

DAILY TORPOR IN A PREGNANT COMMON BLOSSOM-BAT (*SYCONYCTERIS AUSTRALIS*: MEGACHIROPTERA)

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TORPOR and reproduction in mammals are widely viewed as mutually exclusive processes. For most mammals, different energetic and hormonal demands appear to require a temporal sequence of torpor and reproduction within the yearly schedule. Torpor is characterised by a pronounced fall in body temperature and metabolic rate, which results in an overall reduction of energy expenditure (Geiser and Ruf 1995) and in most mammals occurs during the non-reproductive season (Goldman *et al.* 1986; Barnes 1996). Reproduction, on the other hand, requires an increase of energy expenditure for acquiring, processing and transfer of nutrients to the growing offspring (Hoffman 1964; Goldman *et al.* 1986; Thompson and Nicoll 1986; Kenagy *et al.* 1989; Barnes 1996).

Paradoxically, members of a few mammalian taxa, including echidnas (Monotremata), some small dasyurids and feathertail gliders (Marsupialia), and some small insectivores and microchiropterans (Placentalia), are known to display torpor even while pregnant and/or lactating, in spite of the apparently high energy demands (Geiser 1996). Because information about the extent of torpor use in reproductive individuals among the various mammalian taxa is presently limited, we report here observations made during a study on torpor by common blossom-bats (*Syconycteris australis*, body mass 18 g) that extend our knowledge on torpor use during reproduction to a new mammalian suborder.

Syconycteris australis are small, nectar and pollen eating bats of the suborder Megachiroptera that are found along the east coast of Australia north of Myall Lakes (Law 1994a,b). They roost solitarily in foliage within rainforests (Law 1993) and therefore gain no thermal benefits from clustering.

Bats were captured in winter using mist nets on the subtropical north coast of New South Wales, Australia (30° 22' S, 153° 06'E). Captured bats (5 females 3 males) were transferred to the University of New England where they were held in a large holding room (3.5 x 2.1 x 3.0 m) that provided enough space for flight. The room was fitted with leafy branches and wide plastic mesh for roosting and for attachment of feeders to provide *ad libitum* food (Geiser *et al.* 1996). Ambient temperature was maintained at $21 \pm 1^\circ\text{C}$ and relative humidity above 40%. The photoperiod was maintained at 10L:14D (lights on 0700 - 1700 hrs). After 4 weeks of acclimation to captivity, metabolic rate was measured as rate of oxygen consumption (directly proportional to energy expenditure), for about 1 day to test whether and to what extent animals used torpor. The ambient temperature was maintained at 18°C, food and water were not provided during these measurements, and each bat was measured once. The respirometry equipment used has been described previously (Geiser *et al.* 1996).

Six bats (3 females, 3 males) entered torpor during measurements of oxygen consumption at an ambient temperature of 18°C. Bats were usually active for most of the night and metabolic rates ranged from values of about $4 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ during periods of rest to maxima of about $7 - 9 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ during activity (Fig. 1). However, near the time of lights on in the morning, metabolic rates dropped precipitately and the bats entered torpor. The mean minimum metabolic rate during torpor was $0.60 \pm 0.29 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (SD) and the six bats remained torpid for an average of 6.3 ± 2.2 hrs. Spontaneous arousal from torpor, characterised by an overshoot of metabolic rate, usually occurred in the early afternoon (Fig. 1).

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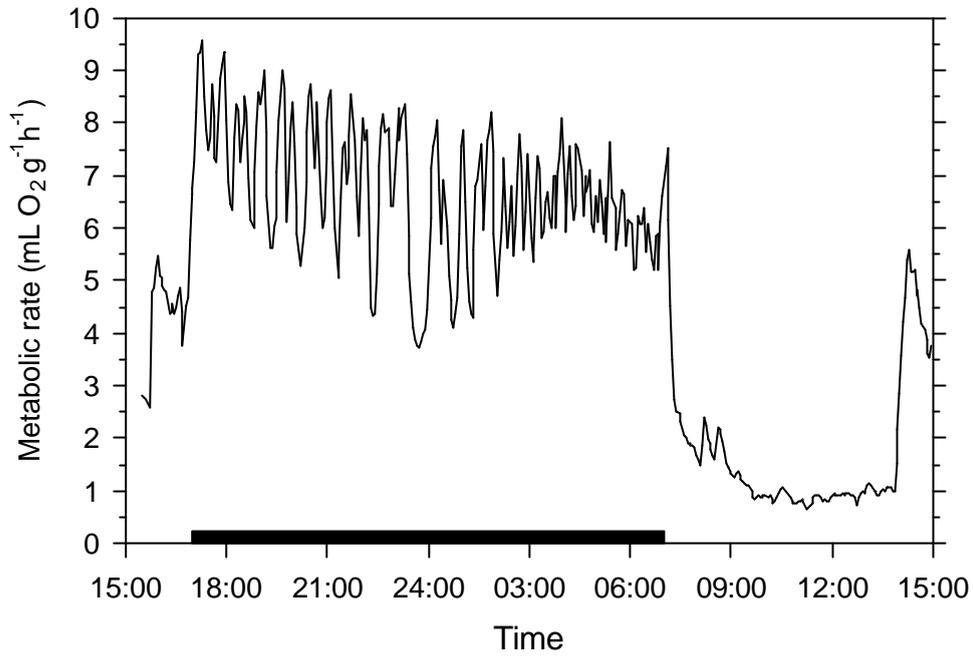


Fig. 1. Oxygen consumption of a male *S. australis* measured at 18°C. The black bar indicates the period of darkness. Note the decline of oxygen consumption around lights on and the spontaneous arousal around 1400 hrs. The torpor pattern shown is representative of that in the other six non-pregnant bats.

