THE ROLE OF TORPOR IN THE LIFE OF AUSTRALIAN ARID ZONE MAMMALS

FRITZ GEISER

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Approximately half of the Australian continent is arid and is characterised by low primary productivity, limited supply of food and pronounced daily fluctuations of ambient temperature (T_a). Despite these adverse conditions the diversity of small mammals in the Australian arid zone is high, although their abundance is generally low. The most successful groups of small arid zone mammals are the dasyurid marsupials, native rodents, and insectivorous bats. A probable reason for the success of the insectivorous dasyurids and bats, which must cope with strong fluctuations in food and water availability, is their extensive use of torpor. Mammalian torpor is characterised by substantial reductions of body temperature (T_b) metabolic rate (MR) and water loss. Small arid zone dasyurids use exclusively daily torpor, some even during the reproductive season, when most mammals maintain strict homeothermy. Dasyurids reduce T_b from ~ 35ºC during normothermia to ~ 15ºC during torpor, the MR during torpor (TMR) is ~ 30% of basal metabolic rate (BMR). Mass loss, and thus water loss, is related to the duration of torpor bouts. Dasyurids usually enter torpor at night or in the early morning and arouse around midday or in the afternoon. Recent evidence shows that desert dasyurids may bask in the sun during rewarming from torpor. This can minimise energetic cost of arousal to a fraction of that required for endogenous warming. Arid zone bats are also likely to use torpor extensively, but few species, specific to the arid zone, have been studied. Nevertheless, widely distributed bats that occur in the arid zone, such as *Nyctophilus geoffroyi*, enter brief torpor for part of the day in summer and prolonged torpor (hibernation) for up to two weeks in winter and can reduce T_b to a minimum of 2 - 3ºC and TMR to ~ 3% of BMR; mass loss and water loss, are minimal during torpor. Patterns of torpor similar to those in bats also have been observed in the insectivorous echidnas and two species of insectivorous / nectarivorous pygmy-possums, which have distribution ranges that include semi-arid and arid areas. In contrast to these species, no detailed information is available on torpor in native Australian rodents, because little work with respect to torpor has been conducted in Australia. However, many arid zone rodents on other continents employ torpor and it is likely that Australian rodents do as well. In addition to reducing energy expenditure and water loss, use of torpor also appears to prolong life span. This is important for bridging adverse conditions and for subsequent re-colonization of areas after droughts and fires in inland Australia. Thus it appears that the success of small insectivorous/nectarivorous mammals and perhaps rodents in the Australian arid zone is partially due to their use of torpor.

Key words: torpor, rodents, bats, marsupials, echidnas, diet, arid-zone, hibernation, metabolism.

F Geiser, Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW 2351, Australia. Email: fgeiser@une.edu.au.

AUSTRALIAN terrestrial mammals consist of approximately 300 species belonging to the subclasses Prototheria (2 species), Marsupialia (~ 150 species) and Eutheria (rodents ~65 species, bats ~ 77 species) (Menkhorst and Knight 2001). These live in a variety of habitats and one might expect that most would be found in coastal regions with substantial rainfall. However, the diversity of small mammals in the Australian arid zone, which comprises ~ half of the continent and receives < 300 mm of average rainfall / year (Colls and Whitaker 1993), is surprisingly high, although their abundance is generally low. While several small Australian mammals (< 10 kg) manage to live in the arid zone (e.g., echidna, marsupial moles, numbat, some bandicoots, two pygmy-possums, and some small macropods) the groups that do especially well are the dasyurid marsupials (~ 47% of all Australian species are found entirely or partially in the arid zone, *n* = 26 species), native rodents (~ 37%, *n* = 24), and insectivorous bats (~ 22%, *n* = 17) (Menkhorst and Knight 2001).

Living in arid areas creates a number of problems for small endothermic mammals, because of limited food and water supply and pronounced daily fluctuations of T_a (Schmidt-Nielsen 1979; Bradshaw 2003). Endotherms have high metabolic rates (MR) and water loss when their T_b is high, so their food and water requirements may quickly exceed available resources. This is especially true for insectivorous and nectarivorous endotherms because food availability declines with T_a while energy requirements increase (Speakman and Thomas 2003). Presumably because of these limitations not all endotherms are permanently homeothermic. Many are capable of entering a state of torpor (Hudson 1973; Lyman *et al.* 1982; Geiser and Ruf 1995), which is characterised by substantial reductions of T_b, MR, water loss and other physiological processes, thereby reducing water and food requirements.

Species capable of entering a state of torpor are often referred to as 'heterothermic endotherms'. Heterotherms during the normothermic season when torpor is not used or during other periods of activity are able to maintain a high T_b via physiological thermoregulation just like homeotherms. However, unlike homeotherms, they are also able to employ torpor during acute or potential energy or water limitations. Heterotherms save energy because; i) thermoregulation at high T_b is abandoned and no energy is required for normothermic thermoregulation, ii) because the T_b falls, temperature effects reduce the MR below the BMR and, iii) some species are able to use metabolic inhibition in addition to temperature effects on MR to further minimise energy expenditure (Malan 1986; Geiser 1988; Guppy and Withers 1999). Consequently, MR can be reduced to a fraction of BMR, which in normothermic individuals represents the minimum maintenance MR (Dawson and Hulbert 1970; Geiser and Ruf 1995). Nevertheless, thermoregulation during torpor is not entirely abandoned. The T_b during torpor is regulated at a species or population-specific minimum via an increase of MR, and this minimum T_b or T_b setpoint is regulated by the hypothalamus (Heller and Hammel 1972).

