

The influence of temperature and photophase on daily torpor in *Sminthopsis macroura* (Dasyuridae: Marsupialia)

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Summary. 1. Body temperatures (T_b) and rates of oxygen consumption (\dot{V}_{O_2}) during torpor of the insectivorous marsupial *Sminthopsis macroura* were determined at different ambient temperatures (T_a) and photophases.

2. Torpor was observed in the morning and usually commenced before the onset of dawn. In the afternoon animals were normothermic. The duration of torpor was usually between 3 and 9 h with a maximum of 17 h and 15 min.

3. All animals entered torpor spontaneously at a T_a of 13 °C, but if food was withheld torpor was induced below 17 °C.

4. An increase in \dot{V}_{O_2} and T_b during torpor was observed below a T_a of about 12 °C. The body temperature below which endothermic arousal is no longer possible (the critical arousal temperature) was less than 15.1 °C.

5. An eight hour phase shift of the dark-light cycle resulted in a corresponding shift in the diurnal torpor-activity cycle and it appears that light is an important cue for the timing of daily torpor.

thermoregulate during torpor, and thus prevent body temperature from reaching a level from which endothermic arousal is not possible, is well documented in placental mammals and birds (Wyss 1932; Hainsworth and Wolf 1970) but has yet to be described for dasyurids.

The insectivorous dasyurid *Sminthopsis macroura* (syn. *larapinta*) occurs widely in semi-arid and arid areas of central and northern Australia (Morton 1983). Its field behaviour is largely unknown, but in the laboratory daily torpor occurs spontaneously from early morning to around noon (Godfrey 1968). In this study we investigate the influence of ambient temperature, photophase and food availability on daily torpor in *S. macroura*, and determine if marsupials, like placentals, regulate their body temperature during periods of torpor above a critical level.

Materials and methods

Adult stripe-faced Dunnarts (*Sminthopsis macroura*, Dasyuridae, Marsupialia) were supplied by the Arthur Rylah Institute, Melbourne and from the South Australian Museum, Adelaide. The animals were individually housed in cages provided with wood shavings and boxes containing nesting material. Water and a mixture of canned and dried pet food were available ad libitum and *Tenebrio* larvae and an egg/gelatin supplement were provided every two weeks. Under these conditions body weight remained constant with individuals ranging between 18 and 28 g. Twelve animals used for the measurements of body temperature (T_b) were maintained at a constant ambient temperature (T_a) of 19 °C with a photocycle of LD 12:12 (light 06.00 to 18.00 h). Seven of these animals were used to determine the diurnal fluctuation of T_b at $T_a = 19$ °C and food ad libitum. Measurements were taken every 8 or 12 h staggered over a 3 day period. After this daily cycle of T_b was established the animals were exposed to different T_a 's between 7 and 25 °C with food ad libitum. T_b was measured at 09.00 h, three hours after the lights went on and at 20.00 h, two hours after the lights went off; these times were assumed to represent the daily minimum and maximum. Animals were not exposed to temperatures different from $T_a = 19$ °C for more than two consecutive

Introduction

Although it is known that many small marsupials of the families Burramyidae (the pygmy possums) and Dasyuridae (marsupial insectivores and carnivores) undergo periods of torpor (see Wallis 1982; Geiser 1985), little detailed information is available from laboratory studies (Lyman et al. 1982). For example, the interactions of the major determinants for torpor in placental mammals, temperature, light and food availability, have not been determined for a marsupial. Similarly, the ability to

