



Daily Torpor, Hibernation, and Heterothermy in Marsupials

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Contents

Introduction	2
American Marsupials	5
Didelphimorphia: Opossums	5
Paucituberculata: Shrew Opossums	7
Microbiotheria: Monito del Monte	7
Australasian Marsupials	8
Dasyuromorphia: Insectivorous/Carnivorous Marsupials	8
Notoryctemorphia: Marsupial Moles	12
Diprotodontia: Possums	13
Heterothermy in Large Marsupials	16
How Many Marsupials Express Torpor?	18
Ecological Aspects of Torpor	18
Concluding Remarks	22
Cross-References	24
References	24

Abstract

Most marsupials are small, and because they are endothermic and have high metabolic rates when active, they lose substantial amounts of energy and water. To deal with such challenges many marsupials are not permanently homeothermic, but rather they are heterothermic and can enter a state of torpor during which metabolic rate (MR), water loss, body temperature (T_b), and other

Dedicated to the memory of Francisco (Pancho) Bozinovic

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physiological functions are temporarily reduced. Torpor is used by both American and Australasian marsupials, including species from nine families ranging in body mass from ~5 g to 1000 g. Daily torpor with a reduction of metabolism and water loss by ~70% and T_b by ~10–20 °C for several hours, typically interrupted by daily foraging, is most common. Multiday torpor (hibernation) is known to occur in the Microbiotheriidae, Burramyidae, and Acrobatidae, which can reduce MR by >90% and T_b by ~30 °C to a few degrees above 0 °C. Hibernating marsupials can remain torpid for several days up to a month before periodically rewarming, perhaps because of the need to drink. As torpor saves so much energy and water it has profound effects on the ecology and biology of many marsupials. Torpor permits survival under adverse seasonal environmental conditions and periods of food and water shortages as well as persisting and reproducing in resource-poor habitats. Torpor can facilitate extreme longevity and assists survival after natural disasters via reduced energy and water demands, which permits reduced foraging and thus predator avoidance. Thus, torpor is a crucial part of the biology and ecology of many marsupial species.

Keywords

Adverse conditions · Daily torpor · Hibernation · Long-term survival · Thermal energetics · Water conservation

Introduction

Extant mammals comprise three groups, the egg-laying mammals (Monotremata, ~5 species), the pouched mammals (marsupials or Metatheria, ~345 species), and the placental mammals (Placentalia or Eutheria, >6000 species). Endothermic mammals evolved from ectothermic reptiles around 200 Mya, which required a many-fold increase in metabolic rate and therefore food requirements (Withers et al. 2016; Lovegrove 2019). The oldest subclass, the egg-laying mammals, diverged from the line leading to the therian subclass about 190 Mya, while marsupials and placental mammals diverged around 140–160 Mya (Bininda-Emonds et al. 2007; O’Leary et al. 2013). Consequently, the three mammalian lineages must have separately survived the Cretaceous-Paleogene (K-Pg) extinction of dinosaurs and many other terrestrial organisms at around 65 Mya (O’Leary et al. 2013; Lovegrove 2019). The use of heterothermy and torpor, the topic of this chapter, provides a functional avenue as to how endothermic mammals could survive this calamity (e.g., Lovegrove 2019) and how they continue to live and reproduce under adverse conditions. Consequently, torpor is an important aspect of the ecology, distribution, and abundance of marsupials.

Of the ~345 extant marsupial species, most (~225) are found in Australia and New Guinea and the rest (~120) are mainly in South and Central America. Extant marsupials are classified into seven orders, the Didelphimorphia and Paucituberculata (American marsupials; Ameridelphia), as well as the

Microbiotheria from the Americas, and the Dasyuromorphia, Peramelemorphia, Notoryctemorphia, and Diprotodontia from Australia and New Guinea. The Microbiotheria are considered to be potential ancestors of Australian marsupials as they belong to the Australidelphia along with the Australian orders, although they occur only in South America (see Riek and Geiser 2014; Withers et al. 2016).

Several biological factors predispose marsupials to the use of heterothermy to balance their energy and water budgets. Marsupials differ from the much more diverse placental mammals in their reproductive biology. The neonates of marsupials are very small, weighing only between ~5 and 900 mg or <1% of maternal body mass, much smaller relatively than neonate placental mammals (Tyndale-Biscoe 1973; Lee and Cockburn 1985). Marsupials are born after a brief period of gestation but have a long developmental period usually in a pouch when they are only partially endothermic while relying on the mother's milk for energy and nutrient supply. At the time young marsupials leave the pouch they are endothermic, but at a much smaller size than that of adults, which has significant implications for their thermal biology and energetics (Tyndale-Biscoe 1973; Geiser 2021).

Adult marsupials have a much narrower range of body masses (~5 g to 90 kg) than placental mammals (~2 g to 190 t) and aspects of their thermal biology also differ (Withers et al. 2016). Functional brown fat, important for heat production via non-shivering thermogenesis for many small placental mammals, is absent in marsupials and they use skeletal muscle for shivering and non-shivering thermogenesis instead (Oelkrug et al. 2015; Withers et al. 2016; Nowack et al. 2017b). Most marsupials have a lower resting body temperature (T_b) during normothermia than placental mammals (marsupials ~33–36 °C, placentals ~34–39 °C) and the basal metabolic rate (BMR) of marsupials (observed when animals are at rest in the thermoneutral zone, or TNZ, where no energy is required for thermoregulation) is on average about 25% below that of typical placental mammals (Dawson 1983).

The small body size of many marsupials means they have a large relative surface area for heat exchange with the environment. Therefore remaining “homeothermic” and regulating a high and constant T_b via physiological thermoregulation requires an elevated and adjustable metabolic heat production to compensate for heat loss at low ambient temperature (T_a ; Withers et al. 2016). However, maintaining a high metabolic rate (MR) relies on a regular intake of food, which is not always possible, especially for small marsupials when periods of low T_a may correspond with low food abundance. Therefore, many marsupials are not permanently homeothermic like some large endothermic mammals and birds (Hetem et al. 2016). Rather, they are “heterothermic” with a temporarily fluctuating MR, water loss, and T_b and, during certain times of the day or year, enter a state of torpor (Boyer and Barnes 1999; Geiser 2021). Torpor is characterized by substantial, controlled, and reversible reductions of MR, T_b , and other physiological functions, and results in considerable energy and water savings. Torpor is used by many birds belonging to several orders as well as members of all three mammalian lineages. Here torpor is defined as a reduction of T_b by 5 °C or more below the normothermic resting T_b or a reduction of MR by more than 25% below the resting MR (RMR) at the same T_a , including the BMR in the TNZ (Withers and Cooper 2010; Geiser 2021). Torpor was originally considered to be characteristic of species with poor thermoregulatory ability and its

prevalence among some groups of marsupials was consistent with the idea that marsupials were inferior thermoregulators compared with placental mammals (see Withers and Cooper 2010). However, marsupials are now considered to be equivalently competent endotherms as placental mammals (e.g., Dawson 1983) and torpor is recognized as a tightly controlled physiological process that provides considerable ecological advantages (Withers and Cooper 2010; Geiser 2021).

A common pattern of torpor expressed by many birds and mammals, including marsupials, is daily torpor. Species expressing this pattern of torpor are referred to as “daily heterotherms.” Daily activity patterns of these species are strongly governed by a circadian rhythm. Daily torpor is often (but not always) used during the rest phase, the torpor bout duration (TBD) is several hours, and typically animals forage daily. During daily torpor, the torpor MR (TMR) is usually reduced to ~30% of the BMR and T_b to ~18 °C on average (Ruf and Geiser 2015). Although it was often assumed in the past that daily torpor is used only occasionally and mainly during energetic emergencies, it is now known that in the field it can be used on a daily basis over several weeks and in the laboratory it can be used “spontaneously” even when food is available. In contrast, multiday torpor in the “hibernators” is known to occur in only a single bird species (the poorwill, *Phalaenoptilus nuttallii*; see Woods et al. 2019), but in many mammalian species of all three mammalian lineages (Geiser 2021). Hibernation is typically expressed during the cold season and is characterized by a sequence of deep torpor bouts during which T_b falls to nearly 5 °C with TBDs lasting for days to weeks. These torpor bouts are interrupted by brief and periodic arousals to normothermia or euthermia when T_b is maintained at high homeothermic levels (interbout euthermia, or IBE) for several hours in most. For most hibernators, the circadian rhythm does not persist during the hibernation season and many hibernators do not forage between torpor bouts during the main torpor season. The TMR of torpid hibernators falls on average to about 5% of BMR, only a fraction of that during daily torpor (Ruf and Geiser 2015).

