Review

Hibernation and daily torpor in Australian and New Zealand bats: does the climate zone matter?[1]

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Abstract. We aim to summarise what is known about torpor use and patterns in Australian and New Zealand (ANZ) bats from temperate, tropical/subtropical and arid/semiarid regions and to identify whether and how they differ. ANZ bats comprise ~90 species from 10 families. Members of at least nine of these are known to use torpor, but detailed knowledge is currently restricted to the pteropodids, molossids, mystacinids, and vespertilionids. In temperate areas, several species can hibernate (use a sequence of multiday torpor bouts) in trees or caves mostly during winter and continue to use short bouts of torpor for the rest of the year, including while reproducing. Subtropical vespertilionids also use multiday torpor in winter and brief bouts of torpor in summer, which permit a reduction in foraging, probably in part to avoid predators. Like temperate-zone vespertilionids they show little or no seasonal change in thermal energetics during torpor, and observed changes in torpor patterns in the wild appear largely due to temperature effects. In contrast, subtropical blossom-bats (pteropodids) exhibit more pronounced daily torpor in summer than winter related to nectar availability, and this involves a seasonal change in physiology. Even in tropical areas, vespertilionids express short bouts of torpor lasting ~5 h in winter; summer data are not available. In the arid zone, molossids and vespertilionids use torpor throughout the year, including during desert heat waves. Given the same thermal conditions, torpor bouts in desert bats are longer in summer than in winter, probably to minimise water loss. Thus, torpor in ANZ bats is used by members of all or most families over the entire region, its regional and seasonal expression is often not pronounced or as expected, and it plays a key role in energy and water balance and other crucial biological functions that enhance long-term survival by individuals.

Additional keywords: body temperature, fattening, heterothermy, metabolic rate, passive rewarming, regions, roosts, season.

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[1]This paper is dedicated to Les Hall whose major scientific interests were the diversity and distribution of Australasian bats. He worked on both insectivorous bats and flying foxes, was an avid caver and was involved in work on many other aspects of the biology of bats including their conservation. He also contributed to our knowledge about the thermal biology of Australian bats (Hall 1982), the topic of this paper. Apart from scientific papers on bats, he produced an excellent field guide on Bats from Eastern Australia with Greg Richards, another giant of Australasian Chiropterology (Hall and Richards 1979), and more recently a book on A Natural History of Australian Bats, Working the Night Shift (Richards *et al.* 2012). We hope he would think this review does justice to the bats.

Introduction

Australia is known as the continent of pouched mammals such as the koala and kangaroos, as well as the egg-laying monotremes, the echidna and platypus, whereas New Zealand as the land of kiwis. Less well known is the fact that these islands are also home to diverse native placental mammals, especially rodents and bats in Australia, but only bats in New Zealand. In contrast to the monotremes and marsupials, Australian bats do not appear to be of Gondwanan origin, and all nine families of extant Australian bats are thought to be derived from the South-east Asian bat fauna (Hall 1984; Richards *et al*. 2012). Australia supports the families Pteropodidae (fruit and blossom-bats); Megadermatidae (ghost bats), Rhinonycteridae (trident leaf-nosed bats), Hipposideridae (leaf-nosed bats), Rhinolophidae (horseshoe bats), Emballonuridae (sheathtail bats), Molossidae (freetail bats), Miniopteridae (bent-wing bats) and Vespertilionidae (evening bats). Although most of the ~90 Australian bat species are considered endemic, endemism is mainly restricted to the insectivorous bats whereas only two of 11 species of pteropodids are currently considered to be endemic (Hall 1984; Churchill 1998).

The diversity of New Zealand bats has declined since the Miocene (Hand *et al*. 2018). New Zealand is home to only two extant bats belonging to two families. The Mystacinidae (short-tailed bats) are now represented by a single extant species (*Mystacina tuberculata*); a second species (*M. robusta*) likely went extinct as recently as 1967 (O'Donnell 2008). The mystacinids, like the kiwis, are believed to be of Gondwanan origin and used to be present in Australia but are now extinct there (Hand *et al*. 2018). In contrast, the single vespertilionid (*Chalinolobus tuberculatus*) likely invaded New Zealand from Australia in the past 2 million years (Hand *et al*. 2018).

Australian bats are found continent wide and live in a variety of climate zones (Fig. 1). These range from tropical regions in the north, subtropical regions and cool-temperate mountain regions in the south-east, Mediterranean regions in the south, and arid and semiarid regions in the centre and west making up over half of the continent. These regions differ substantially in the seasonal change in weather and food availability. Whereas the tropical north receives almost all rainfall in summer and much of it is warm and dry in winter, the opposite is the case in the south where it rains more in winter and summers tend to be hot and dry (BOM 2020). Much of the east coast and associated mountain ranges also receive most rain in summer and some of the mountain areas experience ambient temperatures (T_a) below freezing in winter. The climate of arid and semiarid Australia is typically unpredictable and extreme. Key characteristics include unpredictable and relatively low rainfall, high T_as and high rates of evaporation. Unpredictability in rainfall is more extreme in the northern arid zone (north of 27° S parallel) where rainfall is summer dominated, whereas the area south of 27° is dominated by winter rainfall (Van Etten 2009). Bat diversity falls dramatically with increasing latitude across the Australian continent (Hall 1984).
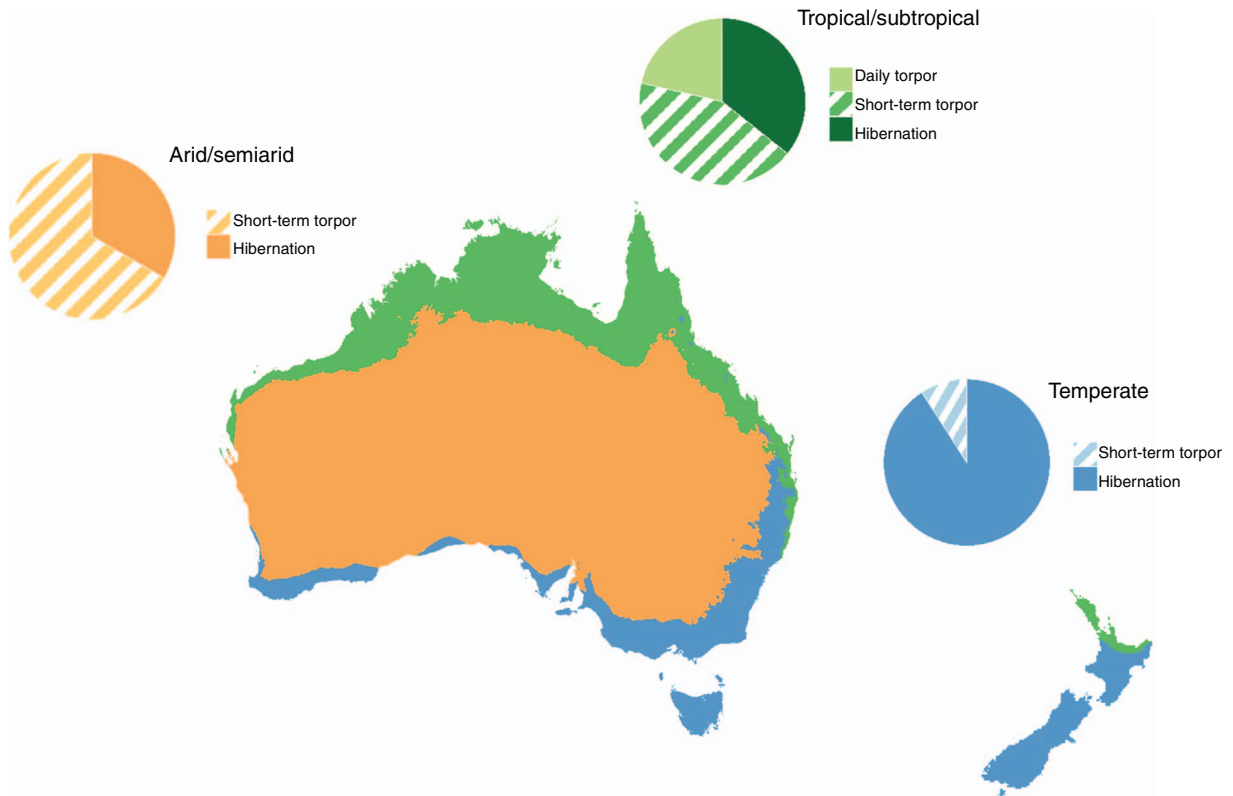
Fig. 1. Climate map of Australia and New Zealand (BOM 2020; NIWA 2020) and patterns of torpor expressed in the different climate zones (numbers for pie charts from Table 1).

