Torpor in Marsupials: Recent Advances

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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 minimize 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) (Archer 1984), whereas the South American Didelphimorphia and Paucituberculata evolved independently (Fig. 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 (Hulbert 1988; Grigg et al. 2004). Historically, marsupials were considered a functionally primitive group and, because they lack thermogenic brown fat (Nicol et al. 1997), considered essential for rewarming from deep and prolonged torpor (i.e. hibernation), it was assumed that they are unable to hibernate (McKee and 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 (Wang 1989; Carey et al. 2003; Geiser 2003; Geiser and Körtner 2004).

Torpor or heterothermy is currently known to occur in 5 of the 7 marsupial orders (Fig. 1) and shows a highly significant phylogenetic signal with torpor being expressed mainly in closely related taxa (Cooper and 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 and 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 (Geiser 2003; Geiser and Körtner 2004; Cooper and Withers 2004). Based on Archer's (1984) phylogeny, and the fact that hibernation occurs in the ancestral microbiotheriids (Fig. 1), it seems likely that hibernation in marsupials is plesiomorphic, whereas daily torpor and homeothermy in the other marsupial orders are derived traits. However, Kirsch et al.'s (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 are now available about torpor patterns of previously unstudied species in the field, especially involving basking during passive rewarming. The purpose of our paper is to synthesize 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 determining whether or not a species is heterothermic. Small species have larger surface area: volume ratios and mass-specific energy requirements that far exceed those of large species (Withers 1992). As in placental mammals (French 1986), torpor characterized by substantial reductions of T_b in marsupials is restricted to species <10 kg (Fig. 2). Torpor occurrence decreases with increasing adult body mass (Fig. 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 and Petajan 1962; Schleucher 1999). The high energy costs of thermoregulation as well as nutrient requirements for somatic growth are likely to provide a 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 very undeveloped in an altricial state at <1% of the mother's body mass and develop slowly at ~half the rate of placentals (Lee and Cockburn 1985; Tyndale-Biscoe and Renfree 1987). Therefore marsupials permit a detailed examination of functional changes during development. With regard to torpor during development, data are available for four insectivorous marsupials (*Sminthopsis macroura* 25g; *Antechinus stuartii* 30g; *A. flavipes* 40g; *Dasyuroides byrnei* 120g; Geiser et al. 1986, 2006; Geiser 1988). In these dasyurids endothermy (maintenance of normothermic T_b during moderate cold exposure) developed 70 to 90 days after birth, and the ability to enter into and rewarm from daily torpor developed soon thereafter. In all species, torpor was longer (2.8 to 6-fold) in the newly endothermic juveniles than when individuals reached adults size (Fig. 4). In *Antechinus*, minimum body temperature (T_b) was ~4.5ºC lower in small juveniles than adults, and in *Sminthopsis macroura*, the deeper and longer torpor bouts in small juveniles reduced total daily energy requirements by ~50% compared to young adults. Thus torpor during development in altricial endotherms is an important adaptation that helps growing young to survive periods of energy shortage, but also may 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: Nagel 1977; Prinzinger and Siedle 1988; Nuesslein and Schmidt 1990; Bae et al. 2003, Geiser et al. 2006).

Torpor and Reproduction

Reproduction, like growth and cold exposure, is energetically demanding for many small endotherms. Torpor could provide an effective means to reduce energy expenditure during the reproductive period if this was required. 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 (Landau and Dawe 1960; Goldman et al. 1986; Nicol and Andersen 2006). However, empirical evidence, including data from the field, does not always corroborate this (Racey 1973; Geiser 1996; Chruszcz and Barclay 2002; 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 ~9 days after the measurement, and, as the gestation period in this species is ~12.5 days (Tyndale-Biscoe and Renfree 1987), she had completed ~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 ~4 h, ~2/3 of that for non-pregnant individuals. The pregnant female raised two young to weaning at the typical 70 days after birth.

