

Daily torpor in relation to photoperiod in a subtropical blossom-bat, *Syconycteris australis* (Megachiroptera)

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Abstract

Daily torpor in many temperate-zone mammals is affected by photoperiod. As little is known about the effects of photoperiod on torpor in subtropical species, we investigated whether, and if so how, torpor use, duration, and depth are affected by acclimation to three photoperiods (short, intermediate, long) in the blossom-bat *Syconycteris australis*. In contrast to many other studies, torpor occurrence, duration, and depth did not significantly respond to photoperiod acclimation in *S. australis*. Interestingly, the trend of a decline in torpor use under long photoperiod was the opposite of that observed previously in *S. australis*, which had been captured from the wild in summer and winter. Our study suggests that some species living in low latitude areas with unpredictable weather like *S. australis* may not use photoperiod for seasonal adjustments in physiology because it is not a reliable cue for food availability.

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1. Introduction

Photoperiod has a pronounced effect on the expression of daily torpor in many mammals. The most common pattern that has been observed in temperate zone species is an increase in torpor occurrence and depth after acclimation to short photoperiod, and a concomitant decline in reproductive organs and activity (Lynch et al., 1978; Steinlechner et al., 1986; Ruf et al., 1989; Geiser and Heldmaier, 1995; Stamper et al., 1999; Körtner and Geiser, 2000). As daily torpor results in a substantial reduction in energy expenditure, to a large extent because of the ~10–20 °C fall in body temperature (T_b) for ~5–10 h (for review: Geiser, 2004), frequent and deep torpor in response to shortening day length is

often interpreted as an appropriate adaptation to life in a predictable environment where photoperiod provides a reliable predictive cue for the imminent arrival of adverse weather and food shortages in winter.

However, not all species respond in such a way. For example, in the insectivorous marsupial *Sminthopsis crassicaudata*, torpor occurrence and depth are not affected by photoperiod, although body mass and testes size do change with photoperiod acclimation (Holloway and Geiser, 1996). As *S. crassicaudata* lives in an unpredictable semi-arid and arid environment with low primary productivity, employment of torpor may be required for survival at any time of the year. Torpor expression in response to photoperiod may also differ among populations. White-footed mice (*Peromyscus leucopus*) from high latitudes increase spontaneous (food provided) daily torpor use in short photoperiod during exposure to mild ambient temperatures (T_a 23 °C),

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whereas low latitude individuals do not enter torpor under the same conditions (Heath and Lynch, 1983). An entirely different seasonal change in torpor patterns has been observed in the blossom bat (*Syconycteris australis*) from sub-tropical Australia. Torpor was short and shallow in *S. australis* captured in winter under short photoperiod, and long and deep in individuals captured in summer under long photoperiod and measured from a week after capture (Coburn and Geiser, 1998). Thus the seasonal change in torpor in *S. australis* was the opposite of those observed for many heterothermic mammals from high-latitude and temperate regions of the northern hemisphere. Nevertheless, it remains to be resolved whether the unusual seasonal change in torpor patterns in *S. australis* is due to seasonal changes in photoperiod, or reflects changes in T_a , rainfall, food availability or other factors. The purpose of the present study was therefore to investigate whether and how daily torpor in *S. australis* is affected by acclimation to different photoperiods.

2. Methods

S. australis are small (~18–20 g), nectar and pollen eating bats of the Suborder Megachiroptera that, in Australia, are found along the east coast north of Myall Lakes (32°19'S, 151°31'E; Law, 1994a, b). They roost solitarily in foliage within rainforests (Law, 1993), therefore gain no thermal benefits from clustering and can experience substantial heat loss when at rest at T_a s that are often well below the thermo-neutral zone. The species is active for most of the night and its mass-specific energy expenditure in the field is one of the highest reported for mammals (Law, 1993; Geiser and Coburn, 1999; Voigt, 2003; Korine et al., 2004). Therefore, daily torpor may be important in minimising and balancing energy use (Bartholomew et al., 1970; Geiser et al., 1996).