Two general patterns of torpor are widely recognised. The first of these, prolonged torpor or hibernation in the hibernators, may last for several day or weeks, but is interrupted by periodic arousals and brief normothermic periods throughout the hibernation season, which usually lasts for ~ 6 months (Wang 1989). However, at high T_a hibernators may exhibit short bouts of torpor lasting less than one day and may even forage between torpor bouts. When exposed to low T_a, the T_b in torpid hibernators usually falls below 10ºC and MR during torpor (TMR) is on average only 5% of the basal MR (BMR). The second common pattern, daily torpor in the daily heterotherms, always lasts less than a day, T_b is usually maintained between 10 and 25ºC and TMR is on average ~ 30% of BMR (Geiser and Ruf 1995). 'Aestivation' is often used to describe daily or prolonged torpor in summer, but, because there is no evidence that it differs functionally from the other torpor patterns, apart from occurring at somewhat higher T_a, this term is not used in this review.

Traditionally torpor in endotherms was seen predominantly as an adaptation of cold climate species. It now is established that torpor occurs in many diverse mammals from a wide range of habitats ranging from the arctic to the tropics and includes species from arid zones (Barnes 1989; Geiser and Ruf 1995; Bartels *et al*. 1998; Lovegrove 2000; Fietz *et al*. 2003). The shift in the perception about torpor in recent years is evident from the literature. A book on desert animals by Schmidt-Nielsen (1979) covers Australian mammals, but torpor in marsupials is not mentioned, and bats are not discussed at all. As is summarised below we now know that in Australia torpor occurs in echidnas, insectivorous/carnivorous dasyurids, pygmy-possums, bats, and perhaps rodents from the arid zone (Table 1). The only groups of small arid zone mammals for which no information on torpor is available are the bandicoots and small macropods (Hulbert and Dawson 1974; Dawson 1989). Thus torpor is very common in Australian arid zone mammals and is likely a crucial key to their success. The purpose of this review is to summarise what is currently known about torpor patterns in Australian arid zone mammals and how it is likely to affect their life.

Echidnas

The short-beaked echidna (*Tachyglossus aculeatus*) is distributed over the entire continent. *T. aculeatus* has been observed to enter prolonged torpor in many areas of Australia including the arid zone (Coleman 1935; Augee *et al*. 1970; Grigg *et al*. 1992; Nicol and Andersen 1996; Grigg and Beard 2000). Whereas torpor bouts with T_b < 10ºC may last for more than two weeks during a ~ 6-month hibernation season in the Australian Alps, the Northern Tablelands and Tasmania (Grigg and Beard 2000; Nicol and Andersen 2000; Frank *et al*. 2001), in the arid zone torpor bouts tend to be shorter and the hibernation season may last only for a few months or less (Nicol and Andersen 1996). In semi arid southwestern Queensland, *T. aculeatus* remained torpid for up to 9 days during winter with T_b of ~ 14ºC and occasionally for one day in summer (Brice *et al*. 2002). Metabolic rates in captive *T. aculeatus* fall to values characteristic of those in other hibernators (Nicol *et al*. 1992), but because of their low BMR,

	BM (g)	N T_b (^{0}C)	M T_b (^{0}C)	Torpor (h)	TMR (ml O_2/g h)	TMR/ BMR	Source
MONOTREMATA							
TACHYGLOSSIDAE							
Tachyglossus aculeatus	2-7^a	32	4	384	0.02	0.13	Grigg *et al.* 1992; Nicol *et al.* 1992
MARSUPIALIA							
DASYURIDAE							
Planigale ingrami	5.8-9.3	34.5		2-4		0.3	Dawson & Wolfers 1978
Planigale tenuirostris	6.6-7.3	34.5		2-4		0.3	Dawson & Wolfers 1978
Planigale gilesi	8.3	32.6	14.3	15.3	0.36	0.25	Geiser & Baudinette 1988
Ningaui ridei	9						Dickman pers. comm. 1999
Ningaui yvonneae	10-13	34.4	15.3	12.3	0.3	0.23	Geiser & Baudinette 1988
Sminthopsis youngsoni	10						Dickman pers. comm. 1999
Sminthopsis ooldea	11						Aslin 1983
Sminthopsis longicaudata	15-20						Burbidge *et al.* 1983
Sminthopsis hirtipes	15						Dickman, pers. comm. 1999
Sminthopsis crassicaudata	17	34.1	13.0	19.5	0.27	0.22	Geiser & Baudinette 1987
Sminthopsis macroura	20-28	34.3	14.0	17.9	0.3	0.29	Geiser & Baudinette 1987
Antechinomys laniger	27	34.8	11.0	16.0	0.14	0.13	Geiser 1986
Pseudantechinus macdonnellensis	31	35	15.7	10			Geiser *et al.* 2002
Dasycercus cristicauda	70-110	33.7	14	12	0.12	0.23	Geiser & Masters 1994
Dasyuroides byrnei	120	34.3	20.4	7.5	0.4	0.54	Geiser & Baudinette 1987
Dasyurus geoffroyi	1^a	35	23.1				Arnold 1976
MYRMECOBIIDAE							
Myrmecobius fasciatus	500	34.4	19.1	15.3			Serventy & Raymond 1973; Cooper 2003
NOTORYCTIDAE							
Notoryctes typhlops	60						Tyndale-Biscoe 1973
Notoryctes caurinus	34	30.8					Withers *et al.* 2000
BURRAMYIDAE							
Cercartetus concinnus	18	34.4	4.7	264	0.046	0.04	Geiser 1987
Cercartetus lepidus	12	33.7	5.9	144	0.052	0.03	Geiser 1987
CHIROPTERA							
VESPERTILIONIDAE							
Chalinolobus gouldii	17.5	34	5		~0.06	0.042	Hosken & Withers 1997
Chalinolobus picatus	6	37.5	12.8^b				Kulzer *et al.* 1970
Nyctophilus geoffroyi	7	35.7	1.4	312	0.037	0.027	Geiser & Brigham 2000; Turbill *et al.* 2003a
Nyctophilus timoriensis	14	33	6^b		0.05	0.033	Hosken 1997
Scotorepens balstoni	7		3.2		0.044		Geiser and Brigham 2000
Vespadelus findlaysoni	5		9.5^b				unpubl. data
RODENTIA							
MURIDAE							
Pseudomys hermannsburgensis	9	36	21^c				Predavec 1997
Mus musculus (introduced)	~15		18.2				Morton 1978a