Captive pregnant mulgaras (*Dasycercercus cristicauda* syn. *blythi*, Dasyuridae) displayed torpor frequently when food was freely available and body mass was increasing (Geiser and 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 ~20ºC) 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 minimize energy expenditure to accumulate fat stores when little energy transfer to young is required (neonate dasyurids weigh between 10 and 18 mg, Tyndale-Biscoe and 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) maintained a higher and more constant T_b than non-pregnant individuals (Christian 2007). During lactation, however, when pouch young were 19 to 34 days old, torpor (T_b 20 to 27ºC) was recorded 8 times in 4 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 minimize energy expenditure during pregnancy and perhaps to store fuel for lactation when they do not enter torpor, 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 and Renfree 1987). Neonate size in mulgaras is not known, but all dasyurids for which data are available have <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 and Geiser 2000) they may employ torpor. The opposite seems to be the case for small dasyurids, which 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, this section examines 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 and Pavey 2007; Warnecke et al. 2008; Körtner et al. 2008). Basking during rewarming from torpor can reduce rewarming costs by 85% (Geiser and Drury 2003), but in the wild published data on basking by torpid mammals 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.

Recent temperature-telemetry data revealed 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. unpublished) in western New South Wales (NSW). The minimum T_b during torpor was 10.5ºC and the lowest T_b observed during basking was 13.8ºC (Table 1). Basking commenced at about 10h30 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 h of darkness and most torpor bouts lasted for ~17 h. Arousal usually commenced at ~10h30 and on three occasions dunnarts emerged while torpid to bask in the sun before T_b rose. The lowest T_b measured during basking was 14.6ºC.

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 to 11 h), activity lasted for much of the first half of the night and arousal commenced earlier (mean 09h56) than in winter, but as in winter ~3 h after sunrise (Warnecke et al. 2008). Basking during torpor was observed for 8/30 bouts, mean T_b at which basking was first observed was 23.9ºC, 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. unpublished). The most common torpor pattern observed was entry ~7 h before sunrise with torpor bouts lasting for ~11 h on average. On two occasions torpid individuals were observed basking and the minimum basking T_b was 19.3ºC (Table 1).

Pseudantechinus macdonnellensis in central Australia in winter entered torpor frequently (~58% of observed days; Geiser and Pavey 2007). Animals were usually active during the afternoon and the first half of the night, entered torpor at ~02h00 and usually remained torpid for ~8 hours. Rewarming began at ~09h45 when animals frequently employed basking with T_b as low as 19.3ºC (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 and Withers 2004) and mulgaras (*Dasycercercus 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 reduce the usually greatest energy demand during torpor and thus further enhances energy savings. Thus, the functions and adaptations of torpor are manifold and complex and it is likely that we currently understand only some of them.

Acknowledgments

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Table 1: Basking in torpid marsupials

Species	Body mass (g)	Basking T_b minimum (ºC)	Source
Planigale gilesi	8	13.8	Warnecke et al. unpublished
Sminthopsis crassicaudata	10	14.6	Warnecke et al. 2008
Sminthopsis macroura	15	19.3	Körtner et al. unpublished
Pseudantechinus macdonnellensis	31	19.3	Geiser & Pavey 2007