It is often assumed that torpid mammals abandon endothermy and become ectothermic. However, torpor is a tightly controlled thermoregulatory state and mammals enter torpor only during short-wave sleep (SWS) when thermoregulating; they do not enter torpor during rapid-eye-movement (REM) sleep when thermoregulation is abandoned, and time in REM sleep decreases with the depth of torpor (see Withers and Cooper 2010). Mammals only thermoconform when T_a and T_b are above the torpor T_b set point, which may occur over a wide range of T_b and T_a . Above the T_b set point MR falls curvilinearly with T_b , largely consistent with a Q_{10} effect. When the T_b reaches its species-specific T_b set point, endothermic thermoregulation via proportional metabolic heat production is activated to maintain T_b at or above this minimum (Heller and Hammel 1972). This is in contrast to hypothermia, during which the reduction of MR and T_b is uncontrolled (Geiser 2021). Moreover, at the end of a torpor bout torpid mammals can achieve rewarming from torpor entirely via endogenous heat production while pathologically hypothermic mammals can only rewarm with the aid of an external heat source.

Torpor is common among marsupials of both the Ameridelphia and Australidelphia (Cooper and Geiser 2008; Geiser and Körtner 2010; Riek and Geiser

2014). Torpor in Australian marsupials was described as early as 1926, when it was stated that pygmy-possums of the genus *Cercartetus* “spend part of the winter hibernating” (Le Souef et al. 1926). For South American marsupials it was reported in 1924 that opossums (*Marmosa elegans*) exhibited hibernation that was just as deep as that of hazel dormice and marmots (Krieg 1924). It is now known that five of the seven marsupial orders contain known heterothermic species and express torpor, and a sixth, the shrew opossums (Paucituberculata, Caenolestidae), are probably heterothermic (González et al. 2020). Only for the Peramelemorphia, the omnivorous bandicoots (Hume 1999), has torpor has not been documented for any species. This chapter describes the diversity of heterothermy in marsupials and then discusses its ecological implications.

American Marsupials

Didelphimorphia: Opossums

The opossums (Didelphimorphia, family Didelphidae) are often confused with the Australian possums (Diprotodontia, see below). However, opossums occur in South and Central America and one in North America north of Mexico and diverged from the Australidelphia about 90 Mya (Bininda-Emonds et al. 2007). The largely insectivorous/carnivorous or omnivorous opossums (Hume 1999) are considered to be the oldest extant marsupial group (Bininda-Emonds et al. 2007). Most carnivorous/insectivorous opossums are small and several use daily torpor (Table 1). Daily torpor in the insectivorous murine opossum (*Gracilinanus*

Table 1 Torpor use by American marsupials

Family/species	Body mass (g)	Torpor pattern
Didelphidae		
<i>Gracilinanus microtarsus</i>	13	Daily torpor
<i>Gracilinanus agilis</i>	30	Daily torpor
<i>Thylamys elegans</i>	30	Daily torpor
<i>Lestodelphys halli</i>	50	Multiday, deep torpor ^a
<i>Micoureus paraguayanus</i>	70	Daily torpor? ^b
<i>Monodelphis brevicaudata</i>	40	Daily torpor
<i>Monodelphis domestica</i>	100	Daily torpor
<i>Marmosa robinsoni</i>	120	Daily torpor
Caenolestidae		
<i>Rhyncholestes raphanurus</i>	~40	Torpor suspected ^c
Microbiotheriidae		
<i>Dromiciops gliroides</i>	30	Multiday, deep torpor

Data from Riek and Geiser (2014), with additional information from Kelt and Martinez (1989)^c, Cooper et al. (2010)^b, and Geiser and Martin (2013)^a

Torpor Pattern: Daily torpor lasts for <24 h with minimum T_b maintained >10 °C. Multiday, deep torpor describes hibernators capable of expressing torpor bouts of >1 day, often lasting for weeks, with minimum T_b typically decreasing to <10 °C

microtarsus, 13 g) lasted for up to 8 h and is lowered T_b to $\sim 16^\circ\text{C}$ (Morrison and McNab 1962). Similar torpor patterns have been recorded for 30 g *G. agilis* and *Thylamys elegans* (see Ruf and Geiser 2015). During daily torpor, small opossums often reduce MR to $\sim 20\text{--}50\%$ of BMR and water loss to $\sim 30\%$ that of normothermic individuals (see Ruf and Geiser 2015). The slightly larger ($\sim 70\text{--}120$ g) omnivorous opossums, the Long-furred Woolly Mouse Opossum (*Micoureus paraguayanus*), Robinson's Mouse Opossum (*Marmosa robinsoni*), the Northern Red-sided Opossum (*Monodelphis brevicaudata*), and the Gray Short-tailed Opossum (*Monodelphis domestica*) also express daily torpor with minimum T_b s from ~ 20 to 25°C (see Cooper et al. 2010; Riek and Geiser 2014).

The Patagonian Opossum (*Lestodelphys halli*, 50 g) lives further south than any other marsupial, inhabiting xeric environments of Patagonia in southern Argentina. It is carnivorous and shows extreme caudal fat storage in autumn when its tail changes from a flat beaver tail-shaped to an incrassated carrot-shaped tail, suggesting that this species faces energy bottlenecks in winter. For captive *L. halli* in autumn the normothermic T_b in resting individuals was $\sim 33\text{--}35^\circ\text{C}$ and increased during activity to $\sim 38^\circ\text{C}$ (Fig. 1). However, after animals had fattened and mainly when food was withheld, T_b was substantially reduced and the animals entered a state of torpor (Geiser and Martin 2013). Occasional spontaneous torpor when food was available was observed (Fig. 1). The minimum T_b measured during torpor was 7.7°C and opossums remained torpid for up to almost 2 days (Fig. 1). As the $T_b\text{--}T_a$ differential during torpor at low T_a was often $<1^\circ\text{C}$ (Fig. 1), it appears that T_b was not defended during torpor at the T_a measured and opossums were still thermoconforming, which is typical for hibernators, not daily heterotherms, so it is likely that the torpor T_b set point is $<7.7^\circ\text{C}$. This opossum was extremely difficult to capture; only two males

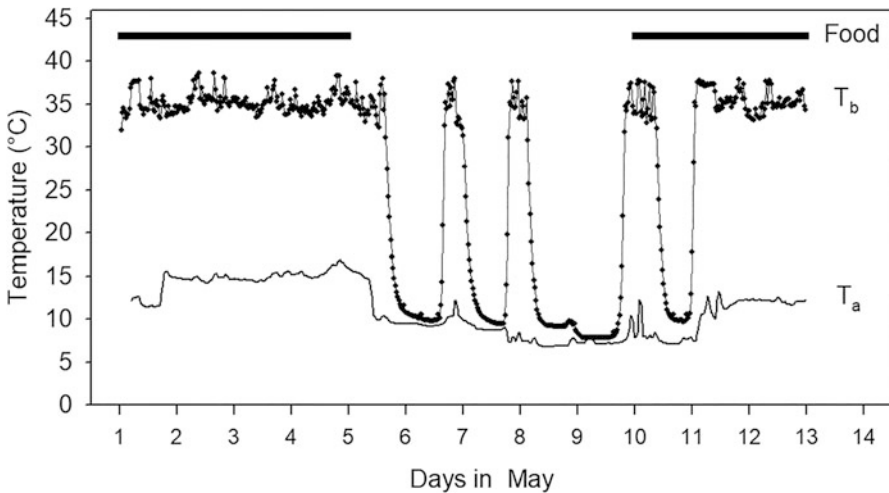


Fig. 1 The body temperature (T_b , measured in 30-min intervals) of *Lestodelphys halli* (~ 50 g) and the corresponding ambient temperature (T_a) as a function of time. The horizontal black bars indicate food was available. (Data from Geiser and Martin (2013))

were caught despite extensive trapping efforts. The low capture rate may have been due to extensive torpor use during late autumn and it is possible the hibernation season had already commenced for the females (Geiser and Martin 2013). The prolonged and deep torpor observed for *L. halli* is the first time this pattern of torpor has been observed among the Didelphimorphia and raises the question of whether some opossums are able to hibernate.

