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Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia)

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Abstract Almost all studies on daily torpor in mammals have been conducted in the laboratory under constant environmental conditions. We investigated torpor and activity patterns in free-ranging sugar gliders (*Petaurus breviceps*, 100 g) using temperature telemetry and compared field data with published information obtained in the laboratory. Body and/or skin temperature and activity patterns of 12 sugar gliders were monitored from autumn to spring. Healthy sugar gliders were active between sunset and sunrise, but on cold or rainy nights activity was substantially reduced. Animals in poor condition occasionally foraged during the day. Eleven gliders were monitored for 8–171 days and all of these entered daily torpor. Torpor was observed on 103 days (17% of observation days), usually occurred on rainy or cold nights, and frequency of torpor changed with season. Torpor bouts lasted between 2 and 23 h (average 13 h) and the body temperature fell to a minimum of 10.4°C. Torpor was thus much deeper, longer and more frequent than in laboratory studies on the same species. Our study shows that cold or wet conditions curtail foraging in wild sugar gliders and that they employ daily torpor regularly during adverse weather. This suggests that minimisation of energy loss by the use of torpor in sugar gliders is pivotal for their survival in the wild.

Key words Climate · Energy · Marsupial · Mortality · Temperature telemetry

Introduction

Many insectivorous and nectarivorous animals must cope with an unpredictable and fluctuating food supply. This problem often is most pronounced during the cold season, but wind, rain, or drought can also reduce food availability. Such energetic bottlenecks are especially challenging for small species because they have high energy costs for maintenance metabolism, thermoregulation, and locomotion (Bartholomew 1982). Most likely because of these energetic constraints many small mammals from the arctic to the tropics enter daily torpor for several hours, usually during the rest phase (Lyman et al. 1982; Wang 1989; Geiser and Ruf 1995; Bartels et al. 1998). Daily torpor in these “daily heterotherms” is characterised by a controlled reduction of body temperature (T_b) and metabolic rates (MR) usually well below the minimum maintenance or basal MR (BMR) of normothermic animals (Lyman et al. 1982; Wang 1989; Geiser and Ruf 1995). Daily heterotherms always remain torpid for less than a day, independent of environmental conditions, and thus differ from hibernators which can enter prolonged torpor and remain torpid for several days or weeks (Geiser and Ruf 1995). Interestingly, almost all studies on daily torpor have been conducted under laboratory conditions, although energy constraints, at least at certain times of the year, are likely to be more pronounced in the field than in the laboratory. Furthermore, captive mammals are usually fatter than conspecifics in the field, and the frequency, depth, and length of daily torpor increases with decreasing body mass (Geiser 1988; Holloway and Geiser 1996). Therefore, data obtained from laboratory studies may underestimate the frequency of daily torpor in free-ranging animals and may not always reflect the natural pattern of torpor.

The small marsupial sugar glider (*Petaurus breviceps*) is potentially faced by food shortages as it feeds predominantly on plant exudates and insects (Smith 1982; Henry and Suckling 1984). Nevertheless, it appears to be well adapted to cope with such challenges as it is common throughout its distribution range, including the colder parts of the great dividing range in south-eastern Australia and Tasmania (Smith 1973). Free-ranging sugar gliders, in comparison to similar-sized non-gliding possums, have relatively low energy demands, which are likely due to social thermoregulation, good insulation, and low-cost locomotion (Fleming 1980; Nagy and Suckling

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1985; Geiser and Stapp 2000). Moreover, energy expenditure in sugar gliders may also be affected by their ability to use daily torpor. However, in captivity, sugar gliders are most reluctant to enter daily torpor and usually do so only after prolonged starvation (Galbraith 1977; Fleming 1980; Dawson and May 1984; Holloway 1998). Since free-ranging sugar gliders have never been observed in torpor, it could be argued that the species is able to survive in the wild by employing energy-saving strategies other than torpor under most circumstances. On the other hand, it is possible that the paucity of information on torpor in the field is due to a lack of observations.

We were interested in whether torpor is used in free-ranging gliders, how often and under what circumstances it is employed, how it is related to activity patterns, and whether patterns of torpor in the wild differ from those of induced torpor previously determined in laboratory studies. To address these topics, we used temperature telemetry to quantify the thermoregulatory and activity patterns of free-ranging sugar gliders on the cool-temperate Northern Tablelands of New South Wales.