Table 1. Summary of body mass and physiological variables in heterothermic arid zone mammals. The longest torpor bouts and the lowest metabolic rate during torpor are reported. BM = body mass, N T_b = normo-thermic body temperature; M T_b = minimum body temperature; BMR – basal metabolic rate; TMR – metabolic rate during torpor; ^{a} kg; ^{b} likely not a regulated minimum body temperature; ^{c} possibly non-regulated hypothermia.

which appears to be partially due to the low normothermic T_b of ~ 32ºC, the TMR/BMR ratio of ~ 13% is larger than in other hibernating species (Table 1, Fig. 1). The low T_b during activity and the low TMR and T_b during torpor will reduce both energy and water requirements and likely contribute to the survival of the species in a large variety of habitats including the arid zone.

Thus prolonged and deep torpor in echidnas is similar to that observed in hibernators from other continents (Geiser and Ruf 1995). As for many other hibernating species, *T. aculeatus* relies heavily on stored fat during the hibernation season, and, unlike daily heterotherms, can survive without eating for weeks or months. However, torpor in *T. aculeatus* appears to be more opportunistic than in strongly seasonal hibernators (Körtner and Geiser 2000a) and may occur at any time of the year.

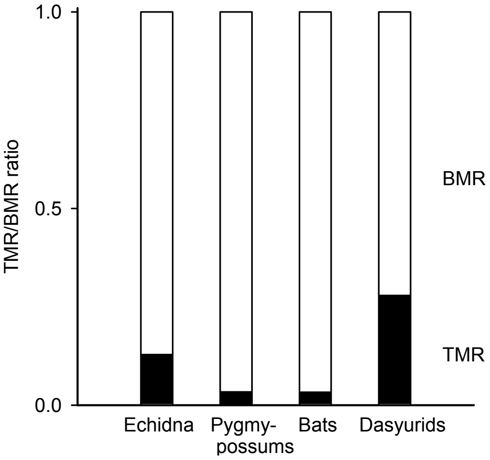

Fig. 1. TMR/BMR ratio in arid zone mammals.

Insectivorous/carnivorous marsupials

The group of Australian arid zone mammals that has been studied most extensively for their use and patterns of torpor are the insectivorous/carnivorous marsupials of the family Dasyuridae (Godfrey 1968; Tyndale-Biscoe 1973; Wallis 1982; Dawson 1989; Dickman 1996; Geiser 2003; Table 1). Heterothermic arid zone dasyurids range in body mass from ~ 6 g in *Planigale* spp. to ~ 1000 g in the western quoll (*Dasyurus geoffroii*). All dasyurids that have been studied use daily torpor exclusively, with torpor bouts lasting for several hours from the late night or morning to the following late morning or early afternoon. Minimum T_b measured during torpor range from 11 to 15ºC in the small species (< 100 g) and ~ 15 to 23ºC in the larger species (> 100 g)(Table 1). Minimum TMR range between 13 and 54% of BMR (Table 1). The reduction in daily energy expenditure by the use of torpor usually is in the range of 10 to 40% of individuals that remained normothermic at the same T_a (Frey 1991; Holloway and Geiser 1995; Song *et al.* 1995; Geiser and Drury 2003). Daily torpor in captive dasyurids does not only occur at low T_a. Animals may enter torpor at T_a between 25 and 30ºC, especially when food is withheld. However, because of the high T_a torpor is shallow and brief (Geiser 1986, 2003; Song *et al.* 1995). Moreover, arid zone dasyurids frequently enter spontaneous torpor when food and water are freely available, which is likely an adaptation to the general resource availability in their desert environment.

Physiological variables associated with the torpor of dasyurids are similar to those in other daily heterotherms found elsewhere in the world, in which torpor lasts on average for several hours and the average minimum T_b is ~ 17°C (Geiser and Ruf 1995). Dasyurids, like other small daily heterotherms, generally do not fatten substantially before the torpor season, and often lose mass before they will use torpor frequently (Morton 1978a,b; Holloway and Geiser 1996; Körtner and Geiser 2000b). Dasyurids appear to rely predominantly on foraging for energy supply in winter (Geiser 2003) and, when food is withheld, perish after a few days (Kennedy and McFarlane 1971).