Paucituberculata: Shrew Opossums

Published data on torpor for the South American shrew opossums (Paucituberculata, family Caenolestidae) are not available. However, various aspects of their biology suggest that they likely use torpor (Kelt and Martinez 1989). They are small and largely insectivorous and inhabit cool, wet, temperate rainforests. The Long-nosed Shrew Opossum (*Rhyncholestes raphanurus*, ~40 g) seasonally stores fat in its tail suggesting periodic food shortages and caudal fat storage has been related to heterothermy (Kelt and Martinez 1989). Temporal variability in the capture of this species, with more numerous captures in late summer (Patterson and Gallardo 1987), also suggests that it may use torpor during cooler periods.

Microbiotheria: Monito del Monte

The single extant species of the marsupial order Microbiotheria (family Microbiotheriidae) is the insectivorous Monito del Monte (*Dromiciops gliroides*, 30 g). It is interesting from an evolutionary point of view, because, despite its exclusively South American distribution, Australian marsupials are thought to have been derived from their ancestor (O'Leary et al. 2013). Therefore, it is likely that all Australian marsupials, including the largely homeothermic kangaroos, koala, and wombats, as well as the bandicoots, evolved from the ancestor of a hibernating species. *Dromiciops* is found along the Andes in the wet forests of southern Argentina and Chile. It can express multiday torpor bouts lasting up to 5 days and thus seems to differ from most didelphid opossums (Table 1). In the wild the species fattens in autumn and disappears during winter, suggesting that it hibernates during this time (Grant and Temple-Smith 1987).

Dromiciops can lower TMR to only ~1% of normothermic RMR and T_b to ~4 °C, similar to many placental hibernators (Bozinovic et al. 2004). Photoperiod combined with food availability is the most important driver of torpor use for *Dromiciops* and females enter torpor even when carrying pouch young and lactating (Nespolo et al. 2021). During torpor, the evaporative water loss of *Dromiciops* was reduced to as little as 21% of normothermic values, but its relative water economy (RWE; metabolic water production/evaporative water loss) was less favorable than during normothermia as torpid *Dromiciops* never achieved water balance. In normothermic animals RWE was positive (i.e., water loss < metabolic water production) at $T_a < 15.4$ °C (Withers et al. 2012).

Australasian Marsupials

Dasyuromorphia: Insectivorous/Carnivorous Marsupials

Dasyuromorph marsupials from Australia and New Guinea are a diverse group of insectivorous/carnivorous mammals. They comprise about 75 species, or ~22% of all extant marsupial species. The families Dasyuridae (insectivorous/carnivorous marsupials), Myrmecobiidae (Numbat), and the recently (1936) extinct Thylacinidae, the Tasmanian “Wolf” or Thylacine, belong to this order (Withers et al. 2016).

Dasyurid marsupials are largely nocturnal or crepuscular, but during winter they may be diurnal (Pavey et al. 2016; Stawski et al. 2015). In normothermic resting dasyurids the T_b typically ranges from 34 °C to 36 °C. Many dasyurids are known to use daily torpor (see Fig. 2) and this has been observed in ~31 species or >50% of all Australian dasyurid species (Table 2). Dasyurids are especially successful in the center of the continent, which is largely arid or semi-arid, and living there likely is facilitated by their extensive use of heterothermy (Withers et al. 2004; Geiser and Körtner 2010). As multiday torpor has not been recorded for any species to date, it is highly likely that most, if not all, heterothermic members of this family use shallow daily rather than deep multiday torpor (Table 2). Use of daily torpor is known for species ranging in body mass from ~5 g planigales (*Planigale* spp.) to ~1 kg quolls (*Dasyurus* spp.; Table 2), so daily torpor is not restricted to only small dasyurids,

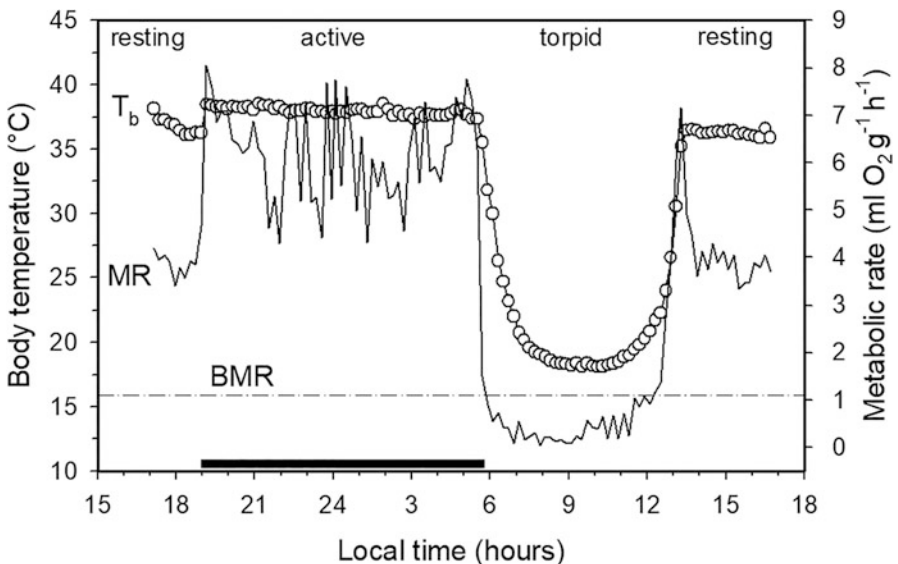


Fig. 2 The body temperature (T_b , measured in 12-min intervals) of a Stripe-faced Dunnart (*Sminthopsis macroura*) (~25 g) and the corresponding metabolic rate measured via oxygen consumption as a function of time. Food was not available during the measurement. The basal metabolic rate (BMR, dash-dotted line) is shown for reference and the black horizontal bar indicates night. (Modified from Geiser (2021))

Table 2 Torpor use by Australian marsupials

Family/species	Body mass (g)	Torpor pattern
Dasyuridae		
<i>Planigale ingrami</i>	6–9	Daily torpor
<i>Planigale tenuirostris</i>	7	Daily torpor
<i>Planigale gilesi</i>	8	Daily torpor
<i>Planigale maculata</i>	10–16	Daily torpor
<i>Ningau ridei</i>	9	Daily torpor ^a
<i>Ningau yvonneae</i>	10–13	Daily torpor
<i>Sminthopsis dolichura</i>	8–9	Daily torpor ^a
<i>Sminthopsis youngsoni</i>	10	Daily torpor ^a
<i>Sminthopsis longicaudata</i>	11	Daily torpor ^b
<i>Sminthopsis fuliginosus</i>	13	Daily torpor ^a
<i>Sminthopsis hirtipes</i>	15	Daily torpor ^a
<i>Sminthopsis crassicaudata</i>	17	Daily torpor
<i>Sminthopsis murina</i>	18	Daily torpor
<i>Sminthopsis macroura</i>	20–28	Daily torpor
<i>Sminthopsis granulipes</i>	26	Daily torpor ^a
<i>Sminthopsis psammophila</i>	35–44	Daily torpor
<i>Sminthopsis douglasi</i>	60	Daily torpor
<i>Antechinomys laniger</i>	27	Daily torpor
<i>Dasykaluta rosamondae</i>	27	Daily torpor
<i>Antechinus agilis</i>	18–30	Daily torpor
<i>Antechinus stuartii</i>	20–60	Daily torpor
<i>Antechinus flavipes</i>	30–70	Daily torpor
<i>Antechinus mimetes</i>	50–100	Daily torpor ^c
<i>Dasyercus cristicauda</i>	70–110	Daily torpor
<i>Dasyercus blythi</i>	60–85	Daily torpor ^d
<i>Phascogale calura</i>	35	Daily torpor
<i>Phascogale tapoatafa</i>	110–135	Daily torpor ^e
<i>Dayuroides byrnei</i>	120	Daily torpor
<i>Dasyurus hallucatus</i>	500	Daily torpor
<i>Dasyurus geoffroyi</i>	1000	Daily torpor
<i>Dasyurus viverrinus</i>	1000	Daily torpor
Myrmecobiidae		
<i>Myrmecobius fasciatus</i>	500	Daily torpor
Notoryctidae		
<i>Notoryctes caurinus</i>	35	Extremely thermolabile
<i>Notoryctes typhlops</i>	60	Torpor suspected ^f
Burramyidae		
<i>Cercartetus concinnus</i>	18	Multiday, deep torpor
<i>Cercartetus lepidus</i>	12	Multiday, deep torpor
<i>Cercartetus nanus</i>	20–40	Multiday, deep torpor
<i>Cercartetus caudatus</i>	30	Multiday, deep torpor ^{g, a}
<i>Burramys parvus</i>	60	Multiday, deep torpor

(continued)

Table 2 (continued)