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

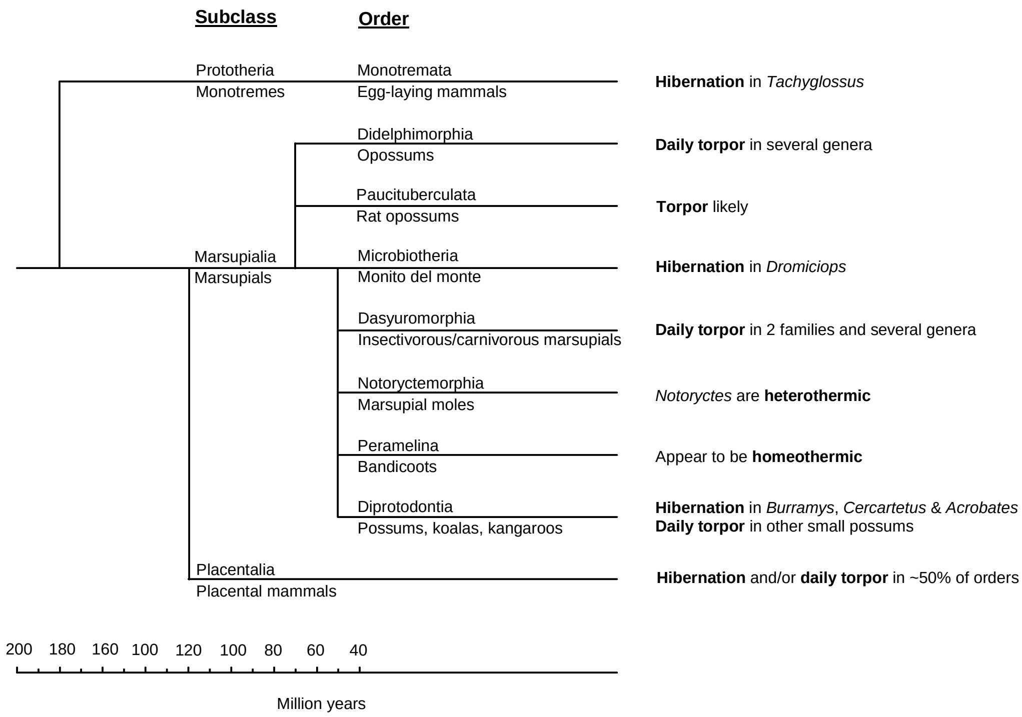

Fig. 2. Frequency distribution of known heterothermic (white) and assumed homeothermic (black) marsupials as a function of body mass (based on 284 species)