Whereas daily energy expenditure decreases with the use of torpor, two major activities raise daily energy expenditure in daily heterotherms and these are foraging and endothermic arousal from torpor. Obviously, in species relying heavily on ingested rather than stored energy resources, foraging must be adequate for replenishing fuel resources and is therefore essential, although torpor use may lower the time required for foraging. On the other hand, energy expenditure for arousal, which is perceived as an unavoidable energetic drawback of torpor (Ellison and Skinner 1992), can be reduced, especially in a desert environment. Recent evidence from arid zone dasyurids shows that, similar to lizards, torpid fat-tailed pseudantechinus (*Pseudantechinus macdonnellensis*), ~ 30 g, bask in the morning and use the sun as an energy source during rewarming (Geiser *et al.* 2002). In winter, *P. macdonnellensis* emerge from their deep rock crevices ~ 2.5 h after sunrise with T_b around 26ºC (basking T_b minimum 19.3ºC), bask until they reach normothermic T_b, and continue to bask for much of the rest of the day. Usually *P. macdonnellensis* sit with their side or back to the sun close to a crevice for escape and alternate sun-exposed sides like sunbathers on a beach (Fig. 2). In the laboratory it has been estimated that passive rewarming via an increase in T_a reduces rewarming costs in stripe-faced dunnarts (*Sminthopsis macroura*) to ~ 35% of active rewarming (Lovegrove *et al.* 1999). During radiant heat assisted passive rewarming by *S. macroura* basking under a heat lamp, its rewarming costs were as low as 15% of that required for active endothermic rewarming at the same T_a, even though the lamp provided much less radiant heat than the sun (Geiser and Drury 2003). Basking during normothermia, which also appears common in arid zone dasyurids (Geiser 2003), allows a reduction of energy expenditure to BMR without thermoregulatory costs over a wide range of T_a

Fig. 2. A basking *Pseudantechinus macdonnellensis.*

(Geiser and Drury 2003). So with the low TMR, access to solar energy during passive rewarming from daily torpor, and access to solar energy during the normothermic rest phase allows a mammal like *S. macroura* to reduce daily energy expenditure by up to 50%. Thus, while the desert environment may be limiting with respect to food availability, the high T_a fluctuations and access to solar radiation provides another potential source of energy that is not commonly available to heterothermic species in cold climates with long and dark winters.

The importance of torpor in arid zone dasyurids is further emphasised by its use during reproduction when many other species are strictly homeothermic and raise MR. Moreover, torpor is employed even during development and growth. Female fat-tailed dunnarts (*Sminthopsis crassicaudata*) entered daily torpor during lactation in the field without adversely affecting the development of the young (Morton 1978a). Captive female mulgaras (*Dasycercus cristicauda*) regularly used spontaneous daily torpor (food and water available) during pregnancy and over the same time period increased their body mass by 35%. Perhaps this strategy helps to build up fat stores for the more energetically demanding period of lactation (Geiser and Masters 1994). In young kowaris (*Dasyuroides byrnei*) at about half adult body mass (~ 50 g), but fully capable of endothermic thermoregulation, torpor is deeper and longer than in adults (Geiser *et al*. 1996). This demonstrates that even during the growth phase, which is usually associated with an increase in energy expenditure, torpor may be employed to conserve energy in desert dasyurids.

As pointed out above, torpor also affects water loss. Unfortunately direct data on water loss in dasyurids are not available, but daily mass loss, which to a large extent is caused by water loss, is related to torpor bout duration in both kultarr (*Antechinomys laniger*) and Giles' planigale (*Planigale gilesi*) (Geiser 1986, 2003); mass loss during long torpor bouts (> 10 h) was ~ 50 - 60% (~ 4 - 6 $\mathrm{mg\,g^{-1}\,h^{-1}}$) of that during shorter bouts (< 10 h; ~ 7 - 12 $\mathrm{mg\,g^{-1}\,h^{-1}}$). In the American mouse *Peromyscus eremicus*, which shows a similar pattern of daily torpor as dasyurids, pulmocutaneous water loss in torpid individuals declined in parallel with TMR to < 50% of that during normothermia (MacMillen 1965) and it is likely that similar relationships occur in dasyurids.

Daily torpor also occurs in numbats (*Myrmecobius fasciatus*) and the pattern of torpor and torpor depth appear similar to that in dasyurids (Cooper 2003). Moreover, marsupial moles (*Notoryctes* spp.) may be heterothermic, but little published information is currently available (Tyndale-Biscoe 1973; Withers *et al*. 2000; Table 1). It is likely that heterothermy in these species has similar effects on energy and water conservation as in the dasyurids.

Pygmy-possums

Two of the pygmy-possums, the western pygmy-possum (*Cercartetus concinnus*) and the little pygmy possum (*Cercartetus lepidus*) extend their ranges from coastal regions into semi-arid and arid regions (Menkhorst and Knight 2001). Unlike the carnivorous marsupials, these insectivorous/

nectarivorous pygmy-possums can remain torpid for one or two weeks when exposed to low T_a, lower their T_b to a minimum of ~ 5ºC and their minimum TMR is ~ 4% of BMR (Table 1, Fig. 1). Even at the relatively high T_a of 19ºC, torpor bouts lasting for two days were observed in captive *C. lepidus*. Both species enter torpor at T_a 26 - 27ºC, although at these high T_a torpor lasted only for part of the day and TMR was ~ 50% of BMR because T_b during torpor remains above the T_a. Mass loss during bouts of > 12 h were ~ 2 $mg\,g^{-1}\,h^{-1}$) in *C. concinnus* and < 1 $mg\,g^{-1}\,h^{-1}$) during a 6-day torpor bout in *C. lepidus* (Geiser 1987), emphasising the effectiveness of long bouts in reducing water and energy requirements.

