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Variable Climates Lead to Varying Phenotypes: “Weird” Mammalian Torpor and Lessons From Non-Holarctic Species

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Mammalian heterotherms, species that employ short or long periods of torpor, are found in many different climatic regions. Although the underlying physiological mechanisms of heterothermy in species from lower latitudes (i.e., the tropics and southern hemisphere) appear analogous to those of temperate and arctic heterotherms, the ultimate triggers and resulting patterns of energy expenditure and body temperature are often noticeably different. Phenotypic flexibility in the patterns of thermoregulation in non-Holarctic species can be extensive (depending on body condition, environmental parameters and species competition) and the factors responsible for inducing heterothermy are more variable in non-Holarctic species. As well as being a regular adaptation to seasonality, heterothermy can also be employed as a response to unpredictability in environmental parameters and as a response to emergency situations. Non-Holarctic heterotherms also challenge the notion that regular inter-bout arousals during hibernation are obligatory and suggest all that is necessary to maintain proper functioning during hibernation is an occasional passive return to—or maintenance of—a relatively high body temperature. The study of non-Holarctic heterotherms has led to the conclusion that heterothermy must be defined on the basis of mechanistic, physiological parameters, and not solely by body temperature; yet we are still limited in our abilities to record such mechanistic parameters in the field. It is now believed that homeothermy in mammals evolved in hot climates via an ancestral heterothermic state. Similar to extant warm-climate heterotherms, early mammals could have relied mainly on passive body temperature regulation with a capacity for short- to longer-term up-regulation of metabolism when needed. Hibernation, as seen in temperate and arctic species may then be a derived state of this ancestral heterothermy, and the study of torpor in warm climates can provide potential models for the energetics of early mammals.

Keywords: hibernation, heterothermy, southern hemisphere, tropics, torpor

INTRODUCTION

Torpor in heterothermic endotherms is a controlled, reversible depression of metabolic rate, and active thermoregulation, well below the usual daily cycle (*sensu* Geiser and Ruf, 1995). Over the last two to three decades, it has become apparent that torpid states in endotherms are employed in a wide range of ecological and physiological settings and under contrasting conditions (Cossins and Barnes, 1996; Geiser and Brigham, 2012; Boyles et al., 2013; Levesque et al., 2016; Nowack et al., 2017). This challenges the “traditional” view of torpor as essentially an adaptation to mismatches between energy supply and demand during cold seasonal northern hemisphere winters (Geiser, 2004b; Heldmaier et al., 2004; McKechnie and Mzilikazi, 2011). Understanding the different underlying causes and initiators of heterothermy is essential if we are to understand how homeothermy evolved (Grigg and Beard, 2000; Lovegrove, 2012). Torpor use in temperate and arctic species is traditionally differentiated into “daily torpor” and “long-term hibernation.” Daily torpor consists of hypometabolic phases of less than 24 h, with regular, euthermic behavior during the usual active phase, whereas hibernation consists of a series of hypometabolic phases (multiday torpor bouts) over several months that are interspersed with regular euthermic arousals. In “classic” hibernators periodic, or inter-bout, arousals occur about once every 1 or 2 weeks and are presumably needed to sustain mammalian life during long-term torpor. Importantly, however, arousals are energetically expensive phases of active rewarming during hibernation (Carey et al., 2003; Murray et al., 2003) and are associated with increased production of reactive oxygen species and cellular damage (Carey et al., 2000; Brown and Staples, 2011; Nowack et al., 2019). Energy savings during hibernation are more pronounced than during daily torpor, but in contrast to daily torpor, hibernation usually requires preparation (e.g., accumulation of fat stores, modifications of the reproductive and digestive system Barnes et al., 1986; Hume et al., 2002; Sheriff et al., 2013 (but see Liu and Karasov (2011) for an example of a subtropical bat species without pre-fattening) and reliably favorable conditions to allow for a quick recovery when animals terminate hibernation with a reduced body condition. Despite the differentiation between daily heterotherms and hibernators, the extent to which species use torpor can vary substantially as we will detail below.

A Global Perspective of Torpor in Mammals: A Continuum of Physiological Responses

Extant non-Holarctic heterotherms, often living in warm, tropical or subtropical climates, are also capable of conserving energy by reducing metabolism. Although temperate and arctic heterotherms usually employ torpor in a seasonal manner to escape unfavorable winter conditions, the responses reported to date for non-Holarctic heterotherms fall on a continuum (Boyles et al., 2013; Levesque et al., 2016). One extreme is represented by largely heterothermic species that have a highly labile body temperature (T_b ; i.e., large daily fluctuations of T_b without actively depressed metabolic rate) and employ torpor

(large daily amplitudes in T_b and depressed metabolic rate) at any time of the year, with longer bouts during the hibernation season (Grigg and Beard, 2000; Turbill et al., 2003; Lovegrove and Génin, 2008; Levesque and Lovegrove, 2014; Lovegrove et al., 2014a,b; Dausmann et al., submitted). At the opposite end of the continuum are species that are physiologically able to exhibit torpor but do so only rarely (and usually in form of short bouts of torpor) in emergencies when immediate survival is at risk (Nowack et al., 2010; Dausmann et al., 2012). An intermediate form between heterothermy on a very frequent basis throughout the year or only rare torpor use under extreme circumstances, would be the “classical,” seasonal use of torpor. In this case, T_b is kept rather constant outside of the hibernation season and animals show a regular adjustment of energy balance to seasonal unfavorable conditions (such as low temperature, high rainfall, low food availability, see **Table 1**).

The number and phylogenetic diversity of non-Holarctic species with documented torpor use is steadily increasing, with the number doubling in some taxonomic orders since 2011 (**Table 1, Figures 1A,B**) (McKechnie and Mzilikazi, 2011). Also, thanks to technological advancements, more physiological data can be obtained in the field, enabling functional insights into heterothermic responses of free-ranging animals with their full physiological potential (Chmura et al., 2018). The purpose of our review is to summarize what is known about torpor use in mammals living outside the Holarctic, including what is traditionally termed sub-tropics and tropics, and the more temperate zones of the southern hemisphere (**Figure 1A**). Therefore, we have synthesized information about the occurrence, the length, minimum T_b and metabolic rate during torpor, as well as the ultimate triggers of torpor use (season, weather, etc.) in heterothermic species outside of the north temperate and arctic zones. We used data from the comprehensive review by Ruf and Geiser (2015) with the addition of more recent descriptions of torpor use in non-Holarctic heterotherms (**Table 1, Figures 1A,B**). We focus on the proximate factors influencing torpor use, as well as the physiological similarities and differences between mammals using torpor in diverse habitats. Following on previous syntheses (Grigg, 2004; Grigg et al., 2004; Lovegrove, 2012), we further discuss how knowledge of these proximate, and the ultimate causes of torpor use in extant tropical heterotherms can provide insight into the ancestral mammal condition.

DO NON-HOLARCTIC HETEROTHERMS FALL INTO THE DAILY-HETEROTHERM—HIBERNATOR DICHOTOMY?

Daily torpor and hibernation patterns in non-Holarctic species are similar to those observed in temperate/arctic animals, albeit with some distinctive differences. As far as it is known, the physiological basis seems analogous: metabolism (and other physiological variables, such as heart rate, respiration rate, etc.) is actively depressed to a fraction of euthermic levels, usually during the daily resting phase or at the end of the activity phase,

TABLE 1 | Non-Holarctic heterotherms, including species distribution, patterns of heterothermy and potential factors inducing torpor where known.

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
Afrosoricida										
Chrysochloridae										
<i>Amblysomus hottentotus</i>	Hottentot golden mole	Africa	Sub/-tropical	71	SB/HIB	8.6	NA	Field	Scantlebury et al., 2008	Opportunistic, not triggered by temperature, HIB in spring and summer n.d.
<i>Eremitalpa granti</i>	Namib desert golden mole	Africa	Sub/-tropical	26	DT	19.3	0.12 ^F	T _b : Field, TMR: LabW	Fielden et al., 1990	
Macroscelidae										
<i>Elephantulus myurus</i>	Eastern rock elephant shrew	Africa	Sub/-tropical	57	SB/PT	7.5	0.078	LabW	Lovegrove et al., 2001; Mzilikazi et al., 2002	Torpor in summer and winter; triggered by cold and food reduction
<i>Elephantulus rupestris</i>	Western rock elephant shrew	Africa	Sub/-tropical	53–61	DT	11.9	NA	Field		Oelkrug et al., 2012
<i>Elephantulus edwardii</i>	Cape rock elephant shrew	Africa	Subtropical/temperate	42–48	SB/PT	9.2	NA	LabW	Geiser and Mzilikazi, 2011	n.d.
<i>Macroscelides proboscideus</i>	Round-eared elephant shrew	Africa	Sub/-tropical	46	DT	9.4	NA	LabW	Lovegrove et al., 1999	Only when food deprived
Tenrecidae										
<i>Echinops telfairi</i>	Lesser hedgehog tenrec	Madagascar	Subtropical	132	SB/PT	12.5	0.026	Lab	Lovegrove and Génin, 2008; Wein, 2010	Year-round, independent of season, temperature and food supply
<i>Geogale aurita</i>	Large-eared tenrec	Madagascar	Subtropical	7	n.d.	24.9	0.15	Lab	Gould and Eisenberg, 1966	n.d.
<i>Hemicentetes nigriceps</i>	Highland streaked tenrec	Madagascar	Subtropical	102	HIB?	NA	NA	LabW	Gould and Eisenberg, 1966; Stephenson and Racey, 1994	n.d.
<i>Hemicentetes semispinosus</i>	Lowland streaked tenrec	Madagascar	Subtropical	133	HIB	22	NA	LabW	Gould and Eisenberg, 1966; Stephenson and Racey, 1994	n.d.
<i>Microgale dobsoni</i>	Dobson's shrew tenrec	Madagascar	Subtropical	45	n.d.	24.2	0.22	LabW	Stephenson and Racey, 1993	n.d.
<i>Microgale talazaci</i>	Talazac's shrew tenrec	Madagascar	Subtropical	44	n.d.	27.4	NA	LabW	Stephenson and Racey, 1993	n.d.