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days and were kept at 19 °C for three days before being exposed to a different temperature. The other five animals were used to determine the influence of light on the timing of daily torpor. These were kept at $T_a = 18$ °C with food ad libitum. They were exposed to an eight hour phase advancement of the dark cycle (darkness 18.00–06.00 h was advanced to 10.00–22.00 h) for 5 days after which the original light regime was reintroduced. T_b measurements were taken at the times of the daily maximum and minimum as determined by the previous experiments. Body temperatures were determined by inserting a 0.5 mm diameter thermocouple probe rectally for 25 mm and reading from a Comark Electronic Thermometer. All thermocouples were calibrated against a mercury thermometer traceable to a National Standard. The six animals used for the oxygen consumption measurements were held in an outdoor facility and thus were exposed to natural day length and temperature cycles. Rates of oxygen consumption (\dot{V}_{O_2}) were measured over a daily cycle at constant air temperatures of 6.5, 10, 14.2 and 17 °C both in winter (June) and summer (November–December). The effect of a reduction of T_a on \dot{V}_{O_2} during torpor was also determined. Food and water were not available to the animals during the period of these measurements. A Servomex model OA 184 paramagnetic oxygen analyser was used together with a Rikadenki Potentiometric Recorder. \dot{V}_{O_2} was determined from the difference between the oxygen content in two parallel circuits, one a room air reference and the other drawing air through a 3 l respirometer chamber containing the animal. Flow rates which kept the ambient oxygen level in the animal chamber above 20% were maintained through calibrated rotameters. All gas values were corrected to dry volumes under standard conditions of temperature and pressure (STPD). For the calculation of mass specific \dot{V}_{O_2} during the prolonged measurement periods, the animals were weighed before and after the experiment and body masses interpolated assuming a constant rate of loss. All measurements were conducted in a quiet controlled temperature room which was acoustically remote from the recording equipment. A video camera was used to observe the animals during the experiment periods. Body temperature and \dot{V}_{O_2} criteria ($T_b < 31$ °C; $\dot{V}_{O_2} < 75\%$ of resting values; see Hudson and Scott 1979) were applied to define periods of torpor. A Students *t*-test was used for comparisons of paired observations.

Results

The typical pattern of \dot{V}_{O_2} of *S. macroura* showed strong diurnal variations (Fig. 1). From a resting period at about 18.00 h with a \dot{V}_{O_2} of 3.81 l O₂/(kg h), \dot{V}_{O_2} declined over the following 30 min and it appeared that the animal was entering torpor. However, after the lights were switched off \dot{V}_{O_2} increased to 6.5–7.7 l O₂/(kg h), a level consistent with the activity period. At midnight the animal entered torpor and \dot{V}_{O_2} fell to a minimum level of 0.19 l O₂/(kg h), which was maintained for about 9 h. This is only 16% of the standard metabolic rate (SMR) predicted from the equation of MacMillen and Nelson (1969) for a dasyurid of body mass 18.5 g. Just prior to the time T_b was measured (09.55 h), \dot{V}_{O_2} was slightly increased (0.38 l O₂/(kg h) above the minimum values observed earlier in the morning, but the T_b was still 20.8 °C which is 4.1 °C above the ambient level

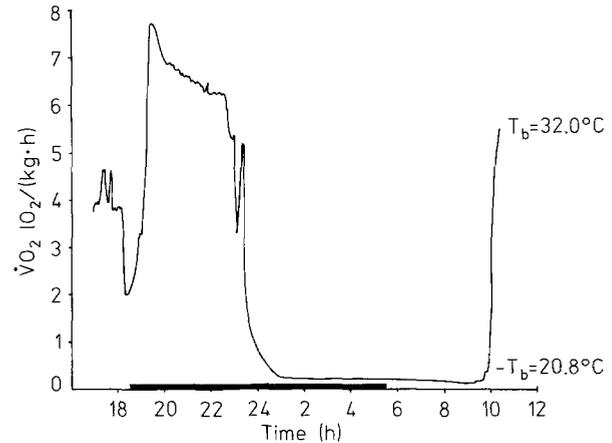


Fig. 1. The rate of oxygen consumption (\dot{V}_{O_2}) of an individual *S. macroura* measured over an 18-hour period at a constant ambient temperature of 16.7 °C. The abscissa represents the local time and the dark bar indicates the period of darkness

of 16.7 °C. After the disturbance caused by the measurement of T_b , \dot{V}_{O_2} increased rapidly and after a period of 22.5 min T_b rose to 32.0 °C. This results in an arousal rate of 0.5 °C/min. In experiments where T_b was not measured the animals aroused spontaneously in the late morning or afternoon. This description is typical of a torpor cycle of *S. macroura* and while the period of torpor was usually between 3 and 9 h at temperatures above 10 °C, a maximum of 17.25 h was observed in one individual. Below 10 °C, shorter torpor periods of 1–4 h occurred.