Materials and methods

The study was conducted between May and October (Australian autumn to spring) 1998 in Imbota Nature Reserve (formerly Eastwood State Forest); (30°35′S, 151°44′E; altitude approximately 1000 m; area approximately 220 ha) located about 10 km southeast of Armidale on the Northern Tablelands (Australia). The tree community of this open woodland includes: broadleaved stringybark, *Eucalyptus caliginosa*; Blakely’s red gum, *Eucalyptus blakelyi*; manna gum, *Eucalyptus viminalis*; yellow box, *Eucalyptus melliodora*; apple box *Eucalyptus bridgesiana*; and fernleaved wattle, *Acacia filicifolia*, as the most common species (Ford et al. 1985).

Twenty Elliott traps baited with honey and provided with Dacron fibre material for insulation were set overnight on small wooden platforms attached to tree trunks at a height of 3–5 m. To attract the gliders to these trapping stations, platforms were sprayed with honey water, and a drop of honey was provided on the platforms for one to three nights prior to trapping. All captured gliders were weighed to the nearest 0.1 g and were individually marked with subcutaneous microchips (Destron-Fearing) and, unless implanted with transmitters, were released on the evening after capture. Overall, 12 individuals (seven females, five males), belonging to three different social groups, were fitted with temperature-sensitive radio transmitters (Sirtrack; single stage; 3 g). Four individuals received implantable transmitters to measure core T_b, five were equipped with transmitters attached to a collar which provided skin temperature (T_{skin}) measurements, and two individuals were fitted with both transmitter types to evaluate how accurately T_{skin} measurements represent core T_b. Transmitters were calibrated in a water bath to the nearest 0.1°C before implantation. Transmitters were implanted intraperitoneally under Forthane anaesthesia (0.75–4% in oxygen) and the animals were allowed to recover for at least 2 days before release at the site of capture. Gliders were tracked between 8 and 171 days, with the exception of one individual which could be tracked only for 6 days (mean, 57 days of measurement/individual; total, 617 days of measurement).

Tagged gliders were radio tracked in 1- to 3-day intervals to identify the nest trees. Occasional night-time observations were performed to locate the exact nest sites and to count the number of individuals using the nest sites. Once the location of nest sites was established, T_b and T_{skin} were recorded automatically in 10-min intervals with receiver/loggers (Körtner and Geiser 1996, 1998) fitted with omni-directional antennae (CDB 151; Titley Electronics) or H-frame antennae (Titley Electronics or Telonics). Several receiver/loggers were distributed throughout the home range of gliders to record T_b also during nightly activity. Most collared animals were monitored only at their nest site, because T_{skin} readings were an accurate reflection of T_b only during periods of rest when the gliders assume a curled position with the transmitter situated near the centre of the animal. However, strong temperature variations of external transmitters during activity allowed us to estimate how long gliders were active during the night. To obtain data on activity- and rest-phase from internal transmitters an additional logger/receiver with a short-range flexible antenna was placed at the bottom of the nest tree and, providing the nest hollow was less than 3 m above the ground, the presence and absence from the nest tree could be measured with this arrangement.

Ambient temperature (T_a) was recorded hourly at the study site with an eight-channel data logger using temperature transducers (AD590; accuracy ±0.35°C). The temperature in one nest hollow was recorded with a collar transmitter after the glider to which it had been initially attached had removed it. Readings from this transmitter permitted us to compare nest temperatures with outside T_a. Daily rainfall for Armidale, measured at 0900 hours, was obtained from the Bureau of Meteorology.

Animals were considered to be torpid when their T_b or T_{skin} fell below 30°C. This threshold was situated at the lower end of the frequency distribution observed for the day-time T_b minimum in this study, and several degrees below the normothermic resting T_b observed in captive sugar gliders (approximately 36°C: Fleming 1980; Dawson and May 1984). The beginning of entry into torpor was defined as the time when T_b started to decline consistently to fall below 30°C, and the end point of arousal when T_b had reached a plateau above 30°C. Timing of torpor entry and arousal from torpor was analysed using a Rayleigh’s test (Zar 1996).