Although the two extant species of New Zealand bats have severely declined, there is some recent improvement for *M. tuberculata*, and both bat species are now restricted to areas of native forests across the two main and offshore islands (O'Donnell *et al.* 2018). The South Island is cool-mountainous and temperate, similar to the North Island; however, the latter also has subtropical regions, mainly in the far north (Fig. 1). Rainfall is high in many areas, especially on the south-west coast of the South Island, whereas the south-east coast and much of the North Island are drier, on average (NIWA 2020).

Bats adjust both behaviour and physiology to live under such varying conditions, which is especially critical for them because they are endothermic (Withers *et al.* 2016). This means that during periods of activity or 'normothermia', bats use a large proportion of their ingested energy for thermoregulation to maintain a high and constant body temperature (T_b) of ~34–38°C (Geiser 2006). Even at high T_as when bats are resting in their thermo-neutral zone (TNZ) and their metabolic rate (MR) can be basal (BMR) because heat loss is minimal, the MR of small species is extremely high, with the mass-specific BMR (BMR g^{-1} body mass) of a 10-g bat being ~7-fold higher than that of humans (Withers *et al.* 2016). At T_as below ~30°C, which approximates the lower end or lower critical T_a of the TNZ in small bats (Riek and Geiser 2013), their large relative surface area results in a steep linear increase of heat loss because the T_b–T_a differential increases as T_a falls. This heat loss, further augmented by their large vascularised wings (Speakman and Thomas 2003), requires compensation through an increase in resting MR (RMR), although, when vasoconstricted, the wings can also serve as 'thermal blankets' (Bartholomew *et al.* 1964). In comparison to BMR at T_a ~30°C, a 4-g little forest bat (*Vespadelus vulturnus*) at T_a 5°C must increase its RMR 12-fold just to maintain a normothermic T_b (Willis *et al.* 2005). Moreover, during flight, bats may further increase MR by >10-fold above that at rest (Speakman and Racey 1991), which is further augmented during high-intensity echolocation (Currie *et al.* 2020). As the food of most bats is also strongly affected by season and weather, many small species simply cannot afford to constantly 'waste' energy for thermoregulation and maintenance of a high T_b when this is not required. This is exemplified by northern Australian bats, most of which exhibit limited foraging when T_a <15°C (Richards 1989). Instead, many bats enter a state of torpor to conserve energy and water and, as we will see below, for several other reasons. Torpor is used by a large number of diverse 'heterothermic' mammals and birds worldwide (Dawson and Hudson 1970; McKechnie and Mzilikazi 2011; Ruf and Geiser 2015; Nowack *et al.* 2020). However, likely due to the combination of the high energetic cost of thermoregulation and flight, and to the often-fluctuating, unpredictable, or temperature-dependent food supply the order Chiroptera probably contains the largest proportion of heterothermic species of all mammalian orders (Hock 1951; Pohl 1961; Lyman 1970; Henshaw 1970; Brigham 1987; Speakman *et al.* 1991; Thomas 1995; Arlettaz *et al.* 2000; Barclay *et al.* 2001; Speakman and Thomas 2003; Willis and Brigham 2003; Stawski *et al.* 2014; Czenze and Dunbar 2020).

Torpor is characterised by controlled reductions of MR and T_b and is extremely effective in minimising energy expenditure, water loss and other bodily functions. In bats, MR during torpor (TMR) is often reduced by 50–95% below that of normothermic resting individuals, and T_b falls by between 5 and 35°C, with a maximum known fluctuation of T_b (measured as skin temperature, T_s) by 43°C, from ~46°C during a heat wave in summer to ~3°C during winter torpor in desert bats (Bondarenco *et al.* 2014). Water loss during torpor in bats is extremely low, typically ~10% of that of normothermic individuals (Hosken and Withers 1997), and the heart rate can be reduced from an incredible ~800 beats min^{-1} during normothermia to only 8 beats min^{-1} during deep torpor in small 10-g bats (Currie *et al.* 2014; Currie 2018). Torpid animals not only benefit from reduced costs for thermoregulation but, as MR during torpor is usually well below BMR, because of a combination of the lowered T_b and metabolic inhibition, other maintenance costs are also substantially reduced (Geiser and Brigham 2000; Nowack *et al.* 2020). Torpid animals may thermo-conform over a wide range of T_a and T_b, but, despite the substantial fall of T_b and MR, they remain endothermic animals and can regulate T_b via an increase of MR at a species- or population-specific minimum (Heller and Hammel 1972; Stawski and Geiser 2011; Currie *et al.* 2018). Apparently, they commit this energy expenditure to avoid organ or tissue dysfunction or damage, which often occurs well above 0°C, or to prevent the loss of the ability to arouse using endogenous heat production (Geiser and Baudinette 1987; Barnes 1989).

Two patterns of torpor are common. Torpor in some species lasts for several hours, often during the rest phase of the day, and this form of torpor is called 'daily torpor' and occurs in the 'daily heterotherms' (Ruf and Geiser 2015). Daily torpor in bats occurs mainly in small pteropodids like blossom-bats and typically is relatively shallow with T_b reduced from ~37°C to ~15–25°C with a reduction in metabolism to ~30–50% of the BMR; the T_b–T_a differential during steady-state daily torpor in thermo-conforming individuals is often ~3–6°C (Stawski *et al.* 2014; Currie *et al.* 2015*a*). Daily heterotherms do not appear capable of continuous multiday bouts of torpor even when exposed to low T_a. In contrast, hibernating species, which include many insectivorous bats, can remain torpid for many consecutive days (Stawski *et al.* 2014). However, the state of torpor in almost all species is interrupted by periodic arousals, including a rewarming to normothermic T_b. These arousals come at a high energetic cost, except in instances where individuals can bask or are exposed to an increase in T_a. Although the torpor bout duration (TBD) of hibernators may last up to several weeks based on data from North American bats (Jonasson and Willis 2012; Czenze *et al.* 2017*a*), TBD is strongly temperature-dependent, and at high T_a it may last for <1 day, as is often observed in hibernating bats in summer. Chiropteran and other mammalian hibernators typically reduce T_b from ~37°C during normothermia to between 0 and 10°C during torpor, the T_b–T_a differential during steady-state torpor in small thermo-conforming hibernators is typically at ~0.5–2°C, often less than for daily heterotherms, and the TMR in small hibernating bats may be as low as 1–5% of the BMR

of normothermic individuals (Stawski *et al*. 2014; Currie *et al*. 2015*a*; Ruf and Geiser 2015) (Table 1). Recently, it has been suggested that daily torpor and hibernation are a continuum rather than distinct patterns (McNab and O'Donnell 2018). However, these conclusions were based on short-term measurements of captive New Zealand bats that produced thermal energetic values well above those measured in the same species or closely related species in the wild (see below), and therefore lack the scientific rigor required for making meaningful comparisons.

Our purpose is to review the available data on torpor and heterothermy (i.e. exhibiting large T_b fluctuations) in Australian and New Zealand (ANZ) bats. We summarise the data in the context of torpor use in the three climate zones: temperate (including cool- and warm-temperate and Mediterranean), tropical/subtropical and arid/semiarid (Fig. 1). Patterns of torpor are affected by latitude in North American bats (Dunbar and Brigham 2010) and it is probable that similar differences occur in ANZ species. Alternatively, it is also plausible that the torpor patterns exhibited by bats are flexible enough to adequately deal with a wide range of challenges. Therefore, in bats with wide distribution ranges we report and compare data when they are available, from more than one region.