The minimum steady state values of \dot{V}_{O_2} during torpor, determined over at least 30 min at different ambient temperatures in winter as well as summer, are compared in Fig. 2. The lowest mean value (0.23 l O₂/kg h) was observed at about 17 °C. An increase ($P < 0.025$) in \dot{V}_{O_2} to 0.48 l O₂/kg h occurred at 10 °C when compared with the combined values at 17 and 14 °C indicating a thermoregulatory increase in \dot{V}_{O_2} at ambient temperatures between 10 and 14 °C. A marked variation in \dot{V}_{O_2} occurred at an ambient temperature of 6.5 °C and the mean value was 1.53 l O₂/kg h.

A similar increase in \dot{V}_{O_2} could be induced by experimentally decreasing T_a after a 2 hour torpor period at a previous T_a of 16 °C. \dot{V}_{O_2} remained at a constant level of 0.24 l O₂/(kg h) as temperature decreased (Fig. 3). When T_a reached 12.4 °C, \dot{V}_{O_2} increased about two fold to a new plateau of 0.43 l O₂/(kg h) at a T_a of 12 °C. When T_a was further decreased to 10.5 °C, \dot{V}_{O_2} was increased to 0.57 l O₂/(kg h), a value close to the \dot{V}_{O_2} measured at a constant T_a of 10 °C (Fig. 2). An increase in T_a thereafter resulted in a decrease in \dot{V}_{O_2} . The

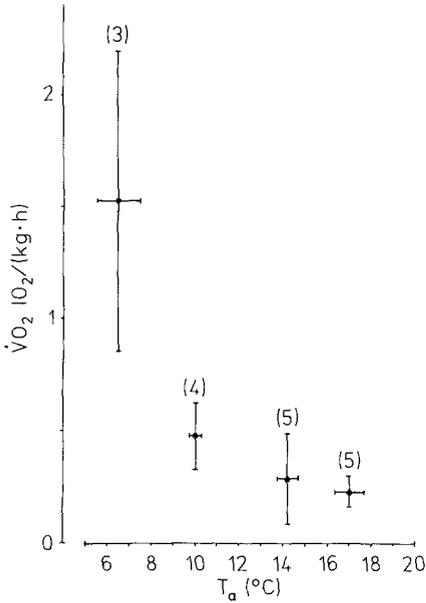


Fig. 2. The minimum rate of oxygen consumption (\dot{V}_{O_2}) during the daily cycle of torpid *S. macroura* exposed to different ambient temperatures (T_a). The points represent the mean \pm standard deviation of the numbers of individuals shown in brackets

reduction in \dot{V}_{O_2} following heating indicates that the increase in \dot{V}_{O_2} below 12.4 °C was largely due to thermoregulation rather than arousal. The animal began to arouse spontaneously at 11.15 h.

The marked daily fluctuations of the body temperatures of seven *S. macroura* kept at 19 °C with a photocycle of LD 12:12 (light 06.00 to 18.00 h) are shown in Fig. 4. The highest body temperatures occurred at night between 20.00 and 24.00 h and ranged between 36.8 and 38.8 °C. At 04.00 h T_b declined to 35.5 °C and a further decrease to 32 °C was observed at 08.00 h. At this time the variation between individual animals was most marked. The body temperatures at 12.00 h were increased to low normothermic levels at about 35.5 °C. T_b was further increased in the late afternoon, after the onset of darkness and throughout the activity period.

This daily T_b cycle of *S. macroura* could be modulated by exposing the seven animals to temperatures between 7 and 25 °C (Fig. 5). The body temperatures in the morning (09.00 h), which were assumed to represent the daily minima, were strongly temperature dependent. The tendency of the animals to enter torpor increased with decreasing temperature. The mean daily T_b minimum of *S. macroura* was about 35 °C at T_a 25.0 °C and it decreased steadily to about 24 °C at T_a 13.0–15.6 °C. The decrease was due to both lower T_b 's in torpid animals at lower T_a 's and a larger proportion of animals in torpor. When T_a was further decreased

