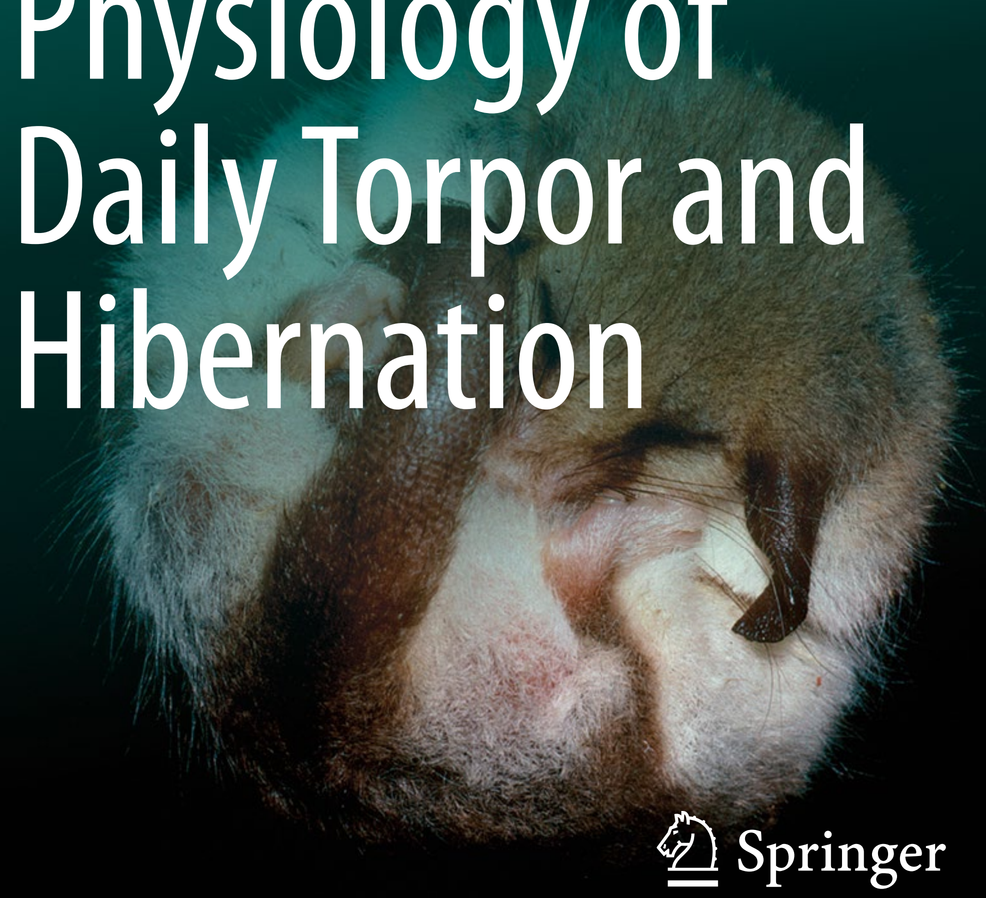
Fascinating Life Sciences

Fritz Geiser

Ecological Physiology of Daily Torpor and Hibernation



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Ecological Physiology of Daily Torpor and Hibernation

Springer

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ISSN 2509-6745 ISSN 2509-6753 (electronic)
Fascinating Life Sciences
ISBN 978-3-030-75524-9 ISBN 978-3-030-75525-6 (eBook)
https://doi.org/10.1007/978-3-030-75525-6

This Springer imprint is published by the registered company Springer Nature Switzerland AG.
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

To my parents Lore and Adolf, for encouraging me to follow my interest in Zoology.

Preface

The last ‘hibernation book’ was published in 1982, nearly 40 years ago, so clearly an update was needed. The options were a book written by a single author or an edited book written by several authors. The second approach was considered because of the vast recent expansion of this field, especially with regard to biochemical and molecular studies, but also on physiological ecology of free-ranging animals. As I was encouraged by colleagues, as well as the publisher, to write one by myself, the final decision was to do that. The emphasis of the book therefore is on organismal biology and primarily covers areas in which I have done some work.

I would like to thank many individuals, in alphabetical order, who were pivotal in undertaking this project. First and foremost, I must thank Mark Brigham, Gerhard Körtner, and Bronwyn McAllan for critically reading manuscripts and providing constructive feedback, which substantially improved the content, structure, logical flow, and writing. Kate McAllan helped with editing the references. Mark Brigham, Ken Cross, and Gerhard Körtner gave me permission to use their photographs of animals. Silvia Herold from Springer showed incredible patience, despite my slow progress. Others who have helped with or contributed to the book in various ways include: Yaara Aharon-Rotman, Artiom Bondarenco, Loren Buck, Christine Cooper, Shannon Currie, Kathrin Dausmann, Lucy Farrow, Sara Hiebert, Lisa Kealhofer, Barry Lovegrove, Bill Milsom, Tetsuo Morita, Roberto Nespolo, Julia Nowack, Chris Pavey, Stephanie Reher, Alex Riek, Thomas Ruf, Anusha Shankar, Carina Siutz, Xiaowei Song, Clare Stawski, Chris Wacker, Craig Willis, and Phil Withers.

I also would like to thank my scientific mentors who positively influenced my scientific career in a way that enabled me to write this book. They are: Paul Bühler, Reinhard Hilbig, and Hinrich Rahmann, from the University of Hohenheim, Stuttgart; Mike Augee and John Raison, from the University of New South Wales and Macquarie University, CSIRO Plant Physiology, Sydney; Russ Baudinette and Ted McMurchie, from Flinders University and CSIRO Human Nutrition, Adelaide; Jim Kenagy from the University of Washington, Seattle; and Roger Seymour from the University of Adelaide.

I wish to thank my students and postdocs for creating a productive, positive, and pleasant environment in the Torpor Lab. Thank you to the doctoral students: Artiom Bondarenco, Nereda Christian, Shannon Currie, Anna Doty, Lisa Doucette, Chris Holden, Jo Holloway, Tracy Maddocks, Daniella Rojas, Xiaowei Song, Clare Stawski, Chris Turbill, Jamie Turner, Chris Wacker, Lisa Warnecke, and Wendy Westman, and postdoctoral and research fellows: Yaara Aharon-Rotman, Christine Cooper, Gerhard Körtner, Eran Levin, Chris Pavey, Gemma Morrow, Julia Nowack, Alex Riek, Clare Stawski, Chris Wacker, and Craig Willis. Also, a thank you to the many Honours and undergraduate research students.

Last but not least, I would like to thank collaborators and sabbatical hosts, sabbatical and other visitors, and close colleagues and friends who have contributed to research projects over many years: Mike Archer, Walter Arnold, Heather Aslin, Michael Barritt, Silke Beckedorf, Claudia Bieber, Adrian Bradley, Anne Brigham, Mark Brigham, Linda Broome, Elliot Burch, Chris Burwell, Qing-Sheng Chi, Dionne Coburn, Christine Cooper, John Coventry, Sharon Crouch, Kathrin Dausmann, Steve Debus, Marine Delesalle, Bruce Firth, Steve Donnellan, Rebecca Drury, Greg Florant, Ted Garland, Kristina Gasch, Julian Glos, Alison Goldzieher, Nicola Goodship, Sue Hand, Fred Harvey, Gerhard Heldmaier, Sara Hiebert, Esa Hohtola, Martin Klingenspor, Noga Kronfeld-Schor, Brad Law, Robert Learmonth, Anaïs Le Bot, Gabriel Martin, Jaya Matthews, Louisa Matwiejczyk, Karen May, Bronwyn McAllan, Andrew McKechnie, Kwezi Mzilikazi, Sae Namekata, Maura Renninger, Thomas Ruf, Elke Schleucher, Ingrid Schmidt, Helen Sink, Meredith Smith, Lina Sprau, Brigitte Stahl, Paul Stapp, Margaret Stawski, Gansukh Sukhchuluun, Steve Swoap, Don Thomas, Mike Thompson, Tom Tomasi, Aaron Trachtenberg, De-Hua Wang, Jing Wen, John Wingfield, Phil Withers, and Lihong Yuan. Apologies if I have forgotten anyone.

Armidale, NSW, Australia Fritz Geiser
March 2021

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About the Author

Fritz Geiser grew up in a small rural village near Heidelberg, Germany. He was fascinated by animals from early in life and studied biology at the University of Hohenheim, Stuttgart. He travelled to Australia after his undergraduate degree on a DAAD scholarship to work at CSIRO at the Macquarie University in Sydney. He received a PhD from the Flinders University in Adelaide, Australia, held a Humboldt Fellowship at the University of Washington in Seattle, USA, and a postdoctoral position at the University of Adelaide. He has worked in Zoology at the University of New England, Armidale, Australia, since 1988, but during this time has conducted projects in Argentina (Patagonia), Austria, Canada, China, Germany, South Africa, and the USA. He is interested in comparative and environmental physiology of animals and most of his work concerns the ecological physiology of birds and mammals especially with regard to hibernation and daily torpor. He has published over 260 papers on these and related topics and was awarded a Madgwick Distinguished Professorship at the University of New England and a Discovery Outstanding Researcher Award from the Australian Research Council.

Author as primary schoolboy feeding a barn-swallow chick that fell out of nest in southwest Germany

Author with tube-nosed bat during fieldwork in tropical Queensland

Chapter 1
Introduction, Background and Definitions

Abbreviations

DH	Daily heterotherm
HIB	Hibernator
IBE	Inter bout euthermia
TBD	Torpor bout duration
MR	Metabolic rate
BMR	Basal metabolic rate
RMR	Resting metabolic rate
TMR	Torpor metabolic rate
TNZ	Thermo-neutral zone
T_a	Ambient temperature
T_b	Body temperature
T_{lc}	Lower critical temperature
T_s	Surface temperature
T_{skin}	Skin temperature
T_{uc}	Upper critical temperature

The diversity of living organisms is vast. New species are still being discovered and the taxonomic relationships of organisms are highly complex. From a functional, thermo-energetic point of view, however, organisms are more easily categorised and understood because there are only two general groups. Living organisms are either are ectothermic (body heat is absorbed from outside) or endothermic (body heat is generated inside).

The majority of living species are ectotherms, including most unicellular organisms, plants, invertebrates and most non-avian and non-mammalian vertebrates, the fish, amphibians and reptiles (Cossins and Bowler 1987; Seebacher and Franklin 2005; Bicego et al. 2007; Pörtner and Farrell 2008; Angilletta 2009; Tattersall et al. 2012). All metabolic processes release heat, but the metabolic rate (MR) and heat production in ectothermic organisms is low. Consequently and because they lack

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_1

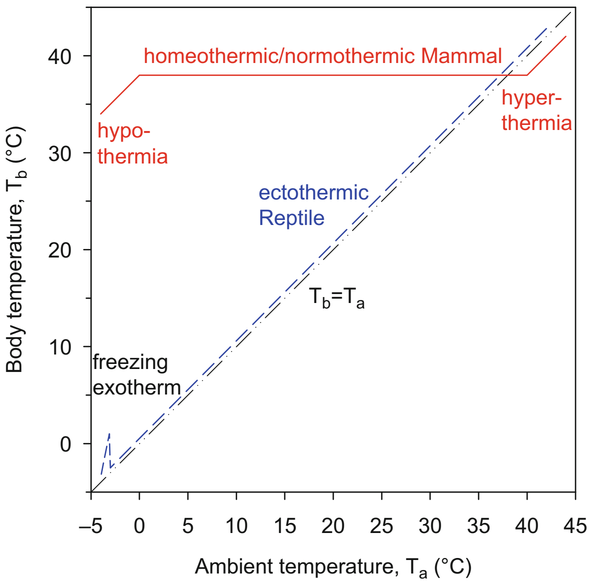

Fig. 1.1 Body temperature (T_b) as a function of ambient temperature (T_a) in a 25-g endothermic mammal (red solid line) and an ectothermic reptile (blue broken line). This size was selected because most endotherms and especially heterothermic endotherms are small. The normothermic T_b of mammals of around 38 °C can be maintained over a wide range of T_a via appropriate adjustments of heat production and heat loss. However, at very low T_a heat loss exceeds heat production and the animals becomes hypothermic, whereas at very high T_a internal heat production and uptake of external heat result in hyperthermia, these states are usually not controlled. In birds similar relationships are observed but the normothermic T_b is around 40 °C. In the ectothermic reptile under steady-state conditions T_b is a direct function of T_a, but slightly above T_a, and at very low T_as the reptile may freeze and this process will result in a freezing exotherm from the release of heat and often is lethal. The black diagonal dash-dotted line represents $T_b = T_a$

thermal insulation and heat easily escapes from the body, their body temperature (T_b) is a direct function of ambient temperature (T_a). Therefore, T_b of ectotherms will fall with T_a and continue to fall to below the freezing point of water, where the animal may freeze (Fig. 1.1). The MR of ectotherms, often measured as standard MR (SMR), is to a large extent determined by T_b, or by temperature effects, and decreases curvilinearly with T_a and T_b (Fig. 1.2). Of course these relationships are only observed under steady-state conditions and exclude behavioural thermoregulation, such as basking in the sun, which is used extensively by terrestrial ectotherms. Although some ectotherms can be partially endothermic, their endothermy is usually restricted to warming of an organ or region of the body to enhance its function, as, for example, the eyes of fish, flight muscles of insects, swimming muscles of large fish, or muscles of incubating large snakes (Hill et al. 2016). Alternatively, endothermy can occur for relative brief periods in the flowers of some plants to attract insect pollinators (Seymour et al. 2003).