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution		M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers
<i>Setifer setosus</i>	Greater hedgehog tenrec	Madagascar	Subtropical	270	SB/HIB	16.5	0.07	T _b : Field, TMR: LabW	Levesque et al., 2013, 2014; Lovegrove et al., 2014a	SB: triggered by cold year-round; HIB: triggered by seasonal dry/food shortage
<i>Tenrec ecaudatus</i>	Tailless tenrec	Madagascar	Subtropical	1500–2500	SB/HIB	16.5	0.027	LabW	Gould and Eisenberg, 1966; Nicoll, 1986 reviewed in Geiser (2004b), Lovegrove et al. (2014b), Treat et al. (2018)	SB: triggered by cold year-round; HIB: circannual rhythms
Carnivora										
Hyaenidae										
<i>Proteles cristata</i>	Aardwolf	Africa	Sub-/tropical	8000–14000	DT	31.2	NA	Field	Anderson, 2004	Possibly water availability
Chiroptera										
Emballonuridae										
<i>Peropteryx macrotis</i>	Dog-faced bat	America	Tropical	5	n.d.	24.2	1.13 ^F	LabW	Genoud et al., 1990	n.d.
<i>Taphozous australis</i>	Coastal sheath-tail bat	Australia	Tropical	23	n.d.	16	NA	LabW	Kulzer et al., 1970	n.d.
<i>Taphozous melanopogon</i>	Tomb bat	Asia	Tropical	26	n.d.	27	NA	Lab	Kulzer, 1965	n.d.
Hipposideridae										
<i>Hipposideros terasensis</i>	Formosan Leaf-nosed Bat	Asia	Subtropical	58	HIB	13.8	0.046	LabW	Liu and Karasov, 2011, 2012	HIB in winter; triggers: n.d.
<i>Macronycteris commersoni</i>	Commerson's Leaf-nosed Bat	Madagascar	Sub-/tropical	54	SB, PT, HIB	27.2	0.026	Field	Reher et al., 2018	HIB and PT in winter, PT and DT in summer, triggers: n.d.
<i>Rhinonycteris aurantia</i>	Orange leaf-nosed bat	Australia	Tropical	7	n.d.	23.6	NA	LabW	Kulzer et al., 1970	n.d.
Megadermidae										
<i>Macroderma gigas</i>	Ghost bat	Australia	Tropical	100	n.d.	32	NA	Lab	Geiser et al., unpub. Data in: Geiser and Stawski, 2011	n.d.
<i>Megaderma lyra</i>	Asian false vampire bat	Asia	Tropical	26	n.d.	30	NA	Lab	Kulzer, 1965	Trigger: n.d. but torpor at high ambient temperatures

(Continued)

TABLE 1 | Continued

Species	Common name		Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers
Molossidae										
<i>Molossus molossus</i>	Pallas' mastiff bats	South America, North America	Tropical	10–12	DT	25.3	0.519	T _b : Field; TMR: LabW	O'Mara et al., 2017	Food availability
<i>Mormopterus loriae</i>	Little northern freetail bat	Australia	Tropical	9	n.d.	10	NA	LabW	Kulzer et al., 1970	n.d.
<i>Ozimops petersi</i> (in paper still <i>Mormopterus species 3</i>)	Inland free-tailed bat	Australia	Subtropical	9	SB/PT	21.3	NA	Field	Bondarenco et al., 2013	Torpor in summer; water saving?
<i>Tadarida aegyptiaca</i>	Egyptian free-tailed bat	Africa	Sub/-tropical	16	SB/PT	6.2	NA	Field	Cory Toussaint et al., 2010	PT at lower ambient temperatures
<i>Tadarida brasiliensis</i>	Brazilian free-tailed bat	Central and South America	Sub/-tropical	11	DT	~15 ^F	0.06	LabW	Soriano et al., 2002	Cold (facultative)
<i>Tadarida condylurus</i> (formerly <i>Mops condylurus</i>)	Angolan free-tailed bat	Africa	Sub/-tropical	28–34	DT	12	NA	Field	Maloney et al., 1999; Vivier and van der Merwe, 2007	Year-round use of torpor triggered by food reduction and cold
<i>Tadarida teniotis</i>	European free-tailed Bat	Africa, Asia, Europe	Subtropical	32	n.d.	16–17	0.04 ^F	LabW	Marom et al., 2006	Cold
Natalidae										
<i>Natalus tumidirostris</i>	Funnel-eared bat	America	Tropical	5	n.d.	23.6	0.67 ^F	LabW	Genoud et al., 1990	n.d.
Nycteridae										
<i>Nycteris thebaica</i>	Egyptian slit-faced bat	Africa	Sub/-tropical	11	n.d.	28.4	NA	LabW	Unpublished data, Cory Toussaint, McKechnie, Brigham in: McKechnie and Mzilikazi, 2011; Cory Toussaint et al., 2013	n.d.; No torpor use found in wild
Phyllostomidae										
<i>Carollia perspicillata</i>	Leaf-nosed bat	America	Sub/-tropical	20	n.d.	22	1.01	LabW	Audet and Thomas, 1997	Food restriction
<i>Glossophaga soricina</i>	Long-tongued bat	America	Sub/-tropical	10	DT	21	0.23	Lab	Kelm and Helversen, 2007	Food restriction
<i>Sturnira erythromos</i>	Hairy yellow-shouldered bat	South America	Tropical	16	DT	~15 ^F	0.2 ^F	LabW	Soriano et al., 2002	Cold (facultative)

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
<i>Sturnira lilium</i>	Yellow-shouldered bat	America	Sub/-tropical	17	n.d.	23	0.5	LabW	Audet and Thomas, 1997	Food restriction
<i>Vampyrops (Platyrrhinus) helleri</i>	Heller's broad-nosed bat	America	Sub/-tropical	15	n.d.	28.5	NA	Lab	Rasweiler, 1973	Food deprivation
Pteropodidae										
<i>Dobsonia minor</i>	Bare-backed fruit bat	Asia	Tropical	74	n.d.	26	0.75 ^F	LabW	McNab and Bonaccorso, 2001	n.d.
<i>Macroglossus minimus</i>	Northern blossom-bat	Asia, Australia	Tropical	16	DT	23.1	0.52	LabW	Bartels et al., 1998	Cold
<i>Megaloglossus woermanni</i>	Long-tongued fruit bat	Africa	Tropical	12	n.d.	26.2	0.80	Lab	Kulzer and Storf, 1980	n.d.
<i>Nyctimene albiventer</i>	Tube-nosed bat	Asia	Tropical	28	DT	25.5	0.67	LabW	Bartholomew et al., 1970	n.d.
<i>Nyctimene robinsoni</i>	Eastern tube nosed bat	Australia	Sub/-tropical	50	n.d.	n.d.	NA	Lab	Hall and Pettigrew, 1995	n.d.
<i>Syconycteris australis</i>	Common blossom bat	Australia	Subtropical	18	DT	17.2	0.47	Lab	Coburn and Geiser, 1998	Food and water deprivation; longer and deeper bouts in summer
Rhinolophidae										
<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	Asia, Australia	Sub/-tropical	8	n.d.	16	NA	LabW	Kulzer et al., 1970	n.d.
Rhinopomatidae										
<i>Rhinopoma cystops</i>	Egyptian mouse-tailed bat	Africa, Asia	Sub/-tropical	12	HIB	1	0.16	Field (T _b) and LabW (MR)	Levin et al., 2012, 2015	HIB in winter; cold, or food shortages
<i>Rhinopoma microphyllum</i>	Greater mouse-tailed bat	Africa, Asia	Sub/-tropical	25	SB/HIB	21 ^F	0.14	LabW	Kulzer, 1965; Levin et al., 2015	SB? for males and non-lactating females in summer, HIB in winter. Cold or food shortages during winter
Vespertilionidae										
<i>Chalinolobus gouldii</i>	Gould's wattled bat	Australia	Wide distribution, tropical	17.5	n.d.	12	0.05	Lab	Hosken and Withers, 1997	n.d.
<i>Chalinolobus morio</i>	Chocolate wattled bats	Australia	Subtropical/temperate	8.1	SB/PT/HIB	3.4	NA	Field	Turbill, 2006	SB? in summer, PT (males) and HIB (females) in winter; trigger: cold

(Continued)