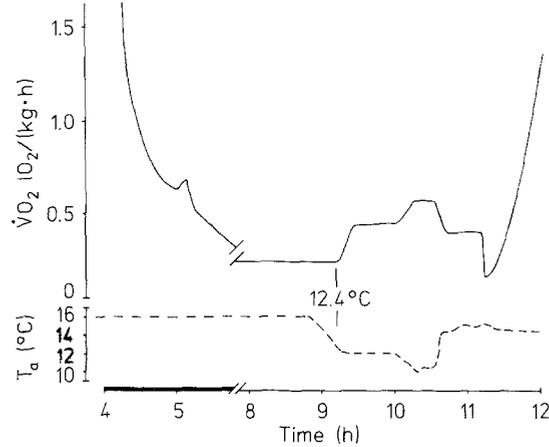


Fig. 3. The rate of oxygen consumption (\dot{V}_{O_2}) of an individual *S. macroura* exposed to changing ambient temperature. The \dot{V}_{O_2} between 06.00 and 07.45 h was constant and was omitted. The temperature (T_a) is indicated by a dashed line, \dot{V}_{O_2} by a solid line. The T_a at which the increase in \dot{V}_{O_2} occurred is indicated. The abscissa represents the local time and the dark bar indicates the period of darkness

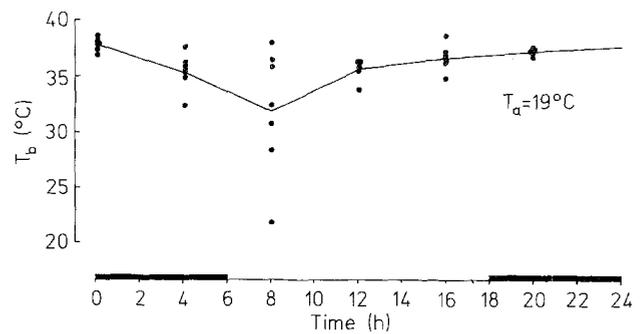


Fig. 4. The daily fluctuations of body temperature (T_b) of seven *S. macroura* at an ambient temperature (T_a) of 19.0 °C. Food was available ad libitum. The points represent individual body temperatures. Measurements were taken every 8 or 12 h staggered over a 3 day period. The abscissa represents the local time and the dark bars indicate the periods of darkness

to 11.2 and 9.3 °C, the T_b minima were increased to about 28 °C because three of seven animals remained normothermic. At 7.1 °C, the mean T_b was similar to that at 15.6 and 13.0 °C. The difference between the mean T_b minima and T_a (ΔT) ranged between 9.8 and 12.4 °C at a T_a above 18.5 °C. The smallest ΔT was 8.4 °C and occurred at a T_a of 15.6 °C. Below 13.0 °C, ΔT was increased to 17.0 °C (T_a = 11.2 °C), 18.2 °C (T_a = 9.3 °C) and 15.8 °C (T_a = 7.1 °C).

The mean T_b during torpor independent of the time of day (Fig. 5) ranged from 24 to 27.2 °C at ambient temperatures above 18 °C. At ambient temperatures less than 16 °C, T_b declined to values between 21.3 and 23.3 °C. Overall the mean value

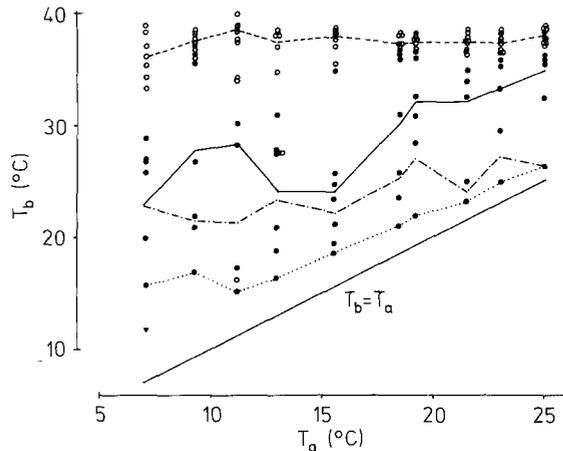


Fig. 5. The daily fluctuations of body temperature (T_b) of seven *S. macroura* exposed to different ambient temperatures (T_a). The photocycle was LD 12:12 and food was available ad libitum. Measurements were taken at 09.00 h three hours after the lights went on and at 20.00 h two hours after the light went off. The symbols indicate the mean T_b of normothermic animals at 20.00 h (\circ —); measurements at T_a 7.1 °C were taken at 11.30 h (\bullet —), the mean T_b at 09.00 h (\bullet —), the mean T_b of animals in torpor at both times (— · — · —), the individual T_b minima (\bullet · · · · ·), and an animal in hypothermia (\blacktriangledown , lower left)