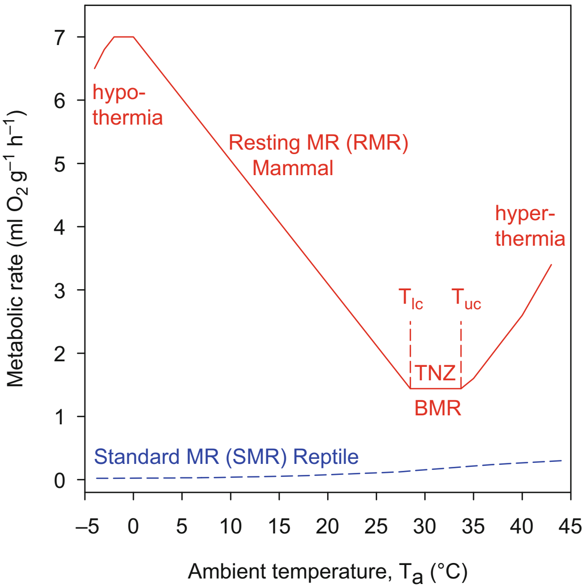

Fig. 1.2 Metabolic rate (MR) as a function of ambient temperature (T_a) in an endothermic mammal (red solid line) and an ectothermic reptile (blue broken line). The resting MR (RMR) of mammals is at or near basal (BMR) in the thermo-neutral zone (TNZ) as there is no thermoregulatory heat production. The TNZ is bordered by the lower critical temperature (T_{lc}) below which the RMR increases proportionally to overcome heat loss to maintain a normothermic T_b, and the upper critical temperature (T_{uc}) above which the RMR must increase to facilitate evaporative cooling. At very low T_a heat loss exceeds maximum heat production, RMR falls, and the animal becomes hypothermic, whereas at very high T_a evaporative cooling is not sufficient to counteract internal heat production and uptake of external heat and hyperthermia results. In birds similar relationships are observed but BMR and RMR are somewhat higher. In the ectothermic reptile under steady-state conditions the standard MR (SMR) falls curvilinearly with T_a and therefore with T_b (Fig. 1.1). The MRs and critical values were calculated for a 25-g mammal or reptile based on Bennett and Dawson (1976), Bradley and Deavers (1980), Bartholomew (1982), Riek and Geiser (2013), White and Seymour (2005); the precise values for hypothermia and hyperthermia are approximations and vary with species

Only a few species are fully endothermic throughout all or most of their life. These include essentially all birds and mammals with over 15,000 species, which can maintain a high and constant T_b over a wide range of T_a via physiological thermoregulation (Fig. 1.1). In endotherms, which typically have insulation in the form of feathers, fur or subcutaneous fat to reduce heat loss from the body surface, heat is produced internally using a number of mechanisms and usually involves the oxidation of sugars or fat. Apart from the heat produced by general metabolic processes, endothermic heat production can be achieved in specialised organs that function as internal heaters and are designed to turn chemical energy directly into thermal energy. The best known example is the brown adipose tissue (BAT) of some placental mammals, in which non-shivering thermogenesis is accomplished in mitochondria via the oxidation of fats (Cannon and Nedergaard 2004; Oelkrug et al. 2015). Other sites for non-shivering thermogenesis are the muscles of birds, mice, pigs and likely many other mammals (Nowack et al. 2017b). However, a main mechanism used in essentially all vertebrate endotherms is shivering thermogenesis. Shivering thermogenesis is a process during which the thermal energy released during asynchonous high-frequency contraction of antagonistic muscles is used to generate heat (Hohtola 2004; Hill et al. 2016). Shivering and non-shivering thermogenesis are often used together to generate heat during cold exposure.

Endothermy brings with it a number of advantages. These include the ability to remain active and continue to foraging over a wide range of T_as throughout the day and night and over a wide range of latitudes and elevations. Endotherms also possess high stamina and peak performance of muscle due to a better oxygen and fuel delivery system (Bennett and Ruben 1979; Nespolo et al. 2017). Moreover, endotherms can assimilate food rapidly and therefore have high growth rates. Their improved cardiovascular, respiratory and metabolic machinery also permits more speedy production of young, which is enabled by increased parental care (Koteja 2000; Farmer 2003).

Although insulation in the form of feathers and fur minimises heat loss from the body to the environment, heat loss still occurs when the animals are exposed to the cold. Therefore the heat produced internally for thermoregulation by endotherms requires a much higher MR than that of ectothermic organisms. This difference is pronounced and is about five-fold at high T_a, but can be up to >100-fold at low T_a in small species (Schmidt-Nielsen 1997; Withers et al. 2016; Figs. 1.1 and 1.2). Unlike in ectotherms, in which MR falls with T_a and T_b, the thermal energetics of endotherms are indirectly affected by T_a. Endotherms have a thermo-neutral zone (TNZ) in which the MR in normothermic (high and constant T_b) and resting endotherms can be minimal or 'basal' (BMR) because the difference between T_b and T_a and heat loss are small. The TNZ is bordered by the upper critical temperature (T_{uc}) at the upper end and the lower critical temperature (T_{lc}, Fig. 1.2) below which heat loss to the environment begins to increase. The TNZ in small endotherms is high often around and above T_a 30 °C. To regulate T_b at a high and constant level over a wide range of T_a, below the TNZ, endotherms must increase heat production proportionally to compensate for heat loss. However, homeothermic thermoregulation is only possible over a limited T_a-range over which MR increases to a maximum (1.1, 1.2). Above the TNZ endotherms also typically increase metabolic rate to facilitate heat loss usually via the evaporation of water, but this is effective only over a rather narrow T_a-range (Figs. 1.1 and 1.2). The normothermic or homeothermic T_b of mammals typically range from around 33 to 38 °C, whereas in birds it is slightly higher at around 38 to 42 °C (Bartholomew 1982; Ruf and Geiser 2015; McKechnie et al. 2017). In Fig. 1.1, 38 °C is used as it is representative for both.

The BMR is the rate of energy expenditure measured under standard conditions and is widely used as a reference point with regard to energy expenditure under different physiological states and thermal conditions (Hill et al. 2016; Withers et al. 2016). BMR is generally viewed as the minimum or maintenance energy expenditure of normothermic animals and is a measure of the cost of living, without thermoregulation, locomotion and other activities. However, as we will see in this book, BMR is definitely not the minimum MR of endotherms. To qualify for a measure of BMR the animal must be at rest during its time of inactivity (no energy is used for movement), under thermo-neural conditions (no energy is used for thermoregulatory heat production), post-absorptive (no energy is used for digestion), non-reproductive (no energy used for reproductive activities or for growing young), and an adult (no energy is used for growth). The resting state may not be reached in small mammals until after several hours and short periods of measurement can result in overestimates of BMR (Cooper and Withers 2009).

The body mass of an animal strongly affects its BMR. The total BMR (i.e. that of the entire animal) increases with body mass as expected, because it is more costly to maintain a large body than a small one. However, on a log-log scale of BMR as a function of body mass, typically a slope between about 0.67 to 0.75 rather than a directly proportional slope of 1.0 is observed (Kleiber 1961; Glazier 2005; White and Seymour 2005; Chap. 5). Therefore between a body mass of 10 g and 10,000 g, the size range that is particularly important for organisms covered in this book, total BMR increases not by 1000-fold but by only ~115-fold. Consequently, the mass-specific BMR, or the BMR per g of body mass of an animal, is not a constant, but is inversely related to body mass, and, on a log-log scale, the slope of this relationship is typically between −0.25 and −0.33 (Kleiber 1961; White and Seymour 2005). The mass-specific BMR increases almost two-fold for a decrease in body mass by one order of magnitude, or increases by almost nine-fold from a 10,000-g to a 10-g animal. So even under thermo-neutral conditions without thermoregulatory energy expenditure and at rest, the mass-specific energy expenditure of a small animal is much higher than that of a big animal, with significant consequences for their energy budgets.

While BMR is a good reference point for other physiological states, its significance with regard to the biology and especially ecology of animals has been overstated (Hulbert 2014). Many animal behaviours such as overall activity or home range are correlated with BMR (e.g. McNab 2002), but in many cases these relationships are not causal. As bigger animals need more food to satisfy their nutritional requirements and must range further it is more costly overall to run and maintain a large than a small organism. This is reflected in the mass-specific energy expenditure of small endotherms in the wild, measured via isotopes as field metabolic rate (FMR, Nagy et al. 1999), which is about 4 to 7-times BMR. This means that BMR is only a small component of the real energy requirement of animals, and even in large animals FMR is still about two-fold of BMR (Degen and Kam 1995; Geiser and Coburn 1999). Thus there is a mismatch between the real energy expenditure in the wild and that for resting animals in the TNZ (Nagy et al. 1999). Some of this mismatch is due to the fact that many small endotherms in the wild rarely experience TNZ conditions because, due to their large surface area, they do not regularly experience T_a that are high enough (Bartholomew 1982). Further, their resting MR (RMR) during cold exposure (Fig. 1.2) and even more so during activity can be many-fold that of BMR. Related to activity, the scaling coefficient for home range size as a function of body mass, which has been correlated with BMR in an attempt to explain the reason for different home range sizes, is about two-fold of that for

BMR (Kelt and Van Vuren 2001; White and Seymour 2005; Körtner et al. 2019), again revealing the lack of a causal link between the two. Moreover, BMR is not a species-specific constant as is sometimes assumed because it can change with season and temperature acclimation (Heldmaier and Steinlechner 1981a; Stawski and Geiser 2020). Therefore in this book, I will used BMR mainly to allow for comparison with other physiological states.

When experiencing T_as above and in the TNZ, active cooling of the body is initiated in endotherms by evaporation of water, which is facilitated by sweating, increased ventilation, gular flutter in birds, or postural changes, but nevertheless requires an increase in MR above the TNZ (Hill et al. 2016; Pessato et al. 2020). The increase in MR above the T_{uc} of the TNZ is curvilinear and is predominantly caused by two factors, the greater energetic demand on muscles or glands for evaporation of water, and the increased T_b that is often associated with exposure to high T_a. However, the ability to maintain a constant T_b under hot conditions, especially when T_a exceeds T_b, is limited before the animal becomes hyperthermic (Figs. 1.1 and 1.2). The T_a at which hyperthermia is induced differs widely among mammals as does their tolerance of high T_b (Bondarenco et al. 2014). In small birds hyperthermia often occurs when T_a exceeds 40 °C, but T_b as high as 45–49 °C have been reported (McKechnie et al. 2017; Freeman et al. 2020). These values are above the T_b that are widely considered to be lethal (Freeman et al. 2020). Although the traditional view is that RMR must increase above the TNZ for cooling (Fig. 1.2), as outlined below, new data suggest that some mammals may use metabolic inhibition to limit or slow the increase of T_b to dangerously high levels (Cliffe et al. 2018; Reher and Dausmann 2021).

Most birds and mammals in the wild thermoregulate below the TNZ for much of the time (Bartholomew 1982), in which T_a-range RMR is inversely related to T_a, (Scholander et al. 1950). This relationship occurs because heat loss is a function of the T_b-T_a differential, i.e. the colder it gets the more heat is lost and must be compensated for by internal heat production. To achieve this, animals must produce enough internal heat to replace the heat leaving the body to the environment, and usually RMR increases linearly (Withers et al. 2016). However, some large species can reduce heat loss at low T_a via peripheral vasoconstriction to reduce their surface temperature, and consequently the relationship may be curvilinear, with a decrease in slope at low T_a (McNab 2002). The scope for an increase in RMR above BMR during cold exposure is often around five to ten-fold (Hinds et al. 1993). At T_as at which heat loss exceeds heat production, the animal becomes hypothermic (Figs. 1.1 and 1.2). In small mammals hypothermia is typically induced by exposure to T_a ranging from −5 to 5 °C, as for example in marsupial dunnarts (*Sminthopsis macroura*; Geiser et al. 2003), but it can be as low as −60 °C in winter-acclimated Djungarian hamsters (*Phodopus sungorus*; Heldmaier et al. 1985).

An analogy for physiological thermoregulation of endotherms is the electricity use of a house. In spring and autumn, when T_a is mild, only appliances and lights will use electricity, since heating and air-conditioning are not required. This is analogous to BMR. When it is hot in summer and an air conditioner is used to cool the house, electricity costs will increase, which is analogous to the increase in

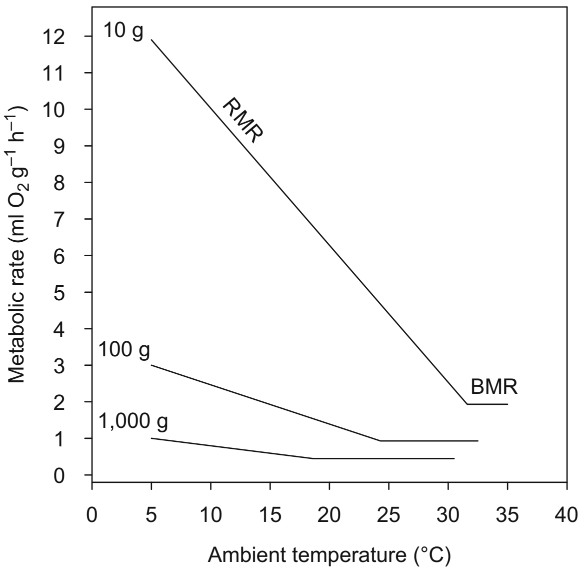

Fig. 1.3 The resting MR (RMR) and the basal MR (BMR) as a function of ambient temperature (T_a) in three mammals ranging from 10 g to 1000 g. Note that in the TNZ, which becomes wider with increasing size (Fig. 1.4), the BMR in the 10-g mammal is about four-fold that of the 1000-g mammal. The RMR at T_a 5 °C is about 12-fold in the 10-g mammal in comparison to the 1000-g mammal, requiring a substantial amount of energy for thermoregulation. The values were calculated for mammals from equations in Bradley and Deavers (1980), Riek and Geiser (2013), White and Seymour (2005)

MR at T_as above the TNZ. When it is cold in winter and a heater is used to warm the house, electricity use will also increase with decreasing T_as, which is analogous to the increase in RMR at T_as below the TNZ.