We define torpor as a reduction in T_b by >5°C below the normothermic resting T_b (Schleucher 2004; Ruf and Geiser 2015) because it is well below the normothermic $T_b \pm 2$°C definition for homeothermy (Hetem *et al*. 2016). Although arbitrary, this value can be reliably used for different body masses or different T_as below the TNZ. If only MR measurements are available, a reduction of MR by >25% below the RMR at the same T_a was used for defining torpor (Hudson and Scott 1979; Ruf and Geiser 2015) and this includes the TNZ (Song *et al*. 1997; Reher *et al*. 2020). The TBD was calculated from the time that T_b or MR remained below these thresholds.

Small-bodied Australian bats of multiple families use torpor extensively (Morrison 1959; Kulzer *et al*. 1970; Hall 1982; Hosken 1997; Hosken and Withers 1997; Coburn and Geiser 1998; Bartels *et al*. 1998; Geiser and Brigham 2000; Dixon and Rose 2003; Turbill *et al*. 2003*a*, 2003*b*; Bondarenco *et al*. 2014; Stawski *et al*. 2014; Stawski and Currie 2016; Doty *et al*. 2016*a*, 2016*b*). Torpor is now also known to occur in both extant species of New Zealand bats (Czenze *et al*. 2017*b*, 2017*c*, 2017*d*; McNab and O'Donnell 2018). Although many ANZ bats experience what might be considered mild thermal conditions for much of the year, it is not correct that torpor is only used by bats living in cooler southern or high-elevation parts of the region. Torpor use by bats has been recorded on both New Zealand and offshore islands and the entire Australian continent including the tropics. Indeed, as we will see below, arid-zone Australian bats that experience extremely hot conditions in summer appear to use torpor to avoid overheating and to conserve both energy and water.

Temperate-zone bats

The thermal biology of bats from temperate regions in New South Wales (NSW), Tasmania, Victoria and Western Australia has been extensively investigated. Early studies were conducted more than half a century ago (Morrison 1959; Kulzer *et al*. 1970). The original work was largely restricted to short-term investigations of captive or wild-caught individuals because of technological limitations, whereas more recent research includes long-term data on thermal biology and energetics from both the field and laboratory (Table 1).

Although most bats from cold northern hemisphere regions hibernate in thermally stable hibernacula like caves, mines or cellars, some Australian bats from cool-temperate regions hibernate in trees. For example, in the New England area of NSW, long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*, hibernate during winter in trees often under exfoliating bark facing the sun or in shallow tree cavities (Turbill and Geiser 2008). These bats are exposed to daily fluctuations of T_a, which result in large daily fluctuations of T_b, conditions considered to hinder expression of hibernation in the past (Henshaw 1970). However, despite partial passive rewarming each day, torpor bouts in mid-winter have been shown to last ~5 days on average with a maximum of 15 days, followed by a full arousal to normothermic T_b (Turbill and Geiser 2008). Normothermic periods after arousals in winter are typically brief (<3 h) (Turbill and Geiser 2008), explaining why capture rates have been reported to be low (Brigham and Geiser 1998). Yet on warm nights it appears that bats do forage, explaining how they survive the winter without obvious prehibernation fattening (Turbill *et al*. 2003*b*, 2008). Increased food resources have also been linked to shorter bouts of torpor in autumn for *N. geoffroyi* (Doty *et al*. 2016*b*). In summer, *N. geoffroyi* uses short bouts of torpor lasting for several hours every day even when it is warm, and on cool days torpor bouts of up to 2 days were observed (Turbill *et al*. 2003*b*). The minimum T_s observed in *N. geoffroyi* was 9.1°C in summer (T_a ~7.5°C) and ~1°C in winter (T_a <0°C). If the values for torpor occurrence of free-ranging *N. geoffroyi* and *N. gouldi* in winter and summer are extrapolated to the remainder of the year, when they are known to also use torpor, they spend ~$^2/_3$ of the year in torpor.

In the laboratory, both *Nyctophilus* species thermo-conformed when torpid over a wide T_a-range from ~25 to 2°C and the mean T_b–T_a differential was just above 1.0°C. However, at very low T_a approximating 0°C, T_b was regulated at minima between ~1 and 2°C (Table 1), measured at T_a ~0–1°C. Importantly, this minimum regulated T_b is different from the minimum T_b measured in thermo-conforming individuals, which simply reflect the T_a to which bats were exposed. Minimum TMR is only 3–5% of the BMR in these species, which is also the case for *N. timoriensis* (Hosken and Withers 1997; Geiser and Brigham 2000) (Table 1). Surprisingly, *N. geoffroyi* does not show a strong seasonal change in the physiology of torpor with TMR remaining at 3–5% of BMR in spring, summer and autumn (Geiser and Brigham 2000) (winter data are not available). Even during the reproductive period in spring, captive *N. geoffroyi* still used torpor when measured overnight at T_a 15°C (Turbill and Geiser 2006). All males, pregnant females and lactating females entered torpor under rather mild thermal conditions, and during torpor, minimum T_b was only ~0.5°C above T_a, while minimum TMR was only ~4% of BMR. Reproductive *N. gouldi* behaved similarly (Turbill and

Table 1. Heterothermy and torpor in Australian and New Zealand bats from different regions

	Body mass (g)	Observation	Source
Temperate regions			
Pteropodidae			
Grey-headed flying fox (*Pteropus poliocephalus*)	700	Heterothermy in free-ranging bats. Minimum measured T_b 32°C.	Walker *et al.* unpubl. data
Mystacinidae			
Lesser short-tailed bat (*Mystacina tuberculata*)	15	Multiday torpor up to 5 days in winter and short bouts in summer. Minimum measured T_s 8.6°C.	Czenze *et al.* (2017*b*, 2017*c*)
Miniopteridae			
Bent-wing bat (*Miniopterus schreibersii oceanensis*)	15	Multiday torpor with torpor bouts up to 12 days after prehibernation fattening. Minimum measured T_b 10°C.	Hall (1982); Kulzer *et al.* (1970)
Vespertilionidae			
Lesser long-eared bat (*Nyctophilus geoffroyi*)	7	Hibernate in winter with multiday torpor up to 15 days, minimum regulated T_b 1.4°C, TMR 3–5% of BMR. Brief normothermic periods, occasional foraging in wild. Short bouts of torpor in summer including during reproduction.	Geiser and Brigham (2000); Turbill *et al.* (2003*b*); Turbill and Geiser (2006, 2008); Turbill (2006*b*)
Gould's long-eared bat (*Nyctophilus gouldi*)	10	Hibernate in winter with multiday torpor up to 11 days, minimum regulated T_b 2.3°C, TMR 3–5% of BMR. Brief normothermic periods, occasional foraging in wild. Short bouts of torpor in summer including during reproduction.	Geiser and Brigham (2000); Turbill and Geiser (2006, 2008); Currie *et al.* (2014)
Greater long-eared bat (*Nyctophilus timoriensis*)	15	Deep torpor in captive bats. Minimum T_b 6°C, TMR 3% of BMR.	Hosken (1997)
Chocolate wattled bat (*Chalinolobus morio*)	8	Hibernate in winter with multiday torpor up to 15 days, T_s <5°C and brief normothermic periods. Short torpor bouts in summer.	Turbill (2006*a*)
Gould's wattled bat (*Chalinolobus gouldii*)	15	Hibernate in winter with multiday torpor up to 5 days, and brief normothermic periods. Minimum T_s −0.2°C, minimum regulated T_b 0.6°C, TMR ~1.5% of BMR, water loss during torpor reduced by ~90%.	Stawski and Currie (2016); Currie *et al.* (2018); Hosken and Withers (1997)
Long-tailed bats (*Chalinolobus tuberculatus*)	9	Shallow torpor in captive bats. Minimum measured T_b >17°C during short-term measurements.	McNab and O'Donnell (2018)
Little forest bat (*Vespadelus vulturnus*)	4	Deep torpor in captive bats. Minimum regulated T_b 5°C, TMR 1–2% of BMR. TBD in free-ranging bats up to 7 days in winter.	Willis *et al.* (2005); Chenery (2018)
Southern forest bat (*Vespadelus regulus*)	5	Deep torpor in captive bats during autumn. TMR (at T_a 13°C) 4% of BMR.	Turbill (2009)
Inland broad-nosed bat (*Scotorepens balstoni*)	10	Deep torpor in captive bats, minimum regulated T_b 3.2°C, TMR ~4% of predicted BMR.	Geiser and Brigham (2000)
Tropical/subtropical regions			
Pteropodidae			
Eastern blossom-bat (*Syconycteris australis*)	18	Daily torpor in captive subtropical bats. TBD ~6 h, minimum regulated T_b 19.3°C, minimum T_{sub} 16°C. Deeper (TMR 34% of BMR) and longer torpor in summer than in winter (TMR 56% of BMR).	Coburn and Geiser (1998); Currie *et al.* (2015*a*)
Northern blossom-bat (*Macroglossus minimus*)	16	Daily torpor for ~6 h in captive tropical individuals. Torpor less pronounced (minimum regulated T_b 23.1°C, TMR ~60% of BMR) than in subtropical *S. australis*.	Bartels *et al.* (1998)
Eastern tube-nosed bat (*Nyctimene robinsoni*)	50	Shallow torpor in captive tropical bats. Large daily T_b-variations in free-ranging tropical bats, but no torpor while fruit abundant.	Hall and Pettigrew (1995); Riek *et al.* (2010)
Megadermatidae			
Ghost bat (*Macroderma gigas*)	100	Heterothermy in captive tropical bats; minimum measured T_b 32°C.	Geiser, Stawski, Pavey, unpubl. data
Rhinonycteridae			