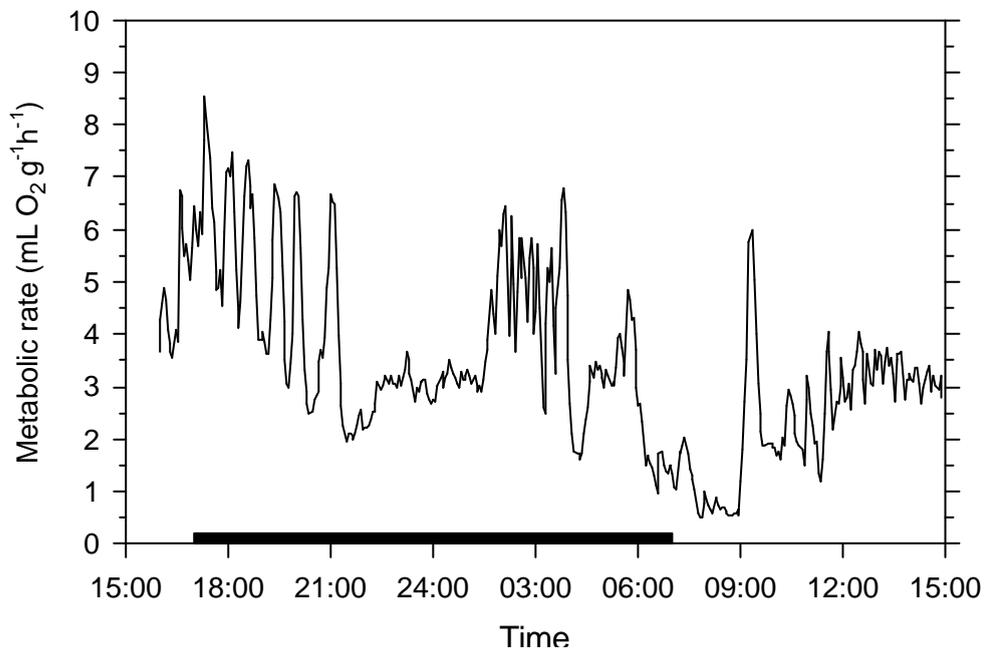


Fig. 2. Oxygen consumption of a pregnant *S. australis*, measured at 18°C. The black bar indicates the period of darkness. Note the decline of oxygen consumption in the morning and the overshoot during arousal at about 0900 hrs.

The remaining two bats were pregnant during our measurements. Both bats gave birth in captivity soon after the measurements. One of these pregnant females entered torpor (Fig. 2). Its minimum metabolic rate during torpor ($0.60 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was identical to the mean of the non-pregnant bats, but the bat remained in torpor for only about 3 hours, roughly half the time of the non-pregnant bats. In contrast to the other seven bats, the second pregnant bat did not enter torpor and its minimum metabolic rate was $2.5 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$.

Our study shows that yet another species of a further mammalian suborder is capable of entering torpor during pregnancy. However, as in tenrecs (Insectivora: Stephenson 1993, Stephenson and Racey 1993), the proclivity towards torpor in the pregnant bats seemed to be reduced, as one individual did not enter torpor and the torpor bout observed in the second pregnant female was shorter than in the other, apparently non-reproductive, bats. Nevertheless, the minimum metabolic rate of the torpid, pregnant bat was reduced to about 46% of the basal metabolic rate of *S. australis* in winter (Coburn and Geiser 1998). The low minimum metabolic rate of the torpid, pregnant bat was similar to that of the non-reproductive bats, suggesting that its body temperature during torpor fell to about 22°C (Coburn and Geiser 1998).

The observation of torpor in a pregnant *S. australis* raises the question how mammals, like ground squirrels, marmots and hamsters, which appear to be strictly homeothermic during the reproductive season (Hoffman 1964; Goldman *et al.* 1986; Barnes 1996), differ from those that show torpor when reproductive. It appears that mammals that produce few or small offspring or spread the reproductive effort and the associated metabolic costs over a long time, like monotremes and many marsupials, may display torpor during the period of reproduction. Monotremes and small marsupials have very small neonates ($< 1\%$ of maternal mass). Moreover, the species of monotremes and marsupials observed in torpor also have slow developmental rates (Geiser 1996) and thus small increases of energy expenditure. At first glance bats do not appear to fulfil these criteria because they have relatively large neonates (13–40% of maternal mass; Ransome 1990). However, bats usually have single young and growth of foetal and young bats is slow, as in many marsupials and monotremes, and energy expenditure at least during gestation is much lower than, as for example, in small rodents (Racey and Speakman 1987; Nicoll and Thompson 1987; Kurta *et al.* 1989, 1990). Tenrecs also have low metabolic rates during much of gestation the time they may enter torpor (Thompson and Nicoll 1986).

It is also evident that species in which torpor has been observed during the reproductive period are insectivorous or nectarivorous. Abundance of most insects (and other arthropods) and nectar strongly fluctuate (McFarland 1985; Paton and Turner 1985; Law 1994a). Occurrence of torpor during reproduction may thus be linked to the food consumed by the mammals. Species that have access to relatively predictable food supplies during the reproductive season, like many herbivorous rodents, may be able to adopt strict homeothermy while pregnant or lactating. In contrast, species with relatively unpredictable, weather-dependent food supplies during the reproductive season may be better off employing torpor for only a small extension of the reproductive period.

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