Heat production and loss in endotherms are also strongly affected by body size because heat exchange occurs over the body surface, which is relatively larger in small than in large animals (Fig. 1.3). As we have seen above, even in the TNZ without heat production for thermoregulatory thermogenesis, the mass-specific BMR, per g of tissue, is much higher in small than large species and increases about four-fold for a mammal weighing 1000 g to one weighing 10 g. As the width of the TNZ is a function of size as well because the relative surface area decreases with increasing size, the T_{lc} of the TNZ, below which thermoregulatory energy expenditure must be activated if the T_b is to be maintained high and constant, is also affected and decreases with size (Fig. 1.4). In mammals, the T_{lc} can be as high as 34.2 °C at a body mass of 5 g, 20.2 °C at 500 g, and 15.5 °C at 5 kg; in very large species it can be near or even below 0 °C (Scholander et al. 1950; Riek and Geiser 2013). When exposed to low T_a of 5 °C, a 10-g endotherm must increase its RMR above BMR by about 12-fold compared to the required RMR increase of a 1000-g endotherm if it aims to remain normothermic (Fig. 1.3). The slope of RMR as a function of T_a is referred to as thermal conductance and is a measure of how much

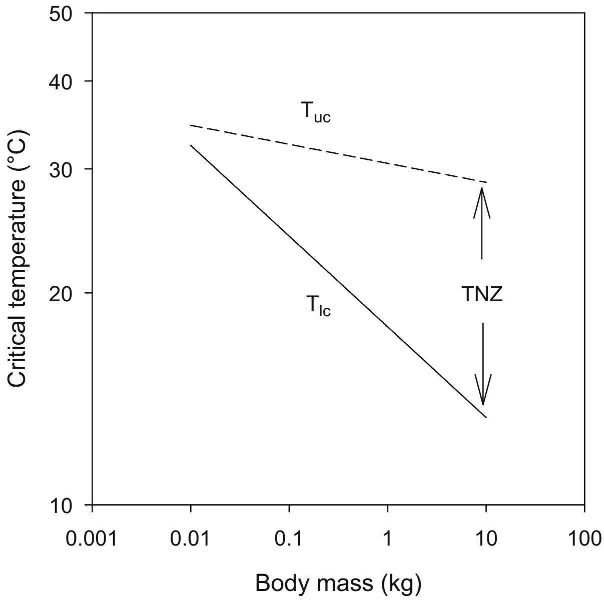

Fig. 1.4 The upper critical temperature (T_{uc}, broken line), the lower critical temperature (T_{lc}, solid line) and the width of the thermo-neutral zone (TNZ, indicated by arrows) as a function of body mass in mammals. Note that TNZ widens with increasing size. The TNZ is the temperature range, in which BMR, the minimum energy expenditure during normothermia, can be maintained. Values calculated from Riek and Geiser (2013)

RMR must increase to compensate for a fall of T_a by 1 °C (Withers et al. 2016). With regard to heat loss and production small endotherms are further disadvantaged, because, on average, large species have thicker and better insulation in the form of feathers or fur and can carry more fat, which can be used both for insulation if deposited subcutaneously and to fuel metabolism (Calder 1996).

Whatever the mechanism of internal heat production, it is always energetically costly as valuable chemical energy is required to fuel it and this must be sustained by the uptake of food. Because most birds and mammals are small and most weigh between about 5 and 200 g (Blackburn and Gaston 1994; Smith et al. 2003), their surface area is relatively large in proportion to the volume of their tissues, heat loss in small endotherms in the cold can be enormous. These high thermoregulatory costs for small birds and mammals can be problematic. The time of year that is of special concern in many, especially high latitude or high elevation regions, is of course winter when T_a is low together with relatively low food availability. To a large extent because of such energetic challenges small endotherms that can fly (birds and bats) and can cover large distances fast and energetically cheaply (Fig. 1.5) can avoid these conditions and migrate often over long distances to more benign areas. Large walkers or runners, such as African or Arctic ungulates, may also migrate because cost of transport per unit body mass decreases with size. In contrast small non-volant

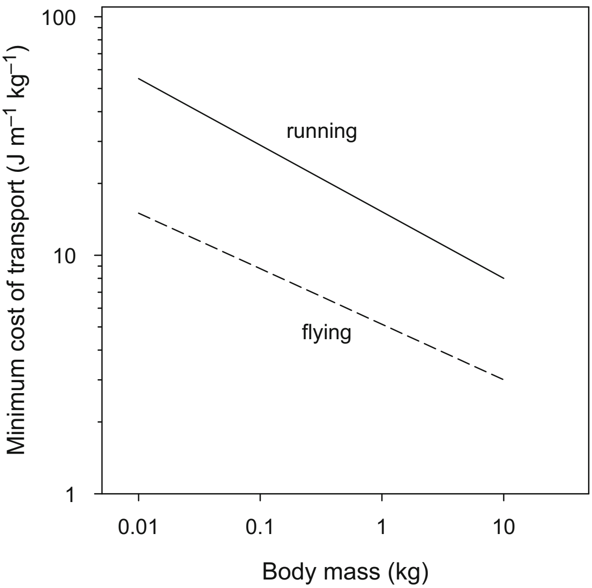

Fig. 1.5 The minimum mass-specific cost of transport per unit of distance required for locomotion in runners and flyers as a function of body mass. Note that both axes are log-transformed, cost of transport increases with decreasing body mass, but running at the same body mass is almost ten-fold more energetically costly than flying, mainly because it is about 10-times slower for a similar energy expenditure. Values calculated from Tucker (1975)

species, such as mice and other small mammals cannot move over long distances because running in small species is slow (Garland et al. 1988) and energetically almost 10-times more expensive than flying over the same distance and at the same body mass (Tucker 1975). Therefore sedentary species have to deal with thermal conditions and food availability in or near their usual home range by using other behavioural and physiological approaches (Körtner et al. 2000).

One effective behavioural approach to reduce heat loss is huddling, as a group of animals has a smaller surface area than a single individual exposed to cold (Gilbert et al. 2010). Huddling is used extensively by small mammals, but also in birds such as penguins, or even passerines (Fig. 3.8). In marsupial sugar gliders (*Petaurus breviceps*) huddling in normothermic groups is common especially when they are not energetically stressed (Nowack and Geiser 2016) and huddling in a group of four reduces energy expenditure by about 50% and lowers the T_{IC} from about 28 to 15 °C (Fleming 1980). Similarly, in two huddling pygmy-possums (*Cercartetus nanus*), RMR at low T_a was about half that of a single individual and the slope of the increase in RMR was also about half in huddling individuals, whereas a nest was less effective (Namekata and Geiser (2009), Fig. 1.6). In all these studies, RMR in huddling animals always remained near or above the BMR measured in the TNZ, an important point with regard to energy conservation (Fig. 1.6).

Prolonged periods of high metabolic heat production in small species, even when huddling is used, can only be sustained by high food intake. During adverse environmental conditions and/or food shortages, the costs of thermoregulation and maintenance may become prohibitively high. Therefore, many endothermic mammals and birds are not permanently homeothermic (homeotherm is from the Greek meaning ‘similar heat’, or to maintain a constant high T_b), but, during certain times

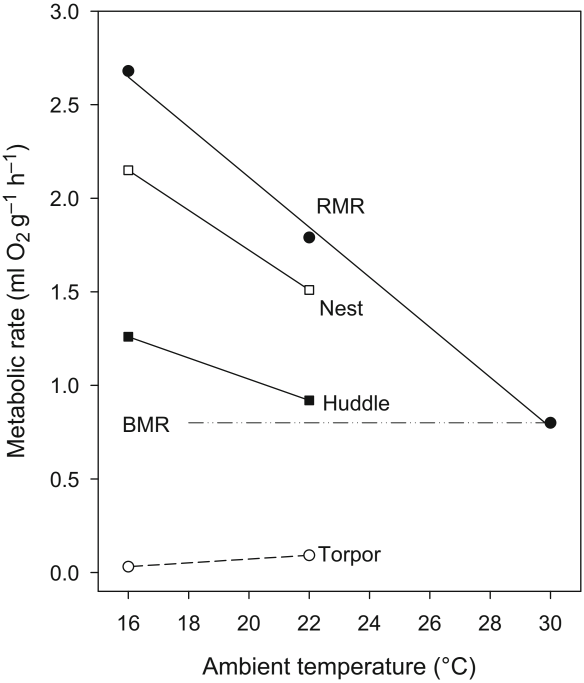

Fig. 1.6 Metabolic rate as a function of ambient temperature in pygmy-possums (*Cercartetus nanus,* ~40 g). Single individuals at rest (RMR filled circles) top, single individuals in nest (squares), two individuals huddling (filled squares), and single individuals in torpor (circles). The value for BMR is indicated by a dash-dotted horizontal line and is below that of huddling individuals, but well above that of torpid individuals. Data from Namekata and Geiser (2009)

of the day or the year, enter a state of torpor (Lyman et al. 1982; Boyer and Barnes 1999; Carey et al. 2003). Torpor in these 'heterothermic endotherms' (heterotherm from the Greek for 'other heat') is characterized by substantial but reversible reductions of MR, T_b and other physiological functions. Importantly, unlike during huddling, MR during torpor can fall well below and often to a small fraction of BMR (Fig. 1.6).

Thus a major function of torpor is to minimise energy expenditure by substantially lowering MR to overcome times of low T_a and food availability. However, as I will show later, torpor is also used to deal with a number of other challenges, including periods of high energetic demands, environmental disasters, or when foraging options are reduced because of high predation pressure. Heterothermy in endotherms has been defined as a large temporal fluctuation of T_b above and below the homeothermic mean in large mammals (Hetem et al. 2016). In this book it is used to describe both rather small T_b fluctuations, but also the large fluctuation of MR and T_b during torpor of mainly small mammals and birds. Hence, mammalian and avian torpor is typified by substantial but controlled temporal reductions in MR, T_b, water loss, heart rate, and other physiological functions. These physiological changes make torpor the most effective mechanism for energy conservation available to endotherms and it is not surprising that it is used by a diverse range of species.

The most common patterns of torpor that have been described are daily torpor in 'daily heterotherms' and multiday torpor or hibernation in 'hibernators'. As the name suggests, daily torpor last only for a few hours, typically during the animal's rest phase, and the animals often are active or forage when MR and T_b are high (Fig. 1.7). Daily torpor in most species is rather shallow, with a reduction of T_b by around 8 to 20 °C. In birds, as for example in passerines which show only small reductions in T_b, daily torpor often occurs at night because most birds are active during the day (Fig. 1.7, top). In small mammals, which are typically nocturnal, daily torpor is often expressed in the second half of the night or in the early morning and is used, for example, by many species of carnivorous marsupials and mice. In these mammals, daily torpor usually is somewhat deeper than in passerine birds with T_b typically falling by around 15 or 20 °C (Fig. 1.7, middle).

The other widely used pattern, is multiday torpor or hibernation. Multiday torpor is expressed during the hibernation season typically from autumn to spring, but in most species hibernation at low T_b does not continue throughout the cold season (Fig. 1.7, bottom). Hibernation is usually characterised by a sequence of multiday torpor bouts with a low T_b (around 5 °C) and a torpor bout duration (TBD) lasting for several days to weeks. However, most hibernators periodically rewarm to normothermic T_b. These rewarming periods and brief periods of rest for several hours are referred to as inter-bout normothermia or inter-bout euthermia (IBE). Unlike in daily heterotherms, IBEs in many hibernators are not used for activity and foraging. The low T_bs during torpor in hibernators are associated with a substantially reduced MRs.

It is widely assumed that restriction of food intake or limited energy stores are the main reason or signal for torpor expression. This is often the case because food restriction in many species increases the use of torpor, and this is referred to as 'induced torpor' (Lynch et al. 1978; Geiser and Baudinette 1987; Tannenbaum and Pivorun 1988; Ruf et al. 1993). However, torpor can also be used in the presence of food and this is referred to as 'spontaneous torpor' (MacMillen 1965; Gaertner et al. 1973; Hill 1975).

In this book I aim to summarise what is currently known about the ecological physiology of daily torpor and hibernation in mammals and birds, and briefly address thermal biology in ectotherms. Previous books specifically on hibernation and daily torpor were published some decades ago by Kayser (1961), Mrosovsky (1971) and Lyman et al. (1982) and the emphasis in these was mainly on physiological aspects of hibernation in captive predominantly northern, cold climate mammals. In recent years, the available information has vastly increased, both with regard to the knowledge of the taxonomic diversity of heterothermy and its geographic range, as well as on ecological aspects of torpor of free-ranging individuals. For both birds and mammals, substantial increases in data for a broad taxonomic diversity have been made at the level of species, families and even orders. Whereas much of the work in the past focussed on cold-climate high latitude species, torpor has now been documented for species living in all climate zones from the arctic to the tropics (McKechnie and Lovegrove 2002; Dausmann et al. 2004; Kronfeld-Schor and Dayan 2013; Ruf and Geiser 2015; Nowack et al. 2020). Torpor is now known to be used by endotherms on every continent.

There are several reasons for the increase in the number of known heterotherms in recent years. These include improvements in technology providing small affordable

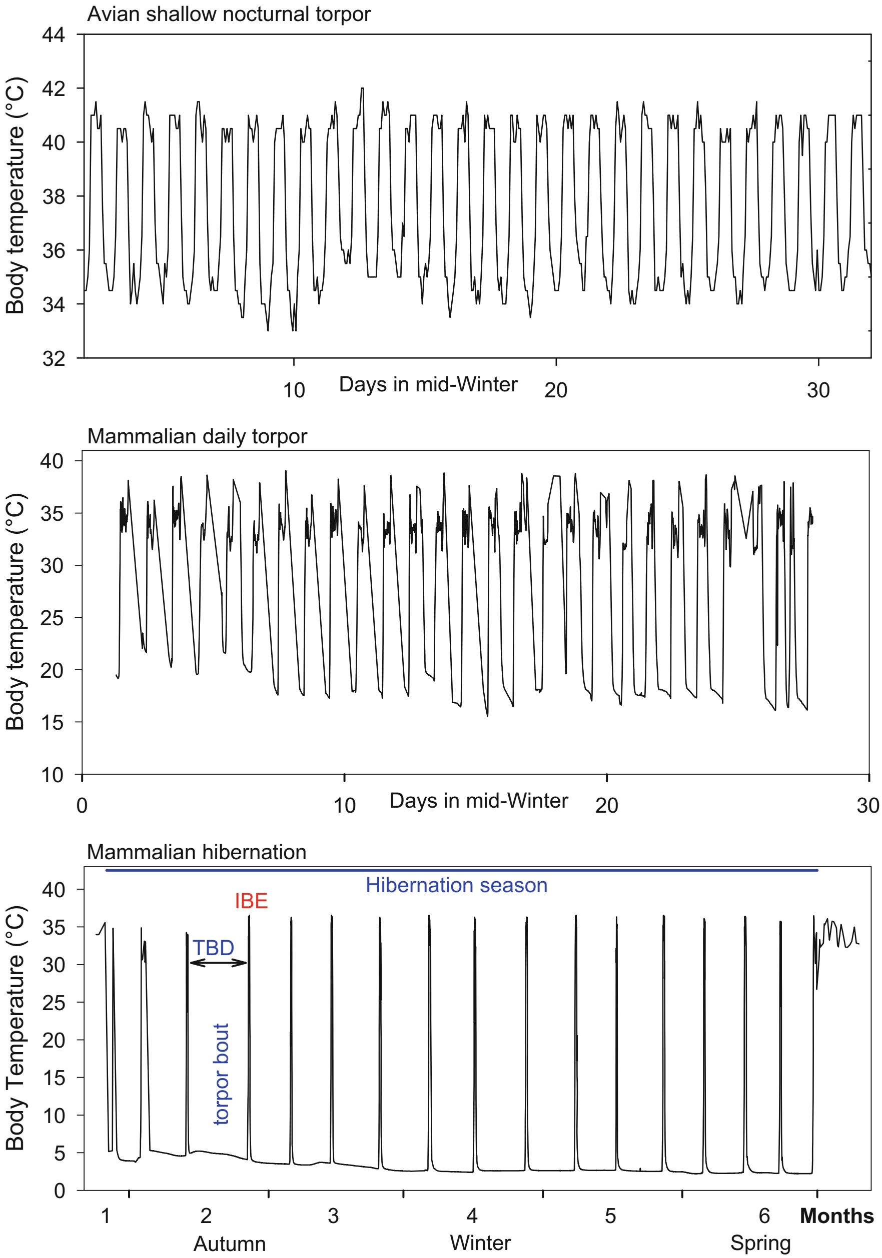

Fig. 1.7 Torpor in a free-ranging heterothermic bird expressing shallow nocturnal torpor (top graph), a free-ranging heterothermic mammal expressing daily torpor (middle graph) and a free-ranging mammal expressing multiday torpor during the hibernation season (blue horizontal bar, top of bottom graph). Note the daily return to high normothermic body temperatures (T_b) and the rather high T_bs during torpor in the two daily heterotherms (top and middle) in contrast to the low T_bs and the periodic arousals to euthermia (IBE red) often after a torpor bout duration (TBD blue) of many days in the hibernator. Data from Körtner and Geiser (1998, 2009) and Geiser (2019)