As for echidnas, the physiological variables of torpor in these pygmy-possums are similar to hibernators in general (Bartholomew and Hudson 1962), but at least in the laboratory torpor appears not strongly seasonal. Prolonged torpor can be induced at any time of the year by exposing individuals to low T_a. The ability of possums to reduce TMR to less than half the BMR at high T_a appears a very useful adaptation in a desert environment. Because torpor in these pygmy-possums is not highly seasonal, it appears to be an adaptation to unpredictable adverse changes in weather and food availability at any time of the year rather than a predictable winter.

Bats

Torpor in Australian bats with wide distribution ranges that include the arid zone suggests that torpor in arid zone bats is widely used. However, species that are restricted to the arid zone have not been studied in detail with regard to torpor. Five of the six families of Australian microbats (insectivorous Microchiroptera; Churchill 1998) contain species that are known to enter torpor, but most of the data are available on the family Vespertilionidae, including those species that extend their distribution into the arid zone (Kulzer *et al.* 1970; Hall 1982; Geiser 2004; Table 1). Most data are available on long-eared bats (*Nyctophilus geoffroyi* and *Nyctophilus timoriensis*), Gould's wattled bat (*Chalinolobus gouldii*) and the inland broad-nosed bat (*Scotorepens balstoni*). These species show much lower minimum T_b (1.4 - 6ºC) and TMR (~ 3 - 4% of BMR) than the dasyurids, but similar values to those found for echidnas, pygmy-possums and many other hibernating species (Hock 1951; Geiser and Ruf 1995). It is likely that these, and many related Australian bats, are capable of prolonged hibernation especially in the southern half of the continent (Lumsden and Bennett 1995; Brigham and Geiser 1998). Data from free-ranging *N. geoffroyi* show that although some foraging does occur in winter this species can remain torpid for up to two weeks (Turbill *et al.* 2003a), which at a low TMR will result in enormous reduction in energy requirements. Prolonged bouts of torpor (2 days) were even observed in summer during cool weather. However, when T_a was high in summer, bats were active for part or most of the night, although torpor during the morning was observed on 100% of roost days (Turbill *et al.* 2003b). In captivity, torpor in *N. geoffroyi* may occur at T_a as high as 27ºC, well above the hibernaculum T_a of many bats (Webb *et al.* 1996). There was a substantial drop of TMR to 25% of BMR at T_a commonly experienced in a desert environment. Similar observations with torpor at high T_a have also been made in the Angolan bat *Mops condylurus* that at times are exposed to hot T_a in their roost (Maloney *et al.* 1999).

In comparison to normothermic individuals (Baudinette *et al.* 2000), torpid bats also exhibit low water loss (Thomas and Cloutier 1992; Hosken 1997; Hosken and Withers 1997). In *N. timoriensis* (*major*) and *Chal. gouldii*, evaporative water loss at low T_a was ~ 10% of that in normothermic individuals, demonstrating that torpor is very effective not only in reducing energy expenditure, but also water requirements. This is also reflected in daily mass loss of *N. geoffroyi* which, when exposed to T_a between 5 and 10ºC and torpid for most of the day, loses only ~ 0.6 $mg\,g^{-1}\,h^{-1}$) (Geiser and Brigham 2000).

Rodents

In contrast to some other Australian arid zone mammals, little is known about torpor in Australian rodents. Predavec (1997) described a torpor-like state in a laboratory study on the sandy inland mouse (*Pseudomys hermannsburgensis*). He reported a minimum T_b of 21ºC in animals captured in November, whereas individuals captured in September were homeothermic. Although torpor use appears likely in this species, the study did not report whether the mice were able to actively rewarm from torpor, and the ~ 2.6-fold difference in BMR between November and September raises questions as to the reliability of the results. Our own observations (Drury, Seckerdiek, McAllan, Geiser, unpubl. data) suggest that captive *P. hermannsburgensis* are reluctant to enter torpor, but reduce heat loss at low T_a by a change in thermal conductance without an apparent drop of core T_b. Those individuals that lowered T_b below 30 ºC were clearly pathologically hypothermic and could not rewarm. It is possible that the same was the case in Predavec's (1997) study. However, unequivocal observations on daily torpor are available for the introduced house mouse (*Mus musculus*) (Table 1), which during the cold season were sharing nests with *S. crassicaudata* (Morton 1978a).

Clearly Australian rodents require further attention with respect to torpor. Desert rodents on other continents use torpor extensively (MacMillen 1965; Schmidt-Nielsen 1979; Lovegrove 2000) and there is no reason to predict that Australian rodents avoid torpor use. However, if heterothermy is employed in Australian rodents, daily torpor rather than prolonged hibernation is the likely pattern.