The proportion of animals in torpor in relation to average nightly T_a and daily rainfall was analysed as data with specified binomial error terms. Principally, the variance of such data is not normally distributed nor is it constant (Crawley 1993). Also, if these data are treated as percentages, information regarding sample sizes is lost. The statistical package GLIM (Crawley 1993) was used to build a model of the logit (natural logarithm of the proportion of animals in torpor [*p*] divided by the proportion of animals not in torpor [*q*]) in relation to nightly T_a and daily rainfall. The odds ratio, the exponential of the logit (ln[*p*/*q*]), can be used to predict the proportion of animals in torpor under any given set of conditions by solution of the following equation: $p=(1+1/\text{odds ratio})^{-1}$.

Linear regressions were performed by the least-square method and numerical values are presented as mean±1 SD for the number of individuals *n*. *N* represents the number of observations.

Results

Group composition and mortality

The sugar gliders fitted with transmitters belonged to three different social groups. Observations of the nest hollows during the onset of activity revealed that most gliders in the study area were not tagged and group sizes varied between three and ten. Group sizes appeared to be rather stable, but especially when gliders changed nest hollows, social groups usually divided for a few days until all group members had eventually moved to the new nest. Such movements were infrequent and in some cases seemed to be attributable to disturbance, because animals changed hollows twice after a member of the group had been trapped the previous night.

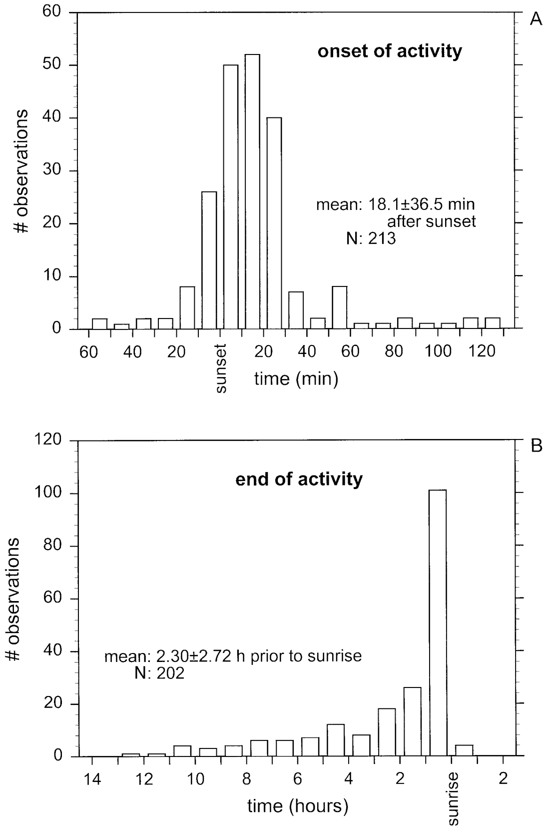

Fig. 1 Timing of onset (**A**) and end (**B**) of activity with respect to sunset and sunrise, respectively (only days with <1.5 mm of rain were included). # = number

Movements between social groups were observed twice, and in one instance a radio-tagged individual joined another group after many or possibly all other group members (initially six observed) had died or disappeared from the study site. The gliders in this particular group, unlike the gliders from the other groups, appeared unhealthy. From the beginning of the study in autumn most of their tail hair was missing and their fur had an ungroomed appearance. Two of them, both tagged, were eaten by unknown predators, one untagged glider was found dead on the forest floor, and the others were never seen again. Not only in this group, but also in the other groups, mortality appeared to be high in both untagged and tagged gliders. Two further tagged and one untagged glider from other groups died from exposure or starvation, and one untagged individual most likely was killed by a predator because only the tail was found.

Body mass and activity patterns

The body mass of gliders trapped between May and July was relatively low and ranged from 85.3 to 115.1 g. Three of the tagged gliders were retrapped in summer and had increased their body mass by 18.3±14.6 g (about 16%).

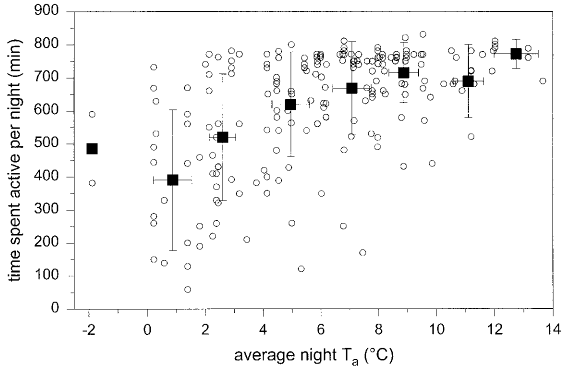

Fig. 2 Time spent active per night as a function of average nightly ambient temperature (T_a; sunset to sunrise). *Circles* represent individual measurements, whereas *squares* represent the average calculated for 10°C intervals. Only data from days with <1.5 mm of rain were included