Species	Value	Notes	Reference
Orange leaf-nosed bat (*Rhinonicteris aurantius*)	7	Torpor in captive tropical bats; minimum measured T_b 23.6°C.	Kulzer *et al.* (1970)
Hipposideridae Leaf-nose bats		No data for Australian hipposiderids, but *H. terasensis* hibernates in subtropical Taiwan. Heterothermy in *H. ater* or other Australian species likely.	Liu and Karasov (2011)
Rhinolophidae Eastern horseshoe bat (*Rhinolophus megaphyllus*)	8	Torpor in captive tropical bats; minimum measured T_b 16°C.	Kulzer *et al.* (1970)
Emballonuridae Coastal sheathtail bat (*Taphozous australis*)	23	Torpor in captive tropical bats; minimum measured T_b 17°C.	Kulzer *et al.* (1970)
Molossidae Little northern freetail bat (*Ozimops halli*)	8.5	Torpor in captive bats; minimum measured T_b 10°C.	Kulzer *et al.* (1970)
Mystacinidae Lesser short-tailed bat (*Mystacina tuberculata*)	15	Multiday torpor >5 days in winter and short bouts in summer. Minimum measured T_s 4.7°C.	Czenze *et al.* (2017*b*, 2017*c*)
Miniopteridae Bent-wing bat (*Miniopterus schreibersii oceanensis*)	15	Torpor in captive tropical bats; minimum measured T_b 25.6°C.	Kulzer *et al.* (1970); Baudinette *et al.* (2000)
Vespertilionidae Eastern long-eared bat (*Nyctophilus bifax*)	9	Torpor in free-ranging subtropical bats in summer and winter with TBD of up to 5.4 days. Torpor during period of reproduction. TMR ~4% of BMR in tropical and subtropical bats in all seasons measured. Minimum regulated T_b 3.4°C in subtropics, T_b 7.3°C in tropics.	Stawski *et al.* (2009); Stawski and Geiser (2010*a*, 2010*b*, 2011); Stawski (2010)
Lesser long-eared bat (*Nyctophilus geoffroyi*)	8	Torpor in free-ranging tropical bats in winter. Minimum measured T_s 19.8°C, TBD ~5 h.	Geiser *et al.* (2011)
Gould's wattled bat (*Chalinolobus gouldii*)	12	Torpor in captive tropical bats. Minimum measured T_b 17.7°C.	Kulzer *et al.* (1970)
Eastern forest bat (*Vespadelus pumilus*)	4.8	Morning and afternoon torpor bouts in free-ranging subtropical bats in summer when insects abundant. Minimum measured T_s 16°C.	Turbill *et al.* (2003*a*)
Large-footed myotis (*Myotis macropus*)	7.8	Torpor in captive tropical bats. Minimum measured T_b 8°C, TBD 8 days.	Kulzer *et al.* (1970)
Arid/semiarid regions **Molossidae** Inland free-tailed bat (*Ozimops petersi*)	9	Torpor in free-ranging bats in winter with TBD up to ~8 days, and in summer, including a heatwave. Summer torpor is relatively longer than in winter.	Bondarenco *et al.* (2013, 2014); Bondarenco (2014)
Southern free-tailed bat (*Ozimops planiceps*)	9	Torpor in captive bats. Minimum measured T_b 20.2°C.	Kulzer *et al.* (1970)
Vespertilionidae Little pied bat (*Chalinolobus picatus*)	6	Torpor in captive bats. Minimum measured T_b 12.8°C.	Kulzer *et al.* (1970)
Inland broad-nosed bat (*Scotorepens balstoni*)	10	Short bouts of torpor on 70% of days in free-ranging bats in summer.	Bondarenco *et al.* (2016)
Little broad-nosed bat (*Scotorepens greyii*)	6	Short bouts of torpor on 83% of days in free-ranging bats in summer.	Bondarenco *et al.* (2016)
Finlayson's cave bat (*Vespadelus finlaysoni*)	5	Torpor in bat netted in harp trap in Ormiston Gorge. Minimum measured T_b 9.5°C on a winter morning.	Geiser and Pavey, unpubl. data

Geiser 2006). This strongly suggests that unlike many other mammals, such as sciurid rodents, which avoid using torpor during reproduction, bats use it extensively and, counter to prevailing dogma that torpor and reproduction are incompatible, it is likely crucial to permit successful reproduction even with limited resources (Stawski *et al.* 2014).

Other temperate-zone bats known to hibernate in trees are wattled bats of the genus *Chalinolobus*. Gould's wattled bat (*Chalinolobus gouldii*) hibernates in winter with a minimum recorded T_s of –0.2°C for free-ranging individuals, and a minimum regulated T_b of 0.6°C and an extremely low TMR at ~1.5% of BMR in captive bats (Hosken and Withers 1997; Stawski and Currie 2016; Currie *et al.* 2018). For free-ranging chocolate wattled bats (*Chalinolobus morio*), hibernation has been observed in winter with bouts up to 15 days and T_s <5°C, along with brief bouts of torpor lasting a few hours in summer (Turbill 2006*a*). These values differ substantially from those for New Zealand long-tailed bats (*Chalinolobus tuberculatus*) from a temperate area (McNab and O'Donnell 2018), which did not reduce T_b below 17°C during short-term measurements in captivity. It is therefore not surprising that the TMR measured was ~10-fold that predicted for small hibernating bats, but of course it needs to be confirmed that *C. tuberculatus* expresses multiday torpor.

Data on hibernation in free-ranging bats are now also available for the tiny little forest bat (*Vespadelus vulturnus*, 4 g), which remained torpid for up to 7 days (Chenery 2018), with captive individuals showing some of the lowest TMRs recorded for any mammal, at 1–2% of BMR (Willis *et al.* 2005). Inland broad-nosed bats (*Scotorepens balstoni*, 10 g) also have TMRs as low as 4% of BMR and a minimum regulated T_b of 3.2°C (Table 1), and Hall (1982) recorded torpor bouts in free-ranging bent-wing bats (*Miniopterus schreibersii oceanensis*) that lasted up to 12 days in a cave in southern NSW in winter (Hall 1982).

No bats from temperate regions of Australia are currently known to be daily heterotherms; however, it is possible that flying foxes, which, unlike the small pteropodids, have distributions that extend into temperate regions, do express daily torpor. For example, limited thermal biology data on adult male grey-headed flying-foxes (*Pteropus poliocephalus*) roosting in Adelaide in winter show that they typically employ shallow early morning dips in core T_b to as low as 32°C (M. Walker *et al.* unpubl. data). Given the variability in their food supply, it would not be surprising if flying fox species inhabiting temperate climates employ shallow daily torpor when energetically stressed. The necessary field data to answer these questions remain an important goal for future research.