TABLE 1 | Continued

Species	Common name		Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers
<i>Lasiurus cinereus</i>	Hoary bat	America	Wide distribution, tropical	33	SB/PT*	2	0.37	LabW	Cryan and Wolf, 2003; Willis et al., 2006	Reproduction, storm
<i>Myotis adversus</i>	Large-footed myotis	Asia	Tropical	8	PT	8	NA	LabW	Kulzer et al., 1970	n.d.
<i>Miniopterus schreibersii</i>	Large bentwing/Schreiber's long-fingered bat	Africa	Tropical	15	n.d.	5	0.24	LabW	Brown (1999)	Torpor in summer and winter, trigger: n.d.
<i>Neoromicia (Pipistrellus) tenuipinnis</i>	White-winged serotine	Africa	Tropical	5	HIB	n.d.	NA	Anecdotal field evidence	Eisentraut (1956)	n.d.
<i>Nyctophilus bifax</i>	Northern long-eared bat	Australia	Tropical	9	SB/PT	9.4	0.046	LabW	Stawski et al., 2009	SB? in summer, PT during winter; triggered by cold, weather condition
<i>Nyctophilus geoffroyi</i>	Lesser long-eared bat	Australia	Wide distribution, tropical	8	SB/HIB	1.4	0.037	LabW	Geiser and Brigham, 2000; Turbill and Geiser, 2008; Geiser et al., 2011	Seasonal, independent of ambient temperature
<i>Nyctophilus gouldi</i>	Gould's long-eared bat	Australia, Asia	Wide distribution, tropical	10	SB/HIB	2.3	0.052	LabW	Geiser and Brigham, 2000; Turbill and Geiser, 2008	HIB in winter, SB? during the rest of the year Trigger: cold
<i>Otonycteris hemprichii</i>	Desert long-eared bat	Africa, Asia	Subtropical	26	n.d.	20–23	0.209 ^F	LabW	Marom et al., 2006	Cold
<i>Scotophilus dinganii</i>	African yellow bat	Africa	Sub/-tropical	29	DT	18.5	NA	Field	Jacobs et al., 2007	n.d.
<i>Scotophilus mhlanganii</i>	recently described	Africa	Sub/-tropical	28	DT	18.2	NA	Field	Jacobs et al., 2007	n.d.
<i>Scotorepens balstoni</i>	Inland broad-nosed bat	Australia	Subtropical	10	DT	15.1	0.044	Field	Geiser and Brigham, 2000; Bondarenco et al., 2016	Torpor in summer; Trigger: n.d.
<i>Scotorepens greyii</i>	Little broad-nosed bat	Australia	Subtropical	6	DT	15.3	NA	Field	Bondarenco et al., 2016	Torpor in summer; Trigger: n.d.
<i>Vespadelus vulturnus</i>	Little forest bat	Australia	Subtropical	4	DT	5	0.014	LabW	Willis et al., 2005	Food withdrawal
Cingulata										
Chlamyphoridae										
<i>Zaedyus pichiy</i>	Dwarf armadillo	America	Subtropical/temperate	700–1500	SB/HIB	12.5	NA	Lab	Superina and Boily, 2007	n.d.
Eulipothyphla										
Erinaceidae										
<i>Atelerix frontalis</i>	Southern African hedgehog	Africa	Sub/-tropical	394–797	SB/HIB	1	NA	Field	Hallam and Mzilikazi, 2011	Seasonal, individuals with high body mass hibernate

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
Soricidae										
<i>Crociodura flavescens</i>	Greater red musk shrew	Africa	Temperate	31.5	DT	n.d.	NA	LabW	Baxter, 1996	n.d.
Marsupialia										
Dasyuromorphia										
Dasyuridae										
<i>Antechinomys laniger</i>	Kultarr	Australia	Wide distribution, tropical	27.4	DT	11	0.14	Lab	Geiser, 1986	Spontaneous torpor at low temperature; torpor induced by food withdrawal at higher temperature.
<i>Antechinus flavipes</i>	Yellow-footed antechinus	Australia	Wide distribution, tropical	30–70	DT	17.8	0.48	LabW	Geiser, 1988; Rojas et al., 2014	Body mass effects torpor stronger than season, frequency increases with age, torpor in response to fires
<i>Antechinus stuartii</i>	Brown antechinus	Australia	Subtropical/temperate	26	DT	18.1	0.66	Field (T _b) and LabW (MR)	Geiser, 1988; Hume et al., 2019	Torpor in response to fires
<i>Dasyercus blythi</i>	Brush-tailed mulgara	Australia	Sub/-tropical	70	DT	10.8	NA	Field	Körtner et al., 2008, 2016	Independent of resource availability; linked to reproduction
<i>Dasyercus cristicauda</i>	Crest-tailed mulgara	Australia	Sub/-tropical	100	DT	13.2	0.12	LabW	Geiser and Masters, 1994; Körtner et al., 2016	Independent of resource availability; linked to reproduction
<i>Dasykaluta rosamondae</i>	Little red kaluta	Australia	Semi-arid	35.5	DT	18 ^F	0.33	Lab	Withers and Cooper, 2009	Food withdrawal
<i>Dasyuroides byrnei</i>	Kowari	Australia	Tropical/subtropical	120	DT	20.4	0.4	Lab	Geiser and Baudinette, 1987	Spontaneous DT, trigger: cold.
<i>Dasyurus geoffroyi</i>	Western quoll	Australia	Subtropical/temperate	1000	DT	23.1	NA	Not known	Arnold, 1976	n.d.
<i>Dasyurus hallucatus</i>	Northern quoll	Australia	Tropical	516	DT	28.4	NA	LabW	Cooper and Withers, 2010	n.d.
<i>Dasyurus viverrinus</i>	Eastern quoll	Australia	Temperate	1000	DT	25	NA	Not known	Moyle, 1999	n.d.
<i>Myrmecobius fasciatus</i>	Numbat	Australia	Subtropical/temperate	n.d.	DT	19.1	NA	Field	Cooper and Withers, 2004	Spontaneous DT, in winter more frequent, deeper and longer; trigger: cold
<i>Ningau i yvonneae</i>	Southern ningau i	Australia	Subtropical/temperate	11.6	DT	15.3	0.3	Lab	Geiser and Baudinette, 1988	Spontaneous DT, trigger: cold. Frequency increased with food withdrawal

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
<i>Planigale gilesi</i>	Giles' planigale	Australia	Subtropical	8.3	DT	14.3	0.36	Lab	Geiser and Baudinette, 1988	Spontaneous DT, trigger: cold. Frequency increased with food withdrawal
<i>Planigale ingrami</i>	Long-tailed planigale	Australia	Tropical	6–9	DT	n.d.	0.48	Lab	Dawson and Wolfers, 1978	n.d.
<i>Planigale maculata</i>	Common planigale	Australia	Tropical	10–16	DT	19.6	0.4	Lab	Morton and Lee, 1978	Triggered by cold, independent of food availability
<i>Planigale tenuirostris</i>	Narrow-nosed planigale	Australia	Wide distribution/tropical	6.6–7.3	DT	n.d.	0.48	LabW	Dawson and Wolfers, 1978	n.d.
<i>Pseudantechinus macdonnellensis</i>	Fat-tailed false antechinus	Australia	Arid-zone	18–33	DT	15.7	NA	Field	Geiser and Pavey, 2007	n.d.
<i>Sminthopsis crassicaudata</i>	Fat-tailed dunnart	Australia	Arid-zone	10	DT	10.8	0.27	Lab	Geiser and Baudinette, 1987; Warnecke et al., 2008	n.d.
<i>Sminthopsis douglasi</i>	Julia Creek dunnart	Australia	Tropical	60	DT	16.9	0.43	not known	Muller, 1996	n.d.
<i>Sminthopsis macroura</i>	Stripe-faced dunnart	Australia	Wide distribution, tropical	20–28	DT	11.3	0.3	Lab	Geiser and Baudinette, 1987; Song et al., 1998; Körtner and Geiser, 2008	Independent of season; triggered by temperature and food/water restriction; deeper at lower temperatures and without food
<i>Sminthopsis murina</i>	Common dunnart	Australia	Wide distribution, tropical	18	DT	15	0.25	Lab	Geiser et al., 1984	n.d.
<i>Sminthopsis ooldea</i>	Ooldea dunnart	Australia	Arid-zone	11	DT	n.d.	0.77	LabW	Tomlinson et al., 2012	n.d.
Microbiotheriidae										
<i>Dromiciops gliroides</i>	Monito del monte	America	Subtropical/temperate	38.9	SB/PT	7.1	0.03	LabW	Grant and Temple-Smith, 1987; Nespolo et al., 2010	Ambient temperature; food availability, but torpor use even when food available
Didelphimorphia										
Didelphidae										
<i>Gracilinanus agilis</i>	Agile gracile opossum	America	Tropical	12–43.6	DT	20	0.3	LabW	Cooper et al., 2009	Lab study only. Capable of torpor at high ambient temperatures

(Continued)

TABLE 1 | Continued

Species	Common name		Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers
<i>Gracilinanus microtarsus</i>	Brazilian gracile opossum	America	Tropical	13	DT	16	NA	LabW	Morrison and McNab, 1962	Lab study only (<i>n</i> = 1). Capable of torpor at high ambient temperatures
<i>Lestodelphys halli</i>	Patagonian opossum	America	Subtropical/temperate	48	SB/PT*	7.7	NA	LabW	Geiser and Martin, 2013	Cold exposure, food withdrawal, but also torpor use when food available
<i>Marmosa robinsoni</i>	Robinson's mouse opossum	America	Tropical	122	DT?	23	NA	LabW	McNab, 1978	n.d.
<i>Monodelphis brevicaudata</i>	Red-legged short-tailed opossum	America	Tropical	40–111	DT?	27	NA	LabW	McNab, 1978	n.d.
<i>Monodelphis domestica</i>	Gray short-tailed opossum	America	Tropical	93	DT	28.6	0.365	Lab	Busse et al., 2014	n.d. but enters torpor at high ambient temperatures
<i>Thylamys elegans</i>	Elegant fat-tailed opossum	America	Wide distribution, tropical	32.1	DT	11 ^F	0.4	LabW	Opazo et al., 1999; Bozinovic et al., 2007	Food reduction
Diprotodontia										
Acrobatidae										
<i>Acrobates pygmaeus</i>	Feathertail glider	Australia	Wide distribution, tropical	14	SB/PT	2	0.042	LabW	Jones and Geiser, 1992; Geiser and Ferguson, 2001	PT in emergency situations
Burramyidae										
<i>Burramys parvus</i>	Mountain pygmy possums	Australia	Temperate	40	HIB	1.8	0.025	LabW	Geiser and Broome, 1991	Seasonal
<i>Cercartetus caudatus</i>	Long-tailed pygmy possum	Australia	Tropical	30	SB/HIB?	n.d.	NA	Lab	Atherton and Haffenden, 1982	n.d.
<i>Cercartetus concinnus</i>	Western pygmy possum	Australia	Temperate/semi-arid	18	HIB	4.7	0.046	Lab	Geiser, 1987	n.d.
<i>Cercartetus lepidus</i>	Tasmanian pygmy possum	Australia	Temperate	12	SB/PT*	5.9	0.052	Lab	Geiser, 1987	n.d.
<i>Cercartetus nanus</i>	Eastern pygmy possum	Australia	Subtropical	20	SB/HIB	1.3	0.018	LabW	Geiser, 1993; Song et al., 1997; Turner et al., 2012	Food withdrawal; opportunistic
Petauridae										
<i>Petaurus breviceps</i>	Sugar glider	Australia	Wide distribution, tropical	130	DT	10.4	0.03	Field (T _b) and LabW (MR)	Fleming, 1980; Körtner and Geiser, 2000; Christian and Geiser, 2007	Reluctant to enter torpor; triggered by rain and cold

