SHORT COMMUNICATION

To use or not to use torpor? Activity and body temperature as predictors

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Abstract When food is limited and/or environmental conditions are unfavourable, many mammals reduce activity and use torpor to save energy. Nevertheless, reliable predictors for torpor occurrence, especially in the wild, are currently not available. Interrelations between torpor use and other energy conserving strategies are also poorly understood. We tested the hypothesis that reductions in normothermic body temperature (T_b) and the period of activity before torpor events could be used as predictors for torpor occurrence in sugar gliders, Petaurus breviceps (body mass, ~125 g), known to display daily torpor in the wild. Occurrence of torpor was preceded by significant (~10-25%) reductions of the duration of the activity phase. Moreover, the normothermic resting $T_{\rm b}$ fell by an average of 1.2°C over 3 days before a torpor event, relative to individuals that did not display torpor. Our new findings suggest that before entering torpor, sugar gliders, which appear to use torpor as an emergency measure rather than a routine energy saving strategy, systematically reduce activity times and normothermic resting $T_{\rm b}$ s to lower energy expenditure and perhaps to avoid employing torpor. Thus, reduced activity and normothermic $T_{\rm b}$ may provide a predictive tool for the occurrence of daily torpor in the wild.

Keywords Torpor · Activity · Body temperature · Sugar glider · Weather · Marsupial

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Introduction

The maintenance of high and constant normothermic $T_{\rm b}$ s of around 37°C represents a considerable metabolic cost for small endotherms. Particularly during cold exposure, the large differentials between $T_{\rm b}$ and ambient temperature $(T_{\rm a})$ result in substantial heat loss and necessitate increased heat production and thus a substantial allocation of energy for thermoregulation (Bartholomew 1982; Speakman and Thomas 2003). In addition, when it is cold, food resources and access to resources are often limited. To reduce energy expenditure when exposed to adverse conditions, many birds and mammals employ daily torpor (Lyman et al. 1982; Geiser 2004). Daily torpor is characterised by a controlled reduction in $T_{\rm b}$ and metabolism to low levels for periods of less than 24 h (Geiser 2004). During daily torpor when $T_{\rm b}$ and metabolic rate (MR) are near their minimum, energy savings between 80% and 90% can be made relative to normothermic thermoregulation at the same T_a (Lyman et al. 1982; Song et al. 1995; Geiser 2004). Although it is well-known that the frequency of daily torpor bouts increases when food is limited and body mass is low, torpor in the wild often appears to be highly unpredictable, especially because under the same environmental conditions some individuals of a population may enter torpor, whereas others do not (Brigham et al. 2000; Schleucher 2004). Consequently, unequivocal functional predictors for the employment of daily torpor are currently not available.

The aim of the present study was to explore the relationship between activity phases and normothermic $T_{\rm b}$ and the use of torpor by wild sugar gliders (*Petaurus breviceps*). Sugar gliders are small (~125 g) nocturnally active, arboreal marsupials (Fig. 1) that feed predominantly on invertebrates and plant and animal exudates (Smith 1982). In colder regions, sap production of eucalypts and



Fig. 1 P. breviceps in the wild. Photograph by Paul Bayne

invertebrate prey decline over winter and it is probable that fluctuating food resources create energetic shortfalls for sugar gliders during these periods (Smith 1982; Körtner and Geiser 2000). Although sugar gliders are able to reduce heat loss by thickening of their pelage, pre-winter fattening (i.e. increasing insulation via subcutaneous fat) and huddling (Fleming 1980; Körtner and Geiser 2000; Holloway and Geiser 2001), cold and wet conditions during winter reduce food availability and make normal foraging energetically expensive. When rainfall or low T_a restricts foraging, gliders risk a negative energy balance. To minimise energy loss, gliders are able to: (1) reduce activity, (2) reduce normothermic $T_{\rm b}$ (and hence MR) whilst inactive and/or (3) use torpor. As no information is currently available on how activity and normothermic $T_{\rm b}$ relate to torpor frequency in wild sugar gliders, we tested the hypothesis that reductions in activity periods and normothermic $T_{\rm b}s$ can be used to predict the occurrence of torpor in the wild. We also aimed to gain a better understanding of which energy-conserving strategies are employed under different environmental conditions experienced in the wild.