Family/species	Body mass (g)	Torpor pattern
Acrobatidae		
<i>Acrobates pygmaeus</i>	12	Multiday, deep torpor
Tarsipedidae		
<i>Tarsipes rostratus</i>	10	Daily torpor
Petauridae		
<i>Gymnobelideus leadbeateri</i>	130	Daily torpor ^h
<i>Petaurus breviceps</i>	130	Daily torpor
<i>Petaurus norfolcensis</i>	230	Daily torpor ⁱ
<i>Petaurus australis</i>	600	Torpor suspected ^j

Data from Riek and Geiser (2014), with additional information from Tyndale-Biscoe (1973)^f, Gotts (1976)^c, Smith (1980)^h, Atherton and Haffenden (1982)^g, Dixon and Huxley (1989)^e, Burbidge et al. (2008)^b, Pavey et al. (2009)^d, Geiser and Körtner (2010)^j, Dausmann et al. (2023)ⁱ, and Cooper and Withers (unpublished observations)^a

Torpor Pattern: Daily torpor lasts for <24 h with minimum T_b maintained >10 °C. Multiday, deep torpor describes hibernators capable of expressing torpor bouts of >1 day, often lasting for weeks, with minimum T_b typically decreasing to <10 °C

although the minimum T_b s of the larger *Dasyurus* spp. appear higher than for the smaller species (Riek and Geiser 2014). For example, captive Western Quolls (*D. geoffroyi*, 1000 g) reduced T_b during torpor to a minimum of 23.1 °C (Arnold 1976). It may be that the relatively large body mass of the biggest species of quoll (*D. maculatus*) and Tasmanian Devil (*Sarcophilus harrisi*) reduces the need for torpor use in this group (Jones et al. 1997). However, despite a lack of torpor observed for free-ranging Eastern Quolls (*D. viverrinus*) during a Tasmanian winter by Jones et al. (1997), torpor was observed in a subsequent study on the species, during which T_b reductions by up to 10 °C for several hours were observed (Moyle in Reardon 1999), suggesting torpor use by these relatively large dasyurids may be highly flexible.

The minimum T_b during torpor for dasyurids ranges from 11 °C for Kultarrs (*Antechinomys laniger*, 27 g) to ~28 °C for Northern Quolls (500 g), and minimum TMRs for captive dasyurids range from about 10–60% of BMR. The duration of torpor bouts is typically 2–8 h, but torpor can last for up to 19.5 h in captivity (Riek and Geiser 2014; Ruf and Geiser 2015). Even torpor bouts of up to 25.9 h have been measured in the wild, but with high T_b s of ~23–26 °C after partial rewarming during the latter hours of the bout (Körtner and Geiser 2009). The absolute evaporative water loss of torpid dasyurids is reduced to as little as 25% of that for normothermic individuals at the same T_a . However, as for the *Dromiciops*, the RWE of torpid dasyurids is less favorable than during normothermia as torpid dasyurids are in negative water balance (e.g., Cooper et al. 2005).

Free-ranging dasyurids usually express more pronounced and deeper daily torpor and TBD is about two-fold of that for individuals in captivity (Warnecke et al. 2008; Körtner and Geiser 2009). Torpor in the wild can be used daily during winter to reduce foraging times to a few hours per day or even eliminate foraging altogether for several days (e.g., Warnecke et al. 2008; Körtner and Geiser 2009). In the arid

zone of Australia, extensive knowledge has been accumulated about wild dunnarts (*Sminthopsis* spp. 17–24 g). In autumn and winter, these small species enter daily torpor essentially every day for about half a day, typically beginning around midnight with arousal the following morning and regularly sun bask, exploiting solar radiation to lower the energetic cost of arousal from torpor (Warnecke et al. 2008), and similar observations have been made for pseudantechinus (*Pseudantechinus macdonnellensis*, ~30 g; Geiser et al. 2002). For the medium-sized mulgaras (*Dasyercus blythi*, ~60–80 g; *D. cristicauda*, ~70–110 g) in arid central Australia, the frequency of torpor use and the TBD were reduced when the proportion of vertebrates in their diet was high, likely because of the larger meal size and energy content of vertebrates (Pavey et al. 2009). Torpor patterns in free-ranging *D. blythi* also differed between sexes with the smaller females (62 g) using torpor more than the males (84 g), although surprisingly, torpor expression was not impacted by habitat or weather (Körtner et al. 2016).

Torpor is not restricted to arid zone dasyurids. In cool-temperate montane forests in southeastern Australia, free-ranging Brown (*Antechinus stuartii*, ~23 g) and Yellow-footed Antechinus (*A. flavipes*, ~30 g) also enter torpor frequently in winter (Parker et al. 2019; Hume et al. 2020). For female Brown Antechinus, torpor was observed on >82% of days in winter with a strong influence of weather; torpor frequency and duration increased with decreasing T_a on cold, dry days (Hume et al. 2020).

Season affects torpor patterns of small dasyurids, but daily torpor is typically expressed throughout most of the year, at least in captivity. Expression of spontaneous torpor (food available) by dunnarts (*S. macroura* and *S. crassicaudata*) held outdoors occurred throughout the year, but torpor frequency was reduced in summer, and this was accompanied by an increase in the regulated minimum T_b and minimum TMR (Geiser and Baudinette 1987). Torpor was over five-fold more frequent when food was withheld. Captive *S. crassicaudata* also increased torpor use in response to an unpredictable food supply (Munn et al. 2010). Thermal biology, including torpor use, is subject to developmental phenotypic flexibility in dasyurids. *S. crassicaudata* reared at low T_a underwent more frequent and deeper torpor bouts than those raised at higher T_a (Riek and Geiser 2012).

Torpor is used during the development and growth of juvenile dasyurids after they leave the mother's pouch when they are endothermic and thermoregulatory energy expenditure is potentially high because of their small size (Geiser et al. 2006). Likely because of this, torpor is often more pronounced in half-grown juveniles than in adult dasyurids. Torpor is used by *Dasyercus* spp. during the period of mating and pregnancy (up to 95% of days) by both captive and free-ranging individuals (Geiser and Masters 1994; Körtner et al. 2008). Pregnant *Dasyercus* spp. apparently use torpor to store fat for the energetically more expensive period of lactation when torpor does not seem to occur (Geiser and Masters 1994; Körtner et al. 2008). The reproductive strategy of antechinus is particularly interesting; males are semelparous and live for only ~11 months before undergoing a complete post-mating mortality, while most females die after weaning of the young at an age of about 1.5 years. For free-ranging Yellow-footed Antechinus, torpor expression was strongly affected by

reproductive condition and sex, although minimum T_b was affected by T_a . Non-reproductive females in the wild used torpor on 60–90% of days, but pregnant females on only 28% of days. However, males before the mating period used torpor on 64% of days while during mating only on ~25% of days (Parker et al. 2019). Thus torpor use in *A. flavipes* is modified similarly by reproductive status as in the medium-sized arid zone *Dasyercus* spp. For many placental mammals living in highly seasonal areas, especially the sciurid rodents and hamsters, torpor is typically but not always avoided during the period of reproduction (McAllan and Geiser 2014; Geiser 2021). However, insectivorous bats use torpor extensively during pregnancy and lactation although torpor is often (not always) less deep and prolonged than for non-reproductive individuals (see McAllan and Geiser 2014). Other placental mammals that are known to use torpor during reproduction include shrew tenrecs (*Microgale* spp.), the Mouse Lemur (*Microcebus murinus*), and the Hazel Dormouse (*Muscardinus avellanarius*; see Geiser 2021).

Numbats (*Myrmecobius fasciatus*, ~500 g) belong to the monospecific family Myrmecobiidae and are exclusively termitivorous in the wild. Numbats were formerly distributed over much of southern and central Australia; however, since European settlement, only two natural populations persist in eucalypt forests in the southwest of Western Australia. Numbats are unusual among marsupials in that they are completely diurnal, timing their activity to coincide with the activity of termites in subterranean soil galleries; consequently, they also avoid activity during extremely hot and cold, wet periods, when termite activity is reduced (Cooper 2011). Numbats use daily torpor during their nighttime rest phase, with a maximum TBD of 15 h and a minimum T_b of 19 °C in the wild and in captivity (Cooper and Withers 2004). Torpor was spontaneous for captive Numbats. In the wild Numbats use fallen logs, tree hollows, or burrows lined with an insulating nest as night retreats which buffer environmental extremes and also provide them with a secure location to enter torpor with minimal predation risk; in winter Numbats enter torpor on 90% of nights. Torpor reduces the daily energy requirements of a Numbat by up to 42%, particularly important for a species feeding on a low-energy density diet (Cooper and Withers 2004). Interestingly, Numbats do not appear to exploit solar radiation to reduce the energetic costs of arousal from torpor, unlike some small dasyurids (e.g., Warnecke et al. 2008), despite a pelt which facilitates extremely high solar heat gain (Cooper 2011).

