

# 33 Torpor in marsupials: recent advances

FRITZ GEISER<sup>1\*</sup>, NEREDA CHRISTIAN<sup>1</sup>, CHRISTINE E. COOPER<sup>1,2</sup>, GERHARD KÖRTNER<sup>1</sup>, BRONWYN M. McALLAN<sup>1,3</sup>, CHRIS R. PAVEY<sup>1,4</sup>, JAMES M. TURNER<sup>1</sup>, LISA WARNECKE<sup>1</sup>, CRAIG K. R. WILLIS<sup>1,5</sup> & R. MARK BRIGHAM<sup>1,6</sup>

<sup>1</sup>Zoology, University of New England, Armidale NSW 2351, Australia

<sup>2</sup>Environmental Biology, Curtin University of Technology, Perth WA 6845, Australia

<sup>3</sup>Physiology, University of Sydney, Sydney NSW 2006, Australia

<sup>4</sup>Biodiversity Conservation, NRETA, Alice Springs NT 0871, Australia

<sup>5</sup>Biology, University of Winnipeg, Winnipeg MB, R3B 2E9, Canada

<sup>6</sup>Biology, University of Regina, Regina SK, S4S 0A2, Canada

\*Author for correspondence: fgeiser@une.edu.au

## Abstract

We report new findings about torpor in marsupials with regard to three energy-demanding processes: (i) development and growth, (ii) reproduction, and (iii) rewarming. Young marsupials use torpor extensively after they develop endothermy, and torpor is generally deeper and longer than in the same individuals when they reach adult size. Adult marsupials also employ torpor during pregnancy and/or lactation to reduce energy expenditure and perhaps to store fat for later use. Moreover, to enhance the energy-conserving potential of torpor, desert marsupials bask during arousal to minimise energy costs of rewarming. We show that the functions of torpor extend beyond merely reducing energy expenditure during food shortages and that torpor can save substantial amounts of energy even during the rewarming process.