Bats ($n = 7$, 4 females, 3 males) were captured in winter using mist nets on the subtropical north coast of New South Wales (30°22'S, 153°06'E). Captured bats were transferred to the University of New England where they were held in a large holding room (3.5 m*2.1 m*3.0 m) that provided enough space for flight. The room was fitted with leafy branches and wide plastic mesh for roosting. Bats were fed a food mixture (500 mL apple juice, 2 bananas, 150 g raw sugar, 150 g "Glucodin", 120 g "Infasoy"), which was blended and frozen. Each day about 75 mL of this mixture was defrosted and diluted to double the volume with water. Food was offered to the bats in plastic feeders. The feeders were washed daily and soaked in Milton anti-bacterial solution to discourage growth of microorganisms. Water was available ad libitum in bird feeders. T_a

was maintained at 21 ± 1 °C and relative humidity above 40%.

Initially after capture on 3 August (Austral winter), the photoperiod was maintained at LD 10:14 (lights on 07:00–17:00 h) to reflect the shortest natural photoperiod bats are exposed to in the wild. After 3 weeks of acclimation to captivity and short photoperiod, metabolic rate (MR) was measured as the rate of oxygen consumption, which is directly proportional to energy expenditure, to test whether, and to what extent, animals used torpor; these measurements were complete by the end of August. The photoperiod was then changed to LD 12:12 on 15 September, to reflect natural spring photoperiod at that time; bats were acclimated to the new photoperiod for 6 weeks and the MR measurements were repeated at the beginning of November. The photoperiod was again changed to LD 14:10 on 4 November to reflect the natural summer photoperiod, animals were acclimated for 5 weeks and MR measurements were finalised in the second week of December. Longer acclimation times were used for LD12:12 and LD14:10 than for LD10:14, because at capture on 3 August, bats had been exposed to natural short photoperiod.

To determine whether bats entered torpor, the MR was measured by open-flow respirometry over ~23.5-h periods beginning in the late afternoon. Each bat was measured once in each photoperiod. Bats were transferred to 0.75-L glass respirometry chambers that were fitted with a wide plastic mesh for roosting. The T_a was maintained at 18 °C, the photoperiod was the same as in the holding room, and food and water were not provided during MR measurements. The respirometry chambers were placed in a temperature-controlled (± 0.5 °C) cabinet. The flow rate (about 450 mL/min) was controlled with rotameters and measured with Omega FMA-5606 mass flowmeters. Oxygen percentage was measured with an Ametek Applied Electrochemistry oxygen analyser (S-3AI) fitted with a high resolution output board (80335SE). Four channels, three animal channels, and one reference channel (outside air) were scanned in sequence with solenoid valves. Each of the four channels was read for 3 min (i.e. the three bats and the reference channel were measured once every 12 min in sequence). The minimum normothermic MR or the minimum MR during torpor (TMR) were determined during the light phase when it remained constant and low for at least 36 min. The T_a inside the respirometer chamber was read to the nearest 0.1 °C with an Omega digital thermocouple thermometer. Outputs from the oxygen analyser, flowmeter and digital thermometer were stored on a PC.

Animals were weighed before and after the 1-day MR measurements. A linear decrease of body mass throughout the MR measurements was assumed for calculation of mass-specific MR at various times during that day.

Animals were considered to be torpid when their MR fell below 75% of the resting MR at same T_a . Torpor bout duration was calculated from the time the MR remained below 75% of resting MR.

Numerical values are expressed as means \pm standard deviation (SD) for the number of individuals (n) that were measured. Body mass, mass loss over the 1-day measurements, torpor duration, and the minimum MR in individuals acclimated to different photoperiod were compared using repeated-measures ANOVA. As torpor variables were not available for the same individuals at all photoperiods tested, mean TMR, mean torpor bout length, and mean time of torpor entry for individuals that entered torpor were compared using a one-way ANOVA. Torpor occurrence was compared by a χ^2 -test.

3. Results

Body mass of bats at the beginning of MR measurements ranged from 18.0 to 25.3 g and remained stable throughout the experimental period (Table 1). Similarly, the loss of body mass over the 1-day MR measurements ranged from 2.0 to 4.9 g (to a large extent due to loss of faeces and urine) and was not significantly affected by photoperiod ($p = 0.90$).