Materials and methods

The study was conducted in late autumn/winter (May–August 2001) in an open Eucalypt/Acacia woodland at the University of New England Newholme Field Laboratory (30° 25'S, 151° 26'E at about 1,000 m altitude) near Armidale in the Northern Tablelands region of NSW, Australia. Ten sugar gliders (5 male; 5 female; capture body

mass 126 ± 8 g) were trapped using Elliott box traps placed on brackets secured to tree trunks ~ 2 m above the ground. Female gliders were non-reproductive during the period of the study. The gliders were implanted intraperitoneally under oxygen/isoflurane anaesthesia (isoflurane 0.5-4% in oxygen) with temperature sensitive transmitters (Sirtrack, 3–4 g) calibrated to the nearest 0.1°C to measure core $T_{\rm b}$. Gliders were released at dusk to the site of capture after 1 day of recovery time. After release, all gliders were radiotracked to their nest trees using a manual radio receiver (Titley Electronics, Regal 2000). The $T_{\rm b}$ was recorded at 10-min intervals using single and multi-channel receiver/ data loggers (Körtner and Geiser 2000) placed at bases of the nest trees. Onset of the activity phase was defined as the time at which a maximum $T_{\rm b}$ within the range for active $T_{\rm b}$ s $(T_{\rm b}=37^{\circ}{\rm C}$ to 39°C) (Fleming 1980; Dawson and May 1984; Körtner and Geiser 2000) was recorded immediately after a period of consistent rise in $T_{\rm b}$ from normothermic resting $T_{\rm b}$ (\geq 30°C to 36°C) or torpor ($T_{\rm b}$ <30°C). Similarly, the time for the termination of the active phase was defined as the time at which a maximum $T_{\rm b}$ (within the range for active $T_{\rm b}$ s) was recorded immediately before a period of consistent drop in $T_{\rm b}$ to resting or torpor values. Animals were considered to be torpid when their $T_{\rm b}$ fell below 30°C for longer than 30 min. $T_{\rm b}$ =30°C was at the lower end of the frequency distribution of normothermic $T_{\rm b}$ s observed in this (fifth percentile=30.6°C) and other studies on sugar gliders, and is several degrees below average normothermic resting values (~36°C) (Fleming 1980; Dawson and May 1984; Körtner and Geiser 2000). Torpor bout length was defined as the time with a $T_{\rm b} < 30^{\circ}$ C because this temperature is widely used for threshold $T_{\rm b}$ defining torpor in marsupials Körtner and Geiser (2000; Geiser 2004). The T_a and nest hollow T_a (in an empty nest hollow) was recorded hourly on site using temperature loggers (DS1921K Thermochron i-Button; resolution $\pm 0.5^{\circ}$ C; accuracy $\pm 1^{\circ}$ C). Rainfall was recorded half hourly on site using a rain gauge data logger (±0.1 mm, Tinytag Plus, Gemini Data Loggers). All nighttime mean, minimum and maximum values for environmental variables were taken from the time of civil sunset of the first night to civil sunrise of the next day.

Statistical analysis was performed using the analysis of covariance (ANCOVA) (1) on the proportion of torpid gliders (arcsine-root transformed) plotted against minimum nightly T_a (nightly rain <1.5 mm and nightly rain >1.5 mm) and (2) average nightly activity of gliders plotted against average nightly T_a (nightly rain <1.5 mm and nightly rain >1.5 mm). Only rainfall readings >1.5 mm were classified as rainfall to eliminate short-term light rain, which did not appear to affect activity, from the analysis. Repeated-measures analysis of variance (ANOVA) was used on (1) torpid and (2) normothermic gliders according to their average daily normothermic T_b and average nightly normothermic activity

on the 3 days before torpor day=0 (torpor days -1, -2 and -3, respectively). Differences between average daily normothermic $T_{\rm b}$ and average daily torpid $T_{\rm b}$ (torpor day=0) were assessed using ANOVA with a post hoc Tukey test. Torpor day=0 represents a day on which some gliders used torpor. Data sets were tested for normality of distribution and homogeneity of variances (Zar 1999). Analysis was performed using StatistiXL version 1.4 and Minitab version 13.1. A level of significance of p=0.05 was used for all statistical analyses and all means are presented ±standard error (SE) for the number of individuals '*n*'. *N*=number of observations.

Results

Sugar gliders showed strong daily fluctuations of $T_{\rm b}$ and occasionally entered torpor (Fig. 2). Of the 10 male and female sugar gliders, 9 used daily torpor on 34 occasions (16 nights) over 102 nights monitored between May and August (4% of all animal-nights; n=10; N=823). Torpor bouts were relatively evenly distributed among individuals with one individual using torpor on eight occasions and two individuals (of the nine that used torpor) using torpor on only one occasion. Torpor bouts always lasted <24 h (393.4± 35.8 min; n=9; N=34). Minimum $T_{\rm b}$ during torpor fell to as low as 14.1°C and averaged 24.0±1.3°C (n=9; N=34).

Fig. 2 Representative changes in body temperature (T_b) of two gliders (from June 8, 2001 to June 16, 2001) over 8 days including the days before two torpor events (a). Unfilled *circles* show the changes in $T_{\rm b}$ for a glider that remained normothermic; filled circles show the changes in $T_{\rm b}$ for a glider that entered torpor. The horizontal black bars represent the time between civil sunset and civil sunrise (a and b). The solid black line indicates nest hollow temperature and the vertical *black bars* indicate rainfall (b): both recorded on site

Gliders used torpor most frequently when it was cold and/ or wet (rainfall >1.5 mm/night) ($F_{1,31}$ =47.11, p<0.001). During normothermia, T_b minima ranged between 30.3°C and 37.5°C (34.5±0.2°C). Low T_a and rainfall negatively influenced the time the gliders spent active ($F_{1,87}$ =36.5, p<0.001). When it was raining or when T_a was low, the gliders curtailed normal nighttime activity, returned to their nests and allowed normothermic T_b to drop to resting levels (see Fig. 2, nights of June 8–9 and June 13–14). If raining ceased within the scotophase (period of darkness), the gliders generally became active again until sunrise or until another episode of rain.