devices (temperature-sensitive transmitters, transponders, and data loggers) that allow measurement of physiological variables (mainly T_b) of free-ranging animals, see Chap. 2. Contributions from scientists from countries not traditionally involved in the study of thermal biology have provided new data on 'exotic' taxa. There is also an increased interest in the biology of heterotherms from an ecological point of view because of their often increased longevity, ability to live and reproduce in resource-poor regions, and their reduced risk of extinction (Geiser and Turbill 2009; Turbill et al. 2011a; Kronfeld-Schor and Dayan 2013; Hanna and Cardillo 2014). Recently torpor also has been shown to enhance survival during natural disasters such as fires (Stawski et al. 2015a, b; Nowack et al. 2016a, b) storms (Nowack et al. 2015) or floods (Barak et al. 2018), and may have been important for colonization of islands or continents by non-flying mammals (Nowack and Dausmann 2015; Nowack et al. 2017a). Consequently the use of torpor has important implications for climate change biology (Levesque et al. 2016). On the other hand, torpor attracts interest from the medical sciences again because of prolonged longevity, but also high thermal and ischaemic tolerances of organs and tissues, and reduced muscle disuse atrophy in heterotherms (Carey et al. 2003; Drew et al. 2007). These ecological and medical interests have resulted in the active involvement of researchers other than and/or in addition to thermal biologists traditionally interested in this scientific domain.

In the following chapters, I first provide some methods on how torpor can be quantified (Chap. 2), then cover the vast diversity and geography of the now known heterotherms (Chap. 3), then provide details of torpor patterns and their expression (Chap. 4) and the physiology and thermal biology of torpor (Chap. 5). This will be followed by addressing seasonal aspects of torpor (Chap. 6), ecological and behavioural aspects of torpor (Chap. 7), the functions of torpor during reproduction and development (Chap. 8), the effects of dietary lipids on thermal biology and torpor (Chap. 9), the evolution of endothermy and torpor (Chap. 10), and concluding remarks (Chap. 11). First however, I will provide some definitions used throughout the book.

Definitions

To explain definitions of torpor, an understanding of the relationships between T_b and T_a (Fig. 1.8) and MR and T_a (Fig. 1.9) is required. The schematic graph (Fig. 1.8) shows T_b as a function of T_a for a typical small heterothermic mammal. Whereas homeothermic and normothermic mammals maintain a constant T_b of around 37 °C over a wide range of T_a (Fig. 1.8), mammals who use torpor can reduce T_b and their T_b follows T_a (i.e. they thermoconform) over a wide range of T_a (diagonal line). However, at low T_a, torpid animals thermoregulate and the T_b becomes stable, in this example at 11 °C (Fig. 1.8). If T_b falls below the regulated T_b value during torpor the animal becomes hypothermic and typically cannot rewarm from the low T_b endogenously. Thus hypothermia can occur both when an

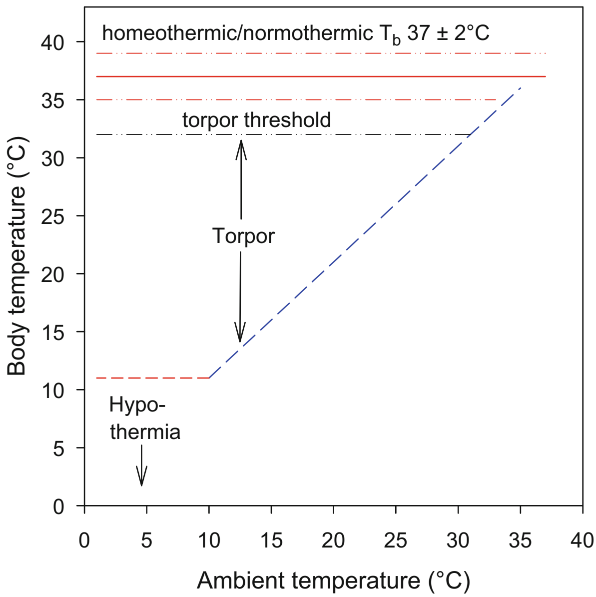

Fig. 1.8 The body temperature ($T_b = 37 \pm 2$ °C) of a homeothermic or normothermic or euthermic mammal (solid red horizontal line) as a function of ambient temperature (T_a). A mean T_b with a variance of ±2 °C (red dash-dotted horizontal lines) is defined as being 'homeothermic' (Hetem et al. 2016). The 'torpor threshold' (T_b 37 − 5 °C = T_b 32 °C) is shown as a function of T_a (black horizontal dash-dotted line). The T_b during steady-state torpor is shown as a diagonal broken line over the T_a-range the torpid animal is thermoconforming (blue), and as a horizontal broken line over the T_a-range the animal is thermoregulating (red). By this definition the animal can be in torpor anywhere in the area (arrows) between the torpor threshold and the broken lines depicting the T_b during torpor, but during steady-state torpor they will approximate the torpor lines. Hypothermia (arrow) indicates the T_b that is below the regulated T_b

animal is attempting to regulate T_b during normothermia (Figs. 1.1 and 1.2) and during torpor (Figs. 1.8 and 1.9).

The MR reflects the relationship between T_b and T_a to a large extent (Fig. 1.9). To maintain a constant high T_b at 37 °C, a homeothermic or normothermic mammal will need to increase its resting MR (RMR) linearly from BMR as T_a falls to compensate for heat loss from the body (Figs. 1.2 and 1.9). Torpid animals, over the T_a range they are thermoconforming, typically reduce their TMR curvilinearly with T_a (Fig. 1.9). When torpid animals thermoregulate during torpor, their TMR must increase, in this example below 10 °C (Fig. 1.9) to maintain T_b during torpor at a constant 11 °C (Fig. 1.8). If the MR falls below the level required for thermoregulation during torpor, the animals becomes hypothermic. Some animals can reduce MR below BMR with only a small or no reduction in T_b (Fig. 1.9). In birds the relationships are similar although their T_bs and MRs are often higher than in mammals.

Many approaches have been used to define torpor (Barclay et al. 2001) and regularly T_b is used to define it because T_b is the variable that is most often

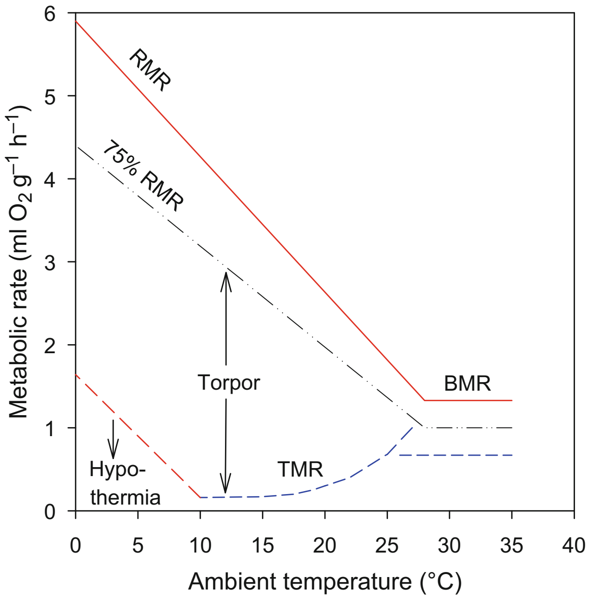

Fig. 1.9 The basal metabolic rate (BMR) and resting metabolic rate (RMR) of a normothermic endothermic mammal or bird (red solid lines), and its minimum torpor metabolic rate (TMR, broken line) as a function of ambient temperature (T_a). The 'torpor' threshold (dash-dotted black line) is defined as a reduction of MR below 75% of the RMR (BMR is equal to RMR in the TNZ) at the same T_a (Hudson and Scott 1979). The minimum TMR falls curvilinearly over the T_a-range the torpid animal is thermoconforming (T_b falls with T_a, blue broken line), or is shown horizontally in animals able to use physiological inhibition in the TNZ (blue broken line). In the T_a-range the torpid animal is thermoregulating (red broken line) TMR increases in parallel to the RMR and T_b is steady (see Fig. 1.8). Hypothermia indicates a MR that is below the TMR used to regulate T_b during torpor, typically animals in this range are unable to rewarm endogenously

measured, especially in free-ranging animals. A simple approach for a single species is one that uses a single torpor threshold for T_b, as for example 31 °C by Hudson and Scott (1979) for mice, which have a normothermic T_b of ~37 °C. However, as the normothermic resting T_b differs widely among different avian (T_b ~ 38 to 42 °C) and mammalian species (T_b ~ 33 to 39 °C) this approach is less suitable for making comparisons among species. Therefore a number of other approaches have been used to better deal with diverse species of different size and under different thermal conditions (see Willis 2007). To be able to easily compare homeothermic and heterothermic endotherms a heterothermy index (HI) has been developed (Boyles et al. 2011), but its disadvantage is that it does not distinguish between short and deep, and long and shallow torpor bouts (Brigham et al. 2011). One straight-forward approach that gets around the problem of different normothermic T_bs, different sizes and exposure to different T_as that has been widely used, is the extent of the T_b reduction below the normothermic resting T_b. As the homeothermic T_b has been defined as the normothermic resting T_b ±2 °C (Hetem et al. 2016; Fig. 1.8) it seems appropriate and conservative to use a fall of T_b by 5 °C below the normothermic resting T_b as torpor threshold (Schleucher 2004; Ruf and Geiser 2015). This permits a comparable and uncomplicated assessment of all species of different sizes and under different thermal conditions. Therefore, a 5 °C T_b reduction below normothermic resting T_b of a species will be the torpor threshold used in this book (Fig. 1.8), although it is arbitrary. By this definition an animal is torpid in the space between the torpor threshold and the T_b in thermoconforming and thermoregulating torpid animals (arrows above and below Torpor, Fig. 1.8). 'Shallow' torpor is expressed by individuals with a T_b that is only slightly below the torpor threshold, whereas 'deep' torpor represents individuals that are near the minimum T_b (or minimum TMR see below) for each species. This torpor threshold also provides an easy way for calculating TBD as the time T_b remains below the threshold, at least at low T_a.

However, relying on T_b as the single criterion for defining torpor can be problematic because a number of species are now known to use torpor at high T_a where T_b can fall very little or not at all (Fig. 1.9). Under such conditions metabolic inhibition can be used to cause a reduction in MR with only a small or no reduction in T_b (Song et al. 1997; Grimpo et al. 2013; Reher and Dausmann 2021). Therefore, when MR measurements are available the definition by Hudson and Scott (1979) of a reduction in MR by 25% below the RMR at the same T_a will be used here. The advantage of this approach is that it can be used at low T_a, but can also be extended into and above the TNZ (Fig. 1.9). So by this definition an animal is torpid in the space between 75% RMR and the minimum TMR of thermoconforming and thermoregulating torpid animals (arrows above and below Torpor, Fig. 1.9). As outlined above 'hypothermia' will not be used to describe a controlled state of torpor (Lyman et al. 1982), but is used to describe uncontrolled reductions of T_b and MR below the range where physiological thermoregulation is possible (Figs. 1.2, 1.8, and 1.9).

MR in most studies referred to in this book was measured indirectly, usually as the rate of oxygen consumption or carbon dioxide production. For simplicity in the text, it will be called 'metabolic rate', but is reported with the unit of the measured variable.

Chapter 2
Quantifying Torpor

Specific and detailed guidelines on how to obtain meaningful measurements of, for example, BMR are provided in a variety of textbooks and other scientific literature. Such guidelines are not available for measurements of physiological variables of torpor. However, interest in the biology of daily torpor and hibernation is shared by many because the extreme physiological states displayed by the animals, which create scientific curiosity, even by scientists not working in the field. Hibernation and torpor also have significant implications for many scientific domains including ecology and biomedicine. While it is possible for non-specialists to read and follow the methods of published papers, understanding them is not always straight forward because the specific details on how to proceed are often not provided. Moreover, typically only a single method required for the specific study is reported. Because the procedures for obtaining reliable torpor data can be frustrating, some general methods and hints rather than guidelines are provided below. These may help in a way that provides meaningful and comparable results, and to avoid the many possible pitfalls of this scientific discipline.

Torpor can be quantified using many different but at the same time appropriate methods. Generally, all methods have advantages and disadvantages, but in essentially all cases, the main and most crucial criterion for obtaining good and meaningful data is patience.