Bats entered torpor under all photoperiods (Figs. 1 and 2). Bats usually were active for most of the night as indicated by the high and variable MR (Fig. 1). Torpor entry occurred in the early morning in the time period from just before to shortly after 'lights on' (Fig. 1A,B,D,F). When 'lights on' was considered as reference point, torpor entry occurred at -20.9 ± 32.8 min (LD 10:14, $n = 7$), -79.4 ± 138.7 min (LD 12:12, $n = 5$), and $+16.3 \pm 33.1$ min (LD 14:10, $n = 4$), but means did not differ among photoperiods ($p = 0.24$). The MR during torpor fell to $\sim 20\%$ ($\sim 50\%$ during shallow torpor) of that in resting normothermic bats. Spontaneous arousals occurred between late morning and early afternoon, and, after arousal characterised by a MR peak, bats usually exhibited a period of rest. When bats did not enter torpor, they also were active for most of the night, but MR during the light-phase did not fall below 75% of

resting MR (Fig. 1C,E). The torpor patterns in male and female bats under different photoperiods were similar. Torpor occurrence was 100% under LD 10:14 and declined somewhat to 57% under LD 14:10 (Table 1). Nevertheless, this apparent decline in torpor occurrence was not significant ($p = 0.159$).

Torpor bout length ranged from 2.8 to 11.4 h. Although mean torpor bout length of all individuals, including those that did not enter torpor and consequently had a bout length of zero, was only 66% under LD 14:10 of that under LD 10:14 (5.8 ± 2.4 h, LD 10:14; 5.6 ± 4.4 h, LD 12:12; 3.8 ± 3.6 h, LD 14:10, all $n = 7$), this apparent difference was not significant ($p = 0.55$) because of the large variance. When the mean torpor bout length of only those individuals that entered torpor was compared, values also did not differ among photoperiods ($p = 0.312$; Table 1).

The daily minimum MR ranged from 0.21 to 2.7 mL O₂ g⁻¹ h⁻¹. The apparent 2.3-fold increase in minimum MR from LD 10:14 to LD 14:10 (0.6 ± 0.27 mL O₂ g⁻¹ h⁻¹, LD 10:14; 1.02 ± 0.78 mL O₂ g⁻¹ h⁻¹, LD 12:12; 1.41 ± 0.95 mL O₂ g⁻¹ h⁻¹, LD 14:10, all $n = 7$) was not significantly different ($p = 0.21$) because of the large variance caused by some individuals not entering torpor. When the TMR of only those individuals that entered torpor was compared (Table 1), TMR values were similar among photoperiods and did not differ ($p = 0.828$).

4. Discussion

We found that *S. australis* exhibits only minor changes in torpor occurrence, duration and depth of torpor in response to photoperiod acclimation. None of the apparent physiological changes were significant, but interestingly the trend was the opposite of that expected from *S. australis* captured in the wild in different seasons.

Physiological variables measured here for *S. australis* were similar to those in previous studies. TMR in torpid individuals was reduced to ~ 20 – 50% of BMR (1.44 mL O₂ g⁻¹ h⁻¹; Geiser et al., 1996), resulting in a

Table 1
Body mass, mass loss, torpor occurrence, and torpor variables in *Syconycteris australis*

| Photoperiod | Body mass (g) | Mass loss (g) | Torpor (%) | Torpor bouts (h) | Minimum TMR (mL g ⁻¹ h ⁻¹) |
|-------------|----------------|---------------|------------|---------------------------|---|
| LD 10:14 | 21.7 \pm 2.0 | 2.8 \pm 0.3 | 100 | 5.8 \pm 2.4 ($n = 7$) | 0.60 \pm 0.27 ($n = 7$) |
| LD 12:12 | 20.5 \pm 1.9 | 2.9 \pm 0.6 | 71 | 7.9 \pm 2.6 ($n = 5$) | 0.61 \pm 0.40 ($n = 5$) |
| LD 14:10 | 19.8 \pm 1.2 | 3.0 \pm 1.1 | 57 | 6.6 \pm 0.9 ($n = 4$) | 0.74 \pm 0.47 ($n = 4$) |

Variables are means \pm 1 SD for the seven bats measured. ' n ' is shown for variables of only those individuals that entered torpor. Mass loss was measured over 23.5 h.

Values did not differ among photoperiods.