Sadly, there are no physiological data for the other dasyuromorph family, the extinct Thylacinidae. However, the large size and high-energy carnivorous diet of the thylacine makes torpor unlikely for this species.

Notoryctemorphia: Marsupial Moles

The marsupial moles (*Notoryctes* spp., family Notoryctidae) are two insectivorous species. They are burrowers that live almost entirely underground in the sand dune deserts of inland Australia. Knowledge about the thermal biology of marsupial moles is scant, but captive *N. caurinus* had a low and labile T_b ranging from

22.7 °C to 30.8 °C (Withers et al. 2000). The low T_b of *N. caurinus* was not associated with any other typical torpor characteristics such as inactivity, unresponsiveness, or a stereotypical torpor posture (P. Withers, 2022, personal communication).

Diprotodontia: Possums

The diprotodont marsupials are found in Australia and New Guinea and include 11 families. Kangaroos, koalas, wombats, possums, and their relatives belong to this marsupial order. Torpor has been observed in four of the “possum” families (Table 2), the pygmy-possums (Burramyidae), feathertail gliders (Acrobatidae), Honey Possum (Tarsipedidae), and the Petauridae, containing small species of both gliding and non-gliding possums (see Riek and Geiser 2014).

The pygmy-possums (Burramyidae) are five species of small insectivorous/nectarivorous marsupials living in Australia and New Guinea. The study of the physiology of torpor of pygmy-possums has a long history and all species that have been investigated in some detail enter multiday torpor and are able to hibernate (see Riek and Geiser 2014). At low T_a , they undergo torpor bouts lasting for up to 4 weeks. Torpid pygmy-possums lower T_b to minima of ~2–6 °C and their minimum TMR is only ~2–4% of BMR, near the minima observed for hibernators in general (Ruf and Geiser 2015). Heart rates of torpid Eastern Pygmy-possums (*Cercartetus nanus*, ~35 g, ~20–50 g body mass range) with a T_b of 8 °C were as low as 8 beats min^{-1} , reduced from 630 beats min^{-1} for normothermic individuals, which is similar to the reduction of heart rate for other hibernators (Swoap et al. 2017). When hibernating at low T_b , all pygmy-possums, like many other hibernating mammals, adopt a spherical posture, with appendages tucked under their body; they retain this posture during the arousal process presumably to minimize heat loss.

Eastern Pygmy-possums are found along the southeastern coast and ranges of Australia. They can fatten extensively permitting individuals weighing about 50 g, when maintained at low T_a of 7 °C and without access to food, to hibernate for up to an entire year fueled entirely by stored fat (Geiser 2007). Frequent arousals occurred early during the hibernation season and mass loss was rapid, but mass loss stabilized when animals began to use multiday torpor bouts after several weeks. A hibernation season of more than the ~6 months typically required in the wild (Geiser 2021) suggests that a large safety margin has been favored by natural selection as a result of the unpredictable rainfall and food availability in their habitat. Hibernation for up to 1 year also shows that torpor expression in the genus *Cercartetus* is not strongly seasonal. During any time of the year prolonged torpor can be induced by exposure to low T_a in captivity. In the wild, multiday and short bouts of torpor have been observed in winter, whereas during summer bouts of torpor for *C. nanus* were typically brief (Turner et al. 2012a).

In a Mediterranean climate in South Australia, free-ranging Western Pygmy-possums (*C. concinnus*, 18 g) hibernated in winter. During the cold season they

exhibited both brief and multiday bouts torpor lasting up to 8 days (Turner et al. 2012b). Western Pygmy-possums have not been examined for torpor expression in summer in the field. However, individuals in captivity, as well as Little Pygmy-possums (*C. lepidus*, 12 g), do enter spontaneous torpor throughout the year. Photoperiod influenced TBD for both *C. nanus* and *C. concinnus* held at a constant T_a of 20 °C and natural photoperiod with an increase in TBD during the short winter photoperiod (Turner and Geiser 2017). Even at high T_a s of 26–30 °C, Eastern, Western, and Little Pygmy-possums entered bouts of torpor, but under these thermal conditions, torpor bouts lasted only for part of the day. However, these brief bouts of torpor do not appear to be daily torpor, as expressed by the daily heterotherms, but rather short bouts of hibernation, apparently limited in duration by the high T_a and consequently high T_b and TMR (Geiser 2021). For *C. nanus* expressing torpor at high T_a s near the TNZ, the TMR was about 50% of BMR (rather than ~3% of BMR at low T_b and T_a), although T_b was reduced by only ~2.5 °C (Song et al. 1997), similar to tropical bats in Madagascar (Reher and Dausmann 2021). The thermal biology of the tropical Long-tailed Pygmy-possum (*C. caudatus*, 30 g), found in northern Queensland and Papua New Guinea, has not been examined in detail, but it is known to undergo torpor (Atherton and Haffenden 1982; Table 2). The largely aseasonal expression of torpor by pygmy-possums of the genus *Cercartetus* suggests that it is an adaptation to unpredictable adverse changes in food availability and the thermal environment throughout the year, not just an overwintering strategy.

The largest species in the burramyid family is the endangered Mountain Pygmy-possum (*Burramys parvus*, ~40–70 g). It is now restricted to high elevations in the Australian Alps of southeastern Australia, but used to have a much wider distribution during the last glacial period in the Pleistocene (Archer et al. 2019). The remnant population of ~2000 individuals lives on/near mountain tops in glacial boulder fields on “sky islands” (Mansergh and Broome 1994). The diet of *Burramys* is highly seasonal; it feeds predominantly on Bogong Moths (*Agrotis infusa*) that migrate to the mountains to aestivate during summer and succulent fruits and seeds from the Mountain Plum-pine (*Podocarpus lawrencei*). Activity and hibernation of *Burramys* are more seasonal than for the other members of the family, reflecting the highly seasonal snow cover and food availability of their mountain habitat (Broome et al. 2012).

For *Burramys*, after autumnal fattening, the hibernation season is about 7 months for adults and 5–6 months for juveniles, lasting from late autumn until spring, but the time of snow melt affects the time hibernation is terminated in the wild (Geiser et al. 1990; Körtner and Geiser 1998). During hibernation *Burramys* are largely aphagic, and their independence from food for >6 months is probably the main reason they survive over winter under snow. *Burramys* remain in subnivean hibernacula until spring food sources are available and therefore highly seasonal torpor is more beneficial than for other pygmy-possums (Körtner and Geiser 1998). Interestingly, *Burramys* bred in captivity and raised under warm thermal conditions did not fatten and never hibernated, although they were held under identical conditions as wild-caught individuals, which did fatten and hibernated for months (Geiser et al. 1990). This developmental plasticity complicates reintroduction of the species to the wild where hibernation is crucial for winter survival. More recently, however, mothers

and young were held under thermal conditions similar to those in the wild and offspring released to the wild survived and have successfully bred (Parrott et al. 2017).

Torpor patterns of *Burramys* are strongly temperature-dependent, with the lowest TMR and the longest TBD occurring at T_a of $\sim 2^\circ\text{C}$, which is the T_a they experience in their subnivean hibernacula (Geiser and Broome 1993; Körtner and Geiser 1998). A change in T_a , caused by the predicted reduction of snow cover due to climate change, will impact the energetics of hibernation and therefore the overwinter survival of this species, an important factor that impacts the demographics and population of this critically endangered species (Broome 2001). Likewise, the availability of liquid drinking water in hibernacula may be important for pygmy-possums to maintain hibernation until food is available in spring. Drinking to maintain water balance is one likely reason why hibernators must undergo periodic arousals from torpor during the hibernation season (Thomas and Geiser 1997). If *Burramys* eat snow to obtain this water, the energy required to melt and then warm the snow to normothermic T_b would reduce the hibernation season by ~ 30 days, compared to only ~ 9 days for drinking liquid water (Cooper and Withers 2014).