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
Tarsipedidae										
<i>Tarsipes rostratus</i>	Honey possum	Australia	Wide distribution	5–15	DT	5.4	0.15	LabW	Collins et al., 1987	Triggered by food shortage and low temperature
Monotremata										
Tachyglossidae										
<i>Tachyglossus aculeatus</i>	Short-beaked echidna	Australia	Wide distribution, tropical	2800	SB/HIB/PT	4	0.03	Field (T _b) and LabW (MR)	Augee and Ealy, 1968; Grigg et al., 1989	Seasonal HIB year-round use of SB?-food withdrawal, cold
PRIMATES										
Lemuridae										
<i>Allocebus trichotis</i>	Hairy-eared dwarf lemur	Madagascar	Tropical	70	SB/HIB?	n.d.	NA	Anecdotal field evidence	Dausmann, 2014	n.d.
<i>Cheirogaleus crossleyi</i>	Furry-eared dwarf lemur	Madagascar	Tropical	350	HIB	9	NA	Field	Blanco and Rahalinarivo, 2010	Seasonal
<i>Cheirogaleus major</i>	Greater dwarf lemur	Madagascar	Tropical	300	HIB	n.d.	NA	Field	Lahann, 2007	Seasonal
<i>Cheirogaleus medius</i>	Fat-tailed dwarf lemur	Madagascar	Tropical	130	HIB	9.3	0.044	Field	Dausmann et al., 2005	Seasonal
<i>Cheirogaleus sibreei</i>	Sibree's dwarf lemur	Madagascar	Tropical	250	HIB	n.d.	NA	Field	Blanco et al., 2013	Seasonal
<i>Microcebus berthae</i>	Madame Berthe's mouse lemur	Madagascar	Tropical	31	DT	6.8	0.09	Field	Ortmann et al., 1997; Schmid et al., 2000	Seasonal
<i>Microcebus griseorufus</i>	Reddish-gray mouse lemur	Madagascar	Tropical	50	SB/PT/HIB	6.5	0.15	Field	Kobbe and Dausmann, 2009; Kobbe et al., 2011, 2014	Seasonal, hibernation depending on body mass
<i>Microcebus murinus</i>	Gray mouse lemur	Madagascar	Tropical	70	SB/PT?/HIB	7.8	0.16	Field	Schmid, 2000; Schmid and Speakman, 2000	Seasonal, hibernation depending on body mass and sex
<i>Microcebus ravelobensis</i>	Golden-brown mouse lemur	Madagascar	Tropical	63	DT	25 ^F	NA	Field	Lovegrove et al., 2014a	Seasonal
<i>Microcebus rufus</i>	Brown mouse lemur	Madagascar	Tropical	40	SB/PT?/HIB?	n.d.	NA	Field	Atsalis, 1999; Randrianambinina et al., 2003	Seasonal
<i>Mirza coquereli</i>	Coquerel's mouse lemur	Madagascar	Tropical	n.d.	DT	n.d.	NA	Anecdotal field evidence	Dausmann, 2008	Seasonal

(Continued)

TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
Lorisidae										
<i>Galago moholi</i>	African lesser bushbaby	Africa	Sub/-tropical	100	DT	13.5	0.09	Field	Nowack et al., 2010, 2013b	Emergency, low body mass, food withdrawal
<i>Loris tardigradus tardigradus</i>	Red slender loris	Asia	Tropical	85–369	DT	n.d.	NA	Field	pers. obs. KAI Nekaris	n.d.
<i>Nycticebus javanicus</i>	Javan slow loris	Asia	Tropical	600	DT	n.d.	NA	Anecdotal field evidence	pers. obs. KAI Nekaris	n.d.
<i>Nycticebus pygmaeus</i>	Pygmy slow loris	Asia	Tropical	450	PT	11	NA	LabW	Streicher, 2004; Ruf et al., 2015	Seasonal
RODENTIA										
Bathergidae										
<i>Cryptomys hottentotus darlingi</i>	Mashona mole rat	Africa	Sub/-tropical	60	DT	26.8	NA	Lab	Bennett et al., 1993	Cold
<i>Fukomys damarensis</i>	Damaraland mole rat	Africa	Sub/-tropical	88–202	n.d.	28.5	NA	Lab	Streicher, 2010; Boyles et al., 2012	Seasonal?
Cricetidae										
<i>Calomys musculinus</i>	Drylands vesper mouse	America	Sub/-tropical	20	DT	28	0.52	LabW	Bozinovic and Rosenmann, 1988	Aridity? Spontaneous torpor when food supplied
<i>Calomys venustus</i>	Córdoba vesper mouse	America	Sub/-tropical	49.5	DT	16.4	0.96	LabW	Caviedes-Vidal et al., 1990	n.d.
<i>Phyllotis darwini</i>	Darwin's leaf-eared mouse	America	Temperate	35.9	DT	17.5	0.19	LabW	Bozinovic and Marquet, 1991	Food withdrawal
Muridae										
<i>Acomys russatus</i>	Golden spiny mouse	Africa/Middle East	Sub/-tropical	50–72	SB/HIB	24	0.25	Lab	Grimpo et al., 2013; Barak et al., 2019	Torpor use at high temperature and increased during food restriction
<i>Aethomys namaquensis</i>	Namaqua rock mouse	Africa	Sub/-tropical	46	n.d.	19.8	NA	Field	Withers et al., 1980	n.d.
<i>Gerbillus pusillus</i>	Least gerbil	Africa	Tropical	13	DT	16.7	0.38	LabW	Buffenstein, 1984	Food deprivation
<i>Mus musculus</i>	House mouse	Worldwide	Wide distribution, tropical	13	DT	20.5	0.7	Lab	Hudson and Scott, 1979; Tomlinson et al., 2007; Schubert et al., 2010	Cold, food deprivation

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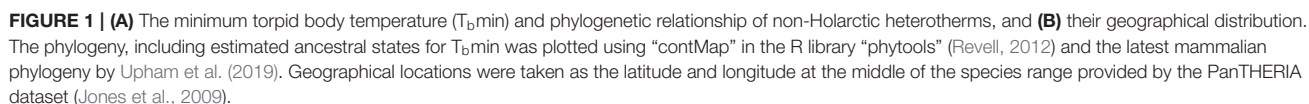
TABLE 1 | Continued

Species	Common name	Distribution	M _b (g)	DT/PT/HIB	T _{min} (°C)	TMR (mLO ₂ h ⁻¹ g ⁻¹)	Lab/Field	References	Potential torpor triggers	
<i>Saccostomus campestris</i>	Pouched mouse	Africa	Sub/-tropical	60–87	DT	21	0.35	Lab	Lovegrove and Raman, 1998; Mzilikazi and Lovegrove, 2002	Year-round, triggered by cold and in females also by food restriction
<i>Steatomys pratensis</i>	Fat mouse	Africa	Tropical	16	DT	13	0.3	Lab	Ellison, 1995	Cold
<i>Petromyscus collinus</i>	Pygmy rock mouse	Africa	Sub-tropical	19	n.d.	15.6	NA	Field	Withers et al., 1980	n.d.
<i>Pseudomys albocinereus</i>	Ash-grey mouse	Australia	Wide distribution, subtropical	28	DT	24.5	1.02	LabW	Barker et al., 2012	Torpor use at 20/25°C, presumably triggered by food withdrawal
<i>Pseudomys hermannsburgensis</i>	Sandy inland mouse	Australia	Wide distribution, tropical	12	DT	17.3	0.85 ^F	LabW	Tomlinson et al., 2007	Hypothermia in response to cold, no spontaneous arousal
<i>Rattus fuscipes</i>	Bush rat	Australia	Wide distribution, subtropical	119–151	DT	23.8	NA	Field	Nowack and Turbill, unpublished data	Torpor use in response to hindered foraging activity
Gliridae (Myoxidae)										
<i>Graphiurus murinus</i>	Woodland dormouse	Africa	Sub/-tropical	45	PT	1.5	NA	Field	Mzilikazi et al., 2012	n.d.
<i>Graphiurus ocularis</i>	Spectacled dormouse	Africa	Subtropical/temperate	67.8	n.d.	<31	NA	LabW	Perrin and Ridgard, 1999	n.d.

Species are chosen on basis of Ruf and Geiser (2015); distributions are based on the IUCN distribution maps. HIB, hibernation (several months); PT, prolonged torpor (several days); DT, daily torpor (<24 h); SB, short torpor bouts undergone by hibernators; n.d., no data; M_b, body mass; T_{min}, minimal body temperature during torpor; TMR, torpid metabolic rate, Lab/Field: Field, evidence from field studies or from wild animals (captured from the field and usually measured within 24 h to a few days) in a field laboratory under natural light and temperature conditions; Lab, evidence from laboratory measurements; LabW, evidence from laboratory measurements on wild animals, i.e., captured from the field and usually measured within 24 h to a few days.

*Termed "hibernation" in the publication, but we further differentiate multiday torpor bouts into prolonged torpor and hibernation based on length.

^F Number estimated from figure.



and T_b adjusts accordingly (Carey et al., 2003; Geiser, 2004a; Heldmaier et al., 2004). Additionally to active depression of metabolic rate, the abandoning of the differential between T_b and ambient temperature contributes substantially to energy savings during torpor bouts, especially in small species. Usually this results in a drop in T_b , the degree of which depends on ambient temperature (and the degree of daily fluctuations thereof), the insulative capacity of the resting site (see below), and the duration of the torpor bout (Hallam and Mzilikazi, 2011; Kobbe et al., 2011).