Trap and Recapture

Perhaps the oldest methods that have been used especially for hibernating animals are trapping and release of individuals in autumn or spring to determine whether or not they have ceased or recommenced above ground activity. This approach has been used extensively for hibernating rodents and lead to a reasonable assessment of the duration of the hibernation season (Kayser 1961; Kenagy and Barnes 1988; Michener 1992; Kawamichi and Kawamichi 1993). Trap and recapture also has been

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_2

successfully used to determine differences in the duration of the hibernation season among sexes and age groups. An advantage of trapping is that body mass and other morphological variables can be measured and tissue or blood-samples can be obtained. A potential drawback of trapping with regard to hibernation is that an animal in a burrow may not necessarily be torpid, but may be normothermic for some time especially in spring before emerging (e.g. Michener 1992; Williams et al. 2011). Similar to repeated trapping is the method of quantifying signs of activity by animals such as digging by echidnas (*Tachyglossus aculeatus*) before and after hibernation (Smith et al. 1989), tracks of bears or simply observing aboveground activity of diurnal rodents, such as marmots. Trapping and release or simple observations are generally not suitable for daily heterotherms, because they forage usually for part of the day even when they use torpor frequently (e.g. Stawski et al. 2015a).

Torpor Use

Captive animals allow the researcher to control environmental variables and frequent access to individuals. Therefore torpor can be quantified by observation or by using some basic equipment especially in species that reduce T_b substantially and have slowed response times when torpid. Often an animal's torpor status can be determined simply by touch or a puff of air. However, as this approach may not always be reliable, it is advisable to use a measuring device to quantify whether the animal is cold, such as a now easily affordable infrared thermometer (see below), to measure surface temperature (T_s). If the T_s of an animal is measured, which is done best on a bare patch of skin or the eye, remember that this is not a precise measurement of core T_b, but measurements of T_s are usually robust enough for determining whether or not an animal is torpid.

A crucial consideration for determining torpor use is that the animal has to be undisturbed and physiologically capable of displaying torpor. In captivity animals often are more likely to enter torpor in their familiar 'home' cage, whereas in unfamiliar surroundings, as for example, respirometry chambers, they may be reluctant to do so, but may use torpor after some repeated trials. Immediately after capture wild animals may be stressed, so it is usually better to wait some time to allow them to settle before commencing studies of torpor use. The time of the year is, of course, also important because many hibernators refuse or are reluctant to enter torpor in summer. It is often advisable to keep the photoperiod the same as that in the wild at the time of capture if no long-term acclimation experiments are conducted. However, if the animal is in captivity for some time or captive bred, a short winter photoperiod is usually best suited to elicit torpor expression. Heterotherms express or enter torpor at certain times of the day and attempts to induce torpor at other times may result in refusal to enter torpor or underestimates of torpor use and overestimates of measured torpor variables.

Often torpor use increases when food and water are withheld or restricted, but how long this can be done must be carefully assessed for each individual and each species. In many daily heterotherms overnight food restriction or withdrawal results in torpor use without negative effects on the animal. However, the animals must be checked regularly when this is first attempted and it is best to feed the animals *ad libitum* for several days after the trial. In hibernators, especially when they are fat and ready to express torpor, food can be withheld for more than 1 day, but many hibernators enter torpor even in the presence of food when measured at the right time of year (MacCannell and Staples 2021).

The best T_a for torpor induction in captive animals is not necessarily an extremely cold T_a. A good starting point is a T_a near the T_a the animals would experience in the wild at the time they express torpor. However, as wild animals typically enter torpor in sheltered places, they rarely experience the outside T_a, but a T_a buffered by soil, wood or other material. If the minimum T_b of a species is known from previous work, a T_a near that T_b likely meets the required condition for expression of torpor in captivity. For many hibernators, the use of a T_a between 2 and 10 °C is often suitable for eliciting torpor. However, daily heterotherms are often more likely to display torpor when exposed to T_as between 10 and 20 °C, and do not become hypothermic at these T_as (MacMillen 1965; Tucker 1966; Geiser and Baudinette 1987). In the field, animals can be expected to display their 'natural' torpor characteristics, but even in their natural surroundings they may be disturbed by recently attached recording devices and it may take days for the animals to get use to the change, although this response again differs among individuals and species.

Sawdust Method and Activity Sensors

For long-term studies of captive hibernating mammals, the most simple and economical approach to determine torpor occurrence and duration is the 'sawdust' method. It is non-invasive, but requires a quiet, cool environment with little or no disturbance. Once the animal has entered torpor and curled up into a ball, as occurs in many mammals, it is possible to determine by a puff of air against its back whether or not it is torpid. If there is no movement, or only slow movement is observed, a small amount of sawdust or fine sand is placed on the animal's back (Fig. 2.1). If the animal does not remove it immediately because of the disturbance, the animal is left in peace and quietly checked again for the presence or absence of sawdust on the next day to minimise disturbance. If the sawdust remains undisturbed, the animal did not arouse since it was last observed, whereas if the animal's back is clean then an IBE has occurred. This approach is appropriate for hibernating mammals, such as pygmy-possums or ground squirrels, especially during mid-winter and at low T_a when they express torpor bouts of several days. Some species even permit being weighed while torpid without arousal if the procedure is done carefully. For such procedures hibernating animals are best handled during the first half of a torpor bout (e.g. on day 2 or 3) because they will have reached steady-state torpor, but are less prone to rewarm than towards the end of the bout. However, if only checked once/day the resolution for TBD by using the sawdust method is, of course, only 1 day.

Fig. 2.1 The ‘sawdust method’. Once an animal has entered into torpor a small amount of sawdust or fine sand, as in this example of the yellow-pine chipmunk (*Tamias amoenus*), is placed on the back of the animal, which will fall off or be removed by the animal during the next arousal (photo F. Geiser)

The sawdust method is not suitable for many bats. It is also less suitable during early hibernation and hibernation at high T_a and usually also not for daily torpor, because at high T_b addition of sawdust will typically induce a premature arousal and removal of the sawdust.

The sawdust method is simple, non-invasive and cheap and it works if done correctly, but it is best to confirm with another method such as an activity meter or infrared motion sensor (e.g. Geiser 2007) that can monitor movement of an individual from outside the cage and detects motion of a warm body during IBEs. The reason for this caution is that torpid hibernators may also move during torpor without arousing and disappearance of sawdust may not be a perfectly reliable measure for IBEs. Once a correlation between the two methods has been established the activity measurement alone may suffice. For bats, which typically hang from a structure, such activity measurements alone may be suitable to determining TBDs and periodic arousals. However thermal cameras may be more suitable for bats and can also be used in the field (see below).

Infrared Thermometers

Infrared thermometers used to be expensive, but now they are relatively cheap, small and precise. Infrared thermometers have been used in a number of torpor studies and have the advantage that measurements can be taken without touching the animal or not handling it as often as for example during rectal T_b measurements. Although the surface of the fur (T_s) is generally well below the core T_b during normothermia, at low T_b during torpor the difference is usually small (Bartonička et al. 2017). However, it is advisable to determine how well T_b and T_s are correlated at a specific T_a, as T_a will affect the relationship (Geiser and Heldmaier 1995). If it is possible to measure eye temperature (T_{eye}), the difference between T_b and is typically smaller than for T_b-T_s and the correlation between T_b and T_{eye} can be strong (Song and Geiser 1997). Good matches between a naked part of skin (T_{skin}) measured via an infrared thermometer and T_b also have been observed in small mammals (Geiser et al. 2019a).

Thermocouples and Thermistors

Temperature measurements can also be done rectally in mammals or in the cloaca of birds with a thermocouple or thermistor to obtain a core T_b value. This requires frequent handing of the animal and the intrusion of a foreign object. Repeated use of this approach may actually discourage animals from using torpor. If such measurements are designed to determine temporal T_b patterns in daily heterotherms the measurements can be staggered over days. It is best to do only one measurement each day at a different time of day because, after the disturbance, animals are likely to behave differently and display a non-representative T_b patterns for the rest of the day (Morton and Lee 1978; Geiser and Baudinette 1985). Such measurements also can be used to get an estimate of torpor use per day. For nocturnal mammals the best time for determining whether or not a species enters torpor based on single measurements/day is usually around 8 or 9 am, after an undisturbed night and a few hours after lights on, but before midday when animals often arouse (Geiser and Baudinette 1985). In diurnal birds, measurements soon after midnight are often suitable (Hiebert 1990). Nevertheless, a single measurement/day probably results in an underestimate of torpor use. In some species, such as hummingbirds, a fine thermocouple inserted into the cloaca and taped to the tail may be tolerated and continuous overnight measurement of core T_b can be obtained (e.g. Wolf et al. 2020). However many other avian and mammalian species will not accept this approach and will try to remove the device and are unlikely to use torpor while it is attached.

Respirometry

Indirect calorimetry, or specifically open-flow respirometry to measure oxygen (O_2) consumption or carbon dioxide (CO_2) production, is a common non-invasive approach for quantifying torpor use and energy expenditure during torpor. Both O_2 consumption and CO_2 production are proportional to energy expenditure during aerobic metabolism (Schmidt-Nielsen 1997). Respirometry is most often used in captivity (Withers 1977b; Lighton 2008), but it also has been used successfully in the wild (e.g. Dausmann et al. 2004). Such respirometry systems typically measure O_2 content and/or CO_2 content of air expired by the animal with a gas analyser over time. Apart from determining torpor occurrence and energy savings gained by using torpor, this approach is especially important at high T_a, where T_b can fall only little or not at all and cannot be used for defining the torpid state (Reher and Dausmann 2021).

For respirometry measurements, an animal is placed into a sealed chamber supplied with a stream of air, and the flow of air through the chamber is measured together with the content of O_2 or CO_2 of air leaving the chamber (Withers 1977b, 2001; Lighton 2008). As O_2 consumption especially is directly related to energy use (Schmidt-Nielsen 1997) it can be used to determine energy expenditure over time and during different physiological states. If MR is to be expressed as a mass-specific value, the body mass must be measured before and after the respirometry trial and the body mass during the trial can be estimated by assuming a linear decline over time. For quantification of torpor it is advantageous for data interpretation and analyses if the T_b of the animals is measured simultaneously and remotely via transmitters, transponders or loggers (described below).

Apart from calibrations of the gas analyser and the flow meter (usually a rotameter or mass flowmeter), respirometry requires several other considerations. One of these is related to what is outlined above, that animals often are more likely to enter torpor if they feel secure. Thus a shelter, perhaps in the form of a cardboard roll for a small quadrupedal mammal, will increase the likeliness of the animal displaying torpor in the respirometer. For birds, a comfortable perch placed into the respirometry chamber is recommended and for bats, a mesh they can hang from.

An important consideration for reliable measurements is to measure T_a inside the respirometer vessel, which reflects the T_a the animal is exposed to, not outside in the temperature cabinet or room. Another fundamental consideration that is sometimes overlooked, is the use of a respirometry chamber of the appropriate size for the animal. The chamber must be big enough to allow the animal to move freely, but small enough to ensure that the 99% equilibrium between the air expired by the animal and the chamber air is reached in a relatively short time (Lasiewski et al. 1966). This can be calculated using the equation:

$$99\%\text{equilibrium} = \text{Respirometer Volume (ml)}/\text{Flow Rate (ml/ min)} * 4.6$$

(Lasiewski et al. 1966)

If the chamber is too big, the time to 99% equilibrium is lengthy and the measurements likely will represent over- or underestimates of O_2 consumption. Generally, a chamber that is about twice the volume of the flow rate/min is suitable for many applications (e.g. a 1000 ml chamber and a 500 ml/min flow rate), which means that 99% equilibrium is reached within about 9 min. This delay can, however, be largely avoided by calculating ‘instantaneous’ values (Withers 2001).

For measurements and calculation of metabolic rates it is important to consider that indirect calorimetry requires the animals to breathe, which is important for torpor studies because during bouts of torpor breathing is often discontinuous (Chap. 5). Therefore, to obtain a measure of metabolism, periods of non-breathing must be integrated with breathing events and it is often best to average measured values over 0.5 to 1 h.

Torpor Induction and the Time to Steady-State Torpor

BMR measurements in small mammals need at least 3–4 h before the true resting state is reached, as required by the definition (Bartholomew 1982; Cooper and Withers 2009). However, in some cases much shorter time periods have been used to measure physiological variables of torpor, although obtaining good steady-state torpor variables often takes much longer than 3–4 h. The time of torpor entry typically is not instantaneous and may occur hours after the beginning of the measurement period. Torpor entry is followed by the cooling of the body, which is curvilinear and slows as T_b approximates T_a because of the reduced rate of heat exchange. Therefore, the time to reach a constant, steady-state torpor T_b from the start of the measurement can take many hours or even days.

Even small (~10-g hibernators), which cool fast, require time to reach a steady-state torpor T_b after torpor entry. If the animal is thermoconforming during the entire entry phase, steady-state torpor occurs after at least around 3–4 h (Currie et al. 2015b, 2018; Fig. 2.2). However, if the animal does not thermoconform and increases MR during torpor entry, as is often the case in laboratory studies, this slows the rate of cooling and the time to reach steady-state torpor can take twice as long (Fig. 2.2). In a 25-g dunnart (*Sminthopsis macroura*, Fig. 2.2), the time from torpor entry to steady-state torpor is ~4 h in a thermoconforming individual (blue). In contrast, in the dunnart that used heat production during torpor entry (red), as indicated by the rise of MR and slow T_b decline during the entry phase, the time to steady-state torpor is increased to ~6 h. Steady-state values at a specific T_a are crucial for comparisons with other individuals or studies because during entry and arousal from torpor T_b and MR values are transient and difficult to compare. In Figs. 1.8 and 1.9 animals are torpid anywhere in the areas indicated by ‘Torpor’, but the values above the steady-state minima at each T_a are not useful for meaningful comparisons.