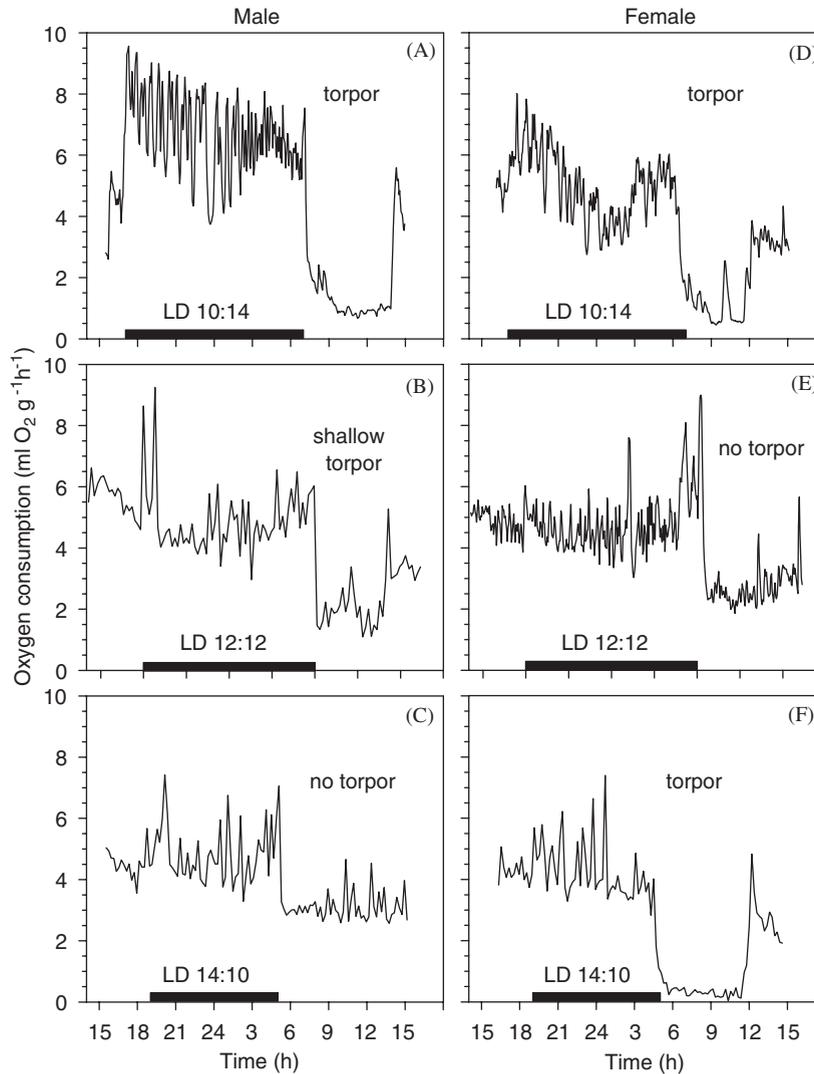


Fig. 1. Daily fluctuations of metabolic rate, measured as the rate of oxygen consumption, in an individual male and an individual female *Syconycteris australis* acclimated to different photoperiods. Torpor occurred in A, D, and F, shallow torpor in B. Bats in C and E remained normothermic (did not enter torpor). The black horizontal bars indicate the dark phase.

reduction of daily energy expenditure by ~20–30% at torpor bouts lasting longer than ~5 h (Coburn and Geiser, 1996). Interestingly, average TMR measured here under all photoperiods (Table 1) were intermediate between summer and winter TMR measured at the same T_a previously (Coburn and Geiser, 1998).