Although we can still differentiate daily heterotherms and hibernators in the non-Holarctic dataset, the distinction becomes a bit more blurry. Notably, it is more common for non-Holarctic hibernators to also use short bouts of torpor that typically last less than 24 h but during which metabolic rate is lowered to levels comparable to those during hibernation phases, e.g., seen in *Nyctophilus* spp. (Geiser and Brigham, 2000; Geiser and Stawski, 2011). To differentiate these from daily torpor use by daily heterotherms, we will refer to those by using the term "short bouts". Furthermore, many non-Holarctic hibernators do not only use short bouts or hibernation, but often also show an intermediate length of torpor, i.e., "prolonged torpor" lasting up to several days with regular activity (several hours to many days) between torpor bouts (Kobbe et al., 2011; Dausmann, 2014).

HETEROTHERMY AS THE NORM, HOMEOTHERMY AS THE EXCEPTION

Although Holarctic heterotherms usually maintain a high and stable T_b during part of the year, examples from the southern hemisphere show us that this is not the case for all heterotherms. At the extreme end of thermolability in heterotherms are the eutherian Tenrecidae, a family of mammals found on Madagascar and the surrounding islands, which have been isolated from the mainstream of mammalian evolution for about 30–56 Myr (Crompton et al., 1978; Everson et al., 2016). They are members of the superorder Afrotheria, a group of mammals whose extant members live predominantly in Africa or are of African origin (Poux et al., 2005). The ecology, behavior and thermoregulatory physiology of these "basoendothermic" mammals have been proposed to be similar to those of the early mammalian endotherms (Lovegrove and Génin, 2008; Levesque and Lovegrove, 2014). All members of this group investigated to date exhibit a generally low basal metabolic rate and highly labile T_b , often closely tracking environmental temperature (Table 1). Even so, the lesser hedgehog tenrec, *Echinops telfairi* (and likely other species of tenrec as well), has functional brown adipose tissue, enabling non-shivering thermogenesis (Oelkrug et al., 2013). In addition to low basal metabolic rates, many species of tenrecs also enter short daily bouts of torpor and long-term hibernation (Table 1). Some species (*E. telfairi*, *Setifer setosus*) seem to maintain euthermy (higher and less variable T_b in the resting-phase) only during reproduction (gestation and/or lactation) (Poppitt et al., 1994; Wein, 2010; Levesque and Lovegrove, 2014; Lovegrove et al., 2014b) presumably to enhance embryonic development and milk production. For males, the

occasional rise of T_b above 30°C might be sufficient to allow sperm production (Fietz et al., 2004).

Outside of the hibernation season (during the austral winter), torpor in *E. telfairi* and *S. setosus* seems to be independent of external stimuli and is employed frequently not in response to seasonality or a scarcity of food or water, but throughout the active season (see Figure 2; Lovegrove and Génin, 2008; Wein, 2010; Levesque et al., 2013, 2014; Dausmann et al., submitted). Interestingly, the thermolability shown by many tenrec species is mirrored by another basoendotherm (dubbed "protoendotherm" by Grigg et al., 2004), the short-beaked echidna, *Tachyglossus aculeatus* (Order Monotremata). Echidnas have a wide distribution in Australia and Tasmania, from cold-temperate to desert habitats, and also occur in tropical areas. They exhibit daily fluctuations in T_b (up to 5°C) and use torpor flexibly (Kuchel, 2003; Grigg et al., 2004; Nicol and Andersen, 2006). Depending on their habitat they increase torpor use during the cold period and either show long-term hibernation (e.g., Tasmania or Australian Alps: Augee and Ealy, 1968; Grigg et al., 1989; Nicol and Andersen, 2002) or prolonged torpor lasting for a few days (Brice et al., 2002; Kuchel, 2003; Western Australian Wheatbelt: Nowack et al., 2016).

Although this form of continuous heterothermy, either via torpor or highly variable T_b , has to date predominantly been found in spiny, terrestrial insectivores such as tenrecs and echidnas, it may possibly exist in other groups. For example, another tropical species that uses torpor on a regular day-to-day basis is the Angolan free-tailed bat, *Tadarida aegyptiaca*. This species uses daily torpor throughout the year and continuously maintains its T_b close to ambient temperatures when at rest (Vivier and van der Merwe, 2007). Given the large phylogenetic range covered by these three groups and the small number of studies investigating thermophysiology in the field, it is likely that there are other species of mammals with similar levels of thermolability that will be revealed with further study.

SEASONAL HETEROTHERMIC RESPONSES

Strictly seasonal use of torpor seems to be less common in lower latitude heterotherms than in their northern counterparts (Table 1). Furthermore, although most species show regular, seasonal use of daily or prolonged torpor, the use of hibernation, in the classical sense of animals disappearing for months at a time, is not as widespread in non-Holarctic species as it is in temperate/arctic mammalian lineages (Heldmaier et al., 2004; McKechnie and Mzilikazi, 2011; Ruf and Geiser, 2015). In contrast to those tenrec species highlighted above that use some form of heterothermic response during most of the year, other species, such as the tailless tenrec, *Tenrec ecaudatus*, are generally believed to only hibernate seasonally (Nicol, 1986). Although based on more recent studies, it is highly likely that they can also use short bouts of torpor outside of the regular hibernation period (Lovegrove et al., 2014b; Treat et al., 2018).

Interestingly, the most strictly seasonal hibernators in the tropics are concentrated in one family of small, nocturnal

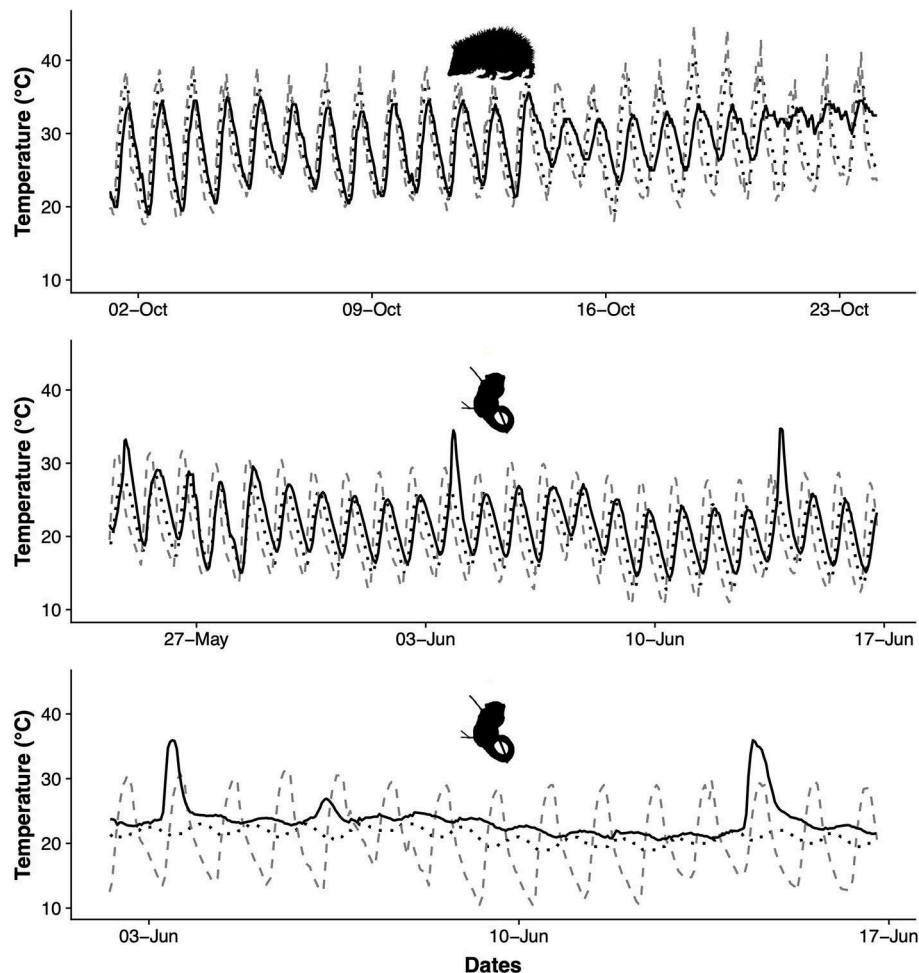


FIGURE 2 | Top panel: Body temperature (black), ambient temperature (dashed gray) and temperature from a nearby nest site (dotted black) of a free ranging greater hedgehog tenrec (*Setifer setosus*) during the Austral winter (dry season). Redrawn from Lovegrove et al. (2014a) and Levesque et al. (2014). Middle and lower panel: Body temperature (black), ambient temperature (dashed gray) and tree-hole temperature (dotted black) of a free ranging fat-tailed dwarf lemur (*Cheirogaleus medius*) during the Austral winter (dry season) in a poorly insulated (middle) or moderately well insulated (lower panel) tree-hole.