Implications of torpor on life in arid zone mammals

While torpor use has direct and obvious advantages for energy and water conservation in arid zone mammals as well as in birds (Geiser *et al*. 2004), it has other potential benefits that are rarely considered in an ecological or wildlife management context. Torpor in Australian mammals appears to be an important survival strategy, because they not only have to cope with seasonal changes in weather and food availability, but also have to survive unpredictable droughts, fire or floods. Frugal use of energy and water may be essential in coping with these challenges. However, use of torpor has other potential advantages. For example, use of torpor during reproduction in desert dasyurids allows them to reproduce on limited food and water availability, which is a truly remarkable achievement for endotherms. Torpor use during the period of development and growth, which is usually associated with an increase, rather than decrease in energy expenditure, also is a potentially crucial adaptation for life in deserts. Finally, because life span in many heterothermic mammals is longer than in related homeothermic species (Lyman *et al*. 1981; Wilkinson and South 2002), they possess the potential of survival of prolonged periods of adverse conditions. While the number of individuals surviving the bad times is likely to be low these individuals can multiply when things improve and maintain a high diversity of Australian arid zone mammals.

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REFERENCES

ARNOLD JM, 1976. Growth and bioenergetics of the Chuditch, *Dasyurus geoffroii*. PhD thesis, University of Western Australia, Perth, WA.

ASLIN HJ, 1983. Ooldea dunnart *Sminthopsis ooldea*. Pp. 54 in *Complete book of Australian mammals* ed by R Strahan. Angus and Robertson: Sydney.

AUGEE ML, EALEY EHM AND SPENCER H, 1970. Biotelemetric study of temperature regulation and torpor in the echidna, *Tachyglossus aculeatus*. *Journal of Mammalogy* **51**: 561-570.

BARTELS W, LAW BS AND GEISER F, 1998. Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). *Journal of Comparative Physiology B* **168**: 233-239.

BARNES BM, 1989. Freeze avoidance in a mammal: body temperatures below 0ºC in an Arctic hibernator. *Science* **244**: 1593-1595

BARTHOLOMEW GA AND HUDSON JW, 1962. Hibernation, estivation, temperature regulation, evaporative water loss, and heart rate of pigmy possums *Cercaertus nanus*. *Physiological Zoology* **35**: 94-107.

BAUDINETTE RV, CHURCHILL SK, CHRISTIAN KA, NELSON JE AND HUDSON PJ, 2000. Energy, water balance, and roost environment in three Australian cave-dwelling bats. *Journal of Comparative Physiology B* **170**: 439-446.

BRADSHAW D, 2003. *Vertebrate ecophysiology*. Cambridge University Press: Cambridge.

BRICE PH, GRIGG GC, BEARD LA AND DONOVAN JA, 2002. Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Australian Journal of Zoology* **50**: 461-475.

BRIGHAM RM AND GEISER F, 1998. Seasonal activity patterns of *Nyctophilus* bats based on mist-net captures. *Australian Mammalogy* **20**: 349-352.

BURBIDGE AA, MCKENZIE NL AND FULLER PJ, 1983. Long-tailed dunnart *Sminthopsis longicaudata*. Pp. 58-59 in *Complete book of Australian mammals* ed by R. Strahan. Angus and Robertson: Sydney.

CHURCHILL S, 1998. *Australian bats*. Reed: Sydney.

COLEMAN E, 1935. Hibernation and other habits of the echidna under domestication. *Victorian Naturalist* **52**: 55-62

COLLS K AND WHITAKER R 1993. *The Australian weather book*. National Book Distributers: Brookvale, Australia.

COOPER CE, 2003. Physiological specialisations of the numbat, *Myrmecobius fasciatus* Waterhouse 1836 (Marsupialia: Myrmecobiidae): a unique termitivorous marsupial. Ph.D. thesis, University of Western Australia, Perth, WA.

DAWSON TJ, 1989. Responses to cold of monotremes and marsupials. Pp. 255-288 in *Animal* *adaptation to cold* ed by LCH Wang. Springer Verlag: Berlin, Heidelberg.

Dawson TJ and Hulbert AJ, 1970. Standard metabolism, body temperature, and surface areas of Australian marsupials. *American Journal of Physiology* **218**: 1233-1238.

Dawson TJ and Wolfers JM, 1978. Metabolism, thermoregulation and torpor in shrew sized marsupials of the genus *Planigale*. *Comparative Biochemistry and Physiology* **59A**: 305-309.

Dickman CR, 1996. Vagrants in the desert. *Nature Australia* **25**: 54-62.

Ellison GTH and Skinner JD, 1992. The influence of ambient temperature on spontaneous daily torpor in pouched mice (*Saccostomus campestris*: Rodentia – Cricetidae) from southern Africa. *Journal of Thermal Biology* **17**: 25-31.

Fietz J, Tataruch F, Dausmann KH and Ganzhorn JU, 2003. White adipose tissue composition in the free-ranging fat-tailed dwarf lemur (*Cheirogaleus medius*; Primates), a tropical hibernator. *Journal of Comparative Physiology B* **173**: 1-10.

Falkenstein F, Körtner G, Watson K and Geiser F, 2001. Dietary fats and body lipid composition in relation to hibernation in free-ranging echidnas. *Journal of Comparative Physiology B* **171**: 189-194

Frey H, 1991. Energetic significance of torpor and other energy-conserving mechanisms in free-living *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae). *Australian Journal of Zoology* **39**: 689-708.

