removed from their nests during daylight hours and placed within a glass respirometry chamber (volume 450 ml). Dry air (20.95% O_2) was drawn through the chamber at a rate of 300 ml · min⁻¹ and flow rate was monitored by a flow meter (Ametek, Pittsburgh) cross calibrated at regular intervals with a custom-built bubble flow meter. Excurrent gas from the chamber was redried by passage through silica gel and then measured for O_2 content using an O_2 analyser (Ametek S-3 A/I, Applied Electrochemistry, Pittsburgh). The time lag between a stepped change in O_2 content of air entering the respirometry chamber and that change being registered to within 5% by the O_2 analyser (95% equilibrium time of the system) was less than 4 min. An analogue voltage output from the analyser representing the O_2 content of the gas was converted to a digital signal once every 10 s and a mean value stored automatically on a microcomputer once every minute. $\dot{V}O_2$ was calculated using the appropriate equation from Withers (1977) assuming a RQ of 0.8. Each dormouse was placed in the respirometry chamber and left for 60 min to grow accustomed to its surroundings after which $\dot{V}O_2$ was monitored for a further 60 min before the dormouse was removed from the chamber and T_b was taken to confirm euthermia ($T_b > 34$ °C). Resting $\dot{V}O_2$ was taken as the mean of the lowest five consecutive measures of $\dot{V}O_2$ during the 60-min measurement period. Estimates of $\dot{V}O_2$ were converted to metabolic rate in watts by assuming a calorific equivalence of O_2 of 20.1 W · ml⁻¹ [for a non-protein RQ of 0.8; Elia and Livesey (1988)].

$\dot{V}O_2$ of the same seven dormice was then determined over longer periods of time also using open-flow respirometry. Three hours before the end of the light period individual dormice were removed from their nests, weighed (± 0.01 g) and then placed in a larger respirometry chamber (volume 5000 cm³) containing a nest box, a branch to climb on and a pot containing water ad libitum. Air flow through the system was maintained at 300 ml · min⁻¹ and the 95% equilibrium time of the system was less than 60 min. A measure of the O_2 content of excurrent gas was taken once every 100 s and a mean value stored to disc once every 5 min. The respirometry chamber was maintained under a 14L:10D light cycle at a temperature of either 25 or 10 °C. Food (rat diet and sunflower seeds) was either available ad libitum or not at all. $\dot{V}O_2$ of each dormouse was determined at each temperature for 37 h with food available ad libitum and then for a further 60 h in the absence of food.

Dormice were taken to be active or torpid when metabolic rate fell above or below 120% and 80% of resting metabolic rate, respectively. In this way an objective analysis of the proportion of time that each individual spent active or torpid under the various conditions could be made. An example of torpor and activity using empirical data is shown in Fig. 1. The effect of individual, T_a (25 or 10 °C) and duration of food deprivation (0, 1 or 2 days) on daily energy expenditure and the mean duration of time spent either active or torpid was determined through full factorial multifactor analysis of variance (Sokal and Rohlf 1981).

The energetic cost of activity and torpor

The additional energetic cost incurred through activity during each light and dark period was estimated by subtracting resting $\dot{V}O_2$ from mean $\dot{V}O_2$ during activity and multiplying by the duration of time spent active. In a similar way the energetic saving achieved by the use of torpor was estimated by subtracting mean $\dot{V}O_2$ during torpor from resting $\dot{V}O_2$ and multiplying by the duration of time spent torpid.

Results

The effect of low T_a and food deprivation on $\dot{V}O_2$ and the use of activity and torpor

An empirical example of temporal variation in $\dot{V}O_2$ is given in Fig. 1. In this particular example the record of $\dot{V}O_2$ commences at the start of the dark period (at time = 19 h). The dormouse immediately became active (as shown by high and extremely variable $\dot{V}O_2$) and remained active until the start of the light period (at time = 29 h) whereupon it ceased activity and fell immediately into torpor. The animal remained torpid until approximately time = 33 h when it aroused but remained at rest but euthermic within the nest. At the start of the next dark period (at time = 43 h) the dormouse became active once again but this time the level of activity was more variable and activity was interspersed with short periods of rest and even of torpor (Fig. 1).