Data on free-ranging New Zealand bats are available for short-tailed bats (*Mystacina tuberculata*) from both main islands and an offshore island. These bats displayed multiday torpor for up to 5 days in winter and short bouts of torpor in summer and all bats that roosted solitarily expressed torpor (Czenze *et al.* 2017*b*). The minimum T_s measured in a temperate area was 8.6°C, unexpectedly higher than that measured on a subtropical island (T_s 4.7°C: Czenze *et al.* 2017*c*). However, both these values were well below the minimum T_b measured for *M. tuberculata* in captivity (~16°C), in part because captive bats were exposed to T_a >9°C (McNab

and O'Donnell 2018), and not enough time was allowed for them to reach steady-state torpor and/or animals were unsettled. This probably also explains the high TMRs reported, which are well above predicted values.

Tropical and subtropical bats

Tropical and subtropical bats are exposed to entirely different environmental conditions compared with temperate-zone bats. Nevertheless, these bats employ torpor and, in fact, the taxonomic representation of torpor use is much greater than in temperate areas (Table 1), extending across a greater number of families and reflecting the greater diversity found in those climate zones (Hall 1984). Records of torpor in tropical and subtropical bats have been available for some time for several species (Table 1). However, the most detailed data available are for eastern long-eared bats (*Nyctophilus bifax*) (Stawski *et al.* 2009, 2014). Free-ranging *N. bifax* hibernate in winter on the subtropical north coast of NSW. All recorded individuals entered torpor on all days in winter and the maximum TBD was ~5.5 days with a minimum T_s of 9.4°C measured at a T_a of 6.5°C (Stawski *et al.* 2009). In summer, maximum TBD in subtropical *N. bifax* was just under 1 day, with a minimum T_s of 16°C and bats expressed torpor on 85% of days (Stawski and Geiser 2010*a*). This is similar to tropical *N. bifax* in Queensland in winter, which used torpor on 95% of days and exhibited similar patterns of T_s fluctuations (Stawski and Geiser 2012). Captive *N. bifax* from subtropical and tropical habitats had a similar TMR at ~4% of BMR, although the minimum regulated T_b was lower in subtropical (3.4°C) than in tropical bats (7.3°C; Fig. 2). Subtropical *N. bifax*, like temperate-zone *N. geoffroyi* (see above), do not significantly change minimum T_b with season (Fig. 3) and the same is the case for the minimum TMR.

A low TMR indicates that energy savings derived from using torpor can be enormous even in tropical and subtropical bats. However, it is important to note that torpor can have additional selective advantages (Stawski and Geiser 2010*b*). In
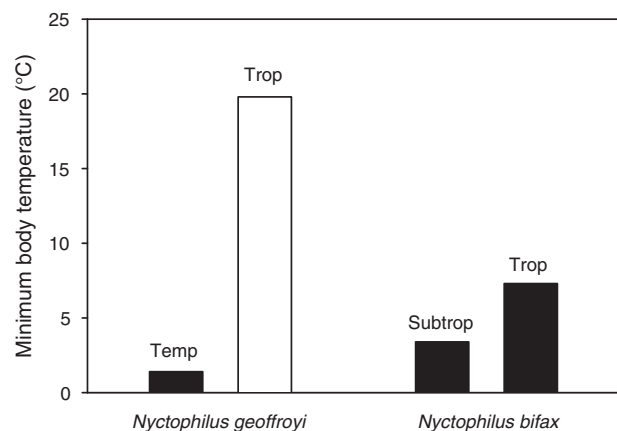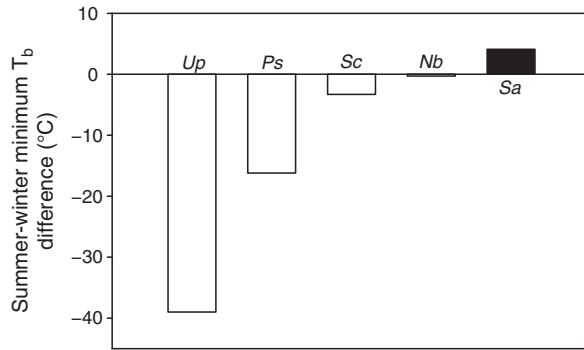

Fig. 2. The minimum body temperature of torpid *Nyctophilus* bats from temperate (Temp), tropical (Trop) and subtropical (Subtrop) areas. Black bars are regulated T_b minima, whereas the white bar is the minimum T_s as observed in the wild, which is not likely a regulated minimum, but simply due to the high T_a experienced. Data are from Table 1.

Fig. 3. The difference in the minimum body temperature (T_b) maintained during summer and winter in representative species: arctic ground squirrels (*Up*, *Urocitellus parryii*: Barnes 1989; Sheriff *et al*. 2012), hamsters (*Ps*, *Phodopus sungorus*, spontaneous torpor: Heldmaier and Steinlechner 1981), dunnarts (*Sc*, *Sminthopsis crassicaudata*: Geiser and Baudinette 1987), long-eared bats (*Nb*, *Nyctophilus bifax*: Stawski and Geiser 2011), and blossom-bats (*Sa*, *Syconycteris australis*: Coburn and Geiser 1998), the exception with a positive change.

Fig. 4. The proportion of the day that eastern long-eared bats (*Nyctophilus bifax*) were torpid or normothermic in a subtropical area as a function of body condition index (BCI) (body mass (g)/forearm length (mm)) in summer when food appeared abundant. Fat bats use more torpor than lean bats (data from Stawski and Geiser 2010*b*).

summer, free-ranging subtropical *N. bifax* expressed more torpor when they were fat than when lean. Bats with a high body condition index (BCI) (body mass (g)/forearm length (mm)) used longer torpor bouts and were torpid for a greater proportion of the day (Fig. 4), but also during the foraging time at night than those with a low BCI. This runs counter to the long-held assumption that torpor is employed only during conditions of negative energy balance. These observations suggest that *N. bifax* uses torpor to extend the availability of stored fat, which minimises the need for foraging. As survival rates during torpor are much better than during activity (Lebl *et al*. 2011) *N. bifax* seems to extend torpor to minimise exposure to predators (Stawski and Geiser 2010*b*).

Free-ranging eastern forest bats (*Vespadelus pumilus*), another tiny tree-roosting species weighing 4.8 g, also expressed torpor in a subtropical coastal region of NSW in summer, even though T_a during the study was mild (14.4–27.2°C) and insects were abundant (Turbill *et al*. 2003*a*). During this time, individuals usually expressed two bouts of torpor per day, the first in the early morning and the second in the late afternoon. Both arousal from morning torpor bouts, which was partially passive because of the rising T_a, and the normothermic period around midday when it was warm would have been energetically cheap. Arousal from afternoon bouts around sunset would have been more costly, yet the use of torpor meant it was less expensive overall than remaining normothermic for the entire afternoon (Turbill *et al*. 2003*a*). Data for winter are not available but it is likely that *V. pumilus* uses multiday torpor bouts like *N. bifax* in a similar habitat (see above).