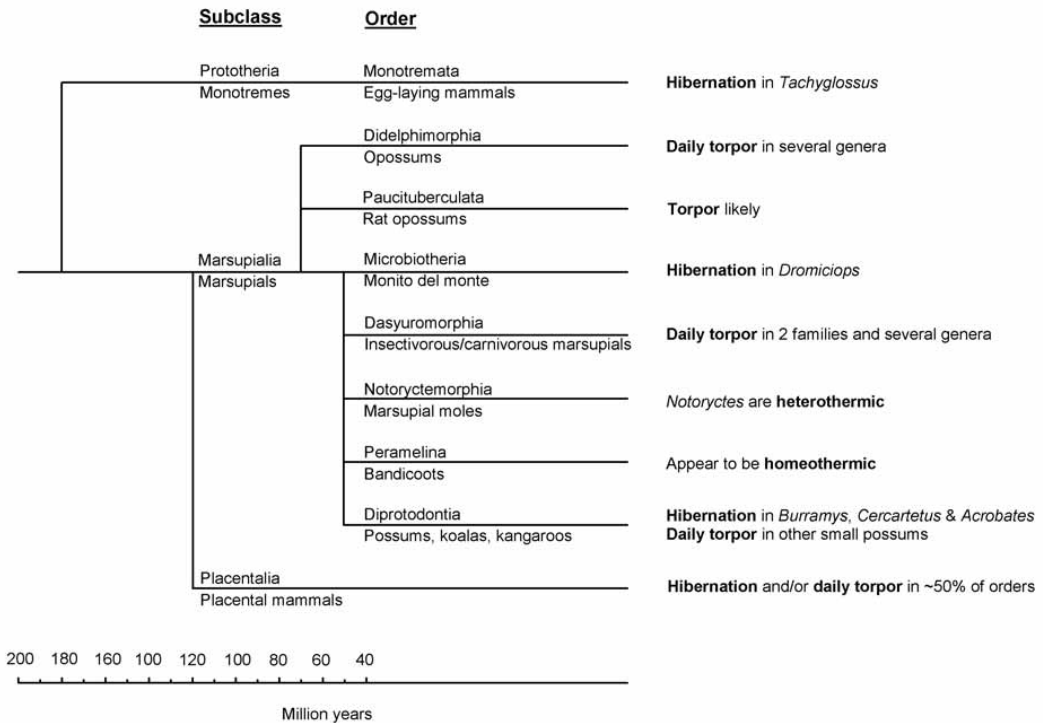
## Introduction

Mammals of the subclasses Marsupialia (Metatheria) and Placentalia (Eutheria) have been independent lineages for ~120 million years (Dawson 1983). Australian marsupials, comprising four orders (Dasyuromorphia, Notoryctemorphia, Peramelina, Diprotodontia), likely evolved from the South American Microbiotheria in the late Cretaceous (~70 million years ago) (Archer 1984), whereas the South American Didelphimorphia and Paucituberculata evolved independently (Figure 1).

The physiology of marsupials is often used to examine the evolution of torpor and hibernation in relation to mammalian endothermy because of their phylogenetic position (Grigg *et al.* 2004; Hulbert 1988). Historically, marsupials were considered a functionally primitive group and, because they lack thermogenic brown fat (Nicol *et al.* 1997), which is considered essential for rewarming from deep and prolonged torpor (i.e. hibernation), it was

assumed that they are unable to hibernate (McKee & Andrews 1990). However, it has now been established that marsupials employ both daily torpor and hibernation, and that, in general, torpor in marsupials is qualitatively similar to that exhibited in monotremes, placentals and birds (Carey *et al.* 2003; Geiser 2003; Geiser & Körtner 2004; Wang 1989).

Torpor or heterothermy is currently known to occur in five of the seven marsupial orders (Figure 1) and is significantly correlated with phylogeny, with torpor being expressed mainly in closely related taxa (Cooper & Geiser 2008). Torpor is also likely to occur in the rat opossums (Paucituberculata). The bandicoots (Peramelina) are currently considered to be homeothermic (Warnecke *et al.* 2007) and so are the large species within the Diprotodontia (Dawson 1983). Hibernation occurs in two orders, the Microbiotheria (Monito del Monte *Dromiciops*) and the Diprotodontia (pygmy-possums *Burramys parvus*, *Cercartetus* spp.; Feathertail Glider *Acrobates*) (Bozinovic *et al.* 2004; Geiser & Körtner 2004). In *Cercartetus nanus*, hibernation entirely fuelled from stored fat/tissue may last for up to an entire year, which to our knowledge, is longer than for any other mammal without access to food (Geiser 2007). Daily torpor occurs in the Didelphimorphia, Dasyuromorphia, Petauridae and Tarsipedidae (Cooper & Withers 2004; Geiser 2003; Geiser & Körtner 2004; Withers *et al.* 1990). Based on Archer's (1984) phylogeny, and the fact that hibernation occurs in the ancestral microbiotheriids (Figure 1),



**Figure 1.** Mammalian evolutionary tree indicating heterothermic and homeothermic marsupial orders (tree modified from Archer 1984; information on thermoregulation from Bozinovic *et al.* 2004; Cooper & Withers 2004; Dawson 1983; Geiser & Körtner 2004; Geiser 2003; Grigg *et al.* 2004; Nicol *et al.* 2008; Warnecke *et al.* 2007; Withers *et al.* 2000).

it seems likely that hibernation in marsupials is plesiomorphic, whereas daily torpor and homeothermy in the other marsupial orders are derived traits. However, Kirsch and colleagues' (1997) marsupial phylogeny, which suggests that the poorly studied rat opossums are the ancestral marsupial group, may not support this interpretation.