The activity phase of sugar gliders contained one to three bouts of activity. On dry nights with less than 1.5 mm daily precipitation, activity usually commenced around sunset (Fig. 1A), and in most cases was terminated 1 or 2 h before sunrise (Fig. 1B). However, the end of the activity phase varied, and occasionally gliders were active for only a short period after sunset and then retreated into their nest hollow (Fig. 1B). The T_a at night appeared to influence activity patterns as sugar gliders were active for only short periods on cold nights (Fig. 2). Rainfall during the night also curtailed activity even during mild nights, and on two wet and cool nights (T_a <13.2°C) there was no activity in some gliders.

Although gliders were generally active at night, some tagged and untagged individuals were observed foraging during the day-time (Fig. 1A). One radio-tagged glider commenced activity as early as 0930 hours in the morning (28 June). Activity during day-time was observed in individuals which appeared to be in poor condition, and these were regularly chased away from feeding sites by other gliders with the onset of the normal activity phase near sunset. One of these diurnally active gliders lost 21.3 g over 37 days, and died from exposure during a rainy night 3 days after shifting activity into the day-time.

Use of torpor and T_b fluctuations

The occurrence of torpor changed with season (Fig. 3). Torpor was occasionally observed in May (autumn) and September/October (spring), but only a fraction of the tagged individuals entered torpor during these times. Torpor was most frequent between late June and mid-August (winter), and on 6 days during this time all of the tagged gliders entered torpor.

Torpor seemed to occur in response to inclement weather conditions (Figs. 3, 4). The percentage of animals entering torpor increased with decreasing T_a during dry weather, but rainfall during the activity phase also

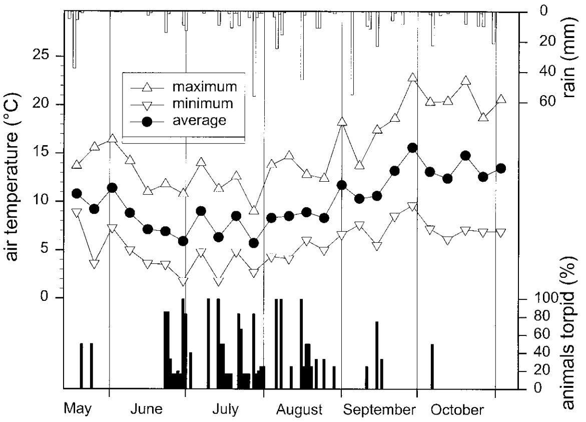

Fig. 3 Rainfall, air temperatures, and percentage of torpid sugar gliders between May and October 1998. Rainfall data were obtained from the Bureau of Meteorology. T_a was measured at the field site

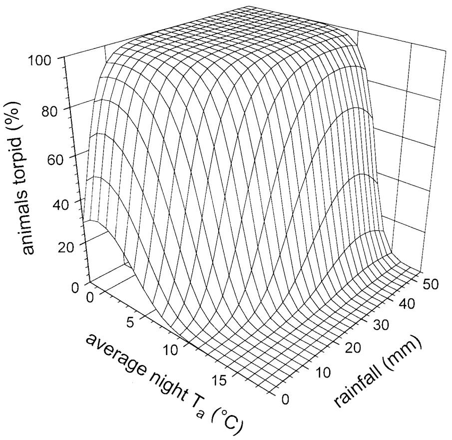

Fig. 4 The response surface constructed from the model showing the percentage of animals entering torpor as a function of average nightly T_a and daily rainfall. The model constructed from the data was: $\ln(p/q)=a+bT_a^2+cR+dR^2$. Coefficients±1 SE were: intercept=–0.6808±0.2027; T_a^2=0.04824±0.0061; R=0.3931±0.0457; R^2=–0.0045±0.0008; all significant at $P<0.05$