In tropical Pine Creek in the Northern Territory in winter when T_a ranged from 16.5 to 34.0°C, free-ranging lesser long-eared bats (*N. geoffroyi*), a species that occurs over the entire continent, including Tasmania, expressed short bouts of torpor on every day lasting, on average, ~5 h (Geiser *et al*. 2011). The minimum measured T_s of *N. geoffroyi* in the wild in this region was high at 19.8°C, but unlike that of tropical *N. bifax* (Fig. 2),
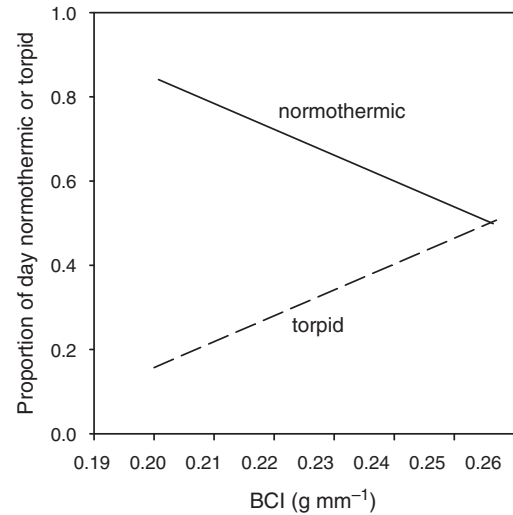
this is unlikely to be a regulated minimum T_b, but rather reflects the high T_a (>16.5°C) to which the bats were exposed. However, the mean TBD of *N. geoffroyi* measured in the tropics was >2-fold that predicted from the TBD versus T_a regression in temperate individuals, suggesting regional plasticity (Stawski and Geiser 2012).

New Zealand short-tailed bats (*Mystacina tuberculata*) also enter multiday torpor on subtropical Hauturu Island in winter. In fact, bats on Hauturu expressed torpor on 98% of observation days in comparison to a temperate area where torpor was used on 95% of days and, as stated above, the minimum T_s in Hauturu (T_s = 4.7°C) was lower than that measured in temperate-zone bats (T_s = 8.6°C: Czenze *et al*. 2017*c*).

For daily heterotherms, detailed information on seasonal daily torpor expression is available for captive blossom-bats (*Syconycteris australis*). Individuals captured on the subtropical east coast of NSW, at the same site where subtropical *N. bifax* was studied, expressed torpor both in summer and winter, but showed a seasonal change in the pattern of torpor (Coburn and Geiser 1998). The typical seasonal pattern of torpor expression in other mammals is lower T_b during torpor in winter and higher T_b or no torpor at all in summer. These seasonal differences from summer to winter can be substantial, with reductions in the minimum T_b ranging from 39°C in arctic ground squirrels (*Urocitellus parryii*) to 0.3°C in long-eared bats (*N. bifax*) (Fig. 3). Blossom-bats show the opposite pattern. Although the occurrence of induced torpor in *S. australis* was similar in summer and winter, average TBD in bats captured in winter was short (5.5 h) and shallow (mean minimum regulated T_b = 23.4°C), whereas for bats captured in summer, torpor was deeper (mean minimum regulated T_b = 19.3°C) and longer (7.3 h) (Coburn and Geiser 1998). Consequently, the mean minimum T_b increased by 4.1°C from summer to winter, unlike

for typical heterotherms (Fig. 3). This unusual seasonal response may be explained by different daylength and food availability. In winter, T_a on the subtropical east coast is still relatively mild and bats can forage for prolonged periods during long nights and thus have the opportunity to access the abundance of flowering plants over a long period. In summer, nights and thus foraging times are shorter and the local availability of nectar is lower. Therefore, the unusual seasonal pattern of torpor use in *S. australis* is actually a highly appropriate physiological adaptation to the ecological constraints imposed by their subtropical habitat and specialised nectar and pollen diet. It is also important to note that the minimum regulated T_b of sympatric, hibernating *N. bifax* was almost 20°C below that of *S. australis*, emphasising the different thermal strategies of the two species. We do not know the reasons for this.

Tropical northern blossom-bats (*Macroglossus minimus*) were captured near Cairns in spring and measured in spring at the University of New England after about three weeks in captivity at T_a 22°C. These blossom-bats used daily torpor on 90% of days when T_a was <24°C and food was withheld (Bartels *et al.* 1998). Torpor was not as deep as in subtropical *S. australis*, with T_b during torpor ~23°C and the minimum TMR at ~60% of BMR.

Other bats known to use torpor in the tropics belong to the families Rhinonycteridae, Rhinolophidae, Emballonuridae, Molossidae and Miniopteridae, but quantitative information on these is limited (Table 1). The ghost bat (*Macroderma gigas*: Megadermatidae) was considered to be homeothermic in the past (Leitner and Nelson 1967); however, captive individuals reduced T_b to a minimum of 32°C (Table 1). Although this is above our threshold definition of torpor, it is possible that this species is also heterothermic.

Arid-zone and semiarid-zone bats

Considering the large daily and yearly fluctuations of T_a and the unpredictable rainfall in arid and semiarid areas, it is of little surprise that bats living there use torpor extensively, similar to dasyurid marsupials in the desert (Körtner *et al.* 2016). However, most of the studies on bats to date have been carried out south of 27°S in regions dominated by winter rainfall and there is little knowledge of torpor in bats from the northern arid zone. The most detailed information is available for a molossid, the inland free-tail bat (*Ozimops petersi*) (Bondarenco *et al.* 2013, 2014). This species is, to a large extent, restricted to arid and semiarid regions. Similar to the vespertilionids described above, *O. petersi*, studied at Sturt National Park in north-west NSW, entered multiday torpor for up to 8 days in winter (Bondarenco 2014) with a minimum T_s of ~3°C. However, even in summer, TBDs up to 2 days have been reported (T_a <15°C), although most lasted for <1 day and often two bouts of torpor on the same day were used (Bondarenco *et al.* 2013), similar to the subtropical *V. pumilus*. In both summer and winter, TBD was strongly related to T_a, but the nature of the relationship differed significantly between seasons (Fig. 5). Although TBD was longer in winter than in summer because of the lower T_a experienced, at the same T_a between ~19 and 21°C, TBD was about twice as long in
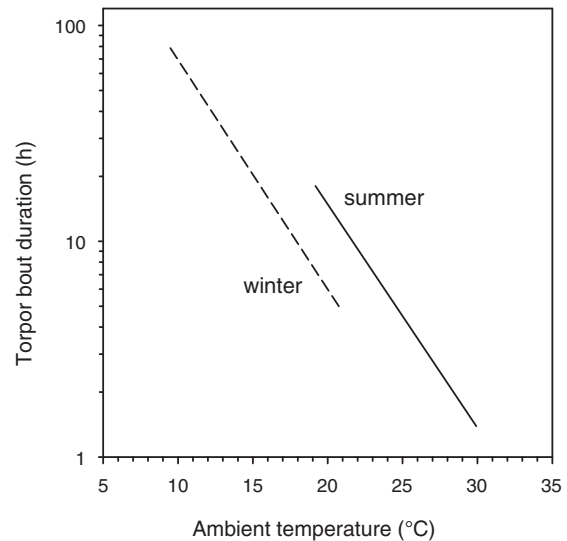

Fig. 5. Torpor bout duration (TBD) on a logarithmic scale as a function of ambient temperature (T_a) in free-ranging inland free-tail bats (*Ozimops petersi*) at Sturt National Park, NSW, in summer and winter. At T_a <15°C bats expressed multiday torpor, at T_a >15°C TBD was <1 day. The regressions differed significantly ($P < 0.01$) between the seasons and TBD was about twice as long at overlapping T_as of 19–21°C. Data are from Bondarenco (2014).

summer than in winter (Fig. 5). This relatively long TBD in summer is likely related to water loss, which is reduced substantially while individuals are torpid (Hosken and Withers 1997). Again, this desert bat shows an unusual seasonal response similar to that of the subtropical *S. australis*, but in this case apparently for water conservation, similar to desert spiny mice (*Acomys russatus*) near the Dead Sea, which also exhibit more pronounced torpor in summer to conserve water (Levy *et al.* 2011).