Figure 2.2 also shows that the widely used torpor threshold definition for T_b (a 5 °C reduction of T_b) (Chap. 1) is more conservative than the torpor threshold for MR (a reduction of MR by >25% below the RMR at the same T_a). In the thermoconforming individual, MR had fallen by ~85% at the time T_b fell by 5 °C. At the point MR had fallen by 25%, T_b had fallen only by 1 or 2 °C. Even in the individual that did not thermoconform, the MR had fallen by ~60% at the time T_b was reduced by 5 °C (Note: with ‘instantaneous’ MR measurements (Withers 2001) these differences would be further exaggerated). However, it is easier to measure T_b than MR in the wild and, even with these differences, T_b is a reasonable proxy for MR, which is the more representative measure of torpor expression. Animals do not

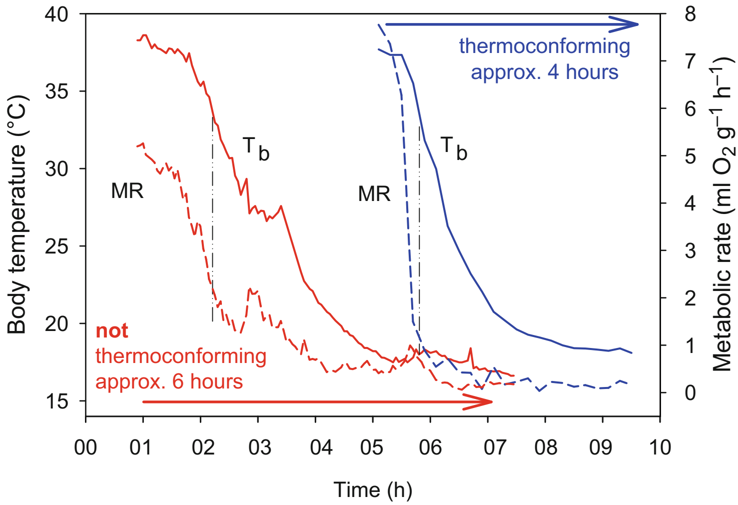

Fig. 2.2 Torpor entry by a thermoconforming (blue right) and not thermoconforming (red left) dunnart (*Sminthopsis macroura*, body mass ~25 g) held at a T_a of about 16 °C. The body temperatures (T_b, solid lines) and metabolic rates (MR, broken lines) are shown as a function of time from entering torpor. The thermoconforming animal reached steady-state torpor values after about 4 h (blue arrow) whereas the non-thermoconforming animal required about 6 h (red arrow). The vertical dash-dotted lines show that at the time that T_b had fallen by 5 °C from torpor entry the metabolism had fallen by >60% in both examples, largely because the normothermic $T_b - T_a$ differential was no longer maintained. Unpublished observations by the author

enter torpor primarily to reduce T_b, but to save energy and water and a reduction of T_b, although it contributes to the MR reduction, is often unavoidable.

The time interval required to reach steady-state torpor increases with increasing body mass. Mammals weighing ~50 g require around 12–20 h to reduce T_b below 10 °C at $T_a < 10$ °C (Fig. 2.3; Geiser and Mzilikazi 2011; Geiser and Martin 2013), 100-g species up to 30 h (Wilz and Heldmaier 2000) and 700-g ground squirrels >25 h (Barnes 1989). In species with a higher minimum regulated T_b of around 15–25 °C and measured at $T_a > 10$ °C the time to reach steady-state torpor from torpor entry is somewhat shorter, but still 3–4 h are required at a body mass of around 20 g (see Fig. 2.2), up to 6 h in 13-g gerbils (*Gerbillus pusillus*, Buffenstein 1985), and around 6 h for animals with a body mass of around 50 g (Lovegrove et al. 2001). Hibernating echidnas (*Tachyglossus aculeatus*, body mass ~4 kg) require 39 h on average to reach a T_b that approximates the steady-state minimum (Nicol and Andersen 2007). More than twice that time is required for similar-sized marmots (*Marmota marmota*) that cooled slowly and required ~68 h for a 30 °C reduction in T_b (Ruf and Arnold 2000). Therefore, measurements that last only a couple of hours overall, with variables of torpor measured within an hour or less of torpor entry will not provide reliable steady-state values. The errors for premature readings of 'BMR' values are often overestimates of ~10–20% (Cooper and Withers 2009). Variables of torpor measured too early can overestimate steady-state values by tenfold (1000%)

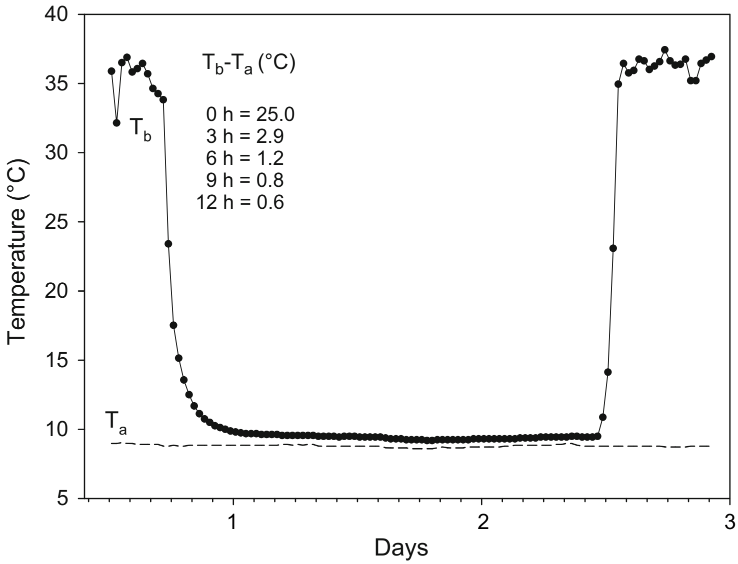

Fig. 2.3 A torpor bout of an elephant shrew (*Elephantulus edwardii*, 45 g). The T_b measurements (filled circles) were taken in 30-min intervals over ~2.5 days. The T_a is shown as a broken line. The T_b-T_a differentials at different times are shown from torpor entry; the minimum of 0.6 °C was reached after 12 h. Data from Geiser and Mzilikazi (2011)

or more. Obviously, such data are not suitable for making meaningful comparisons with other studies or species.

External Thermal Sensors

As electronic equipment for measurement of temperature becomes cheaper, smaller and more sophisticated, such devices are widely used to quantify torpor over many days without requiring disturbance of the animal. Often thermocouples or temperature data loggers placed under the animal in a nest can non-invasively measure T_s or T_{nest} and record the data over time (French 1985; Willis et al. 2005a). Thermocouples may be less suitable for rodents, which tend to chew them, but they have been used to quantify torpor use of perching hummingbirds (Hiebert 1992). Of course these data are only of value if the animal actually sits on or is near the measuring device and often the data from such measurements are incomplete because the animal moved away from the recording device. Infrared thermometers that record the surface temperature over time and point towards an animal in, for example a nest tube, are also suitable for such measurements and may be more reliable because close proximity of the animal to the recording device is not as crucial (Warnecke 2012). Generally, non-invasive measurements that use external sensors and require little interference with the animal are most suitable for quantifying the timing of entry and arousal or how often torpor is used.

Temperature-Sensitive Radio Transmitters, Data Loggers and Heart Rate Transmitters/Loggers

To obtain a detailed long-term measure of variables about torpor, a widely used approach for quantification of torpor is the attachment of external electronic devices. These have been used in the wild, in aviaries or outside enclosures, or during respirometry in captive animals. Electronic devices can be temperature-sensitive radio-transmitters (with individual frequency and a temperature-dependent pulse rate), or temperature loggers (capable of storing temperature readings as a function of time), which remain with/on the animal as it moves or forages. External devices are attached either as collars, back-packs, or via glue (Barclay et al. 1996; Dausmann 2005). External transmitters have a long range for their size, so it is easy to detect animals from a distance, in extreme cases >1.5 km for a 0.5-transmitter, but usually detection range is from around 100 m (Turbill et al. 2003b). External transmitters or loggers that transmit or record T_s over time are usually more reliable for small (~10 g) species such as small bats or birds, with small T_b-T_s differentials of often <2 °C (Barclay et al. 1996; Dausmann 2005; Romano et al. 2019) and as little as on average 0.4 °C (Bondarenco et al. 2014). An error of <2 °C seems acceptable if the T_b during torpor falls by 10 or 20 °C or more, however when the T_b of a species only falls by ~5 °C or less below the normothermic T_b it can be difficult to obtain meaningful data and interpret them correctly. In larger species, which usually maintain a greater thermal gradient between the core and the periphery, T_b-T_s differentials are much bigger (Körtner et al. 2001). However, even for medium-sized species, such measurements can be valuable if the position of the recording device is, for example, at the centre of a curled-up individual during rest or torpor (Körtner and Geiser 2000b; Dausmann 2005). Nevertheless, other disadvantages of externally attached devices are that they can be removed within brief periods by the animal, but this differs among species. External devices also can damage the skin or may cause an animal to get caught in branches or when they enter small openings of burrows, tree holes or nest boxes.

If measurements of precise core T_b are required, internal transmitters or temperature loggers are the best approach. Although these require surgery, it has been established that for long-term studies implanted devices are more suitable than external devices from an animal ethics point of view because they typically do not interfere with foraging of the animals. Since the data quality from internal devices is often better, typically fewer individuals are required for a meaningful data set (Rojas et al. 2010; White et al. 2013). Temperature-sensitive transmitters must be calibrated before use to get reliable data. Although temperature-sensitive transmitters have the added advantage of informing about home range, foraging and activity of an animal

(Körtner et al. 2016), when the transmission range of the transmitter to the receiving device is exceeded, which is often within 10–50 m for small internal devices, data are not recorded. However, absence of an animal from the receiver can also be used to estimate the activity period if it returns to the same roosting/nesting site. Because of their narrow range, small internal transmitters can make it difficult to radio-track tagged animals. Relatively large external transmitters on the other hand, often have enormous signal ranges that can even be received by satellites. Temperature loggers have the advantage of providing continuous thermal data with a time stamp and without missing points, but unlike transmitters, they do not provide information about other biological aspect, especially with regard to foraging or activity of the animals. However, the thermal data obtained do not only inform about torpor expression, but can also provide information about the timing of key reproductive events (Williams et al. 2011).

Other biologgers, some of whom are external, can provide data about light, acceleration and location using GPS (Nowack et al. 2016a; Evans et al. 2016; Williams et al. 2016). In some instances, a combination of both transmitters and temperature loggers has been used to improve the quality and quantity of the data set (Nowack et al. 2016a), but the animal must be large enough to carry both. Transmitters that can measure heart rate are now available and have been used in free-ranging bats to estimate MR, which correlates well with heart rate during normothermia and torpor (Currie et al. 2014; O'Mara et al. 2017). Further, small data loggers that can measure both heart rate and T_b are now commercially available.

Transmitter and Logger Size

It is often stated that devices carried by animals should be <5% of the animal's mass (Rojas et al. 2010). Importantly, this 5% value was not obtained by empirical measurements on quadrupedal mammals and, with current technology, would preclude work on many small species, which are often the most interesting with regard to heterothermy. However, when selecting appropriate masses of equipment for implantation or attachment to animals it must be considered that the relative capacity to carry mass is not a constant, but decreases with increasing body mass (Schmidt-Nielsen 1977). To illustrate this, human neonates weigh only about 4% of their mother's body mass, whereas in small, terrestrial, placental mammals, with a body mass of 10 g, neonate litter masses can be up to 36% of maternal mass and is still around 24% of maternal mass in a 100-g mammal (Blueweiss et al. 1978). Obviously these small pregnant mammals are able to adequately move in the wild. Whereas these high percentage values exceed what appears reasonable for masses to use for implanted or attached devices they demonstrate the ability of small mammals to carry devices.

Empirical evidence on running speed supports the interpretation of a substantial load carrying capacity by small mammals (Rojas et al. 2010). In two small terrestrial mammal species, weighing 13 and 17 g, maximum running speed, considered to be a

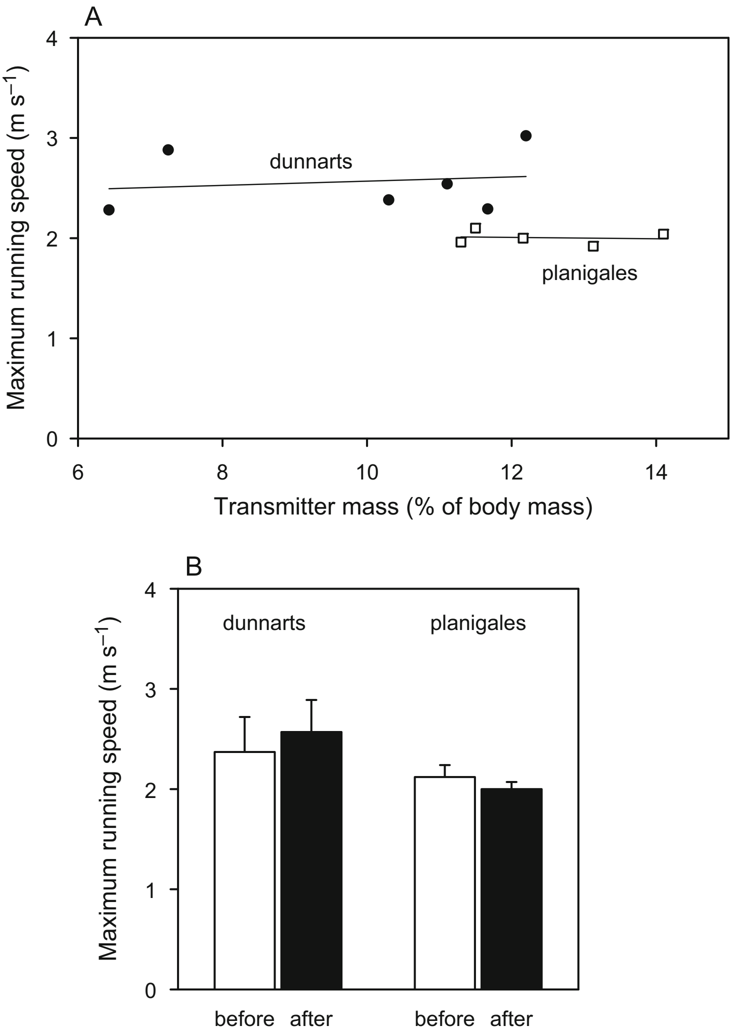

Fig. 2.4 (**a**) The maximum running speed of dunnarts (*Sminthopsis crassicaudata*, 17 g, filled circles) and planigales (*Planigale gilesi*, 13 g, squares) as a function of transmitter mass (% of body mass). In dunnarts transmitters between 6 and 12% of body mass did not affect running speed, and in planigales between 11 and 14% of body mass. (**b**) The bar graphs show means with SD of maximum running speed before (white bars) and after (black bars) the transmitter implant, which were almost identical, for the same individuals (data from Rojas et al. 2012)

crucial trait for successful predator avoidance, was unaffected by transmitter masses between 6 and 14% of body mass (Fig. 2.4a). Moreover, the running speed of the same individuals did not differ significantly before and after implantation of the device (Fig. 2.4b). Data from that work also suggest that there are no long-term negative effects associated with implanted transmitters, with implanted females successfully producing young. This led to the recommendation by the authors for transmitter/logger masses in small (<30 g) non-flying mammals to be <10% of the animal's body mass because this is less than half of neonate litter mass. This mass will ensure that transmitters have large enough ranges and long enough battery lives, both of which are a function of size/mass. At that size/mass, meaningful data collection and therefore ethical experimentation will be ensured, however, as empirical work shows, it does not hinder animal performance.