Malagasy lemurs, the Cheirogaleidae (**Table 1**). It is likely that all species of this family (i.e., the genera *Allocebus*, *Cheirogaleus*, *Microcebus*, *Mirza*) are heterotherms, with the exception of members of one genus (*Phaner*, which has a very specific feeding regime that does not change seasonally) and most species of this family studied to date become torpid during the austral winter under free-ranging conditions (Dausmann, 2008, 2014). Thus, heterothermy in lemurs is a seasonal response, decreasing energy and water demands drastically thereby facilitating survival during the harsh (cold and dry) conditions of the Malagasy winter (Schmid and Speakman, 2000; Schmid et al., 2000). During the dry season in winter, temperatures decline across all habitats of Madagascar, although the extent varies. All dwarf lemurs (*Cheirogaleus*) are obligate hibernators in their natural environments (Petter, 1978; Hladik et al., 1980; Dausmann, 2008, 2014), from the eastern rainforests to the western dry forests. They hibernate either in tree hollows or buried underground

between 3.5 and 8 months, depending on the seasonality of their habitats (Blanco et al., 2013; Dausmann, 2013; Dausmann and Blanco, 2016). As applies to most hibernators, this strategy requires preparation as well as sufficiently favorable conditions for recovery when hibernation is terminated, and reproduction needs to commence promptly. Thus, it can only be expressed in fairly predictable habitats. More flexible responses are shown by the mouse lemurs (*Microcebus*- over 20 species at present count). Most likely, all species are heterotherms and every mouse lemur species studied up to date has shown some form of seasonal torpor (**Table 1**). Some of these species have also shown months-long hibernation, however, in each case, only some individuals in a population did so, and individuals alternated between occasional torpor, short bouts of torpor, prolonged torpor and months-long hibernation both within and between winter seasons (Schmid and Ganzhorn, 2009; Kobbe et al., 2011). *Allocebus* and *Mirza* species have

been reported or presumed to exhibit daily torpor during winter, albeit at different and flexible frequencies, however data have yet to be recorded (Dausmann and Warnecke, 2016; **Table 1**).

Most lower latitude hibernators, such as many bat species (see **Table 1**), short-beaked echidnas, *Tachyglossus aculeatus* (Grigg et al., 1989), and eastern pygmy-possums, *Cercartetus nanus* (Turner et al., 2012), are not strictly seasonal in their use of torpor and though they will use hibernation in winter, they also undergo shorter bouts of torpor during the rest of the year (see Opportunistic Torpor below). However, like the lemurs mentioned above, there are some species, which show a strict seasonal use of torpor (either daily or prolonged torpor) such as the Southern African hedgehog, *Atelerix frontalis* (Hallam and Mzilikazi, 2011), the African lesser bushbaby, *Galago moholi* (Nowack et al., 2010, 2013b), pygmy slow loris, *Nycticebus pygmaeus* (Streicher, 2004; Ruf et al., 2015), the Damaraland mole-rat, *Fukomys damarensis* (Streicher, 2010), and the Mountain pygmy possum, *Burramys parvus* (Geiser and Broome, 1991). However, it has to be noted that sufficient data on year round torpor use are lacking for most species with most measurements restricted to the winter when torpor is expected (Levesque et al., 2016).

OPPORTUNISTIC TORPOR

Similar to the tenrecs and echidnas mentioned above, a number seasonal heterotherms also employ torpor independent of season, if the conditions are sufficiently challenging (**Table 1**). Opportunistic torpor enables these species to respond promptly to unpredictable environmental changes, such as prolonged droughts or cold spells, as well as to an unusual shortage of food. For example, the eastern and rock elephant shrews, *Elephantulus myurus* and *E. rupestris*, routinely show short daily bouts of torpor during the winter, but also use daily torpor opportunistically throughout the year, presumably triggered by low temperatures and high air humidity (Mzilikazi and Lovegrove, 2004; Oelkrug et al., 2012). Furthermore, echidnas and marsupial antechinus (*Antechinus* spp.) have recently been reported to intensify torpor use in response to the threats of and the reduced food availability after fires (Stawski et al., 2015; Nowack et al., 2016). Other species, such as sugar gliders, *Petaurus breviceps*, or golden spiny mice, *Acomys russatus*, have been observed to use or intensify torpor in response to storms or floods (Nowack et al., 2015; Barak et al., 2019). Similarly, many non-Holarctic bat species exhibit prolonged torpor during winter (up to several days; reviewed by Geiser and Stawski, 2011) while also using opportunistic short bouts of torpor in other seasons. For example, the Northern long eared bat, *Nyctophilus bifax*, uses prolonged torpor (up to 5.4 days) during winter, but short bouts of torpor in response to cold weather conditions during summer (Stawski et al., 2009). Another, only recently studied, example is the Malagasy bat, *Macronycteris commersoni*. This species roosts in hot caves ($\geq 32^\circ\text{C}$ year-round) and displays a whole spectrum of different torpor responses during summer and winter (Reher et al., 2018). In summer, individuals may remain euthermic or

enter torpor bouts lasting up to 6 days (sometimes coinciding with cyclones), while in winter their responses range from short torpor bouts, over prolonged torpor to hibernation with single bouts lasting up to 16 days; the triggers for the duration of torpor use remain unknown (Reher et al., unpublished data).

Other species also show opportunistic torpor independent of season, but in response to ambient conditions or food and water supply (**Table 1**). Amongst those are the pouched mouse, *Saccostomus campestris*, which entered torpor in the laboratory over a wide range of ambient temperatures and independent on photoperiod (Lovegrove and Raman, 1998; Mzilikazi and Lovegrove, 2002), the pichi, *Zaedyus pichiy*, which has been reported to use short bouts of torpor in spring after the hibernation season (Superina and Boily, 2007), the monito del monte, *Dromiciops gliroides* that entered torpor in the laboratory when kept under long photoperiod and relatively warm temperatures (20°C) (Bozinovic et al., 2004; Nespolo et al., 2010), and the striped faced dunnart, *Sminthopsis macroura* (Geiser and Baudinette, 1987; Song et al., 1997). In contrast, opportunistic use of heterothermy has been observed in only a handful of Holarctic species. The edible dormouse, *Glis glis*, for example, has been shown to re-enter hibernation already in July and to remain torpid until the following year (up to 11 months in total) in non-mast years when reproduction is skipped (Bieber and Ruf, 2009; Hoelzl et al., 2015).

RARE USE OF TORPOR

Not all heterotherms use torpor on a regular basis. A few species are known to be physiologically capable of employing torpor but do so only under adverse conditions and instead remain homeothermic whenever possible. A well-studied example is the African lesser bushbaby, *Galago moholi*. This species was long thought to be strictly homeothermic, despite cool environmental temperatures and a lack of food present in its habitat during winter. However, Nowack et al. (2010) detected sporadic daily torpor in a small fraction of the population. Since even these few (primarily juvenile and subadult) individuals became torpid only on single occasions, this suggests an unusual or specific trigger and is clearly not a regular seasonal response (Nowack et al., 2010, 2013b). Instead, behavioral and nutritional strategies are used by *G. moholi* to facilitate survival in winter, including larger sleeping groups, better insulated sleeping places, and changes in diet (Nowack et al., 2013c). In *G. moholi*, heterothermic phases are always shorter than 24 h and individuals have unusual difficulties rewarming to euthermic levels on cold days. The fact that *G. moholi* possess brown adipose tissue and the ability to use non-shivering thermogenesis suggests that individuals only enter torpor when their internal energy stores are depleted and that they have to rely on exogenous heat to return to active T_b (Nowack et al., 2013a).

Other heterothermic species which have been found to use torpor only rarely are the sugar glider, *Petaurus breviceps* (Christian and Geiser, 2007) and the feathertail glider, *Acrobates pygmaeus* (Jones and Geiser, 1992). Torpor use in *P. breviceps* seems to be triggered by especially cold and rainy days when

animals remain in their nests instead of foraging (Körtner and Geiser, 2000; Nowack et al., 2015), enabling them to occur over a wide range of climatic conditions and even in cold temperate areas (snow and freezing conditions overnight). *A. pygmaeus* commonly exhibit bouts of short torpor but seem to be able to extend torpor use and undergo prolonged bouts when cold stressed (8–12°C; Jones and Geiser, 1992). Further examples of reluctant use of torpor are found in the rodent family. Although most Australian ash-gray mice, *Pseudomys albocinereus*, remained euthermic over a range of ambient temperatures when studied in the laboratory, one individual became torpid at 20 and 25°C (Barker et al., 2012). Body temperature recordings also suggest that Australian bush rats (*Rattus fuscipes*), which have a large geographical distribution, including tropical moist forests, can use torpor to compensate for lost feeding opportunities (unpublished data Nowack and Turbill). On the other hand, sandy inland mice (*Pseudomys hermannsburgensis*), who are also endemic to Australia, responded to food deprivation and low ambient temperature by becoming hypothermic without being able to arouse spontaneously (Tomlinson et al., 2007). More in-depth studies of species with large latitudinal ranges will provide better understanding of the flexibility of these responses.

Heterothermy as a singular response to acute emergency situations has to our knowledge not been reported for Holarctic mammals. This strategy, however, could be conceivable for members of the Sciuridae, which includes the classic hibernators (ground squirrels and chipmunks in the clade Marmotini). Interestingly, tree squirrels (sub-family Sciurinae) including European red squirrels (*Sciurus vulgaris*), have not been observed to enter torpid states (Dausmann et al., 2013), although it appears likely that closely-related flying squirrels are capable of shallow torpor (Olson et al., 2017). Tropical and sub-tropical sciurids have not been studied and more field studies are clearly needed to elucidate the potential for rare use of torpor in otherwise homeothermic mammals.