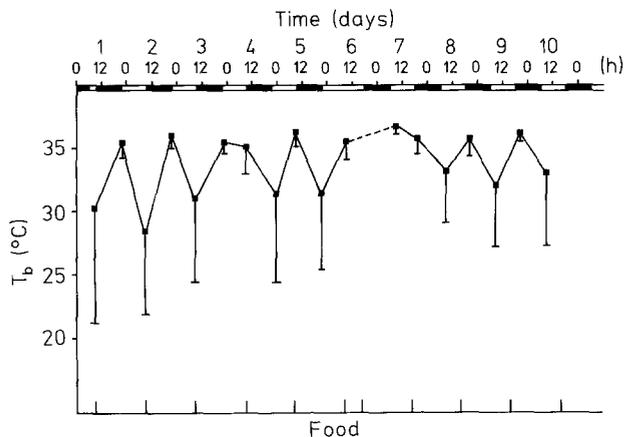


Fig. 6. The daily fluctuations of body temperature (T_b , mean with SD) of five *S. macroura* at $T_a=18$ °C, exposed to an altered photophase. The abscissa represents the local time and the numbers of days. The dark bars indicate the periods of darkness. The times when food was exchanged are shown as vertical stroke

of T_b during torpor was not strongly effected by T_a at the measured range and appeared to be constant at ambient temperatures below 16 °C.

The lowest individual body temperatures measured at a T_a higher than 11.2 °C (at 09.00 h) were 1.2 to 3.9 °C above T_a , with the higher ΔT values at the lower temperatures (Fig. 5). At 9.3 and 7.1 °C, ΔT was increased to 7.6 and 8.7 °C, respectively. Thus while the increase in ΔT for the individual T_b minima occurred below $T_a=11.2$ °C, ΔT

for the mean daily T_b minima increased below $T_a=13.0$ °C. The lowest T_b measured during torpor was 15.1 °C. One animal at a T_a of 7.1 °C had a T_b of 11.6 °C but was unable to arouse after disturbance by the T_b measurement and was not included in the mean torpor values. This individual was however able to arouse after partial rewarming and survived.

The assumed daily T_b maxima measured at 20.00 h were largely independent of ambient temperature. The mean T_b over the ambient range of 9.3 to 25 °C varied from 37.2–38.4 °C if the single incidence of torpor at T_a 11.2 and 13.0 °C is excluded. The maxima at 7.1 °C were measured post arousal at 11.30 h in order to reduce the cold stress. These measurements show a slightly lower mean value of 36.0 °C.

The diurnal T_b cycle of *S. macroura* can be altered by the photophase (Fig. 6). After the advancement of the dark cycle from 18.00–06.00 h to 10.00–22.00 h, the previous daily torpor-activity cycle with 2 to 3 of the 5 animals in torpor at around 09.00 h was maintained for further two days. On day four the animals adjusted their daily cycle to the new light regime, remained normothermic at about 09.00 h and entered torpor before midnight for two consecutive days (day 4 and 5). After five days exposure to reversed light the original light regime was reintroduced. This resulted in no incidence of torpor on day 7 at the measured times and body temperatures remaining at around 36 °C. On day 8 the animals already had returned to their original daily cycle with torpor in the early morning and activity in the evening; this pattern was maintained until day 10. Fig. 6 also shows that the time at which the old food was removed and new food was supplied (after the T_b measurements) did not influence the timing of torpor. On days 2 and 3 the daily peak in T_b occurred about 12 h after feeding and torpor about 24 h after feeding. On days 4, 5, 8, 9 and 10 (Fig. 6) this situation was reversed and torpor was observed about 12 to 14 h after feeding.

Discussion

The diurnal cycle in body temperature of *S. macroura* is influenced by temperature, food and photophase. In summer and winter animals entered torpor at ambient temperatures below 17 °C when no food was available. For some individuals spontaneous torpor (when food was provided) occurred in the morning at T_a as high as 25 °C, but for others ambient temperatures as low as 13 °C were required to induce torpor. At T_a below 13 °C, the

tendency to enter spontaneous torpor was reduced which was most likely due to a reduced torpor duration. A similar reduction in the number of animals entering torpor below a specific temperature was previously reported for *Peromyscus* spp. (Morhardt 1970). Maximum body temperatures were observed in the evening (20.00 h), the time of the peak activity period of the species (O'Reilly et al. 1984), however at a T_a of 11.2 and 9.3 °C two animals which had been active at 16.00 h were observed in torpor. Godfrey (1968) observed that although the highest mean T_b occurs after 18.00 h, some individuals had lower body temperatures of 32 to 33 °C even at relatively high T_a of 21 °C. The maximum duration of torpor (17.25 h) is almost double that reported for *S. macroura* (Godfrey 1968) and even longer when compared with values from most other dasyurids (see Wallis 1982).