Feathertail gliders (*Acrobates pygmaeus*, $\sim 12\text{--}14$ g, and *A. frontalis*, $\sim 12\text{--}19$ g) and the Feather-tailed Possum (*Distoechurus pennatus*, $\sim 40\text{--}50$ g) of the family Acrobatidae are small insectivorous/nectarivorous marsupials found in Australia and New Guinea. Feathertail gliders use torpor both in the wild and in captivity (Frey and Fleming 1984; Geiser and Ferguson 2001). In captive *A. pygmaeus*, torpor lasted up to 8 days; the minimum T_b was as low as 2°C , and at a T_a of 5°C , the TMR was only about 1% of the RMR of normothermic animals, and only 6% of the BMR in the TNZ (Geiser and Ferguson 2001). Although the pattern of torpor for feathertail gliders is similar to that of pygmy-possums (Burramyidae), *A. pygmaeus* does not fatten extensively unlike the pygmy-possums and many other hibernators, being more similar to some bats (Geiser 2021). Free-ranging feathertail gliders had a more or less constant body mass of about 13.5 g from autumn to spring and aroused daily from torpor during that time (Frey and Fleming 1984). Torpor in captive-bred feathertail gliders was less pronounced (shorter TBD, higher minimum T_b) than that expressed by wild-caught individuals, suggesting developmental phenotypic plasticity (Geiser and Ferguson 2001). Torpor expression also differed for gliders from different habitats, with animals in montane regions entering deeper torpor than those from subtropical coastal areas (Geiser and Ferguson 2001). Data on torpor in the Feather-tailed Possum from Papua New Guinea are not available, but it is likely that they are heterothermic, since they are small, feed on insects and fruit, and often nest alone in tree hollows.

The Honey Possum (*Tarsipes rostratus*, 10 g) is the only extant species in the family Tarsipedidae and is restricted to southwestern Australia where high floral diversity ensures a year-round supply of flowering plants which provide the nectar and pollen on which this species feeds. In the wild, Honey Possums use torpor mainly during the cold season between autumn and spring, but a few individuals were observed torpid during summer (Bradshaw and Bradshaw 2012). In captivity, the species attains a torpor T_b as low as $\sim 5^\circ\text{C}$, similar to that of hibernators on average. The minimum TMR was also similar to that of small hibernators, but they

did not remain torpid for more than 10 h (Withers et al. 1990), indicating an unusual torpor pattern of deep, but brief (<24 h) torpor. Presumably the very small size of the Honey Possum (5–15 g) facilitates daily rewarming from a very low T_b . It is possible that longer-term field studies (logistically challenging due to the very small size of this species) might reveal multiday torpor, consistent with that observed for other small possums and their low T_b during torpor. However, the restriction of Honey Possums to a region with year-round food availability suggests that longer-term hibernation to withstand seasonal food shortages, as seen for *Burramys*, is not an element of Honey Possum biology.

Daily torpor is widespread among the largely insectivorous/nectarivorous Petauridae, but hibernation has not been documented despite long-term field studies (Table 2). Daily torpor has been observed for Sugar Gliders (*Petaurus breviceps*, 130 g), the similar-sized non-gliding Leadbeater's Possum (*Gymnobelideus leadbeateri*), and Squirrel Gliders (*P. norfolcensis*, 230 g; Dausmann et al. 2023) and there are anecdotal reports about torpor use by the much larger Yellow-bellied Glider (*P. australis*, 600 g Table 2). Captive *P. breviceps* reluctantly enter periods of shallow daily torpor, mainly when food is withheld, and use a combination of huddling and torpor to reduce energy expenditure (Nowack and Geiser 2016). In torpid *P. breviceps* in captivity, the minimum TMR is approximately 10% of that for normothermic and resting individuals (see Ruf and Geiser 2015).

Torpor expression by *P. breviceps* is strongly affected by captivity. Free-ranging gliders in a cool-temperate area entered torpor more frequently and T_b decreased to a lower level (mean minimum T_b 12.9 °C) than captive gliders (mean minimum T_b 22.2 °C), even though the latter were held under outdoor conditions that were thermally similar to those in the wild (Geiser et al. 2007). In free-ranging *P. breviceps* at an elevation of ~1000 m in southeastern Australia, daily torpor, interrupted by arousal around dusk, was often observed over a sequence of several days during periods of cold and wet conditions, often preceded by a three-day reduction in normothermic T_b before entry into daily torpor (Christian and Geiser 2007). The minimum torpor T_b was 10.4 °C and gliders remained torpid for up to 23 h (mean 13 h; Körtner and Geiser 2000). Torpor among petaurids appears to be driven at least partly by resource availability, not just as a response to low T_a . Free-ranging Sugar Gliders expressed torpor during a subtropical cyclone in Royal National Park south of Sydney, even though thermal conditions were mild, presumably to reduce the need to forage and improve the chance for survival during the cyclone (Nowack et al. 2015). Wild Squirrel Gliders (*P. norfolcensis*) in the Warrumbungle National Park of southeastern Australia expressed more torpor in spring than winter, perhaps to deal with short-term food restrictions (Dausmann et al. 2023).

Heterothermy in Large Marsupials

Most marsupials for which torpor has been observed are small and weigh less than 100 g; the median body mass for marsupials expressing torpor is 30 g (Tables 1 and 2). For comparison, the median body mass for all mammalian daily heterotherms is

26 g and that for mammalian hibernators 68 g (Ruf and Geiser 2015). The largest marsupials for which torpor has been documented are the quolls, weighing ~0.5–1 kg. This body mass is well below the maxima of ~7–9 kg of short-beaked echidnas (*Tachyglossus aculeatus*: monotreme) and marmots (placental) that undergo periods of extended and deep hibernation, with T_b s well below 10 °C. This may be because the occurrence and patterns of torpor use among marsupials are strongly affected by phylogeny (Cooper and Geiser 2008). The dasyurids, the family to which the largest non-herbivorous extant heterothermic marsupials belong, only use short-term daily torpor as opposed to deeper, multiday hibernation. It is energetically inefficient to rewarm a large body mass daily, perhaps precluding daily torpor from the larger dasyurids, or it is not required because of their large size. Large folivores and grazers, which rely on foregut or hindgut fermentation, are also less likely to use torpor due to the requirement of maintaining a high and stable T_b to facilitate microbial fermentation. Most Australian biomes also lack the extreme seasonal cold and snow cover which drive seasonal hibernation and inactivity of even herbivores at higher latitudes and elevations.

Despite a lack of torpor at large body mass, less pronounced heterothermy with a smaller fluctuation of T_b (<5 °C below the normothermic resting T_b) is not restricted to small mammals, but it occurs also in larger species including larger marsupials (Brown 1984; Hetem et al. 2016). For some large species core T_b may vary considerably, in particular in response to restricted energy or water availability. The average daily T_b amplitude for large mammals typically ranges from 0.8 °C to 3.7 °C, but may become more extreme under conditions of resource shortage (see Geiser 2021). Large mammals also have the capacity to use regional heterothermy, lowering surface temperature and so reducing heat loss at low T_a , although core T_b may remain high (Withers et al. 2016). Heterothermy of medium to large mammals (body mass >1 kg) is most commonly reported for placental mammals from Africa and the northern hemisphere, but also occurs among Australian marsupials.

Kangaroos and wombats (families Macropodidae and Vombatidae, respectively) appear homeothermic but in reality do not have a “constant” core T_b . Captive Quokkas (*Setonix brachyurus*, ~2.5 kg) had daily T_b fluctuations from ~35 to 38 °C (Kinnear and Shield 1975), while core T_b of free-ranging Western Gray Kangaroos (*Macropus fuliginosus*, 50 kg) fluctuated daily by about 4 °C, from 34 °C to 38 °C (Maloney et al. 2011; Hetem et al. 2016). Interestingly, the kangaroos appeared to anticipate heat storage requirements on hot days by decreasing T_b more on mornings with high solar radiation (Maloney et al. 2011). For Southern Hairy-nosed Wombats (*Lasiorchinus latifrons*, 30 kg) caged outdoors, T_b was strongly affected by T_a and ranged from T_b minima of ~31 °C, at T_a < 20 °C, to T_b maxima of ~39 °C as T_a approached 40 °C (Wells 1978). Core T_b of free-ranging Common or Bare-nosed Wombats (*Vombatus ursinus*, ~30 kg) at Kosciuszko National Park in the southeastern Australian Alps (elevation 1200 m) fluctuated from ~34.5 °C to 37 °C (Brown 1984).