Mean resting $\dot{V}O_2$ (SMR) was 4.05 (SD = 0.50) and 1.31 ml · g⁻¹ · h⁻¹ (SD = 0.11) at 10 and 25 °C, respectively (mean BM = 26.44 g, SD = 4.16). Mean $\dot{V}O_2$ was higher during the dark period than during the light period (paired comparison $t_{40} = 8.4$, $P < 0.001$) and,

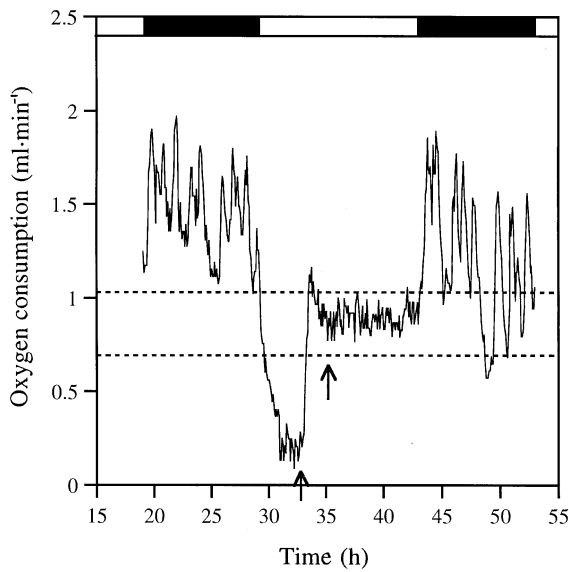


Fig. 1 An empirical example of variation in oxygen consumption ($\dot{V}O_2$) with time in a single *G. murinus* under summer conditions (25°C, 14L:10D) with food available ad libitum. The upper and lower dotted lines show the lower and upper boundaries of activity [$\dot{V}O_2 > 1.2$ times resting $\dot{V}O_2$ (in this case resting $\dot{V}O_2$ was 0.88 ml·min⁻¹, hence the lower boundary for activity was 1.06 ml·min⁻¹)] and torpor [$\dot{V}O_2 < 0.8$ times resting $\dot{V}O_2$ (in this case the upper boundary for torpor was 0.70 ml·min⁻¹)], respectively. The commencement and termination of arousal from torpor are indicated by the vertical arrows. The horizontal solid bars at the top of the graph indicate the timing of the dark period

when $\dot{V}O_2$ was averaged over each 24-h cycle (one dark period plus one light period), there were significant and independent effects of individual, T_a and duration of food deprivation on mean $\dot{V}O_2$ (GLM full factorial ANOVA, $P < 0.05$). The decline in mean DEE (kJ·24 h⁻¹) with duration of food deprivation was logarithmic (Fig. 2; $F_{1,8} = 97.9$, $P < 0.001$) with DEE declining significantly more rapidly at 25°C (11% per day) than at 10°C (31% per day) (Fig. 2; $F_{1,8} = 29.6$, $P < 0.001$).

There were significant and independent effects of T_a and of duration of food deprivation on both the mean duration of time spent active and the mean duration of time spent torpid ($P < 0.05$; Figs. 3, 4). There was also significant interindividual variation in the use of torpor ($P = 0.002$) but not in the use of activity ($P > 0.05$). When food was available at 25°C almost all of the dark period and most of the light period was spent active. However, although four individuals became torpid during the light period at 25°C when food was available ad libitum, the use of torpor during the dark period at 25°C was only noted once dormice had been deprived of food for 3 days (Fig. 4). At 25°C three individuals never entered torpor during the dark period even after 3 days of food deprivation and of these, two

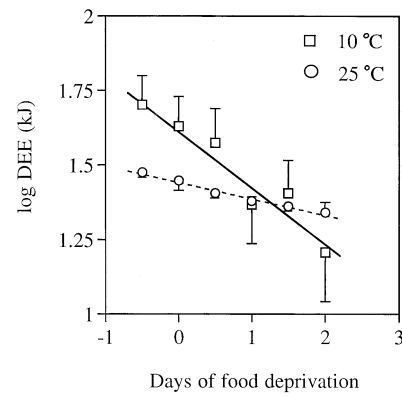


Fig. 2 The effect of food deprivation on mean daily energy expenditure of seven summer-acclimated adult *G. murinus* at either 25 or 10°C. Errors are ± 1 SEM. Day 0 runs from the beginning of the light period before food was removed to the end of the first dark period after food was removed. Day 0.5 runs from the beginning of the first dark period after food was removed to the end of the first light period after food was removed, and so on. The solid line represents the least squares regression at 10°C: $y = 1.61 - 0.188x$, $r^2 = 0.94$, $F_{1,5} = 60.5$, $P = 0.001$. The dotted line represents the least squares regression at 25°C: $y = 1.44 - 0.055x$, $r^2 = 0.98$, $F_{1,5} = 177.3$, $P < 0.001$