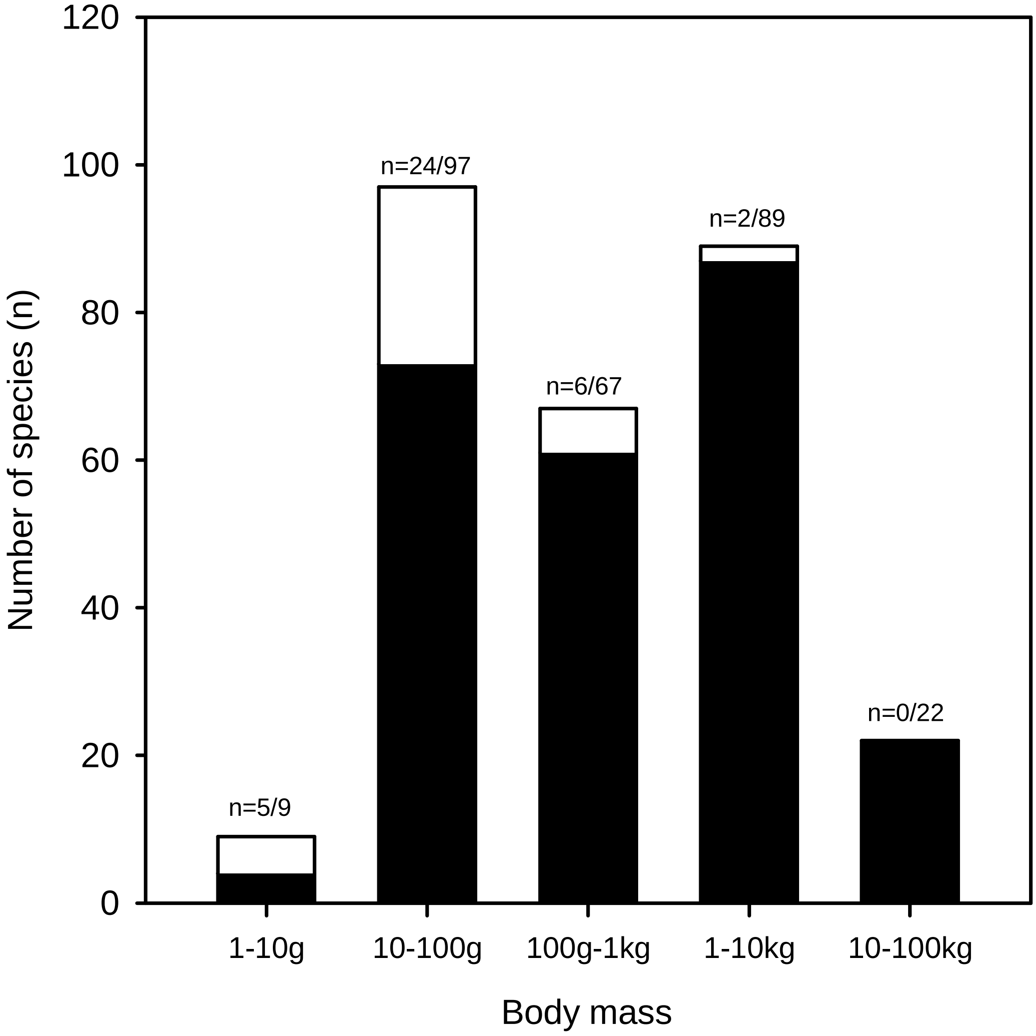

Fig. 3. Known torpor occurrence vs body mass in marsupials (r^2=0.98)

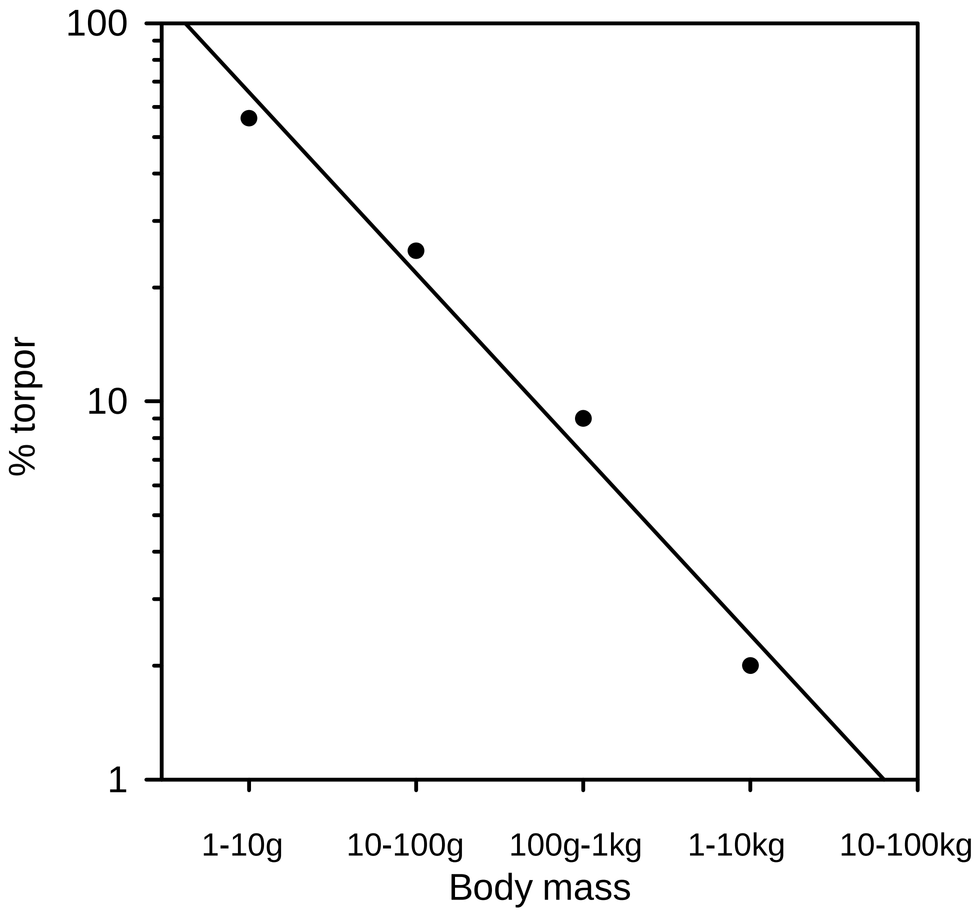

Fig. 4. Duration of torpor in small newly endothermic young in comparison to young adult marsupials. *Sminthopsis* = *Sminthopsis macroura*, *Antechinus* = *Antechinus stuartii* & *A. flavipes*, *Dasyuroides* = *Dasyuroides byrnei* (data from Geiser et al. 1986, 2006; Geiser 1988).