Torpor has also not been reported to date for medium-sized bandicoots (Peramelemorphia) and phalangerid possums (Table 2). However, daily T_b fluctuations from ~32 to 39 °C were observed for the Greater Bilby (*Macrotis lagotis*, ~1500 g, Thylacomidae) in captivity (Kinnear and Shield 1975), similar to those of

both free-ranging (T_b 33.4–39.8 °C) and captive (T_b 33.0–39.9 °C) Southern Brown Bandicoots (*Isodon obesulus*, ~1100 g, Peramelidae; Warnecke et al. 2007). Western Ringtail Possums (*Pseudocheirus occidentalis*, 850 g, Pseudocheiridae) had daily T_b fluctuations of ~36–39 °C in captivity (Kinnear and Shield 1975). For captive brushtail possums (*Trichosurus* spp., ~2 kg) T_b was positively affected by T_a , differed among populations and species, and T_b fluctuations were largest (~33–37 °C) in *T. vulpecula johnstonii* from tropical Queensland (Cooper et al. 2018). Although T_b fluctuations of medium-large mammals are considerable and can have important energetic and hygric implications, they do not approach the more extreme heterothermy observed for small torpid heterotherms described in the first section of this chapter.

How Many Marsupials Express Torpor?

Using the information summarized here it is possible to make an educated guess as to how many marsupial species may use torpor. It is hard to separate the species that are truly not heterothermic from those that have not yet been studied, those which did not undergo heterothermy when studied (especially during short-term examinations), studies that did not report heterothermy, or studies specifically designed to discourage animals from becoming heterothermic. Despite these caveats, reasonable estimates can be made at the family level (Table 3). Even though these appear to be rather conservative, it seems that about 43% of marsupial species, or 150 of 347 marsupial species, are likely to use torpor. Most probably this represents an underestimate considering the limited information on especially the American marsupials, many of which are small and have not had their thermal biology investigated. Consequently, expression of torpor is part of the life of a large proportion of marsupial species with implications for their feeding, foraging, and reproductive biology and their ecology in general.

Ecological Aspects of Torpor

The capacity for small mammals to enter torpor was appreciated by Aristotle and Pliny, with Gessner commencing work on this phenomenon in the 1550s and Buffon in the 1750s (Withers and Cooper 2010). Since these first early experiments, torpor has been studied extensively, mainly by physiologists, and has been associated with survival in extremely cold climates characterized by seasonal ice and snow. Much early work focused on rodents, reflecting their diversity, propensity for torpor, and broad distribution in the northern hemisphere's temperate regions, along with bats, tenrecs, and hedgehogs (Withers and Cooper 2010; Geiser 2021). More recently many other functions of torpor that are crucial to the survival of species in the wild have been uncovered (Geiser and Brigham 2012; Nowack et al. 2017a; Turbill et al. 2019), informed in no small part by the recognition of, and studies into, marsupial torpor use. As torpor results in a substantial reduction of MR and water loss, it is a

Table 3 Extant marsupial families and torpor expression

Family	Numbers of species	Number of species using torpor ^a	% of species using torpor
Didelphidae	112	56	50
Caenolestidae	7	4	57
Microbiotheriidae	1	1	100
Dasyuridae	76	69	90
Myrmecobiidae	1	1	100
Notoryctidae	2	2	100
Peroryctidae	1	0	0
Thylacomidae	2	0	0
Peramelidae	20	0	0
Phascolarctidae	1	0	0
Vombatidae	3	0	0
Burramyidae	5	5	100
Phalangeridae	26	0	0
Pseudocheiridae	18	0	0
Petauridae	11	6	55
Tarsipedidae	1	1	100
Acrobatidae	3	3	100
Hypsiprymmodontidae	1	0	0
Potoroidae	10	0	0
Macropodidae	45	0	0

Number of species from Nowak (2018) with the exception of the Acrobatidae, which are now considered to be three species rather than two

^aEstimated number of species based on known and predicted torpor use based on the size of related species

crucial adaptation for life in resource-poor environments and survival of adverse conditions, not just those characterized by seasonal cold and snow cover, but a range of temperate, tropical, and arid habitats, and for enabling reproduction. Aspects that are specifically relevant for marsupials are addressed below.

As highlighted above, dealing with environmental change as a consequence of seasonal conditions is an important function of marsupial torpor. This may simply refer to the survival of cold periods when food supply is limited, or in direct response to typically low T_a , but also may comprise a seasonal physiological change with more pronounced winter torpor, allowing marsupials to withstand seasonal challenges.

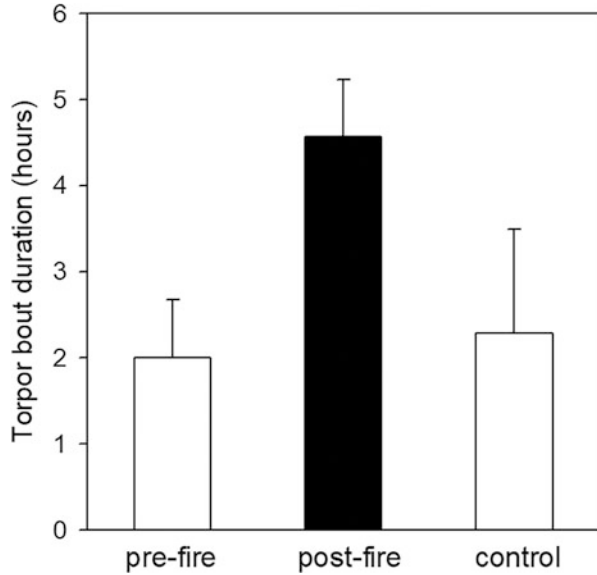
About 70% of the Australian continent is arid or semi-arid, receiving less than 500 mm of annual rainfall. This region is characterized by high solar radiation, high rates of evaporation, and large diel temperature fluctuations, together with low primary productivity and little free water availability. These conditions pose considerable challenges for maintenance of homeostasis for endothermic mammals; nevertheless, there is a surprising diversity of small mammals in Australia's deserts (Withers et al. 2004). The advantages of torpor for energy conservation in arid

habitats are obvious and torpor has been identified as an important factor in the success of many small mammals in Australian deserts, in particular small insectivorous dasyurid marsupials (Geiser 2004). Despite the focus on torpor, and indeed other physiological research on energetics, water balance can be of more immediate concern for animals than energy balance and is especially problematic in arid habitats. Torpor reduces absolute water requirements; a lower T_b reduces EWL from both respiratory and cutaneous avenues, and lower MR is associated with reduced ventilatory parameters and further reduction in respiratory EWL. Reduced energy requirements also reduce urinary and fecal water loss. Dunnarts increase torpor use in response to water as well as food restriction (Song and Geiser 1997), and EWL decreases during torpor for both marsupial daily heterotherms (e.g., Cooper et al. 2005, 2010) and long-term hibernators (e.g., Withers et al. 2012) from arid and more mesic environments. Despite the considerable absolute water savings, which presumably are important for water conservation when free drinking water and pre-formed water sources are limited or unavailable, torpor results in less favorable RWE than normothermia. Periodic arousals are likely essential for maintenance of water balance (Thomas and Geiser 1997), resulting in increased energy expenditure. Water balance may therefore be a limiting factor for torpor use.

Torpor plays an important role in facilitating reproduction for adults and in the development and growth of the young. As reproduction in many Australian marsupials commences in winter, torpor allows for reduction in the energetic costs of thermoregulation and apportioning of energy toward reproduction. Torpor during reproduction (not necessarily in winter) either during pregnancy, lactation or both has been observed for many marsupial species (McAllan and Geiser 2014). Torpor during pregnancy has been documented for dasyurids (dunnarts, mulgaras, and antechinus) and burramyids (*C. nanus*; G. Morrow, unpublished data). Torpor during lactation has been observed for microbiotheriids (Monito del Monte), dasyurids (dunnarts), burramyids (*C. nanus*; unpublished), acrobatids (Feathertail Glider), and petaurids (Sugar Glider). Although torpor expression during reproduction typically results in an extension of the reproductive period, this seems well compensated by the successful production of offspring and an increase in fitness of the parent.