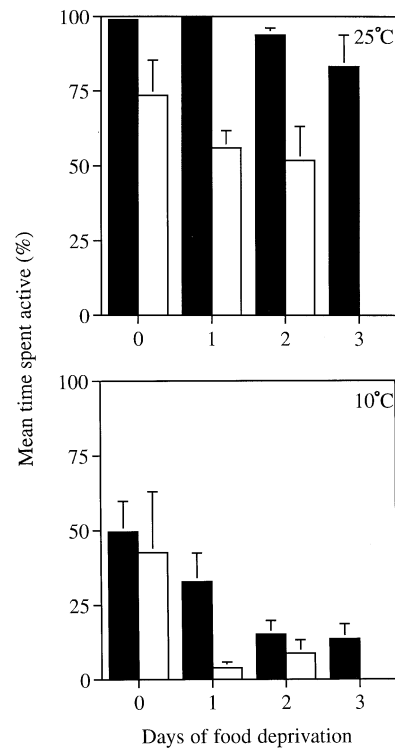


Fig. 3 The effect of food deprivation on the mean percentage of time spent active in seven summer-acclimated adult *G. murinus* at 25 and 10°C during the dark (dark bars) and the light (light bars) period. Errors are ± 1 SEM. See Fig. 1 for definition of activity

also never used torpor during the light period. Only one individual became torpid during the dark period when food was available at 10°C. On food deprivation at 10°C all seven individuals went torpid during the

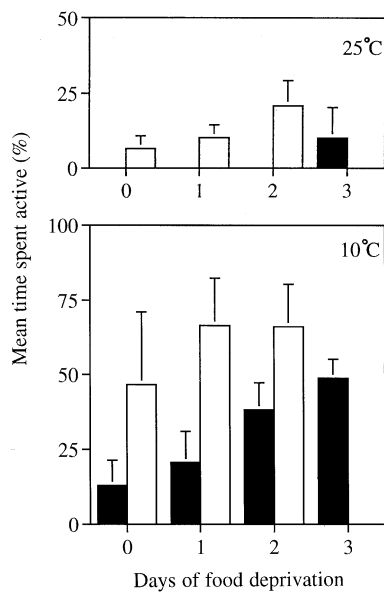


Fig. 4 The effect of food deprivation on the mean percentage of time spent torpid in seven summer-acclimated adult *G. murinus* at 25°C and 10°C during the dark (dark bars) and the light (light bars) period. Errors are ± 1 SEM. See Fig. 1 for definition of torpor

Table 1 The relative contribution of increased torpor use and reduced activity to the reduction in daily energy expenditure (DEE) resulting from a single day of food deprivation in seven summer-acclimated *G. murinus*

Ambient temperature	% of reduction in DEE accounted for	
	10°C	25°C
Increased use of torpor in dark period	4.2	0.0
Increased use of torpor in light period	50.6	2.5
Reduced activity in dark period	0.0	58.5
Reduced activity in light period	0.4	61.9

light period after 2 days of deprivation and during the dark period after 3 days of deprivation.

The relative contribution of increased use of torpor and reduced activity to the reduction in daily energy expenditure shown when dormice were deprived of food for a single day is shown in Table 1. These data do not add up to 100%, in part because of the time lag in the response of the system to changes in $\dot{V}O_2$, but primarily because the data refer only to gross changes in behaviour and ignore changes in $\dot{V}O_2$ that occurred between the upper boundary of torpor and the lower boundary of activity (Fig. 1). At 10°C the primary mechanism for reducing DEE was to increase the use of torpor during the light period, while at 25°C the primary mechanism was to reduce activity during both the light and the dark periods (Table 1).

Duration of clearly discernable torpor bouts ranged from 1.5 to 22.2 h at 10°C and 1.8 to 11.0 h at 25°C and

Table 2 Characteristics of torpor bouts and subsequent spontaneous arousal in summer-acclimated *G. murinus*. SMR is standard metabolic rate. Errors are ± 1 SD

Ambient temperature	10°C	25°C
<i>n</i> individuals	6	3
Body mass (g)	24.4 \pm 4.3	26.6 \pm 5.5
SMR (ml O ₂ · g ⁻¹ · h ⁻¹)	4.37 \pm 0.4	1.29 \pm 0.0
Torpor bout duration (h)	8.49 \pm 3.61	2.85 \pm 0.61
Torpid $\dot{V}O_2$ (ml O ₂ · g ⁻¹ · h ⁻¹)	1.55 \pm 0.73	0.66 \pm 0.19
Duration of arousal (h)	2.33 \pm 0.60	1.18 \pm 0.13
$\dot{V}O_2$ during arousal (ml O ₂ · g ⁻¹ · h ⁻¹)	3.84 \pm 0.72	2.01 \pm 0.35

thus never exceeded 24 h in length. The mean characteristics of clearly discernable torpor bouts are given in Table 2.