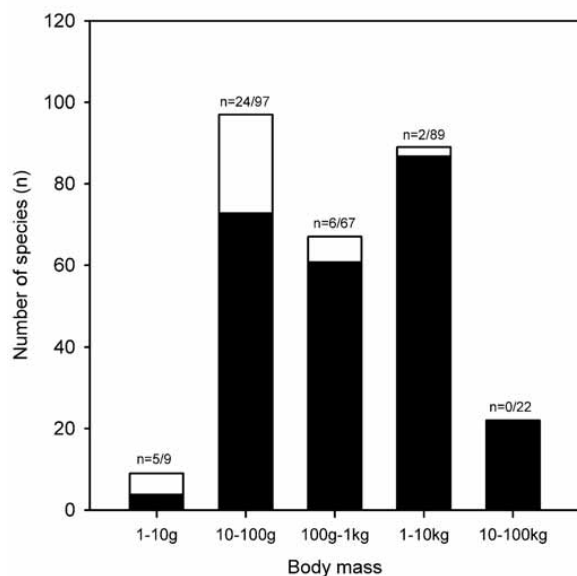
Research on torpor in adult marsupials has produced new knowledge about the biology of torpor in general. Moreover, recent work suggests that during reproduction and juvenile development, torpor functions for more than simply reducing energy expenditure during food shortages or cold stress in winter. New data now exist about torpor patterns of previously unstudied species in the field, especially involving basking during passive rewarming. The purpose of our paper is to synthesise these new findings. Specifically, we examine modifications in the use of torpor with regard to three energy-demanding processes: (i) development and growth, (ii) reproduction, and (iii) rewarming from torpor and the implications of basking.

## Torpor in relation to size and development

Adult body size is one important factor that determines whether or not a species is heterothermic. Small species have larger surface-area-to-volume ratios and mass-specific energy requirements that far exceed those of large species (Withers 1992). As in placental mammals (French 1986), torpor, characterised by substantial reductions of body temperature ( $T_b$ ), in marsupials is restricted to species < 10 kg (Figure 2). Torpor occurrence decreases with increasing adult body mass (Figure 3), suggesting a strong link between size and heterothermy.

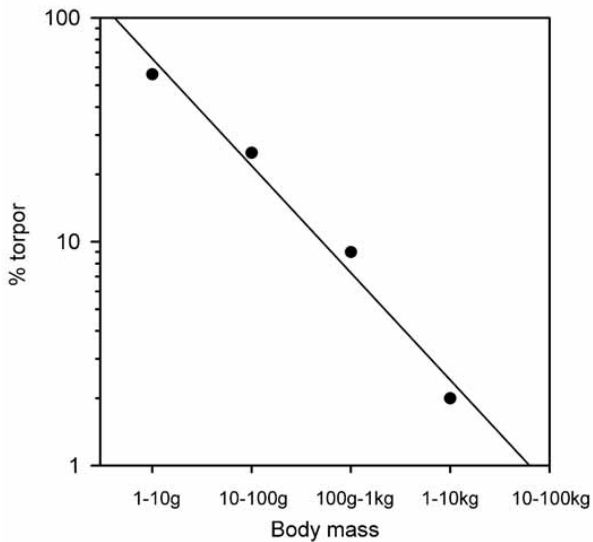
Whereas the relationship between torpor use and size has long been recognised (Morrison 1960; Willis *et al.* 2005), little is known about the impact of size on the development of endothermy and heterothermy. Altricial mammals and birds are poikilothermic at birth or hatching, but become endothermic at ~30–50% adult size (Morrison & Petajan 1962; Schleucher 1999). The high energetic costs of thermoregulation, as well as nutrient requirements for

**Figure 2.** Frequency distribution of known heterothermic (white) and assumed homeothermic (black) marsupials as a function of body mass (based on 284 species)