Flying animals are likely more affected by added mass than non-flying animals. However, in small bats, relative neonate body mass also increases with decreasing body mass (~20% at 100 g, ~30–40% at 10 g) and even in the largest species measured neonate mass is >10% of the maternal mass (Hayssen and Kunz 1996). Similarly, in birds, relative egg mass increases exponentially with decreasing body mass (Rahn et al. 1975). Small birds (<100 g) have egg masses of ~10–20% of the birds' body mass and only when body mass of birds exceeds 1 kg, is egg mass ~ 5% of the mother's mass (Rahn et al. 1975). Therefore, it comes as no surprise that larger birds are more affected than smaller birds by transmitters weighing 5% of body mass (Caccamise and Hedin 1985). In partridges (*Perdix perdix*, ~500 g) even 8 and 11-g transmitters weighing <3.5% of body mass, externally attached as necklace, negatively affected survival (Homberger et al. 2021), but available smaller devices were not tested. With regard to transmitter mass in bats, added loads resulted in a significant drop in maneuverability (Aldridge and Brigham 1988). However, the authors emphasize that bats of varying body masses require different sizes of transmitters and that 5% should not be a 'one size that fits rule'. Nevertheless, transmitters weighing around 5% of the body mass have been successfully used in many long-term studies on small free-ranging bats and birds and this size appears to be a sensible approach for many species. Of course, if smaller devices are available and suitable for the work, they should be used preferentially.

Transponders

Temperature-sensitive transponders are even smaller than modern transmitters and loggers. These transponders can be tiny (e.g. 14 mm × 2 mm) and lightweight (~0.13 g). Different models are available, some with only small temperature ranges, whereas others function over a range of ~5–43 °C, which is important for quantifying deep torpor. Transponders are often implanted subcutaneously, and when calibrated prior to use, they provide reliable and repeatable measurement of subcutaneous temperature (T_{sub}), which is a good approximate for core T_b (Wacker et al. 2012; Currie et al. 2015a, b). A significant disadvantage of transponders is their small range, often only a few cm, and therefore they are often not suitable for work on free-ranging animals, but they have been successfully used in captivity (Freeman et al. 2020).

Thermal Cameras

Thermal cameras have become more affordable, precise and reliable and have been used to quantify thermal biology of animals in the field and laboratory (Tattersall 2016). For example, during development of endothermy in altricial small animals it is difficult to measure T_b with most other equipment, but thermal cameras can be used to measure T_s non-invasively and the measured values can approximate T_b when the young are still naked or partially naked (e.g. Geiser et al. 2019a).

Thermal cameras have been used to quantify movement of torpid bats in mines by measuring T_s. These measurements also reveal periodic rewarming of bats (Bartonička et al. 2017) and can be used to determine TBD non-invasively in the wild. When a small patch of fur was removed to assess how T_{skin} differs from T_s, the thermal image revealed that T_s and T_{skin} were almost identical at low T_b during torpor, as expected, but during arousal the T_s-T_{skin} differential increased significantly, approaching 10 °C. However, most importantly, T_s measurements were sensitive enough to detect rewarming events (Bartonička et al. 2017).

Chapter 3
Diversity and Geography of Torpor and Heterothermy

In this chapter, the diversity of heterotherms, where they live and how they differ from each other is covered in detail. When data from free-ranging animals were available these were used preferentially, but information on captive animals is also included. As the extent of available data differs substantially among taxa, the information provided reflects what is known about a specific group to a large extent. To put the information on heterothermic endotherms into context with other organisms, I will address terrestrial ectotherms first.

Ectotherms

As noted above, the MR in ectotherms is low and therefore their T_b is a function of T_a (Fig. 1.1). Consequently, when exposed to cold, many terrestrial ectotherms enter a state of torpor (Ultsch 1980; Storey and Storey 2011). Often this torpid state is referred to as 'winter dormancy' or 'brumation', but the term hibernation also has been used and that seems appropriate because it does not make any assumptions about the underlying physiology and simply describes a prolonged period at low T_b (Ultsch 1980; Wilsterman et al. 2021). In some ectothermic species T_b falls well below 0 °C, and the low T_b is made possible by super-cooling of body fluids. Often antifreeze proteins are used to inhibit the growth of ice (Storey and Storey 2011, 2013). These species often hibernate deep in the soil or in mud at the bottom of lakes to avoid freezing. If freezing does occur, as indicated by a freezing exotherm (releasing heat) from the release of energy during the freezing process (Fig. 1.1), it is lethal for many organisms. However, some invertebrates and also some vertebrates, for example the wood frog (*Rana sylvatica*), box turtle (*Terrapene carolina*), and the European lizard (*Lacerta vivipara*) are freeze tolerant (Storey and Storey 2011, 2013). Surviving freezing in these vertebrates is possible if ice crystals are restricted to extracellular spaces. These animals have high concentrations of small molecules such as glucose which function as cryoprotectants to protect cells.

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_3

Although T_b follows T_a in ectotherms and the process of dormancy may appear to be entirely passive, some ectotherms can adjust MR in winter to values well below those in summer. For example, tropical Australian frillneck lizards (*Chlamydosaurus kingii*), which perch in trees during the winter dry season, have substantially reduced field metabolic rates (28%) despite small (~2.5 °C) reductions of selected T_bs, in comparison to the warm season (Christian and Bedford 1995). In American spade-foot toads (*Scaphiopus* spp.), during underground dormancy, MR was approximately 20% of individuals resting on the ground at the same T_a (Seymour 1973). Similarly, during aestivation, which can last for years in some species, the northern Australian burrowing frogs (*Cyclorana* spp.) significantly reduced the size of the digestive tract and reduced MR by using metabolic inhibition (Storey and Storey 1990; Guppy and Withers 1999; Withers and Thompson 2000; Cramp and Franklin 2005; Withers and Cooper 2010).

Due to their low internal heat production, ectotherms must rely on behavioural thermoregulation to raise T_b after hibernation. European green lizards (*Lacerta viridis*), measured in the same thermal gradient, select low T_bs in winter and high T_bs in summer. This seasonal change in behavioural thermoregulation, is controlled by the seasonal change in photoperiod and the corresponding level of melatonin (Rismiller and Heldmaier 1988). Typically, after a period of uninterrupted hibernation lasting essentially from autumn to spring, terrestrial ectotherms select thermally favourable sites and rewarm passively from the low T_b. However, in South American tegu lizards (*Salvator merianae*) dormancy during winter months is followed by the reproductive period during which time they not only use behavioural thermoregulation, but increase heat production and express partial endothermy (Tattersall et al. 2016). Moreover, in some species hibernation is interrupted by basking and periodic arousals during winter, as for example in goannas (*Varanus rosenbergi*) in South Australia (Rismiller and McKelvey 2000), and rattlesnakes (*Crotalus horridus*) in Tennessee (Nordberg and Cobb 2016), reminiscent of mammalian hibernators. Given that other reviews about hibernation in ectotherms are available (Ultsch 1980; Guppy and Withers 1999; Storey and Storey 2011), I will not elaborate further about them but move on to the main topic of this book on the diversity of torpor in endotherms. I will return to behavioural thermoregulation in relation to dietary lipids in part relating to ectotherms later in the book.

Torpor in Endotherms

Birds

Birds are a highly diverse class of vertebrates with >10,000 species and they are distributed all over the world. On average birds have higher normothermic T_bs and BMRs than do mammals. Avian T_bs range between ~38 and 41 °C when at rest (Dawson and Hudson 1970; Reinertsen 1983; McKechnie and Lovegrove 2002; Schleucher 2004). Birds, especially flying species, are smaller on average than mammals, with a body mass range of ~2 g in hummingbirds to ~12 kg in swans, pelicans, bustards and the Andean condor. Birds typically rely on high energy foods such as insects, seeds, fruits and nectar that can become seasonally unavailable. The insulation of birds in the form of feathers is typically excellent, and is more adjustable than the hair of mammals, so heat loss at low T_a can be minimized (Biebach 1978). Most birds can fly and therefore are highly mobile permitting them to avoid adverse conditions by migration. Nevertheless, both migratory and sedentary birds use torpor (Geiser and Brigham 2012). However the number of known avian heterotherms is currently far fewer than for mammalian heterotherms (McKechnie and Lovegrove 2002; Ruf and Geiser 2015), which is to some extent due to the lack of data. The reasons for less available information about torpor in birds likely includes the difficulty of keeping many birds in captivity, the assumption that migration pre-empts torpor use resulting in reduced research effort, and the fact that if they survive, many captive birds tend to be either fat or stressed and therefore not likely to express the thermal biology characteristic of birds in the field (Körtner et al. 2000; Geiser et al. 2000; Schleucher 2004; Cooper et al. 2008). Another potential reason for the underestimation of avian torpor is that when perching, birds often form a ball shape in the cold both when torpid and asleep. These birds also remain firmly attached to their perch due to their weight, which tightens the tendons around the heel, causing the toes to lock around the perch (Backus et al. 2015). Consequently, in contrast to many mammals, it is visually less obvious whether or not they are torpid.

Torpor, with a T_b reduction of >5 °C from normothermic resting values, as used for definition of torpor in this book, has now been observed in at least 13 (Table 3.1) of the currently ~30 recognized avian orders (Reinertsen 1983; McKechnie and Lovegrove 2002; Schleucher 2004; Pough and Janis 2019). If smaller reductions of T_b by <5 °C below resting T_b are considered, this number would increase further (see McKechnie and Lovegrove 2002 and below). The relatively low number of heterothermic birds in comparison to mammals (see below) is still somewhat surprising, because on average birds are smaller than mammals (Blackburn and Gaston 1994). The resulting surface area/volume relationships and high heat loss, despite the adjustable thickness of feathers, appear to demand more use of torpor in birds because it would be energetically beneficial. Therefore it is highly likely that more study of free-ranging birds will increase the number of heterothermic species. With regard to large species, there are no records on torpor in the mostly large, flightless ratites, although torpor in large king penguin chicks (~8 kg) has recently been described (Eichhorn et al. 2011). Currently, the avian groups that contain most heterothermic species are small and as adults, avian heterotherms weigh between 2 and 500 g (Ruf and Geiser 2015). Most known heterothermic species belong to the nightjars and relatives (Caprimulgiformes), swifts (Apodiformes), hummingbirds (Trochiliformes) and songbirds (Passeriformes) (Tables 3.1 and 3.2).

Table 3.1 Orders of birds and mammals expressing torpor or heterothermy

Birds	
Galliformes, landfowl	Shallow nocturnal torpor in quail, including during development
Caprimulgiformes, nightjar-relatives	Hibernation in poorwills, nocturnal torpor in many species
Apodiformes, Swifts	Nocturnal torpor in several species, including during development
Trochiliformes, hummingbirds	Nocturnal torpor common in many species ranging in body mass from ~2 to 24 g
Cuculiformes, cuckoos	Shallow torpor in roadrunners and smooth-billed ani
Columbiformes, pigeons	Nocturnal torpor in several species including rather large fruit doves
Ciconiiformes, raptors	Nocturnal torpor in African pygmy-falcons, but needs verification
Sphenisciformes, penguins	King penguin chicks express torpor; small penguins may also use it
Procellariformes, petrels	Storm petrel chicks express torpor when parents fail to provide food
Strigiformes, owls	Shallow torpor in snowy and scops owl, torpor could not be verified as yet in small northern owls
Coliiformes, mouse birds	Several mousebird species express nocturnal torpor in captivity
Coraciiformes, kingfishers	Torpor in the very small tody and the very large kookaburra
Passeriformes, songbirds	Shallow nocturnal torpor with high minimum T_b in several songbirds
Mammals	
Monotremata, egg-laying mammals	Hibernation in the short-beaked echidna, including during reproduction
Didelphimorphia, opossums	Several small to medium-sized opossums express daily torpor, the Patagonian opossum remained torpid for almost 2 days
Microbiotheria, monito del monte	The single member of this order the Monito del Monte hibernates
Dasyuromorphia, carnivorous marsupials	Daily torpor in many dasyurids and the numbat, basking during rewarming common
Notoryctemorphia, Marsupial moles	Sand swimming marsupial moles have a labile T_b
Diprotodontia, possums	Hibernation in pygmy-possums and feathertail glider, daily torpor in *Petaurus* gliders and relatives
Afrosoricida, tenrecs, golden moles	Several tenrecs and perhaps golden moles hibernate, shrew tenrecs express daily torpor
Macroscelidea, elephant shrews	Small elephant shrews mainly seem to use daily torpor, but torpor bouts up to 2 days have been observed
Tubulidentata, aardvark	Substantial heterothermy during drought
Xenarthra, armadillos, sloth, anteaters	Hibernation known for a medium-sized armadillo, and appears to occur in small armadillos. Substantial reductions of T_b in sloths and anteaters, but uncertain whether this was regulated
Lipotyphla, insectivores	Several hedgehog species hibernate, shrews use daily torpor
Chiroptera, bats	Many insectivorous bats from many families hibernate; small blossom/fruit bats, leaf-nosed bats and some tropical families use daily torpor

(continued)

Table 3.1 (continued)

Pholidota, pangolins	Fasted giant and tree pangolins substantially reduce T_b, but it is not certain whether this was regulated
Carnivora, carnivores	Bears hibernate with a rather high T_b of ~30 °C, badgers, skunks and aardwolf also express torpor
Primates, primates	Malagasy fat-tailed lemurs, loris, and perhaps mouse lemurs hibernate, bushbabies and other mouse lemurs express daily torpor
Rodentia, rodents	Hibernation diverse in many species and families including ground squirrels, chipmunks, marmots, dormice, pocket mice, jerboas and large hamsters; daily torpor is used by small hamster relatives and mice

Table 3.2 Geographic distribution of heterothermy and torpor in birds and mammals