Our photoperiod acclimation experiment strongly suggests that the previously observed seasonal changes in individuals captured from the wild, with a more pronounced and longer torpor in summer than in winter (Coburn and Geiser, 1998), cannot be explained by seasonal changes in photoperiod. The trend of a somewhat less pronounced torpor in long photoperiod, as observed here, is the opposite to that in the previous

study (Coburn and Geiser, 1998), which further emphasises that photoperiod is an unlikely factor explaining previously observed seasonal pattern. There is a slight possibility that our bats in spring were refractory to a change in absolute photoperiod. However, we argue that this explanation is unlikely, because the photoperiodicity of other Australian mammals also appears to differ from high-latitude species. For example in *Antechinus stuartii*, which is sympatric with *S. australis*, exposure to natural shortening of photoperiod in autumn is associated with a decline in torpor frequency and depth (Geiser, 1988). Moreover, in contrast to many other mammals, *A. stuartii* is known to use rate of photoperiod change rather than absolute

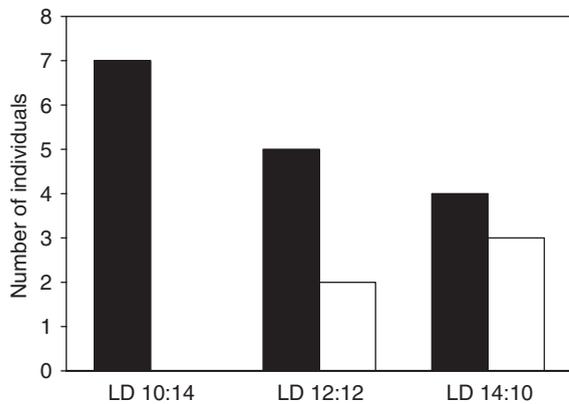


Fig. 2. Occurrence of torpor in *Syconycteris australis*. Dark bars indicate number of individuals that entered torpor, light bars number of individuals remaining normothermic.

photoperiod for seasonal adjustments of physiology (McAllan and Dickman, 1986; McAllan et al., 1991). In *Sminthopsis crassicaudata*, photoperiod acclimation during autumn and winter, when many mammals appear to be sensitive to photoperiod, did not affect torpor patterns (Holloway and Geiser, 1996). Thus, in some Australian mammals the response to photoperiod acclimation seems to differ from, for example, the Siberian hamster *Phodopus sungorus*, which is often used for the investigation of seasonal functional changes because of its predictable photoperiodic response. The lack of response to photoperiod seen here in subtropical blossom-bats, the ‘unusual’ photoperiodic response observed in some other small low-latitude mammals in the northern hemisphere and Australia (Heath and Lynch, 1983; Geiser, 1988; Körtner and Geiser, 1995; Holloway and Geiser, 1996), and the increase in diversity of mammalian taxa towards the equator, raise the question of whether the often-generalised pattern of photoperiodicity of torpor in high-latitude *P. sungorus* is rather the exception than the rule. We contend that photoperiodic data from high-latitude species are unlikely to be representative for species in other climate zones and that influences other than photoperiod must be responsible for the unusual seasonal change in torpor in subtropical *S. australis*.

A possible candidate could be change in T_a as *S. australis* is exposed to substantial seasonal thermal changes in the wild. However, the usually observed response is an increase in torpor depth and length during cold exposure (Ruf et al., 1993) not deeper and longer torpor after warm exposure as in *S. australis* captured in summer in the wild (Coburn and Geiser, 1998).

Time in captivity also could have had an effect on torpor occurrence and depth as our bats were held for almost half a year since capture. It has been demonstrated previously that torpor use can decline substan-

tially after animals have been maintained in captivity for some time (Körtner and Geiser, 1995). Thus the apparent decline in torpor occurrence may not be related to photoperiod at all, but may reflect the prolonged time in captivity.

Another potential influence on seasonal changes in torpor is food availability in the wild. Contrary to the pattern observed in high-latitude and temperate climates, where food availability generally declines in winter, the opposite is true for nectar availability on the subtropical and south-eastern Australian coast (Ford, 1979; Armstrong, 1991). In these areas, nectar, a major food source of *S. australis*, is much more abundant in winter than summer. Perhaps food availability in the field is reflected in the pattern of torpor expressed in individuals captured in different seasons.

Our findings raise the question as to why photoperiod does not appear to be used in subtropical *S. australis* as a cue for seasonally adjusting torpor patterns, as occurs in many other species. Although nectar availability on the Australian east coast generally increases in winter, which could be predicted by photoperiod, flowering and therefore nectar availability are highly variable among years (Law et al., 2000). Therefore bats must be prepared for unpredictable change in food availability (Lovegrove, 2000), must adjust torpor to match food availability, and cannot rely on a highly constant cue like photoperiod.

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