Geiser F, 1986. Thermoregulation and torpor in the Kultarr, *Antechinomys laniger* (Marsupialia: Dasyuridae). *Journal of Comparative Physiology B* **156**: 751-757.

Geiser F, 1987. Hibernation and daily torpor in two pygmy-possums (*Cercartetus* spp. Marsupialia). *Physiological Zoology* **60**: 93-102

Geiser F, 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? *Journal of Comparative Physiology B* **158**: 25-37

Geiser F, 2003. Thermal biology and energetics of carnivorous marsupials. Pp. 234-249 in *Predators with pouches: the biology of carnivorous marsupials* ed by M Jones, C Dickman and M Archer. CSIRO: Melbourne,

Geiser F, 2004. Energetics, thermal biology, and torpor in Australian bats. Pp. **??-??** in *Functional and evolutionary ecology of bats* ed by A Zubaid, GF McCracken and TH Kunz. Oxford University Press: **city?**.

Geiser F and Baudinette RV, 1987. Seasonality of torpor and thermoregulation in three dasyurid marsupials. *Journal of Comparative Physiology B* **157**: 335-344.

Geiser F and Baudinette RV, 1988. Daily torpor and thermoregulation in the small dasyurid marsupials *Planigale gilesi* and *Ningaui yvonneae*. *Australian Journal of Zoology* **36**: 473-481.

Geiser F and Masters P, 1994. Torpor in relation to reproduction in the Mulgara, *Dasycercus cristicauda* (Dasyuridae: Marsupialia). *Journal of Thermal Biology* **19**: 33-40.

Geiser F and Ruf T, 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* **68**: 935-966.

Geiser F and Brigham RM, 2000. Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). *Journal of Comparative Physiology B* **170**: 153-162.

Geiser F and Drury RL, 2003. Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *Journal of Comparative Physiology B* **173**: 55-60.

Geiser F, Matwiejczyk L and Baudinette RV, 1996. From ectothermy to heterothermy: the energetics of the Kowari, *Dasyuroides byrnei* (Marsupialia: Dasyuridae). *Physiological Zoology* **59**: 220-229.

Geiser F, Goodship N and Pavey CR, 2002. Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften* **89**: 412-414.

Geiser F, Körtner G, Maddocks TA and Brigham MR, 2004. Torpor in Australian birds. Proceedings, 23rd International Ornithological Congress, Acta Zoologica Sinica. In press.

Godfrey GK, 1968. Body temperatures and torpor in *Sminthopsis crassicaudata* and *S. larapinta* (Marsupialia: Dasyuridae). *Journal of Zoology, London* **156** : 499-511.

Grigg G and Beard L, 2000. Hibernation by echidnas in mild climates: hints about the evolution of endothermy? Pp. 5-19 in *Life in the cold: 11th International Hibernation Symposium* ed by G Heldmaier and M Klingenspor. Springer Verlag: Berlin, Heidelberg.

GRIGG GC, AUGEE ML AND BEARD LA, 1992. Thermal relations of free-living echidnas during activity and in hibernation in a cold climate. Pp. 160-173 in *Platypus and echidnas* ed by ML Augee. Royal Zoological Society of New South Wales: Sydney.

GUPPY M AND WITHERS PC, 1999. Metabolic depression in animals: physiological perspectives and biochemical generalisations. *Biological Reviews* **74**: 1-40.

HALL LS, 1982. The effect of cave microclimate on winter roosting behaviour in the bat, *Miniopterus schreibersii blepotis*. *Australian Journal of Ecology* **7**: 129-136.

HELLER HC AND HAMMEL HT, 1972. CNS control of body temperature during hibernation. *Comparative Biochemistry and Physiology* **41A**: 349-359.

HOCK RJ, 1951. The metabolic rates and body temperatures of bats. *Biological Bulletin* **101**: 289-299.

HOLLOWAY JC AND GEISER F, 1995. Influence of torpor on daily energy expenditure of the dasyurid marsupial *Sminthopsis crassicaudata*. *Comparative Biochemistry and Physiology* **112A**: 59-66.

HOLLOWAY JC AND GEISER F, 1996. Reproductive status and torpor of the marsupial *Sminthopsis crassicaudata*: effect of photoperiod. *Journal of Thermal Biology* **21**: 373-380.

HOSKEN DJ, 1997. Thermal biology and metabolism of the greater long-eared bat, *Nyctophilus major* (Chiroptera: Vespertilionidae). *Australian Journal of Zoology* **45**: 145-156.

HOSKEN DJ AND WITHERS PC, 1997. Temperature regulation and metabolism of an Australian bat, *Chalinolobus gouldii* (Chiroptera: Vespertilionidae) when euthermic and torpid. *Journal of Comparative Physiology B* **167**: 71-80.

HUDSON JW, 1973. Torpidity in mammals. Pp. 97-165 in *Comparative physiology of thermoregulation* ed by GC Whittow. Academic Press: New York.

HULBERT AJ AND DAWSON TJ, 1974. Thermoregulation in perameloid marsupials from different environments. *Comparative Biochemistry and Physiology* **47A**: 591-616.

KENNEDY PM AND MCFARLANE WV, 1971. Oxygen consumption and water turnover of the fat-tailed marsupials *Dasycercus cristicauda* and *Sminthopsis crassicaudata*. *Comparative Biochemistry and Physiology* **40A**: 723-732.

KÖRTNER G AND GEISER F, 2000a. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. *Chronobiology International* **17**: 103-128.