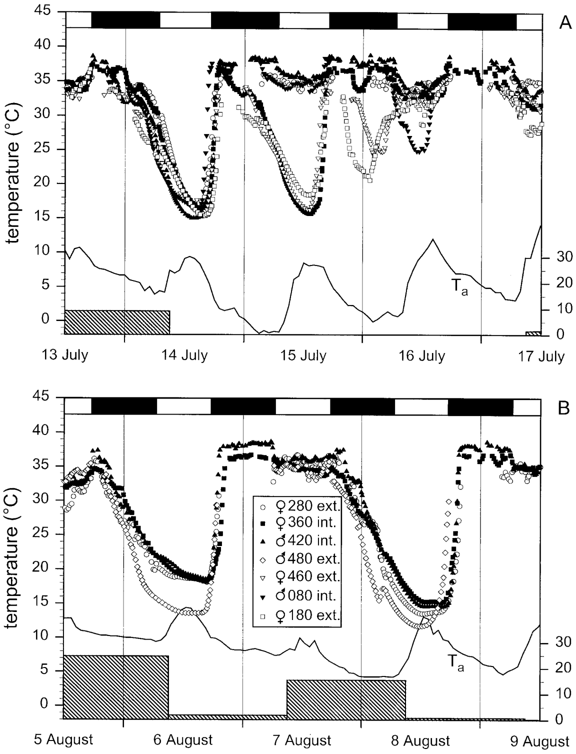

Fig. 5 Two examples for torpor in sugar gliders. Symbols represent individual body temperature (T_b; *filled symbols*) or skin temperature (T_{skin}; *clear symbols*) measurements and T_a is represented by a *solid line*. Rainfall (measured daily at 0900 hours) is indicated by the *bar graph* at the bottom of the graph. The dark phase is indicated by the *black bars* above the graph. Intense rainfall (14 July, 6, 8 August) induced torpor in all monitored gliders, whereas only half of the animals entered torpor on cold dry nights (15–16 July)

induced torpor at a relatively high T_a of up to 15°C (Fig. 4). The final model constructed for the occurrence of torpor in respect to climate had the following form:

$$\ln(p/q)=a+bT_a^2+cR+dR^2$$

where p is the proportion of animals in torpor, q the proportion of animals not in torpor, T_a nightly air temperature, and R daily rainfall (coefficients in figure heading). The significance of the quadratic terms for T_a and rainfall suggested a curvilinear relationship, but could also be attributed to relatively few high rainfall events and nights with very low T_a. A response surface constructed from the model showing occurrence of torpor in relation to T_a and rainfall (Fig. 4) suggested that the likelihood that an animal entered torpor at zero rainfall was about 30% at T_a=–2 to +2°C and increased to 100% when daily rainfall was greater than 20 mm. At T_a>10°C, torpor only occurred on wet days, and at T_a=15°C, torpor was very infrequent and occurred only when daily rainfall was >30 mm. Perhaps due to the large impact of environmental conditions on use of torpor, episodes of torpor were often (particularly in response to heavy rainfall), but not always, synchronised among individuals. Interestingly, synchronisation of torpor not only occurred among members of one group, but also among groups inhabiting different nest hollows (Fig. 5).

Temperature records, available for 12 individual sugar gliders over a total of 617 days, showed that during rest normothermic T_b was generally about 32–34°C and increased to 38°C during the activity phase. On 106 occasions (days in torpor/days monitored, 3–57%, n=11) T_b dropped below 30°C and gliders entered torpor. Both males and females entered torpor (Fig. 5) and all individuals did so, with the exception of one glider, which was monitored for 6 days only because of transmitter failure. Torpor bouts were always shorter than 24 h (mean 13.14±5.31 h, n=11, N=106), and on three occasions more than one torpor bout/day was observed. The longest torpor bout observed was 23 h. Torpor entry usually occurred during the night (Fig. 6), the normal activity phase for sugar gliders (mean entry time: 0248 hours,

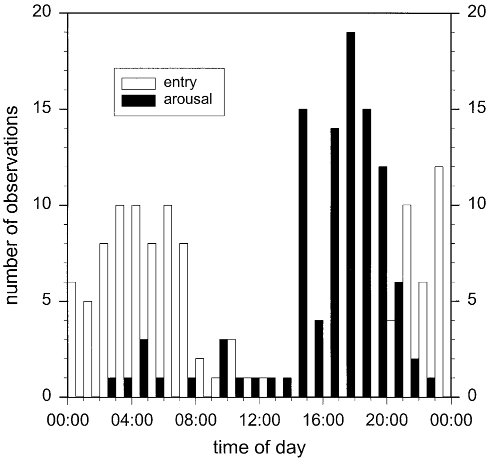

Fig. 6 Timing of entry into and arousal from torpor. Both events were significantly non-random ($P<0.001$), but arousals appeared to occur within a narrower time period than torpor entries (entry mean 0248 hours, $r=0.574$, $N=105$; arousal mean 1713 hours, $r=0.691$, $N=102$)