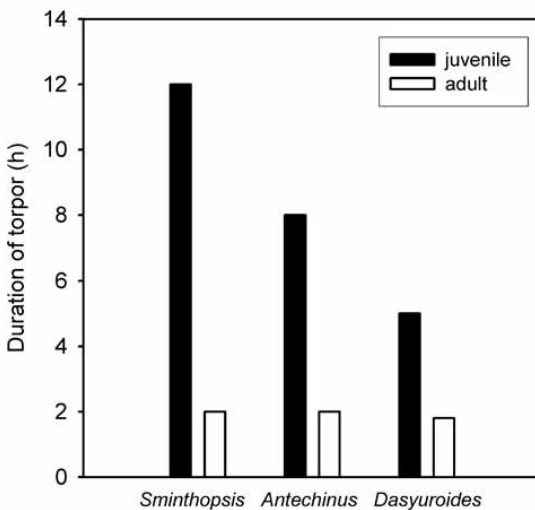
somatic growth, are likely to provide strong selective pressure for heterothermy after endothermy develops because individuals presumably profit from entering torpor to help alleviate the energetic disadvantages of small size.

Marsupials are born extremely undeveloped in an altricial state at < 1% of the mother's body mass and develop slowly at about half the rate of placentals (Lee & Cockburn 1985; Tyndale-Biscoe & Renfree 1987). Marsupials therefore permit a detailed examination of functional changes during development. With regard to torpor during development, data are available for four insectivorous marsupials (*Sminthopsis macroura* 25 g, *Antechinus stuartii* 30 g, *A. flavipes* 40 g, *Dasyuroides byrnei* 120 g; Geiser 1988; Geiser *et al.* 1986, 2006). In these dasyurids, endothermy (maintenance of normothermic  $T_b$ ) during moderate cold exposure) develops 70–90 days after birth, and the ability to enter into and rewarm from daily torpor



**Figure 3.**

Known torpor occurrence vs body mass in marsupials ( $r^2 = 0.98$ )



**Figure 4.**

Duration of torpor in small newly endothermic young in comparison to young adult marsupials. *Sminthopsis* = *Sminthopsis macroura*, *Antechinus* = *Antechinus stuartii* & *A. flavipes*, *Dasyuroides* = *Dasyuroides byrnei* (data from Geiser 1988; Geiser *et al.* 1986, 2006).

develops soon thereafter. In all species, torpor was longer (2.8–6-fold) in the newly endothermic juveniles than when individuals reached adult size (Figure 4). In *Antechinus*, minimum  $T_b$  was  $\sim 4.5^\circ\text{C}$  lower in small juveniles than in adults, and in *Sminthopsis macroura*, the deeper and longer torpor bouts in small juveniles reduced total daily energy requirements by  $\sim 50\%$  compared to young adults. Thus torpor during development in altricial endotherms appears to be an important adaptation that helps growing young to survive periods of energy shortage, but may also facilitate somatic growth because valuable nutrients are not wasted on thermoregulation. Despite these obvious advantages, the importance of torpor during development in altricial mammals and birds has largely been overlooked as an important energy allocation and survival mechanism (but see Bae *et al.* 2003; Geiser *et al.* 2006; Nagel 1977; Nuesslein & Schmidt 1990; Prinzinger & Siedle 1988).

## Torpor and reproduction

Reproduction, like growth and cold exposure, is energetically demanding for many small endotherms. Torpor may provide an effective means to reduce energy expenditure during the reproductive period. Nevertheless, it is widely assumed that energy-conserving mechanisms such as torpor and the energetically costly requirements for reproduction are functionally incompatible and that reproductive animals are reluctant or refuse entirely to enter torpor (Goldman *et al.* 1986; Landau & Dawe 1960; Nicol & Andersen 2006). However, empirical evidence, including data from the field, does not always corroborate this (Chruszcz & Barclay 2002; Geiser 1996; Racey 1973; Stephenson & Racey 1993; Willis *et al.* 2006).

Torpor in reproductive marsupials is known from five species, including recent quantitative data on three. A female dunnart (*Sminthopsis macroura*, Dasyuridae) was pregnant during respirometry measurements and entered torpor nevertheless (Geiser *et al.* 2005). She gave birth  $\sim 9$  days after the measurement, and, as the gestation period in this species is  $\sim 12.5$  days (Tyndale-Biscoe & Renfree 1987), she had completed  $\sim 30\%$  of pregnancy when she entered torpor. Her minimum metabolism during torpor was similar to that of 10 non-pregnant females, but torpor lasted for only  $\sim 4$  hr, about two-thirds of that for non-pregnant individuals. The pregnant female raised two young to weaning at the typical 70 days after birth.