American and Australian marsupials not only have to deal with seasonal changes in weather, many populations also often have to cope with fires. Torpor may appear an unlikely adaptation to deal with fire, and in the extensive 2019 fires in Australia, the use of torpor to facilitate postfire survival, although documented, was widely ignored. However, since torpor saves both energy and water, it permits reduced foraging post fire and also reduces predation risk. It is therefore of crucial importance for ensuring that populations of small marsupials can persist in burnt areas. Postfire torpor use has only been examined for Australian marsupials. In the wild, antechinus typically show a doubling of torpor expression and duration and a concomitant reduction in activity in comparison to prefire conditions and control sites (Fig. 3). As recently burnt sites provide little ground protection and attract predators, a reduction in foraging is of crucial importance (e.g., Stawski et al. 2015). In captivity a combination of charcoal substrate and wood smoke increases the use of torpor

Fig. 3 The duration of torpor bouts (means with SE) for Brown Antechinus (*Antechinus stuartii*) before a prescribed fire, after the fire, and at an unburnt control site at the time of the fire. The means differ significantly and were accompanied by a reverse response for the duration of activity which was about halved after the fire. (Data from Stawski et al. 2015)



beyond food restriction for some heterothermic marsupials such as the Yellow-footed Antechinus (*A. flavipes*) and arboreal Sugar Gliders (*P. breviceps*), suggesting that these cues signal an imminent period of food shortage and increased risk (Stawski et al. 2017; Nowack et al. 2018). These findings not only have implications for survival of extant species, but also likely were of crucial importance in enabling survival of small mammals during the K-Pg extinction event, which probably contributed to the persistence of the three mammalian lineages. Long-term survival without food, enabled by the use of torpor, likely was a crucial adaptation in aiding persistence.

At the other extreme of environmental challenges are floods and also storms. These occur regularly all over the world and are a threat to many species living in flood plains and other flood-prone areas and arboreal species during storms. Sugar Gliders, although typically expressing torpor mainly during cold and wet winter nights, substantially increased torpor and reduced activity use during a category 1 cyclone in a subtropical area, although the T_a remained rather mild, suggesting that they used torpor to increase survival during the storm (Nowack et al. 2015). With regard to floods, which like fires, kill many but not all individuals, animals must survive with wet fur, increased heat loss (Withers et al. 2016), and limited or no food availability. Unfortunately, to our knowledge, data on torpor use during floods are not available for marsupials. However, captive spiny mice (*Acomys russatus*) from Israel, which naturally live in desert Wadis commonly affected by floods, entered torpor after the cage was flooded. In one flooded individual, the torpor bout lasted for ~2.3 days, seven times longer than the average reported for this species (Barak et al. 2018). It seems prudent that this adaptation is investigated in marsupials since many species inhabit flood plains that regularly are inundated by water.

While survival of adverse conditions is important for contributing to an animal's fitness, its life span also is crucial, because long-lived species potentially can produce more offspring than short-lived species. One drawback of small size is, that most small mammals are short-lived and that includes many marsupials (Lee and Cockburn 1985). However, not all small mammals have a short life span. Small hibernating species tend to live much longer than homeothermic species (Turbill et al. 2011). Hibernating bats have especially great longevity, but this is affected by their ability to fly, which is also correlated with longevity. However, for small hibernating mammals in general, maximum life span is still 50% longer than in non-hibernators (Turbill et al. 2011). With regard to marsupials, small heterothermic possums have considerable longevity despite their size, up to 11 years for hibernating Mountain Pygmy-possums (Mansergh and Broome 1994). These small possums can live and reproduce that long despite the fact that marsupials are considered to be "short-lived" (Lee and Cockburn 1985). There can be little doubt that the ability to express multiday torpor, with extremely reduced MR and predator avoidance due to a reduction in activity, contributes to that (Turbill et al. 2011). For marsupial daily heterotherms, however, life span is usually only 1–5 years (Jackson 2007), but this is complicated by post-mating die-off by male antechinus and other dasyurids.

All the advantages of torpor listed above also seem to be reflected in the rate of extinction of mammals, in Australia especially. Australia is often singled out as the continent with the most mammal extinctions over the past 200 years since European settlement. However, what is typically not mentioned in this context is that similar extinctions have also happened elsewhere in the world, often caused by habitat destruction and the introduction of rats and mice and new predators, only earlier.

Of the 61 confirmed extinctions of mammal species worldwide over the past 500 years, only 4 (6.5% of species) were likely to have been heterothermic (Geiser and Turbill 2009). Considering that two-thirds of mammals are rodents and bats, many of which are heterothermic, the small proportion of extinct heterotherms is astonishing. Specifically for Australian marsupials (Geiser and Turbill 2009; Hanna and Cardillo 2014), homeothermic bandicoots and macropods suffered many extinctions, whereas heterothermic dasyurids and pygmy-possums, although many suffered range reductions, do not include any extinct species. Consequently, it appears that using torpor is associated with many ecological gains and the large number of species using it demonstrates the selective advantages of this trait.

Concluding Remarks

Many marsupials are heterothermic, with few species remaining strictly homeothermic despite their general endothermic physiology. The extent of heterothermy used by marsupials is influenced by phylogeny and body size. It is among the smaller marsupials, especially dasyuromorphs <1000 g and non-phalangerid possums <100 g, that the most profound variation of T_b , and associated energy and water expenditure, is observed. Dasyuromorphs and small gliders use daily torpor, whereas the Monito del Monte, pygmy-possums, and feathertail gliders can undergo multiday

hibernation in addition to using short-term torpor. A hibernation period of >1 year fueled by body fat for Eastern Pygmy-possums is the longest reported for any mammal. Nearly half of all marsupial species are predicted to use torpor or hibernation. However, T_b data for even the largest species (kangaroos and wombats) and those groups traditionally considered to be strict homeotherms (bandicoots and phalangerid possums) show considerable diel and seasonal fluctuation of T_b by some 3–7 °C related to activity, T_a , and availability of food and water.

The prevalence of heterothermy among marsupials is a testament to its critical importance in facilitating persistence of these animals in their environment. Daily torpor and, in particular, multiday hibernation are associated with a profound decrease in resource requirements as a consequence primarily of decreased thermoregulatory costs, but also due to the low T_b and MR below BMR and extended periods of inactivity. Once considered evidence of a primitive physiology, torpor and hibernation are now understood to be sophisticated, tightly controlled elements of the thermal biology of many marsupials and other heterothermic endotherms. Studies of marsupial torpor have contributed substantially to understanding the utility of torpor in a variety of ecological and life-history contexts, most notably the role of facilitating survival in a range of resource-restrictive situations, not just allowing for inactivity during the non-breeding cold or snowy winter months in highly seasonal temperate habitats. Torpor allows marsupials to survive both predictable and unpredictable periods of food and water shortage, permits persistence in resource-poor habitats, facilitates longevity, and ever-more importantly can promote survival following extreme environmental events such as storms and fire.

Despite the many advantages, there are risks or costs to daily torpor and hibernation, including a reduced ability to respond rapidly to environmental cues, less-optimal conditions for physiological function, an unfavorable water balance, and the energetic costs of arousal to normothermia. For some marsupials, especially larger species, these costs are prohibitive and consequently the occurrence and extent of heterothermy are restricted. However, the high number of heterothermic species is clear evidence that these costs can be overcome by many species. The underrepresentation of heterothermic species among mammalian extinctions worldwide, and especially among Australian marsupials, shows the selective advantages of this trait, and it is probable that heterothermy allowed all three mammalian lineages to survive and persist beyond the K-Pg mass extinction event that decimated faunal diversity worldwide.

What are the future directions for the study of marsupial heterothermy? There is now a considerable knowledge of the breadth, phylogenetic and allometric patterns, and physiological process and consequences of heterothermy of marsupials, especially Australian species, although information about tropical species remains scant. Thermal and energetic drivers and responses of daily torpor and hibernation have been well described, although there is less information concerning how water availability influences torpor and the absolute and relative consequences for water balance. Further descriptions of heterothermy and quantification of the effects on energy and water balance for species that are currently poorly studied, have an unusual biology, or are of conservation concern will be of value, but the major

opportunities for future thermal research of marsupials are applying current understanding of the occurrence, costs, and benefits of heterothermy to conservation and management of species, populations, and landscapes. Incorporating information about how marsupials use daily torpor and hibernation can better-inform landscape management strategies such as prescribed burning to improve both conservation and welfare outcomes. Research activities, captive husbandry, and breeding programs, along with translocation and reintroduction attempts, will benefit from considering the opportunities and restrictions offered by the heterothermic physiology of many marsupials. In the face of a changing climate, conservation biologists and environmental managers are encouraged to consider the role of torpor in the persistence of marsupials. Climate niche modeling that attempts to predict future distributions and inform long-term management decisions in the face of climate change can be improved by taking a mechanistic approach and incorporating physiological data; heterothermy has profound effects on these physiological variables and needs to be considered to ensure model accuracy. The physiological flexibility of heterothermic marsupials which employ daily torpor and hibernation are predicted to best position these species to withstand the challenges of human-induced environmental change and persist under future climatic conditions.

Cross-References

- ▶ [Activity Patterns of American Marsupials](#)
- ▶ [Energy and Water Balance of Marsupials](#)
- ▶ [Food Habits and Activity Patterns of Australasian Marsupials](#)

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