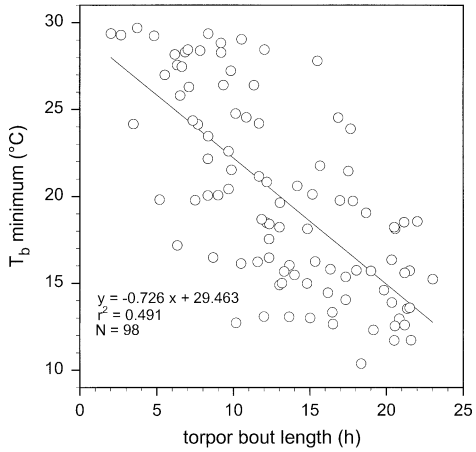

Fig. 7 Daily minimum core T_b and T_{skin} during torpor as a function of torpor bout length. The calculated regression was significant. For abbreviations, see Fig. 5

length of mean vector $r=0.57$, $N=105$, $P<0.001$). Arousal was observed on most occasions shortly before sunset (mean arousal time: 1713 hours, $r=0.69$, $N=102$, $P<0.001$), but occasionally torpor was extended into the following night and arousal occurred up to 3.95 h after sunset (Fig. 6).

The minimum T_b recorded during torpor bouts ranged from just below 30°C to a minimum of 10.4°C (internal transmitter). The mean minimum T_b for all torpor bouts including those where a steady state low T_b had not been achieved was 12.7±2.0°C ($n=5$; internal transmitters) and 12.9±1.5°C ($n=10$; all transmitters). The minimum T_b reached during torpor was negatively correlated with torpor bout length (Fig. 7), but neither variable was correlated with the minimum day-time or average T_a of the day of the torpor bout. The daily minimum T_b during torpor was on average attained in the early afternoon (mean time for daily minimum T_b: 1311 h, $r=0.617$, $N=100$, $P<0.001$) significantly later than the daily minimum T_a ($P<0.001$; time difference: 4.31±4.23 h). This delay is probably explained by the thermal inertia of the nest hollow. Due to insulation and the shielding against solar radiation the nest temperature of one monitored hollow showed a significant time-lag. The daily minimum hollow temperature was delayed by 1.83±3.07 h ($P<0.001$), but the daily maximum temperature by 4.84±1.23 h ($P<0.001$), because in the early morning outside T_a increased rapidly due to solar radiation.

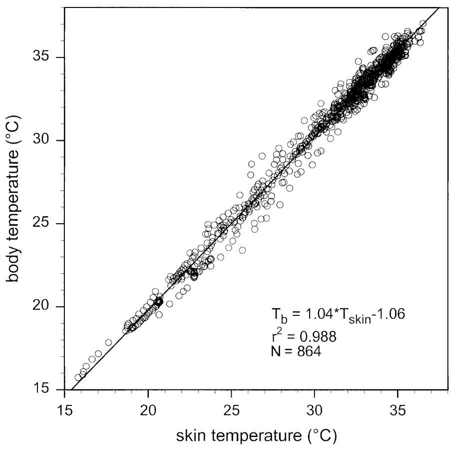

Fig. 8 T_b of resting animals as a function of T_{skin}. Over the whole temperature range the differential between T_b and T_{skin} was on average <1°C. For abbreviations, see Fig. 5

Differences between core T_b and T_{skin} monitored in two gliders differed according to state of activity. In resting animals, T_b and T_{skin} were closely correlated ($r^2=0.988$) and T_b-T_{skin} differentials were on average <1°C over the whole range of T_b recorded (Fig. 8). In contrast, T_b-T_{skin} differentials during activity increased substantially and usually ranged between 2 and 14°C.

Discussion

Our study provides the first detailed data on use of daily torpor in a free-ranging mammal. It shows that daily torpor is frequently used by wild sugar gliders and its occurrence appears to be strongly influenced by T_a and rainfall. Torpor was observed between May and October (Australian autumn, winter, and spring), and was much deeper and longer than in laboratory studies. Our results suggest that torpor is frequently used by heterothermic mammals in the wild and that it plays a key role in their survival.