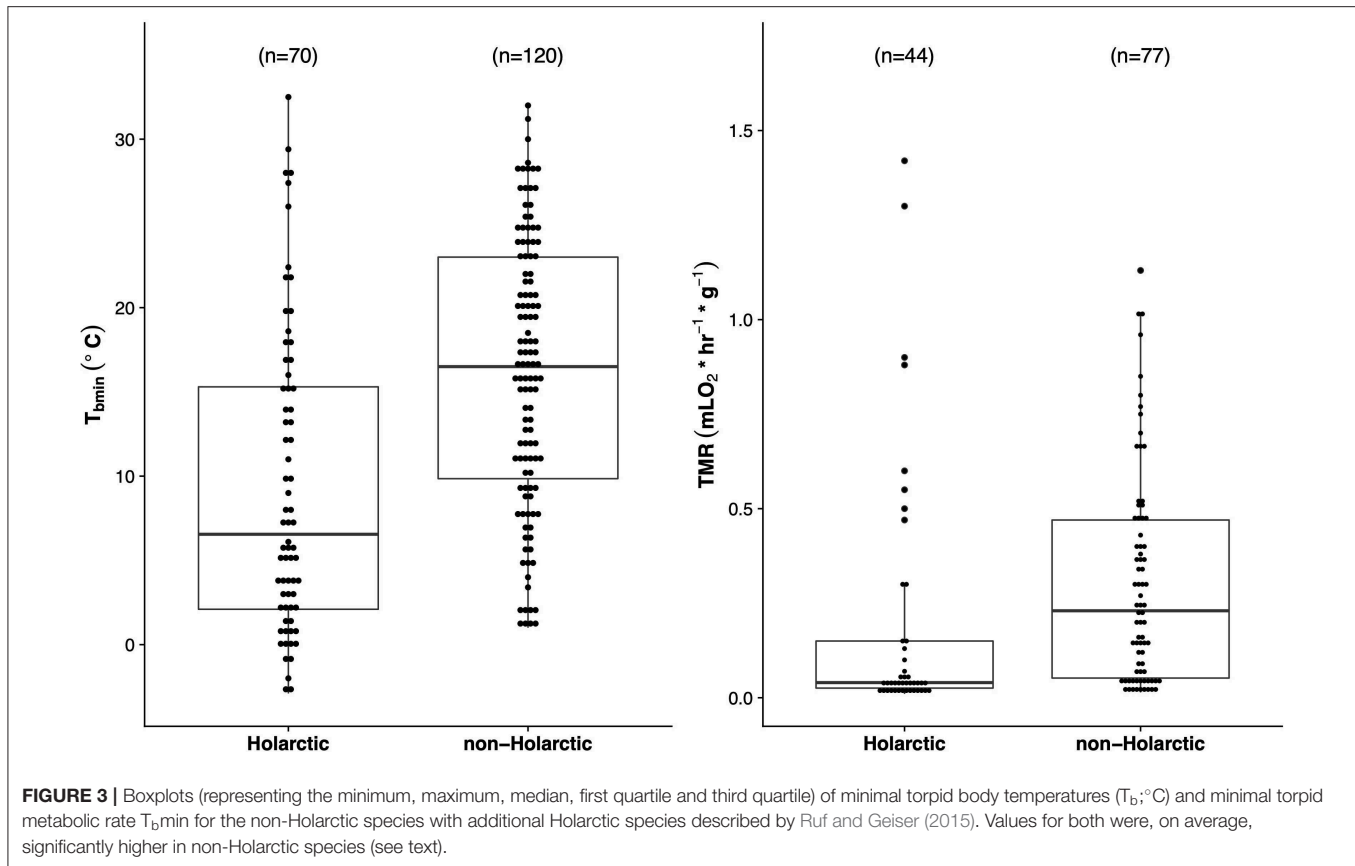
Differences in Body Temperature Are Related to Climate

One could assume that the clearest difference between tropical and Holarctic heterotherms is that T_b does not fall to extremely low levels. Indeed, with the exception of higher elevation habitats, ambient temperature rarely falls to life-threatening temperatures below 0°C in the tropics even during winter, and thus individuals should not need mechanisms to avoid freezing. The record holders, in terms of low T_b , amongst mammals are the Arctic ground squirrel, *Spermophilus parryii*, and the European hazel dormice, *Muscardinus avellanarius*, both regulating a decrease in T_b down to as low as −2.9°C during hibernation without freezing (Barnes, 1989; Pretzlaff and Dausmann, 2012). Nonetheless, heterotherms from non-temperate or arctic areas can sometimes approach this temperature, and the southern African hedgehog, *Atelerix frontalis*, which is also one of the largest of all subtropical heterotherms (400–800 g), has been observed to hibernate with a T_b as low as 1°C (Hallam and Mzilikazi, 2011). In lemurs and tenrecs, the lowest T_b during hibernation recorded to date is

6.5°C in *M. griseorufus* (Table 1; Kobbe et al., 2011), but more commonly T_b is higher between 10°C and 30°C. Indeed, lemurs and tenrecs continue to hibernate even at T_b s >30°C (Figure 2). Similarly, eastern pygmy-possums (*Cercartetus nanus*) become torpid within their thermo-neutral zone and golden spiny mice (*Acomys russatus*) even use torpor at ambient temperatures as high as 35°C (Song et al., 1997; Grimpot et al., 2013).

To imperically test for differences in minimal torpid T_b and torpid metabolic rates between Holarctic and non-Holarctic species we used the “plgs” function in the R package “caper” [R version 3.6.2 (Orme et al., 2013; R Development Core Team, 2019)] on data from species in Table 1 and Holarctic species from Ruf and Geiser (2015) and controlled for phylogenetic relatedness using the mammal phylogeny by Upham et al. (2019). We tested for differences between torpor T_b using “tbmin~distribution” and in metabolic rate using “torpidMR~mass+distribution.” Holarctic species had significantly lower minimum torpid T_b ($p = 0.001$), and torpid metabolic rates ($p < 0.0001$) than non-Holarctic species, despite a high degree of overlap in both values between the two groups (Figure 3). However, in most, if not all, of these examples from non-Holarctic species the lowest T_b measured was bounded at the lower end by the coldest ambient temperatures, it is therefore difficult to predict if torpor patterns in non-Holarctic species would be similar at colder temperatures. The study of tropical heterotherms emphasizes that heterothermy must be defined on the basis of mechanistic, physiological parameters, such as significantly decreased metabolic rate (or heart rate), and not solely by T_b (Dausmann et al., 2004; Kobbe et al., 2011; McKechnie and Mzilikazi, 2011; Canale et al., 2012). However, our analysis has shown that we only have metabolic rate data from about half of the studied species (52% Holarctic and 57% of Non-Holarctic). Furthermore, the metabolic rate data in Table 1 do not necessarily represent minimum torpid metabolic rate for a species as they might have been taken in one study while longer/deeper torpor bouts have been recorded in another study in which only T_b has been measured (as in the case of *Acomys russatus*) or because metabolic rate data have been obtained under a (field-)laboratory setup while T_b has been obtained from free-ranging animals; in fact only eight studies that report torpor metabolic rates of non-Holarctic species have been measuring metabolic rates of animals in the field.

The low risk of freezing in most tropical heterotherms has consequences for several aspects of their physiology including fat metabolism. In the fat-tailed dwarf lemur, *C. medius*, the main fuel during hibernation is monounsaturated oleic acid, which is synthesized preferentially from dietary carbohydrates obtained before food supply diminishes (sugary fruits; Fietz et al., 2003). This fat is stored in large quantities in the tails as triglycerides, resulting in an almost doubling of body mass (Fietz and Dausmann, 2007). Temperate hibernators, on the other hand, profit from a high content of polyunsaturated fatty acids (PUFAs) during hibernation. A diet rich in n-6 PUFAs has been shown to lead to longer and deeper torpor bouts (Geiser and Kenagy, 1987; Giroud et al., 2013) and thus higher energy savings during winter as they increase the activity of the sarcoplasmic reticulum Ca^{2+} ATPase (SERCA) and thus counteract the suppressed enzymatic



activity and allow for greater fluidity of cell membranes at low temperature. Interestingly, n-3 PUFAs have a so far unexplained negative effect on torpor use (Giroud et al., 2013, 2018) and a diet rich in n-3 PUFAs has been shown to not only significantly reduce torpor use in temperate zone heterotherms but also in the tropical daily heterotherm, *Microcebus murinus* (Vuarin et al., 2016). However, the amount of n-6 and n-3 PUFAs in the diet is unlikely to be critical for tropical heterotherms as they usually do not hibernate at T_b s close to freezing (Goldman, 1975; Frank, 1991; Vuarin et al., 2016). They may thus avoid autoxidation and the production of toxic fatty acids peroxides, which are by-products of the metabolism of essential fatty acids.

Different Triggers of Torpor Use

Although torpor use in temperate and arctic regions is usually triggered by photoperiod, low temperatures, and limited food ability, the data summarized in **Table 1** clearly shows the variety of factors that are triggering torpor in non-Holarctic species. As mentioned above, even during winter months, cold does not seem to be a necessity for tropical and subtropical hibernators and torpor bouts are often caused by seasonal low water availability instead of low food availability. Interestingly, mouse-tailed bats (*Rhinopoma*) are even considered incapable of entering torpor during cold periods (Kulzer, 1965). Levin et al. (2015) found that two species of mouse-tailed bats (*Rhinopoma cystops*, *Rhinopoma microphyllum*) hibernated in a geothermally heated

cave in winter with a stable ambient temperature of 19–23.8°C although colder caves were available. Both species showed the lowest torpor metabolic rate at $\sim 20^{\circ}\text{C}$ and aroused at ambient temperature below 16°C (Levin et al., 2015). Thus, the availability of warm caves has allowed them to expand their subtropical distribution range from semi-arid and warm regions in Asia and Africa into southern Israel, the northern edge of their distribution (Levin et al., 2008, 2015). Similarly, the lesser long-eared bat (*Nyctophilus geoffroyi*) uses short bouts of torpor in tropical northern Australia in winter where ambient temperatures do not drop below 16.5°C (Geiser et al., 2011). Opportunistic torpor is often triggered by unpredictability in environmental parameters, such as unseasonal food or water shortages (e.g., droughts or fires), conditions that are less frequently encountered on an unpredictable basis in temperate and arctic regions.