During a summer heat wave, when T_a exceeded 48°C, the highest T_as measured at Sturt National Park in four decades, *O. petersi* also used torpor in the morning (Fig. 6). The T_b then increased with a ~5-h delay after T_a because the bats were roosting in well insulated dead trees, and it appears that bats were thermo-conforming for most of this time even when T_a approached 48°C. The highest T_s reached was 46°C. This lag in T_b resulted in a delay of the time before T_b reached critically high values that require evaporative cooling. The response observed for *O. petersi* is similar to that of Savi's pipistrelle (*Hypsugo savii*) in the Vesuvius National Park, Italy, in summer and perhaps this high heat tolerance is responsible in part for the pipistrelle's recent range extension (Ancillotto *et al.* 2018). However, the thermal tolerance of both *O. petersi* and *H. savii* is even more extreme than that of the heat-tolerant Angolan free-tailed bat (*Mops condylurus*), which largely thermo-conformed up to T_as of 40–45°C with only a small increase in MR despite increased evaporative cooling (Maloney *et al.* 1999), and similar observations have been made for African nightjars (O'Connor *et al.* 2017). When captive *O. petersi* were exposed to high T_a near the TNZ they used metabolic inhibition (Bondarenco 2014) similar to that used by pygmy possums (*Cercartetus nanus*), spiny mice
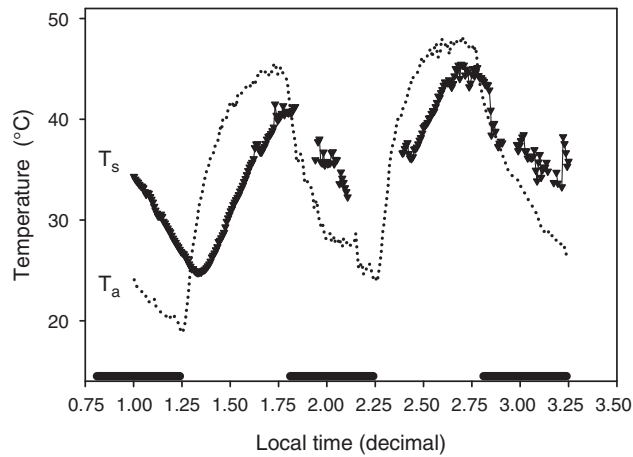
Fig. 6. The fluctuations of ambient temperature (T_a) and skin temperature (T_s) of free-ranging inland free-tail bats (*Ozimops petersi*) during a desert heat wave on 11 and 12 January 2013. Note the lag of T_s by several hours behind T_a, both during torpor entry and passive rewarming on Day 1, because the bat was roosting in a well insulated tree. Although T_s data are missing for the early morning of Day 2, the shape of the curve suggests that the bat again entered torpor at that time, but it nevertheless reached maximum T_s of 46°C at a T_a of 48°C in the late afternoon. Black horizontal bars indicate night. Data are from Bondarenco *et al.* (2014).

(*Acomys russatus*), and roundleaf bats (*Macronycteris commersoni*) from Madagascar (Song *et al.* 1997; Grimpo *et al.* 2013; Reher *et al.* 2020). It appears that metabolic inhibition, in combination with passive rewarming, helps these species to slow the rise of T_b at high T_a, thus conserving water and allowing the bats to avoid overheating.

Arid-zone broad-nosed bats (*Scotorepens greyii* and *S. balstoni*) with a wider distribution than *O. petersi* and free-ranging at Sturt NP have been observed to use torpor on >70% of days in summer (Bondarenco *et al.* 2016). The TBD was 6.5 h on average in *S. greyii*, and 8.3 h in *S. balstoni* with a minimum T_s of ~15°C in both species (Bondarenco *et al.* 2016). The little broad-nosed bat (*S. greyii*) also used torpor in the heat wave described above, but its thermal tolerance at high T_a was likely reduced because they were roosting in poorly insulated trees and seem less well adapted to the arid zone (Bondarenco *et al.* 2014, 2016). Little pied bats (*Chalinolobus picatus*) caught near Broken Hill in autumn were found to use torpor in captivity (Table 1); the minimum measured T_b of 12.8°C was intermediate between those measured in summer in *Scotorepens* and *O. petersi* in winter. Finlayson's cave bat (*Vespadelus finlaysoni*) netted in a harp trap in central Australia in winter had a minimum measured core T_b of 9.5°C in the morning (Table 1).

Regional comparisons

A meaningful comparison of physiological variables of bats from different regions requires detailed measurements conducted under similar conditions and using a similar experimental approach, which limits a statistical comparison of the available data. Of course, this is difficult for free-ranging

individuals under different thermal conditions, although the longest TBD expressed by a species may reflect a species' maximum performance. While TBD measurements under standard conditions in the laboratory may seem a better approach, it is likely that the TBD in hibernating species is compromised by the laboratory environment, at least if measurements are not conducted over months, which is difficult to do in captive insectivorous bats.

The minimum regulated T_b of hibernating bats that is defended during torpor is a reliable variable that can be compared among regions (Fig. 2). As expected, the lowest T_bs have been measured in hibernating bats from temperate regions (Table 1) with a mean T_b of 2.5 ± 1.7°C ($n = 5$ species), somewhat lower than the mean of 4.4°C in mammalian hibernators in general (Ruf and Geiser 2015). As data on the minimum regulated T_b are available for only single ANZ species from the tropics and subtropics, no averages can be compared, but the single minimum regulated T_bs for *N. bifax* were 3.4°C (subtropical area) and 7.3°C (tropical area). No minimum regulated T_b data have been published on arid-zone bats. These data suggest that the minimum regulated T_b is indeed lower in bats from cold than warm areas, as expected from other hibernators (Ruf and Geiser 2015). However, the maximum difference of 6.7°C between T_b 0.6°C (temperate-zone *C. gouldii*) and 7.3°C (tropical *N. bifax*) is much less than the ~17°C difference in the mean minimum T_a in winter between New England (–0.5°C) and tropical Queensland (16.9°C, lowest T_a measured T_a 7.8°C: BOM 2020), from where these bats originated. This suggests that the minimum regulated T_b is selected by the mean minimum T_a in New England, perhaps because it is near 0°C, whereas in the tropics it seems to be selected by extreme T_a minima.

The mean maximum TBD measured in the wild (Table 1) revealed similar regional patterns as the minimum regulated T_b and was 10.0 ± 4.4 days for temperate-zone bats ($n = 7$ species), 8 days for the single arid/semiarid-zone bat *O. petersi*, and 5.4 days for *N. bifax* from a subtropical area and 1.4 days from a tropical area. This suggests a longer TBD in cold than in warm areas, as has been observed for hibernators in general with shorter TBDs at lower latitudes (Ruf and Geiser 2015). Of course, the acute temperature-dependence of TBD needs to be considered in this comparison (see Fig. 5). Therefore, despite the possibly compromising effects of captivity, it would be desirable to measure TBDs of hibernating bats from different climates under the same conditions to see what their physiological capabilities are with regard to the time they can remain torpid. Unlike the minimum regulated T_b and the TBD, the minimum steady-state TMR was rather similar (~2–5% of BMR) among hibernating bats from different habitats (Table 1) and seasons.

In daily heterotherms, obvious differences were observed between the subtropical *S. australis* and the tropical *M. minimus*, both expressing daily torpor. Differences between these two species are evident for the minimum regulated T_b (19.3 versus 23.1°C), the minimum TMR (34–56% of BMR versus ~60% of BMR), but the TBD was similar at ~6 h on average (Table 1). As mentioned above, it is surprising that to date no daily heterotherms have been described in arid and temperate regions, although this pattern of torpor is commonly

used in both climate zones by Australian marsupials and northern hemisphere rodents (Warnecke *et al.* 2008; Levy *et al.* 2011; Körtner *et al.* 2016).

So overall, it appears that, although there are regional differences, these are not as pronounced as one might expect. It appears that a flexible use of torpor and the enormous scope for adjusting torpor patterns and physiology suffice in dealing with prevailing conditions without the need for major regional modifications.