KÖRTNER G AND GEISER F, 2000b. Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* **123**: 350-357.

KULZER E, NELSON JE, MCKEAN J AND MÖHRES FP, 1970. Untersuchungen über die Temperaturregulation australischer Fledermäuse (Microchiroptera). *Zeitschrift für vergleichende Physiologie* **69**: 426-451.

LOVEGROVE BG, 2000. Daily heterothermy in mammals: coping with unpredictable environments. Pp. 29-40 in *Life in the cold: 11th International Hibernation Symposium* ed by G Heldmaier and M Klingenspor. Springer Verlag: Berlin, Heidelberg.

LOVEGROVE BG, KÖRTNER G AND GEISER F, 1999. The energetics of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *Journal of Comparative Physiology B* **169**: 11-18.

LUMSDEN LF AND BENNETT AF, 1995. Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research* **22**: 217-240.

LYMAN CP, O'BRIEN RC, GREEN GC AND PAPAFRANGOS ED, 1981. Hibernation and longevity in the Turkish hamster, *Mesocricetus brandti*. *Science* **212**: 668-670.

LYMAN CP, J.S. WILLIS JS, MALAN A AND WANG LCH, (eds) 1982. *Hibernation and torpor in mammals and birds*. Academic Press: New York.

MACMILLEN RE, 1965. Aestivation in the cactus mouse *Peromyscus eremicus*. *Comparative Biochemistry and Physiology* **16**: 227-247.

MALAN A, 1986. pH as a control factor in hibernation. Pp. 61-70 in *Living in the cold* ed by HC Heller, XJ Musacchia, and LCH Wang. Elsevier: New York.

MALONEY SK, BRONNER GN AND BUFFENSTEIN R, 1999. Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: a small mammal that uses hot roosts. *Physiological and Biochemical Zoology* **72**: 385-396.

MORTON SR, 1978a. Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy* **59**: 569-575.

MORTON SR, 1978b. An ecological study of *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae) III: Reproduction and life history. *Australian Wildlife Research* **5**: 183-211.

NICOL SC AND ANDERSEN NA, 1996. Hibernation in the echidna: not an adaptation to the cold? Pp. 7-12 in *Adaptations to the cold: 10th International Hibernation Symposium* ed by F Geiser, AJ Hulbert and SC Nicol. University of New England Press: Armidale, Australia.

NICOL SC AND ANDERSEN NA, 2000. Patterns of hibernation of echidnas in Tasmania. Pp. 21-28 in *Life in the cold: 11th International Hibernation Symposium* ed by G Heldmaier and M Klingenspor. Springer Verlag: Berlin, Heidelberg.

NICOL SC, ANDERSEN NA AND MESCH U, 1992. Metabolic rate and ventilatory pattern in the echidna during hibernation and arousal. Pp. 150-159 in *Platypus and echidnas* ed by ML Augee. Royal Zoological Society of New South Wales: Sydney.

PREDAVEC M, 1997. Variable energy demands in *Pseudomys hermannsburgensis*: possible ecological consequences. *Australian Journal of Zoology* **45**: 85-94.

SCHMIDT-NIELSEN K, 1979. *Desert animals: physiological problems of heat and water*. Dover Publication: New York.

SERVENTY V AND RAYMOND R, 1973. Torpidity in desert animals. *Australia's Wildlife Heritage* **14**: 2233-2240.

SONG, X., G. KÖRTNER AND F. GEISER, 1995. Reduction of metabolic rate and thermoregulation during daily torpor. *Journal of Comparative Physiology B* **165**: 291-297.

SPEAKMAN JR AND THOMAS DW, 2003. Physiological ecology and energetics of bats. Pp. 430-490 in *Bat ecology* ed by TH Kunz and MB Fenton. University of Chicago Press: Chicago.

THOMAS DW AND CLOUTIER D, 1992. Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. *Physiological Zoology* **65**: 443-456.

TURBILL C, KÖRTNER G AND GEISER F, 2003a. Daily and annual patterns of torpor by tree-roosting microbats. *Comparative Biochemistry and Physiology* **134A**, Suppl.1, 25.5: S93

TURBILL C, KÖRTNER G AND GEISER F, 2003b. Natural use of heterothermy by a small, tree-roosting bat during summer. *Physiological and Biochemical Zoology* **76**: 868-876.

TYNDALE-BISCOE H, 1973. *Life of marsupials*. Edward Arnold: London.

WALLIS RL, 1982. Adaptation to low environmental temperatures in the carnivorous marsupials. Pp. 285-290 in *Carnivorous marsupials* ed by M Archer. Royal Zoological Society of New South Wales: Sydney.

WANG LCH, 1989. Ecological, physiological, and biochemical aspects of torpor in mammals and birds. Pp. 361-401 in *Advances in comparative and environmental physiology* ed by LCH Wang. Springer Verlag: Berlin, Heidelberg.

WEBB PI, SPEAKMAN JR AND RACEY PA, 1996. How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology* **74**: 761-765.

WILKINSON GS AND SOUTH JM, 2002. Life history, ecology and longevity of bats. *Ageing Cell* **1**: 124-131.

WITHERS PC, THOMPSON GG AND SEYMOUR RS, 2000. Metabolic physiology of the north-western marsupial mole, *Notoryctes caurinus* (Marsupialia: Notoryctidae). *Australian Journal of Zoology* **48**: 241-258.