The Advantages of Passive Arousals

Torpor at relatively high ambient temperatures still offers energetic savings, but without some of the major disadvantages. Many vital bodily functions can continue to operate at the comparatively high torpid T_b of non-Holarctic heterotherms and warming to euthermic levels is relatively inexpensive because animals can mostly rely on energy-saving, passive rewarming (Dausmann et al., 2009). An Australian desert bat, the inland free-tailed bat *Ozimops petersi* (former *Mormopterus* species 3; Lumsden, 2019), for example, can arouse from torpor without

an obvious active thermogenic support (Bondarenko et al., 2013). Moreover, individuals can start being active at relatively low T_b , and then activity itself can be used as a means of heat production. Ortmann et al. (1997) first observed the so-called two-step arousal in a species of mouse lemur (*M. murinus*). Individuals rewarming from torpor initially use passive means via exogenous heat sources to raise their T_b to about 27°C before employing endogenous heat production, which keeps metabolic rate (and energy expenditure) during the rewarming process low. Since then, this mechanism has been verified in many other tropical heterotherms that closely synchronize their arousal times with the onset of rising environmental temperature which they may supplement by basking (Lovegrove et al., 1999; Schmid, 2000; Geiser et al., 2002; Mzilikazi et al., 2002; Geiser and Drury, 2003; Dausmann et al., 2005; Lovegrove and Génin, 2008; Warnecke et al., 2008; Kobbe et al., 2011; McKechnie and Mzilikazi, 2011; Nowack et al., 2013b; Dausmann et al., submitted). Although mostly observed in species inhabiting relatively warm habitats, a recent study found that Djungarian hamsters (*Phodopus sungorus*), originally inhabiting Asian steppes, actively seek the heat of a basking lamp when rewarming from torpor under laboratory conditions (Geiser et al., 2016). This finding suggests that the use of passive rewarming might also be common in Holarctic heterotherms.

Perhaps one of the most surprising discoveries from warm climate hibernators is that periodic arousals, thought to be essential to proper functioning during hibernation, are not necessarily needed (Dausmann et al., 2005; Lovegrove et al., 2014b). Depending on the nature of the hibernaculum (insulative capacities) and ambient temperature, the T_b of tropical species can fluctuate widely during hibernation (daily fluctuations of T_b can exceed 25°C per day). Under these conditions, when T_b occasionally rises passively above about 30°C, the expensive arousals are abandoned in *Cheirogaleus* (Figure 2). In contrast, individuals hibernating in better insulated sites (large trees or underground), which have a lower but more stable T_b , show regular periodic arousals, just like their temperate or arctic counterparts (Dausmann et al., 2004, 2005). Similarly, the common tenrec (*Tenrec ecaudatus*) forgoes arousal completely while hibernating in an underground burrow where T_b s remain above 25°C for the winter (Lovegrove et al., 2014b). Although the ultimate factors necessitating periodic arousals in hibernators remain enigmatic (proposed explanations include reduction of oxidative stress and sleep debt, production of gene products, activation of the immune system, limitation of neurophysiological damage; Carey et al., 2003), it seems clear that the capacity to attain a high T_b passively determines whether or not arousals are required (Dausmann, 2014). For example, arctic ground squirrels, *S. parryi*, consistently sleep during arousals (Daan et al., 1991). Their electroencephalography shows the decrease in slow wave activity as would be expected when sleep debt had increased during the preceding phase of torpor. Thus, it has been postulated that the need for sleep slowly accumulates during torpor and that returning to euthermia is periodically required to sleep (Daan et al., 1991; Trachsel et al., 1991). Indeed, *C. medius* display aspects of sleep (rapid eye movement sleep) during the phases of passively heated warmer T_b during

hibernation (in contrast to phases of low T_b), possibly preventing the accumulation of sleep debt, and ensuring brain function and memory consolidation in individuals with highly fluctuating T_b (Krystal et al., 2013). To date, the only other mammal to not exhibit periodic arousals besides hibernating lemurs and tenrecs (Dausmann et al., 2004; Lovegrove et al., 2014b) are black bears, *Ursus americanus*, hibernating at T_b of >30°C (Tøien et al., 2011). The opportunity to abandon periodic arousals not only saves energy, but also limits the damaging high level of oxidative stress resulting from the increased production of reactive oxygen species during active rewarming (Carey et al., 2003; Giroud et al., 2009).

INTER- AND INTRASPECIFIC PHENOTYPIC FLEXIBILITY OF TORPOR USE IN THE TROPICS

Most interestingly, the distinction between the use of short torpor bouts and hibernation is less clear-cut in non-Holarctic heterotherms (Mzilikazi and Lovegrove, 2004; Cory Toussaint et al., 2010; Kobbe et al., 2011; Canale et al., 2012). Whereas, most Holarctic species usually either hibernate or use daily torpor, warmer climate species often show a mixed use of shorter and longer bouts. In the tropics, there is more variation between closely related species at the same site, between populations of the same species at different sites, between individuals within a population, and even in individuals between years (Dausmann, 2014). As outlined above, some species can switch between hibernation (several months), prolonged torpor over several days, becoming torpid for a few hours sporadically or daily (opportunistic) use of short torpor bouts, or remaining homeothermic. As the best examples of this phenotypic flexibility come from southern Madagascar, the driest and least predictable habitat of the island, we suggest that this flexibility may enable tropical species to inhabit not only seasonal, but also unpredictable habitats. It enables species to respond to the context of specific environmental parameters and their own body condition. For example, in the lemur *Microcebus griseorufus* and the bat *Macronycteris commersoni* all of these responses have been observed in different individuals in the same population at the same site (Kobbe and Dausmann, 2009; Kobbe et al., 2011; Reher et al., 2018). Similarly, western rock elephant shrews, *E. rupestris*, are highly heterothermic in South Africa, whereas the closely-related cape rock elephant shrews, *E. edwardii*, at the same site remain mostly homeothermic, although the species is capable of short to prolonged bouts of torpor (McKechnie and Mzilikazi, 2011; Boyles et al., 2012). Hottentot golden moles, *Amblysomus hottentotus longiceps*, and southern African hedgehogs, *A. frontalis*, seem to be capable of diverse thermoregulatory responses at the same site, and under the same conditions in captivity (Scantlebury et al., 2008; Hallam and Mzilikazi, 2011). Despite hibernation being a more fixed response, there is also variation in thermoregulatory patterns during hibernation, such as in dwarf lemurs and tenrecs, where the insulative properties of the hibernacula determine the

occurrence and extent of daily T_b fluctuations and the occurrence of periodic arousals.

Furthermore, the duration of hibernation can be flexible between different populations of the same species, depending on the duration of the period of scarceness in the particular habitat. For example, *C. medius* hibernates up to 8 months in the western dry forests of Madagascar, but only 3.5 months in the south-western littoral forests, where the dry season is much shorter (Lahann and Dausmann, 2011). Differences in thermoregulatory patterns might also emerge as a result of competition with other, closely related sympatric species. Only half as many individual *M. griseorufus* entered hibernation in a habitat where the larger *M. murinus* is present in the littoral forest in the south of Madagascar, compared to where *M. griseorufus* occurs alone in the spiny forest of the south-west (Kobbe et al., unpublished data). As hibernation is thought to be the more advantageous strategy in *Microcebus* species (higher energy savings; predation avoidance), *M. griseorufus* could be outcompeted for access to food before the hibernation period by the larger *M. murinus*, limiting pre-hibernation fattening. If true, then *M. griseorufus* may have to resort to short or prolonged torpor episodes to cope with the Malagasy winter in areas where it occurs together with *M. murinus*.

TROPICAL ORIGINS OF HETEROTHERMY, AND ENDOTHERMY, IN MAMMALS

It now seems increasingly likely that endothermy in mammals evolved from the ancestral ectothermic condition via a heterothermic state (Grigg et al., 2004; Geiser and Stawski, 2011; Lovegrove, 2017). All extant mammals are capable of metabolic heat production (Lovegrove, 2012), but the degree to which they regulate their T_b , both in terms of absolute temperature and level of variability, varies considerably (Boyles et al., 2013; Clarke and O'Connor, 2014). Mammals evolved under climatic conditions similar to modern day tropics, where ambient temperature is high for most of the year, and the costs of maintaining a comparatively high, stable T_b , especially at a lower level ($\sim 32^\circ\text{C}$ like in tenrecs and echidnas) would be relatively low (Levesque et al., 2013). This notion is supported by the fact that early mammalian ancestors had small body masses, were nocturnal, and mostly insectivorous (McNab, 1978; Kemp, 2006; O'Leary et al., 2013), similar to the hedgehog tenrecs. Moreover, it has been postulated that small mammals in particular cannot sustain the high rates of evaporation necessary

to maintain a T_b more than 2°C below ambient for more than a few hours (Crompton et al., 1978), because of substantial water loss needed for evaporative cooling. Often, tropical and subtropical heterotherms inhabit dry environments and water savings might even be more essential for survival than energy savings (Schmid and Speakman, 2000; Dausmann, 2014). Water loss, however, could be avoided if T_b is regulated slightly above ambient, and the outward flow of heat is varied by insulation, therefore, a switch to a diurnal activity pattern in some species would have necessitated higher T_b s (Crompton et al., 1978), which in turn were only made possible with the evolution of the scrotum (Lovegrove, 2019). The evolution of endothermy in mammals is an emergent property of the evolution of various characteristics that aid in either heat production (e.g., thermogenesis, UCP1) and heat dissipation (e.g., insulation, external scrotums) and happened to a different degree across the mammalian lineage (Lovegrove, 2012, 2019; Seebacher, 2018; Jastroch and Seebacher, 2020). By studying the added level of variability in many thermoregulatory traits, torpor use in particular, observed in species in the tropics and subtropics can help shed further light on how endothermy evolved in mammals.

Although advances in understanding the ecological and physiological underpinnings of tropical heterothermy have been substantial, many questions remain. For example, we need to learn more about how blood parameters (lactate levels, as a proxy for hypoxia in the tissue), immunocompetence and sleeping patterns in tropical hibernators differ compared to hibernators with continuously low T_b , especially if we wish to disentangle hibernation specific and low T_b specific physiological responses, which could help elucidating the evolution of homeothermy.

AUTHOR CONTRIBUTIONS

JN and KD conceived of the idea and wrote the first version of the manuscript. DL ran the analyses and prepared the figures for the manuscript. All authors contributed to the final version of the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer FG, declared a past collaboration with the authors to the handling editor.

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