Passive rewarming

Endogenous rewarming from torpor is energetically expensive, compromising the energy savings achieved during torpor, especially in cold climates and during short torpor bouts (Geiser *et al.* 2004). However, it has been documented (described above) that tree-roosting bats reduce these costs by using partially passive or entirely passive rewarming from torpor with the daily increase of T_a (Fig. 6). Although the assumption may be that passive rewarming occurs only in warm areas, it appears to be rather widespread in mammals from different climates (Lovegrove *et al.* 1999; Geiser *et al.* 2004; Nowack *et al.* 2020). Since the roost T_a of bats under sun-exposed bark are warmed to several degrees above outside T_a during the day (Turbill *et al.* 2003*b*) it seems likely that the roosts selected by *Nyctophilus* bats play an important part in minimising energy expenditure, partly by allowing them to exploit the metabolic benefits of torpor while at the same time minimising arousal costs (Turbill 2006*b*). The T_s of *N. geoffroyi* and *N. gouldi* in temperate NSW show large daily fluctuations while they remain in hibernation, but on days when bats rewarm to normothermia, the increasing T_a resulted in partially passive rewarming initially, followed by endogenous rewarming later (Turbill and Geiser 2008). When captive *N. geoffroyi* was exposed to a summer T_a-cycle increasing from 13°C at night to 27°C during the day, the critical T_a at which active rewarming was initiated was a function of time of day, suggesting an underlying circadian rhythm (Turbill *et al.* 2008). When heating commenced at 0600 hours the average critical arousal T_a where endogenous rewarming began was ~25°C, whereas when it commenced at 1200 hours it was ~20°C, apparently ensuring that the time when afternoon normothermia was reached was not substantially delayed (Turbill *et al.* 2008). The critical T_b for active arousal often is ~20°C in bats, and potentially is related to maximising cardiac capacity as the cardiovascular system is integral for heat production during arousal (Currie *et al.* 2015*b*). Captive *N. gouldi* held in outdoor aviaries in a temperate region in winter selected warmer black boxes over colder white boxes, especially when food was restricted, apparently also to passively rewarm and maintain normothermic T_b for longer at reduced energetic costs (Doty *et al.* 2016*a*). Partial passive rewarming also has been observed in *M. tuberculata* from temperate New Zealand (Czenze *et al.* 2017*c*).

In tropical and subtropical *N. bifax* and *N. geoffroyi*, partial passive rewarming from torpor is regularly observed (Stawski *et al.* 2009; Geiser *et al.* 2011). However, passive rewarming is most extreme in arid-zone bats. Broad-nosed bats used entirely passive rewarming on 45% of days (*S. greyii*) and on 29% of days (*S. balstoni*) in summer (Bondarenco *et al.* 2016) and entirely passive rewarming was also used by *O. petersi* (Fig. 6).

Clearly, passive rewarming from torpor is used by many bats in diverse habitats. This may not be surprising since respirometry data for temperate-zone *N. geoffroyi* and *N. gouldi* revealed that passive rewarming can reduce the cost of rewarming by 55–68%, the time required for rewarming, and also minimises exposure to oxidative stress and demand on the cardiovascular system (Turbill *et al.* 2008; Currie *et al.* 2015*b*). In arid-zone bats, energy savings from passive rewarming are likely to be even greater.

Season and fattening

Many mammalian hibernators undertake substantial prehibernation fattening, often characterised by a 40–60% increase in body mass, a large proportion of which is stored fat (Sheriff *et al.* 2012; Bieber *et al.* 2014). Although bats are limited by how much fat they can carry because of the consequences for manoeuvrability in flight (Aldridge and Brigham 1988), similar seasonal changes have been observed in northern bats such as Eurasian horseshoe bats (*Rhinolophus ferrumequinum*), which weighed 21.3 g (16% fat reserves) in late autumn and 14.6 g (4% fat reserves) in spring (Ransome 1990). Fattening has also been observed in the Australian little forest bat (*V. vulturnus*) in temperate southern NSW, which showed a clear change in amount of lipid stored (relative to dry carcass mass) ranging from ~10–20% in December to ~50–65% in June (Tidemann 1993). Similarly, the body mass of *N. gouldi* captured in the Australian Capital Territory increased from ~10–11 g in late summer to 12–13 g in early winter (Phillips and Inwards 1985). Cave-roosting bent-wing bats (*M. schreibersii oceanensis*), increased body mass from ~14 to 18 g in the temperate Northern Tablelands of NSW, whereas coastal, subtropical individuals from the Northern Rivers area exhibited little or no autumnal fattening (Dwyer 1964). In temperate-zone *N. geoffroyi* in the Northern Tablelands of NSW, no obvious autumnal fattening was observed, with bats weighing ~7–8 g in all seasons captured (Turbill *et al.* 2003*b*, 2008; Turbill and Geiser 2008) and similar observations have been made in coastal, subtropical *N. bifax* (Stawski and Geiser 2010*b*). Thus, even in Australian bats expressing multiday torpor and showing autumnal fattening, body mass changes are much smaller than in hibernating rodents or northern bats, and seem especially low in the subtropics, likely because they can forage to some extent in winter, unlike many northern hemisphere cold-climate bats (Brigham 1987). This may also explain why their patterns of torpor in winter are not as predictable as those of some northern hemisphere hibernators.

For daily heterotherms, the single species, the subtropical blossom-bat (*S. australis*), for which data on seasonal expression of daily torpor and seasonal body masses are available, males captured in summer weighed 18.0 g and in winter 17.5 g (Coburn and Geiser 1998). This is consistent with other observations that many daily heterotherms do not substantially change body mass with season.

A seasonal change in physiology?

As some ANZ bats enter torpor both in summer and winter and even during reproduction, the question arises whether they undertake adaptive seasonal changes in physiology, as is also the case for several other heterothermic taxa (Geiser 2020). For subtropical blossom-bats (*S. australis*), which change their torpor physiology from summer to winter, this clearly is the case, but in the opposite direction from what is usually observed (Fig. 3). However, for *Nyctophilus* bats for which seasonal data are available, the change from winter to summer was not pronounced (Geiser and Brigham 2000; Stawski and Geiser 2011). In *N. bifax*, the regulated minimum T_b during torpor did not change significantly between summer and winter (Fig. 3). For *N. gouldi*, cardiac electrophysiology and heart rate in torpor remained unchanged across summer, autumn and winter (Currie 2018). Similarly, TMR of non-reproductive *Nyctophilus* bats from temperate, subtropical and tropical habitats, did not significantly change with season from ~3–5% of BMR, as predicted for small hibernators (Geiser and Brigham 2000; Stawski and Geiser 2011). Moreover, reproductive *N. geoffroyi* and *N. gouldi* from a temperate climate also entered torpor for most measurement days in captivity and also had TMR at ~4% of BMR (Turbill and Geiser 2006). Thus the seasonal change in physiology in Australian bats seems to be small and the substantive seasonal differences observed for TBD with multiday torpor in winter and often TBD of <1 day in summer seems to reflect mainly the change in T_a because TBD is strongly temperature-dependent (Fig. 5).

Conclusions

Our review shows that ANZ bats use torpor extensively to reduce energy expenditure and water loss. Torpor also plays a crucial role in enabling reproduction and allows predator avoidance. Although there are some physiological differences among bats from different climate zones, these are not as extensive as one might expect, but it appears that torpor is flexible enough to deal with the prevailing and often unpredictable environmental conditions by appropriate adjustments of thermal energetics. As torpor is used by essentially all ANZ bat families, and because some species are torpid for more than half the year, it obviously plays a key role in their biology and ecology.

Although considerable advances have been made recently on the understanding of thermal energetics of ANZ bats, it is painfully obvious that for many species, especially from the tropics and subtropics, physiological data do not exist at all, whereas for others we still must rely on a paper from the seventies compromised by the technological limitations at the time. Considering the availability of small tracking devices that permit quantification of physiological and behavioural traits in the field that are crucial for bat conservation, we hope that this paper will encourage more such work on more species. We also need greater insight into the thermal biology and energy conservation in larger bats and bats living in hot climates that may not necessarily use deep torpor but may have mechanisms for reducing metabolism without expressing substantial reductions in T_b. This could be assessed in the wild by using heart rate telemetry and in the laboratory via respirometry. Finally, we need to understand better whether the patterns of hibernation interrupted by bouts of foraging found in most ANZ bats could safeguard against white nose syndrome, which fatally interferes with long-term hibernation in North American bats.

Abbreviations

ANZ, Australian and New Zealand; BMR, basal metabolic rate; MR, metabolic rate; RMR, resting metabolic rate; T_a, air temperature; TBD, torpor bout duration; T_b, body temperature; TMR, torpor metabolic rate; TNZ, thermo-neutral zone; T_s, skin temperature; T_{sub}, subcutaneous temperature.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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