In contrast to the results of our field study, captive sugar gliders enter daily torpor only reluctantly (Galbraith 1977; Fleming 1980; Dawson and May 1984; Holloway 1998). Under field conditions torpor was employed on average more than once per week in the cold season when adverse weather conditions curtailed foraging. Furthermore, the minimum T_b of 10.4°C during torpor in free-ranging gliders was well below values previously recorded from laboratory experiments (minimum T_b=15.6°C, average T_b=24.1°C; Fleming 1980; Holloway 1998) and bouts of torpor in captive gliders were much shorter than in the field. The only other telemetry study on daily torpor in free-ranging mammals using natural nesting sites we are aware of is that by Frey (1991) on the small marsupial *Sminthopsis crassicaudata*, and another on white-footed mice (*Peromyscus leucopus*) inhabiting artificial next boxes (Vogt et al. 1983). Both studies indicated that torpor patterns (i.e. T_b, bout length, and frequency) in the field are similar to those in the laboratory; however, limited quantitative data were provided. Other studies have been conducted under semi-natural conditions and resulted in torpor patterns similar to those found in the laboratory (Tannenbaum and Pivorun 1988). However, the individuals used had the opportunity to fatten during periods of ad libitum feeding, and energy constraints may have been less severe than in the wild. Laboratory studies suggest that, on average, daily torpor bouts last for a maximum of about 11 h (Geiser and Ruf 1995), about half of that observed here. Clearly, more studies are needed to establish the precise natural pattern of daily torpor in various mammalian taxa, and how it compares to the pattern in captivity.

Sugar gliders have a wide distribution range, which extends from tropical New Guinea, along the Australian east coast including its mountain ranges, to cool-temperate Tasmania where they were introduced in 1835 (Smith 1973; Henry and Suckling 1984). As they mainly eat plant exudates, and to a lesser degree insects (Smith 1982; Nagy and Suckling 1985), food sources are likely to fluctuate on a seasonal basis and to be temperature dependent, because insect activity and the production of nectar or tree sap normally decrease at low T_a (Smith 1982; Racey and Swift 1985). Smith (1982) concluded that because sugar sap production of eucalypts is limited during winter in the colder parts of their distribution range, gliders must rely heavily upon *Acacia* gum (water-insoluble carbohydrate polymers produced in response to insect damage). *Acacia* gum is also produced mainly in summer, but can remain on the trees throughout winter. While acacias were present in the understorey of the study site, gliders were mainly observed feeding upon sap from *E. melliodora* and *E. bridgesiana*, which appeared to be the preferred food source at this site.

Feeding was also affected by apparent competition with conspecifics and other species. The established feeding sites were not only used by gliders, which were observed to fight for the right of access (see also Smith 1982), but also by red wattlebirds (*Anthochaera carunculata*) during the day. The aggressive behaviour of dominant gliders also appeared to be the reason for the shift of the activity period of some gliders toward the day-time in order to gain access to feeding sites, because at sunset these individuals were driven off by other gliders.

It appears that during winter food is a limiting commodity for sugar gliders and this situation is worsened on cold or rainy nights. This reduced food availability and increased energy expenditure apparently made foraging uneconomical, as gliders were observed to retreat early at night into their nest hollows, where huddling in well insulated leaf nests minimised thermoregulatory costs (Fleming 1980; Hayes et al. 1992; Boix-Hinzen and Lovegrove 1998). A group of only four huddling gliders can shift the lower critical temperature of the thermoneutral zone from 27°C to 15°C, which approximately halves the resting MR (Fleming 1980). Since group sizes observed in our study were usually larger than four, perhaps because group sizes of gliders show a tendency to increase towards winter (Henry and Suckling 1984), it is likely that huddling gliders in their nests use little energy on normothermic thermoregulation.

Nevertheless, huddling as a means of energy conservation is limited as MR cannot be reduced below BMR. Therefore, during adverse weather, which prohibited foraging, gliders even in large groups reduced energetic costs below that of the BMR by entering torpor. Entry into torpor often occurred shortly after gliders returned to their nest hollow in the early evening, but also could occur late at night or near sunrise. The variation in the timing of torpor entry probably reflects differences in weather patterns and hence food availability (Hiebert 1990), and thermoregulatory cost in relation to T_a (Geiser 1986). Early torpor entries were associated with long torpor bouts and low T_b, but, surprisingly, the minimum T_b, although correlated with torpor bout length, was independent of T_a. It therefore is likely that huddling in a large group and the insulation of the nest provide a relative independence from outside T_a.