It is clear from the present study that T_b is regulated above a critical temperature in *S. macroura* and although an increased metabolic rate at 8 and 11 °C when compared with the values at 16 °C was reported for torpid sugar gliders, *Petaurus breviceps* (Fleming 1980) and a murine opossum, *Marmosa* sp. (Morrison and McNab 1962) respectively, the temperature at which the increase occurs has not been determined. The thermoregulatory ability of birds and placental mammals during torpor has been reported in a number of cases (e.g. Wyss 1932; Hainsworth and Wolf 1970; Frey 1980; Heldmaier and Steinlechner 1981). The lowest T_b measured in torpid *S. macroura* in this investigation was 15.1 °C; considerably lower than the reported 18 to 21 °C for several other dasyurid species (see Wallis 1982). However recent studies (Geiser et al. 1984, and unpublished) revealed T_b minima around 13.5 to 15 °C for *S. murina* and *S. crassicaudata*, suggesting that at least some dasyurid species may be able to arouse from body temperatures below 15 °C. Critical arousal temperatures in the range 12 to 20 °C have been reported for tenrecs in Madagascar (Kayser 1961) and for several North American rodents (Hudson 1965; Tucker 1965; Morhardt 1970; Gaertner et al. 1973). In contrast with *Peromyscus* spp. (MacMillen 1965; Morhardt and Hudson 1966), *S. macroura* was able to survive T_b 's a few degrees below the critical arousal temperature if partially rewarmed.

In winter, the average daily T_a minimum in the distribution range of *S. macroura* is between 3 and 9 °C with maxima as high as 18–24 °C (Climate of Australia 1983). This mild regime suggests potential cold exposure for only a few hours in the early morning, the time the animals enter torpor in the laboratory, and presumably shelter in the

wild. Basking, a common observation in dasyurids in captivity and in the field, would allow them to conserve energy during the second non-active but normothermic period in the afternoon.

The relatively slow arousal rates previously reported for some marsupials when compared with placentals such as hibernating bats (Eisentraut 1934; Kulzer 1965), birch mice (Johansen and Krog 1959) or dormice (Eisentraut 1929), has been related to their apparent lack of brown fat. However, the arousal rates of several small placental heterotherms of comparable body size are around 0.5 °C/min (e.g. Hudson 1965; Morhardt 1970; Gaertner et al. 1973), similar to those for *S. macroura* (this study) and *S. crassicaudata* (Godfrey 1968). Even higher arousal rates of 0.6 to 0.7 °C/min have been observed for the marsupials *Marmosa* sp. and *Cercartetus concinnus* (Morrison and McNab 1962; Geiser 1985). Considering the small amount of data available for marsupials and the large inter-specific variation in the arousal rates found in placental mammals, a significant difference may not exist between the two groups. It appears that the rate of arousal is an adaptation for the requirements of a particular species and since slow rewarming is energetically cheaper and without the excess of a massive \dot{V}_{O_2} overshoot, it may be well suited for daily torpor.

There appears to be general agreement that the daily rhythms of T_b and \dot{V}_{O_2} in mammals which enter torpor are endogenous (see Rath and Kulzer 1976) and we have no evidence that this does not hold for *S. macroura*. However, the transient time between the setting of a new light regime and full response by the animals was only three days, and a similar pattern emerged for the reversal to the former regime. It has been previously shown in *S. macroura* that re-entrainment of the activity cycle to reverse light regime is particularly rapid (O'Reilly et al. 1984), but we do not know if this facility is common to other small marsupials.

This study shows that ambient temperature and food availability are the primary determinants of torpor in *S. macroura* but the light/dark cycle is used as a cue for the timing of the process. In this marsupial daily torpor does not differ qualitatively from that described in placental mammals and hence represents another example of a physiological convergence between the two groups.

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