On the 3 days preceding a torpor event, individuals that entered torpor spent less time active (431.1±45.0 min; n=9; N=78) than gliders that did not enter torpor (502.6± 27.5 min; n=10; N=188) ($F_{1,265}=4.95$, p=0.027) (Fig. 3a). On these 3 days, gliders that entered torpor also significantly reduced their normothermic resting $T_{\rm b}$ s (33.6± 0.2°C; n=9; N=78) relative to the $T_{\rm b}$ s of gliders that remained normothermic (34.8±0.9°C; n=10; N=188) on torpor day=0 ($F_{1,265}=26.8$, p<0.001) (Fig. 3b). In addition, average normothermic $T_{\rm b}$ s of gliders on each of the 3 days before torpor day=0 were lower among gliders that remained normothermic on torpor day=0 and those that were torpid on that day (Tukey's post hoc test; "torpor day -1": T=2.95, p=0.037; "torpor day -2": T=3.55, p=0.0051 and "torpor day -3": T=3.037, p=0.029).



Fig. 3 a Average period of activity phase of gliders that entered torpor (dark bars) on torpor day=0 and the 3 days before day=0 and average period of activity of gliders (white bars) that remained normothermic on day=0 and the 3 days before day=0 (torpor n=9; normothermic n=10). **b** Average normothermic resting $T_{\rm h}$ of gliders that entered torpor (dark *bars*) on day=0 and 3 days before day=0 and average normothermic resting $T_{\rm b}$ of gliders (white bars) that remained normothermic on day=0 and 3 days before day=0 (torpor n=9; normothermic *n*=10). *Horizon*tal line at $T_{\rm b}$ =30°C indicates $T_{\rm b}$ below which torpor was considered to occur



Discussion

Our study provides the first evidence of a concurrent decline of the activity phase and normothermic $T_{\rm b}$ in freeranging sugar gliders before entry into daily torpor. By simultaneously reducing normothermic resting $T_{\rm b}$ and durations of activity, sugar gliders are able to reduce energy expenditure at times when foraging is unproductive and may result in a negative energy balance. Because gliders reduced their activity period over the 3 days preceding their entry into torpor (Fig. 2a), it appears that increased foraging time may be insufficient to compensate for energy expenditure associated with activity and increased thermoregulatory costs at low $T_{\rm a}$. Those gliders that were able to remain active for longer may have had better foraging experience and/or were more dominant individuals with better access to food resources Körtner and Geiser (2000). Over time, reductions in foraging will result in reduced insulative body fat reserves and ultimately body mass. A reduction of activity (intensity rather than duration) before torpor onset was previously observed in other heterothermic mammals (Phodopus sungorus, Burramys parvus) in captivity (Ruf et al. 1991; Körtner and Geiser 1995).

By allowing resting T_b to drop by a small extent (Fig. 2b), gliders are able to make savings in resting metabolic rates (RMR) (Fleming 1980). A decline of 1.2°C in T_b by gliders

as observed here before a torpor episode results in a saving of approximately 6% in RMR (Fleming 1980; Holloway and Geiser 2001).

If energetic savings from lower normothermic resting $T_{\rm b}$ s and reduced activity are insufficient to offset reductions in food uptake over multiple days, torpor is an effective option to further minimise energy loss because MR can be reduced to ~20% of normothermic values (when minimum torpid $T_{\rm h}$ =24.0°C) (Fleming 1980). Thus in gliders, torpor is apparently employed as a last resort rather than a routine energy saving strategy or a strategy aimed at preventing loss of condition or minor weight loss. Rather, the use of torpor depends on the timing and duration of both rainfall events and periods of low $T_{\rm a}$. Some other heterothermic species such as chipmunks (Tamias striatus), similar to sugar gliders, avoid torpor if they have access to food (Humphries et al. 2003), whereas others such as ground squirrels (Spermophilus saturatus) and mountain pygmypossums (Burramys parvus) hibernate even with surplus food (Geiser and Kenagy 1990; Körtner and Geiser 1995).

Our study suggests that in wild sugar gliders, torpor episodes are preceded by reductions in normothermic T_b and the duration of the activity phase in an attempt to minimise energy expenditure when foraging is likely to be unproductive. Torpor follows when these avenues are no longer sufficient. Our observations therefore may provide a predictive tool for torpor occurrence in the wild. Nevertheless, further investigations are needed to verify that species using torpor less and more frequently than sugar gliders exhibit similar patterns of activity phase and normothermic $T_{\rm b}$ reduction before torpor use.

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