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Short communication

Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia)

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Mammalian reproduction is an energetically expensive process. In addition to normal energetic costs for maintenance, locomotion and thermoregulation, reproduction requires energy expenditure to acquire and process nutrients, produce milk, and transferring nutrients to growing offspring with the consequent increase in metabolic rate (MR) (Farmer 2003). Torpor in heterothermic mammals, on the other hand, results in an overall reduction of energy expenditure and is characterised by a pronounced fall in body temperature and MR (Geiser and Ruf 1995). For most mammals, these different energetic, and also hormonal, demands appear to require a temporal sequence of reproduction and torpor within the yearly schedule and thus, torpor usually occurs during the non-reproductive season (Goldman et al. 1986; Barnes 1996; Stamper et al. 1998; Mzilikazi and Lovegrove 2002). Not surprisingly then, there is a widely held view that torpor and reproduction in mammals are mutually exclusive processes.

Nevertheless, members of a few mammalian taxa, including echidnas (Monotremata), some small dasyurids and feathertail gliders (Marsupialia), and some small insectivores and bats (Placentalia), are known to enter torpor while pregnant and/or lactating (Racey 1973; Morton 1978; Geiser 1996; Chruszcz and Barclay 2002; Willis 2005). It appears that species with small litters or offspring or those that spread the costs associated with reproduction over a long time, may be able to enter torpor during reproduction. However, information on torpor by reproductively active mammals is limited and is currently restricted to only a few of the large number of known heterothermic mammals.

We tested whether marsupial dunnarts, *Sminthopsis macroura*, a small species (~25 g) of the family Dasyuridae (Fig. 1) can enter torpor while reproductively active. *S. macroura* is insectivorous, has a slow rate of development, and lives in the arid and semi-arid area of inland Australia where conditions of limited food and water availability, which promote torpor use, occur regularly (Godfrey 1969; Geiser et al. 1998). A similar-sized closely related species (*S. crassicaudata*) with similar thermal and developmental biology has been observed in torpor in the field while lactating (Morton 1978). *S. macroura* is therefore suitable for addressing the question whether torpor may be employed during reproduction.

We studied 12 adult, female *S. macroura* (body mass 24.0 ± 3.0 g) that were captive-bred at the University of New England in Armidale. Individual reproductive condition

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Fig. 1. A stripe-faced dunnart, *Sminthopsis macroura*.

was classified following McAllan et al. (1991). When exhibiting oestrus, each female was paired with a male for the duration of the oestrous period. Of the 12 individuals studied, two did not exhibit oestrous cycles during the reproductive season, two were paired with males at the time MR measurements were conducted, and the remaining eight exhibited oestrous cycles during the reproductive season and were paired with males prior to MR measurements. We did not know at the time of measurements whether or not the animals were pregnant; this was determined after the measurements during weekly assessment of reproductive condition. When not paired for mating, dunnarts were maintained individually in cages as described in Geiser et al. (1998) under the natural photoperiod of Armidale at an ambient temperature (T_a) of 20 °C. Cages were cleaned weekly when animals were weighed and reproductive condition assessed. To determine whether or not individuals entered torpor, the MR of each animal was measured as the rate of oxygen consumption once over 23–24 h (Geiser et al. 1998). Food and water were not provided and T_a was 16.8 ± 0.5 °C. These measurements were also used to quantify minimum MR during torpor (TMR), and average daily MR (ADMR). Torpor was defined as MR falling below 75% of the resting MR at the same T_a and torpor bout duration as the time period when MR was $<75\%$ resting MR. Measurements were conducted between late July and mid-September (late winter/early spring) within the normal reproductive season for the species (Godfrey 1969). Numerical values are presented as mean ± 1 standard deviation (SD) for "n", the number of individuals.

Of the 12 dunnarts measured, 11 were not pregnant. Ten of these individuals entered torpor and one remained normothermic (Fig. 2). The 12th dunnart, the lightest individual measured (19.2 g), was pregnant during our measurements. This individual entered torpor (Fig. 2A) and gave birth approximately 9 days after the measurement.