Captive pregnant mulgaras (*Dasyercercus cristicauda* syn. *blythi*, Dasyuridae) displayed torpor frequently when food was freely available and body mass was increasing (Geiser & Masters 1994). Field data confirm that wild mulgaras also employ daily torpor during pregnancy (Körtner *et al.* 2008). A lactating female with neonate pouch young remained homeothermic in mid-August; however, she entered deep torpor ( $T_b \sim 20^\circ\text{C}$ ) almost daily in late July and early August prior to parturition (Körtner *et al.* 2008). This suggests that, as in captivity, free-ranging pregnant mulgaras minimise energy expenditure to accumulate fat stores when little energy transfer to young is required (neonate dasyurids weigh between 10–18 mg; Tyndale-Biscoe & Renfree 1987) to prepare for the more energy-demanding lactation period. Free-ranging males occasionally displayed shallow torpor during the mating season in early winter, but after mating in late winter, they often employed deep and long daily torpor (Körtner *et al.* 2008).

Unlike these two dasyurids, free-ranging pregnant Sugar Gliders (*Petaurus breviceps*, Petauridae) maintain a higher and more constant  $T_b$  than non-pregnant individuals (Christian

2007). During lactation, however, when pouch young were 19–34 days old, torpor ( $T_b$  20–27°C) was recorded eight times in four females. One of these females was still lactating 70 days after she gave birth and thus torpor did not impair development of young. Dominant males did use torpor occasionally up to two weeks before females were pregnant, but remained homeothermic for the two weeks immediately prior to female pregnancy (Christian 2007).

Thus, torpor use during reproduction appears to differ between female dasyurid and petaurid marsupials. Whereas dasyurids employ torpor to minimise energy expenditure during pregnancy and perhaps to store fuel for lactation when they are less likely to enter torpor (but see Morton 1978), Sugar Gliders show constant high  $T_b$  during pregnancy and display torpor occasionally during lactation. A potential explanation for these differences in torpor use is neonate size. While other reproductive variables are similar among the three species (considering the smaller size of the dunnarts), the size of neonates differs substantially and is almost 20-fold larger in Sugar Gliders (194 mg) than in dunnarts (10 mg; Tyndale-Biscoe & Renfree 1987). Neonate size in mulgaras is not known, but all dasyurids for which data are available have ~10–20-mg neonates. The development of larger and more developed neonates may demand homeothermy during pregnancy in Sugar Gliders, whereas during lactation when energy expenditure of Sugar Gliders is low (Holloway & Geiser 2000) they may employ torpor. The opposite seems to be the case for small dasyurids, which tend to have higher rates of metabolism during lactation (Westman *et al.* 2002). For males, torpor appears to be used occasionally during the mating period, at least, in mulgaras, although it is shorter and shallower than after the mating season. Dominant male Sugar Gliders appear to avoid torpor during much of the mating season, perhaps because they have to produce sperm and can huddle in large groups.

## Basking and torpor

Whereas the previous sections considered torpor use in relation to other functions, in this section we examine energy expenditure during torpor *per se*. Endothermic rewarming from torpor is energetically expensive and reduces the savings accrued from daily torpor and often results in death of light individuals during hibernation if they arouse too frequently. Desert dasyurids in the field, which use daily torpor in winter on up to 100% of days, employ basking during rewarming apparently to lower energy expenditure during arousal (Geiser & Pavey 2007; Körtner *et al.* 2008; Warnecke *et al.* 2008). Basking during rewarming from torpor can reduce rewarming costs by 85% (Geiser & Drury 2003), but published data on basking by torpid mammals under natural conditions was restricted to only two species (Geiser *et al.* 2002; Mzilikazi *et al.* 2002) and therefore it was not known whether these findings have implications for others.