Since combined use of huddling and torpor cannot prevent a negative energy balance it is likely that accumulation of body fat stores in autumn, observed in southern populations (Henry and Suckling 1984), is a further strategy used to overcome short-term starvation inflicted by inclement weather. As such seasonal changes in body mass also occur in captive gliders held in outside enclosures with a constant food supply (Holloway and Geiser 1997), it appears that the body mass threshold of gliders changes with season. The low body masses observed here in winter do not refute this, but indicate that either food availability was not high enough in autumn to allow pre-winter fattening or that fat stores had been already been depleted in May when our study commenced. It appears that gliders at our study site also change body mass with season, as individuals recaptured in the following summer had significantly higher body masses than in winter.

Sugar gliders did not use torpor in order to facilitate body weight gain as observed in some captive mammals that undergo daily torpor (Kenagy 1989; Hiebert 1990; Geiser and Masters 1994). Despite the potential energetic advantages, sugar gliders rarely entered torpor after they were able to forage for most of the night, and then probably did so only if feeding was not very successful. We believe it unlikely that the occurrence of torpor was limited by a potentially increased risk of predation during the day, because predation events appeared to occur predominantly when animals were active. It seems more likely that the food consumed in the previous night required a high T_b to facilitate digestion and nutrient processing (Carey 1989; Ruf and Heldmaier 1992) and that gliders avoid torpor when the gut is full. This interpretation is supported by the observation that during times when foraging was brief and food was apparently in short supply, torpor could occur over a sequence of several days (Figs. 5). However, this extensive use of torpor is likely to also be enhanced by low internal energy stores. Whatever the reasons for torpor induction, torpor in sugar gliders is apparently employed to lower energy loss at times when foraging is not feasible or futile, but, unlike huddling and sheltering, it does not appear to be part of their regular daily routine.

As free-ranging sugar gliders do not appear to use torpor spontaneously, but only in response to low food supply or energy stores, it is not surprising that they are reluctant to enter torpor in captivity. Captive sugar gliders are usually considerably heavier than wild conspecifics (captive mass 132 g; Fleming 1980). Usually starvation was necessary for torpor induction in the former (Fleming 1980; Holloway 1998), and it is likely that body fat reserves influenced use of daily torpor as in other small marsupials (Geiser 1988; Holloway and Geiser 1996). Because torpor was not always synchronised between all gliders we monitored, not even within a group, differences in use of torpor may have been due to differences in energy reserves. While heavy rain induced torpor in all gliders, low T_a during the night did so in only some individuals. It thus appears likely that rain has a greater impact upon food availability than low T_a. As food resources at low T_a are diminished, dominant animals in good condition may have been able to monopolise the few remaining food sources and could afford to remain normothermic.

Given that rain seems to be more problematic than low T_a, is likely that the unusually wet winter of 1998 (June–August 1998: 267 mm versus 154 mm long-term average) resulted in below average conditions and may explain the relatively high mortality observed. As mortality was not restricted to tagged individuals, we believe it unlikely that it was caused by the attached radio transmitters. We found untagged and undamaged dead sugar gliders in the study area suggesting that they died of starvation. However, only three radio-tagged animals died apparently from starvation and most losses were probably due to predation. Potential nocturnal predators such as foxes, cats and boobook owls (*Ninox novaeseelandiae*) were abundant in the area (Henry and Suckling 1984; Suckling 1984). Moreover, the early onset of activity and occasional diurnal activity of some individual gliders potentially exposes them to diurnal predators such as little eagles (*Hieraaetus morphnoides*; one transmitter was close to a nest) and brown goshawk (*Accipiter fasciatus*). Thus, the low food availability and the resulting shift of the activity period are the most likely reasons for the high mortality rates.

Obviously, winter in the cool parts of the distribution range is energetically challenging for small mammals depending on a fluctuating food source. Although sugar gliders have a relatively low energy expenditure, possibly because of the low costs of travelling by gliding and because of social thermoregulation (Fleming 1980; Nagy and Suckling 1985), inclement weather induced torpor regularly. As we observed a high occurrence of torpor at relatively high T_a during wet weather, it is likely that daily torpor is used by many sugars gliders at high altitudes throughout their distribution range and at low altitudes in their southern range. As our study revealed more frequent and more pronounced torpor in the field than in previous laboratory studies, it is likely that the role of daily torpor in the biology of small mammals has been underestimated.

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