Discussion

Summer-acclimated *G. murinus* from the highveld in South Africa use daily torpor as a response to either food deprivation or exposure to cold. Some individuals also use daily torpor spontaneously, i.e. in the presence of food and at high (25°C) T_a . By measuring T_b Lachiver and Petter (1969) found a similar response to either food deprivation or exposure to cold in captive *G. murinus* from central Africa during the summer and suggested that spontaneous torpor also occasionally occurred in some individuals in the population they were studying. However, Lachiver and Petter (1969) also suggested that animals from their study population were incapable of spontaneous arousal (i.e. arousal in the absence of exogenous heat) in summer once T_b had dropped below about 14–15°C. Although we did not have the facility to measure T_b during torpor bouts, individuals entering torpor in the present study were apparently always capable of subsequent spontaneous arousal even at T_a of 10°C. *G. murinus* therefore appears to use daily summer torpor in a way similar to that of members of the Glirinae in northern Europe [e.g. *Eliomys quercinus*, Montoya et al. (1979); *Glis glis*, Rothwell and Stock (1986)] as an energy saving mechanism when exposed to low energy availability and/or high thermoregulatory energy demand.

Torpor in mammals that use controlled hypothermia tends to be more prevalent in winter than in summer even when food is freely available (Hill 1975; Elliot et al. 1987; Fowler and Racey 1987; Fowler 1988; Ruf et al. 1991). The category of torpor employed [daily torpor or hibernation; Geiser and Ruf (1995)] also tends to be associated with season; for instance, torpor induced by food deprivation in summer-acclimated *Phodopus sungorus* does not have the characteristic depth, timing

and duration of spontaneous torpor bouts in winter (Steinlechner et al. 1983). In most cases hibernation is associated with winter while, given the correct stimuli, daily torpor can occur at any time of the year and it seems likely that not all species that use daily torpor are also physiologically capable of hibernation (Geiser and Ruf 1995). Torpor noted in the present study would generally be classified as daily torpor (Geiser 1994; Geiser and Ruf 1995). However, *G. murinus* from the same population as those used in the present study also appear to be capable of entering a hibernal state (Ellison and Skinner 1991). Ellison and Skinner (1991) found that each of three winter-acclimated *G. murinus* from the southern African high veld could easily be induced to utilise torpor by exposure to low temperature (10–15 °C). T_b taken during daylight hours under these conditions indicated that these individuals spent most of the daytime in deep torpor, while metabolic measures using open-flow respirometry showed torpor bouts to be frequently in excess of 24 h (Ellison and Skinner 1991). Mean $\dot{V}O_2$ during torpor at 10 °C was also much lower (0.27 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) than that noted in the summer-acclimated individuals in the present study (Ellison and Skinner 1991; Table 2). Even so, while mean $\dot{V}O_2$ during daily torpor in summer-acclimated *G. murinus* fell well within the range reported for minimum $\dot{V}O_2$ during daily torpor in other mammal species (Geiser and Ruf 1995), mean $\dot{V}O_2$ during torpor in winter-acclimated *G. murinus* was still almost four times the upper limit to the range of minimum $\dot{V}O_2$ during hibernation in other mammal species (Geiser and Ruf 1995). However, it should be noted that this relatively high rate of hibernal metabolism is based on a limited amount of data so far available for *G. murinus* [three individuals over comparatively short periods of time; Ellison and Skinner (1991)].

Torpor was not the only energy-saving mechanism displayed by dormice in response to food deprivation in the present study. While the major response at 10 °C was to increase the use of torpor, the major response at 25 °C was to reduce activity while remaining euthermic (Table 1). In part this temperature dependence of response reflects the large amount of time spent active by dormice at 25 °C when food was available (Fig. 3). However, a further contributory factor may have been a difference in the relative benefits of torpor for energy conservation at the two temperatures. At 10 °C the time-specific energetic cost of arousal was less than SMR (Table 2). As the energetic cost of torpor was also less than SMR (Table 2) an individual will always save energy by entering torpor regardless of how short the duration of the torpor bout. However, at 25 °C the energetic cost of arousal was 0.72 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ greater than SMR (Table 2), equivalent to a total additional $\dot{V}O_2$ of 0.85 ml $O_2 \cdot g^{-1}$ for an average arousal of 1.18 h duration (Table 2). Thus, an individual will only save energy by becoming torpid if a torpor bout is longer than 1.35 h. Any bout of torpor of less than

1.35 h will result in a net increase in energy expenditure above standard metabolism.

In summary, we determined the effect of food deprivation and cold on the level of activity and the use of torpor in summer-acclimated *Graphiurus murinus*. Individual dormice responded to both food deprivation and short-term exposure to cold by reducing activity and increasing the amount of time they spent in daily torpor. Such response is in accordance with the use of daily torpor as a mechanism for balancing daily energy budget and is similar to that reported for other dormouse and small mammal species that are capable of using controlled hypothermia.

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