**Table 1.** Basking in torpid marsupials.

Species	Body mass (g)	Basking $T_b$ minimum (°C)	Source
<i>Planigale gilesi</i>	8	13.8	Warnecke <i>et al.</i> unpubl. data
<i>Sminthopsis crassicaudata</i>	10	14.6	Warnecke <i>et al.</i> 2008
<i>Sminthopsis macroura</i>	15	19.3	Körtner <i>et al.</i> unpubl. data
<i>Pseudantechinus macdonnellensis</i>	31	19.3	Geiser & Pavey 2007

Recent temperature-telemetry data reveal that basking during rewarming occurs in four desert-dwelling dasyurids. These include new data for two arid-zone dunnarts and a planigale and published observations on the rock-dwelling *Pseudantechinus* (Table 1).

*Planigale gilesi*, the smallest species investigated (8 g), displayed daily torpor on 100% of winter observation days (Warnecke *et al.* unpubl. data) in western New South Wales (NSW). The minimum  $T_b$  during torpor was 10.5°C and the lowest  $T_b$  observed during basking was 13.8°C (Table 1). Basking commenced at about 10:30 and lasted 40–125 minutes.

In winter, *Sminthopsis crassicaudata* in western NSW displayed torpor on 100% of observation days and basked frequently with the entire body exposed to the sun (Warnecke *et al.* 2008). Activity was brief and occurred in the late afternoon to early evening. Torpor entry often occurred within the first 3 hr of darkness and most torpor bouts lasted for ~17 hr. Arousal usually commenced at ~10:30 and on three occasions dunnarts were observed to emerge while torpid to bask in the sun before  $T_b$  rose. The lowest  $T_b$  measured during basking was 14.6°C.

In autumn, when ambient conditions were predictably milder, *S. crassicaudata* at the same site still entered torpor on 30 of 31 days. Most torpor bouts in autumn were shorter (~5–11 hr), activity lasted for much of the first half of the night and arousal commenced earlier (mean 09:56) than in winter, but as in winter ~3 hr after sunrise (Warnecke *et al.* 2008). Basking during torpor was observed for 8 out of 30 bouts, mean  $T_b$  at which basking was first observed was 23.9°C, and dunnarts in autumn exposed only part of their body to the sun, which likely accounts for the slower rewarming rates than in winter.

*Sminthopsis macroura* in south-western Queensland entered torpor on 99.5% of days over several months in winter (Körtner *et al.* unpubl. data). The most common torpor pattern observed was torpor entry ~7 hr before sunrise with torpor bouts lasting for ~11 hr on average. On two occasions, torpid individuals were observed basking and the minimum basking  $T_b$  was 19.3°C (Table 1).

*Pseudantechinus macdonnellensis* in central Australia entered torpor frequently in winter (~58% of observed days; Geiser & Pavey 2007). Animals were usually active during the afternoon and the first half of the night, entered torpor at ~02:00 and usually remained torpid for ~8 hr. Rewarming began at ~09:45 when animals frequently employed basking with  $T_b$  as low as 19.3°C (Table 1).

Whereas the marsupials described above employ basking during rewarming from torpor in the wild, this behaviour does not appear to be displayed by two other species, Numbats (*Myrmecobius fasciatus*; Cooper & Withers 2004) and mulgaras (*Dasyercus blythi*; Körtner *et al.* 2008). It is possible that in these species risks from exposure to predators outweigh energy savings gained by basking.

In summary, our review shows that torpor use is not merely for energy conservation during acute adverse conditions. Torpor during development may enhance survival during growth and help spare valuable nutrients required for growth. Torpor during reproduction may be used to facilitate accumulation of fat for future energy demands. Basking during rewarming is employed to minimise the usually greatest energy demand during torpor and thus further enhances energy savings. The functions and adaptations of torpor are therefore manifold and complex and it is likely that we currently understand only some of them.

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