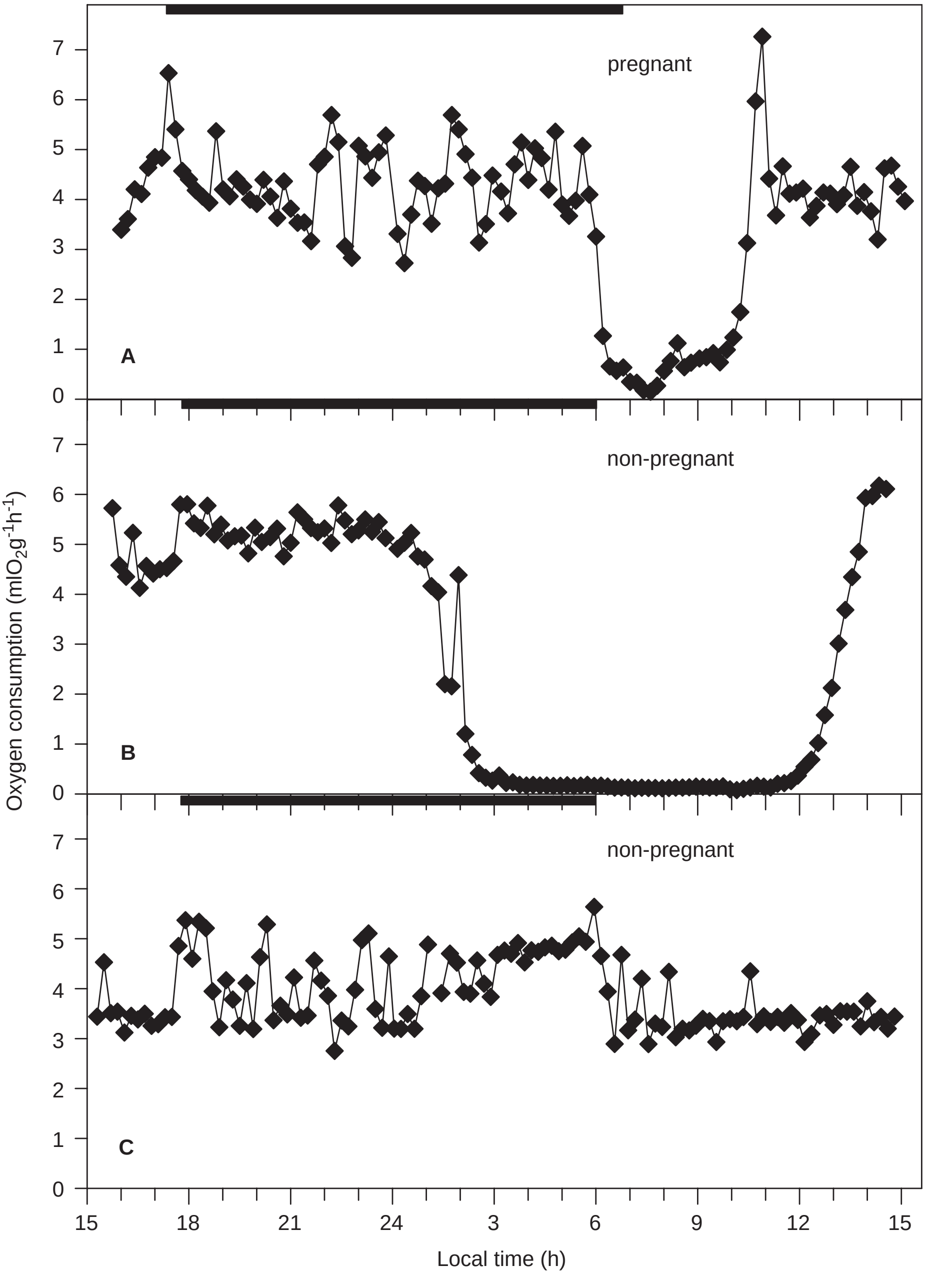

Fig. 2. Oxygen consumption of female dunnarts (*Sminthopsis macroura*) measured over 1 day at 16.8 °C. Female (A) was pregnant and entered a ~4 h torpor bout lasting from ~06:00 to ~10:00 h, female (B) was non-pregnant and entered a ~10 h torpor bout lasting from ~02:00 to ~12:30 h, and female (C) was non-pregnant and the only individual that remained normothermic. The black bar indicates the period of darkness. The torpor pattern shown for the non-pregnant dunnart (B) was one of the longest observed.

As the gestation period in this species is ~12.5 days (Godfrey 1969), the female had completed ~30% of pregnancy on the day she entered torpor. Its minimum TMR ($0.23\,\mathrm{ml\,O_2\,g^{-1}\,h^{-1}}$) was even less than the mean TMR of non-pregnant animals ($0.32 \pm 0.35\,\mathrm{ml\,O_2\,g^{-1}\,h^{-1}}$, $n = 10$), but the pregnant dunnart only remained in torpor for 4.05 h, somewhat shorter (65%) than the average torpor bout length of the non-pregnant individuals (6.25 ± 2.96 h). The ADMR of the pregnant female ($31.7\,\mathrm{kJ\,day^{-1}}$) was among the lowest measured in the non-pregnant females that entered torpor ($36.5 \pm 5.5\,\mathrm{kJ\,day^{-1}}$), and the ADMR of all individuals entering torpor was lower than that of the individual remaining normothermic ($49.6\,\mathrm{kJ\,day^{-1}}$). The pregnant female raised two young successfully, weaning them about 70 days after birth as expected (Godfrey 1969).

Our study documents another mammalian species capable of entering torpor during pregnancy. While the general torpor variables of this female were similar to that in the non-pregnant individuals, it remained in torpor for a shorter period than most of the non-pregnant individuals. Nevertheless employing torpor substantially reduced its ADMR and consequently food and water requirements. As the minimum TMR of the pregnant dunnart was similar to that for non-pregnant dunnarts, we estimate from the body temperature–ambient temperature differential during torpor for the species (Geiser et al. 1998) that its minimum body temperature was about 20 °C.

The observation of torpor in a pregnant dunnart raises the question of how mammals, which appear to be strictly homeothermic during the reproductive season (e.g. ground squirrels, marmots and hamsters) (Goldman et al. 1986; Barnes 1996; Mzilikazi and Lovegrove 2002), differ from those that exhibit torpor when reproductive. It appears that mammals with small litters or individual offspring or those who spread the reproductive effort and the associated metabolic costs over a long time, like monotremes, many marsupials, insectivores and bats may display torpor during the period of reproduction (Racey 1973; Geiser 1996). Thus it appears that a low MR during parts of the reproductive season is one of the traits required for torpor expression during pregnancy or lactation.

Species for which torpor has been observed during the reproductive period are also insectivorous or nectarivorous. Abundance of most insects (and other arthropods) and nectar fluctuate (Csada and Brigham 1994; Law 1994). 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 may improve fitness via the ability to use torpor. What remains to be resolved is the relative importance of reproduction and diet in determining torpor expression during reproduction.

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