Africa and Madagascar
Nightjars, doves, owls, perhaps small raptors, mouse birds, passerines (sunbirds)
Tenrecs, golden moles, elephant shrews, aardvark, hedgehogs, shrews, bats, perhaps pangolins, carnivores, primates (lemurs, bushbabies), rodents (dormice, jerboas, pouched mice, rock mice)
Antarctica
King penguin chicks
Asia
Quail, nightjars, swifts, doves, passerines (martins)
Hedgehogs, shrews, bats, carnivores (bears), primates (tarsiers), rodents (dormice, ground squirrels, hamsters, jerboas)
Australia and New Zealand
Nightjars (frogmouth, owlet nightjar), swifts, doves, kingfishers (kookaburra), passerines (woodswallows, honey eaters)
Monotremes (echidna), marsupials (carnivorous marsupials, possums), bats, rodents (mice)
Europe
Quail, nightjars, swifts, passerines (martins)
Hedgehogs, shrews, bats, carnivores (bears, badgers), rodents (dormice, marmots, ground squirrels, hamsters, mice)
North America
Nightjars, hummingbirds, swifts, cuckoos (roadrunner), doves, storm petrel chicks, owls, todies, passerines
Shrews, bats, carnivores (bears, badgers, skunks), rodents (pocket mice, marmots, ground squirrels, chipmunks, deer mice)
South America
Nightjars, hummingbirds, cuckoos (ani), passerines (manakins)
Marsupials (monito del monte, opossums), armadillos, perhaps anteaters and sloths, bats, rodents (leaf-eared mice, harvest mice, vesper mice)

Landfowl, Galliformes

Landfowl typically are rather heavy, ground-dwelling, diurnal birds which usually are granivorous or omnivorous. They are often reluctant to fly and are distributed all over the world with the exception of some oceanic islands and Antarctica (Pough and Janis 2019). A study of captive Japanese quail (*Coturnix coturnix*), one of the smaller galliforms at ~150 g, showed that food deprivation for four days resulted in a reduction of T_b by 5 °C from 41.5 to 36.5 °C, much greater than when food was available. This fasting-induced T_b fluctuation was similar at high and low T_as (Hohtola et al. 1991). The low T_b was maintained for much of the night, but T_b increased shortly before daybreak. Shallow nocturnal torpor has also been observed for a short period during the development of precocial king quail at a body mass of around 15 g (*Coturnix chinensis*, adult body mass ~50 g) (Aharon-Rotman et al. 2020). Surprisingly, other galliform birds, even those living in cold environments such as ruffed grouse (*Bonasa umbellus*) do not appear to enter torpor, but instead use behaviours such as snow roosting and fat storage to minimize heat loss (Shipley et al. 2019).

Nightjars and Relatives, Caprimulgiformes

The Caprimulgiformes have a world-wide distribution with the exception of far northern and southern latitudes and some deserts (Holyoak 2001). Unlike many other birds, nightjars and their relatives are nocturnal and many roost on the ground. Many nightjars use torpor for energy conservation, and torpor in arid zone individuals is especially common (Brigham et al. 2006, 2012). Most nightjars are largely insectivorous, but the large tawny frogmouth (*Podargus strigoides*, 500 g) may also eat snails, bird eggs and small vertebrates.

The only known avian hibernator, the American common poorwill (*Phalaenoptilus nuttallii*, 45 g; Brigham 1992; Fig. 3.1), a migratory species, belongs to the caprimulgiforms. Poorwills breed in the western USA and southwestern Canada. They overwinter in Arizona, California and Mexico during which time they display multiday bouts of torpor. It has been suggested for some time that poorwills hibernate (Jaeger 1948) but long-term data on free-ranging birds have only recently become available (Woods et al. 2019). Poorwills in Arizona and California enter torpor frequently in winter, often on the ground in the open in rocky Canyons or at the base of *Opuntia* cacti. It appears that poorwills can remain in one spot for most of winter because winter roost sites were delineated by a horizontal mat of yellow grass with a green fringe outlining the bird's body (French 1993). Radio-telemetry data show that on sunny days T_{skin} of free-ranging birds fluctuated by >25 °C due to passive rewarming by the sun. When poorwills were artificially shaded they remained inactive for up to 45 days and displayed torpor bouts of 4–7 days, with T_{skin} falling below 5 °C (Woods et al. 2019). Qualitatively this pattern of torpor expression, with passive T_b fluctuations, is similar to that observed on fat-tailed

Fig. 3.1 A torpid poorwill (*Phalaenoptilus nuttallii*, 45 g), the only known avian hibernator, sitting in the open on the ground. Note the bird's excellent camouflage, its closed eyes, and the transmitter antenna extending from the bird's neck to the top left corner of the picture. The picture was taken in the Okanagan Valley of British Columbia. (photo and copyright, Mark Brigham)

lemurs in Madagascar (Dausmann 2014; Dausmann and Warnecke 2016). During their reproductive period in southern Canada, poorwills entered short bouts of torpor (up to 36 h) regularly in spring and autumn but only rarely when they were reproductively active (Brigham 1992; Kissner and Brigham 1993). The physiology of hibernation in poorwills appears be similar to that of mammalian hibernators, with the expression of autumnal fattening, the capability to express multiday torpor bouts in winter, a minimum T_b of ~3 °C, and an extremely low TMR at ~5% of BMR, similar to that of similar-sized mammals (Withers 1977a; Woods 2002; Ruf and Geiser 2015).

All other heterothermic caprimulgiforms investigated to date use daily torpor, often during the second half of the night, and/or in the morning. The known heterothermic species include the European nightjar (*Caprimulgus europaeus*, 80 g) which, after substantial loss of body mass from 86 g to 32 g, entered daily torpor with a T_b of about 20 °C and recovered without apparent ill-effects after feeding (Schlegel 1969). Similarly, after 6 days of fasting *C. europaeus* displayed daily torpor with a reduction of T_b from 35.2 to 19.3 °C (Peiponen 1965) and in another study, T_b fell to near 10 °C (Peiponen 1970). Australian spotted nightjars (*Eurostopodus guttatus*, 75 g; Dawson and Fisher 1969) also entered torpor after losing body mass in captivity. As these data are over five decades old and relied heavily on starvation to induce torpor, data on free-ranging individuals for these species would be highly desirable to gain insight on how and when torpor is expressed and its ecological significance in the wild. Free-ranging common North American nighthawks (*Chordeiles minor*, 80 g) rarely express shallow torpor. This

Fig. 3.2 A tawny frogmouth (*Podargus strigoides*, 500 g), the largest bird known to use torpor as an adult, is distributed all over the Australian continent (photo and copyright F. Geiser)

is similar to whip-poorwills (*Caprimulgus vociferous,* 55 g), which reduced T_s to a minimum of 20 °C on average and TBD was ~6 h, but torpor only occurred on 12 night out of 346 bird-nights of observation (Fletcher et al. 2004; Lane et al. 2004). With the exception of poorwills, available data on free-ranging caprimulgiforms suggest that they reduce their T_b during torpor to minima ranging from ~10.5 °C in the South African freckled nightjar (*Caprimulgus tristigma,* 70 g; Smit et al. 2011) to 29 °C in the Australian tawny frogmouth (*Podargus strigoides*) weighing 500 g (Körtner et al. 2000). Frogmouths are the largest adult bird known to use torpor with a T_b reduction of ~10 °C (Körtner et al. 2000, 2001).

Observations on the tawny frogmouth (*P. strigoides*, Fig. 3.2), are of special interest because of their size and because they reveal the potentially large differences in torpor expression between captive and free-ranging birds. Frogmouths which are sedentary, are distributed all over the Australian continent and roost in the open on tree branches. Two independent studies on captive frogmouths (Fig. 3.3) suggested that they are strictly homeothermic (McNab and Bonaccorso 1995; Bech and Nicol 1999) with an unusually precise normothermic T_b of 38.1 ± 0.07 °C (McNab and Bonaccorso 1995). Nevertheless, despite the large size of the species, they are almost

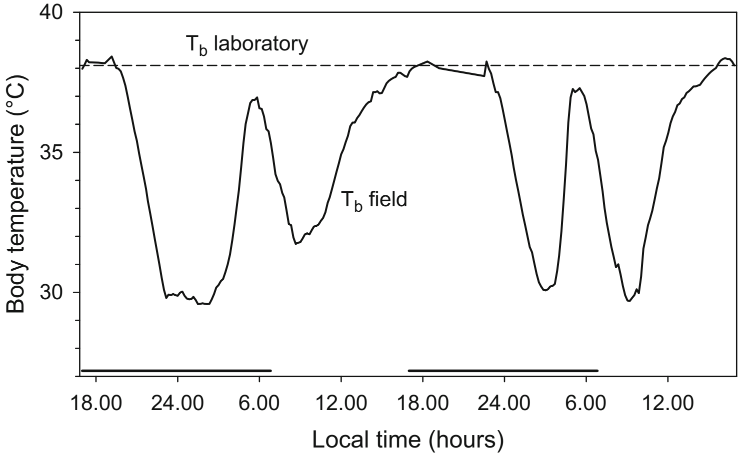

Fig. 3.3 Body temperatures in tawny frogmouths (*Podargus strigoides*, 500 g) over 2 days in the field (solid line) in comparison to the mean 38.1 ± 0.07°C measured in captivity (broken line). Data from Körtner et al. (2001) and McNab and Bonaccorso (1995)

tenfold bigger than most other birds for which torpor has been described, frogmouths did enter torpor in the wild with a reduction of core T_b from ~39 °C to ~29 °C (Körtner et al. 2000, 2001). Free-ranging frogmouths in a forest at ~1000 m elevation in south-eastern Australia entered torpor on cold winter nights, when daily T_a ranged between about 0 and 15 °C (average night T_a 4.4 °C). Torpor was expressed on up to 60% of observation days, typically after a brief period of activity after dusk (Fig. 3.3). The nocturnal torpor bout lasted for 7 h on average, was followed by endogenous rewarming, and flight and then re-positioning at a new roost with a camouflaged background. Frogmouths then entered a second ~3.5-h torpor bout in the morning, which was usually terminated by partial passive rewarming in the sun (Körtner et al. 2000, 2001) and probably reduced the energetic costs of rewarming (see Chap. 7). Torpor in frogmouths was expressed only from autumn to spring in the wild and interestingly captive individuals on *ad libitum* food showed a strong (~40%) seasonal change in body mass with lowest body mass in summer and the highest in early winter, unlike the pattern observed for many other daily heterotherms (Stulberg et al. 2018).

Detailed long-term data are also available on free-ranging Australian owlet-nightjars (*Aegotheles cristatus* 50 g), a much smaller species. Owlet-nightjars belong to the family Aegothelidae and are found in New Guinea, Australia, the Moluccas, and New Caledonia (Holyoak 2001). Owlet-nightjars are distributed all over the Australian continent, are insectivorous, and heterothermic, and unlike most other nightjars they roost in tree hollows and crevices. Birds in a montane forest in eastern Australia frequently entered torpor in the early morning in winter, with T_b falling from maxima of 42 °C to a minimum of 22 °C (Brigham et al. 2000). The morning torpor bout lasted for ~4 h with a maximum of 9 h, and birds rewarmed near midday, likely using radiant heat from the sun, because they were observed basking. For about 30% of observations owlet-nightjars re-entered a second torpor bout in the afternoon, before arousing for the nocturnal activity period. Owlet nightjars also display torpor in arid central Australia. Torpor was more frequent during a period of drought than during a wet year, and birds roosting in tree hollows expressed torpor more frequently than those roosting in thermally buffered rock crevices; low arthropod abundance increased torpor use (Doucette et al. 2011, 2012). Owlet-nightjars also entered torpor in captivity, but torpor was shallower and shorter than for individuals in the field (Doucette and Geiser 2008; Geiser et al. 2000).

Free-ranging freckled nightjars (*Caprimulgus tristigma,* 70 g), from a semi-arid region of the Karoo in South Africa exhibited the lowest measured T_{skin} of 10.5 °C for any *Caprimulgus* nightjar which typically seem to express daily torpor (Smit et al. 2011). Therefore, it was hypothesized that this species may be able to use multiday torpor similar to poorwills, but so far this has not been confirmed. Torpor expression in freckled nightjars was not strongly affected by T_a, but rather by moonlight. When moonlight was available nightjars foraged, whereas in the absence of moonlight they became inactive and displayed torpor (Smit et al. 2011). Insect availability was high throughout the entire project so it appears that foraging opportunities provided by lunar light affected torpor patterns. The lowest T_{skin} were measured in torpid birds on the nights after the new moon (Smit et al. 2011).

Swifts, Apodiformes

Like nightjars, swifts are also found world-wide with the exception of the far north, large deserts, many oceanic islands and Antarctica. Swifts are diurnal aerial predators, and can remain in the air for months, including during sleep at night (Rattenborg 2006; Hedenström et al. 2019). However, to my knowledge there are no data on swifts using heterothermy during flight, which seems likely because of their small size, high heat loss, diet of aerial insects such as swarms of termites, ants and beetles, and the ability of flight in bats and birds at T_bs below 30 °C (Chap. 7). Common swifts (*Apus apus*) fly and soar to altitudes of up to 3600 m with an average of 2300 m and are exposed to T_as ranging from 2.4 to 12.5 °C with an average of 3.6 °C during clear weather (Gustafson et al. 1977); these T_as are close to those experienced by mammalian hibernators in their hibernacula (Chap. 6).

Although it has been known for some time that European common swifts (*Apus apus*, 42 g) can use daily torpor as juveniles and as adults after food withdrawal (Koskimies 1948), data about heterothermy for this avian group remain scant. Some other swifts are known to use torpor, including the American white-throated swift (*Aeronautes saxatalis*, 30 g; Bartholomew et al. 1957), the Australasian needletail swift (*Hirundapus caudacutus*, 85 g; Pettigrew and Wilson 1985), the glossy swiflet (*Collocalia esculenta*, 7 g), perhaps the uniform swiftlet (*C. vanikorensis*, 12 g) from New Guinea (McNab and Bonaccorso 1995), and the small tropical silver-rumped spinetail from Malaysia (*Rhaphidura leucopygialis*, 12 g; Shipley et al. 2015).

The rather large needletail swift entered torpor every night over several nights in captivity and body mass declined during that time. On one night when cloacal T_b

was continually monitored, T_b fell from 38.5 °C to 28 °C and the bird remained torpid for 10 h. The bird aroused using endogenous heat production the following morning after human disturbance (Pettigrew and Wilson 1985). Needletail swifts not only display torpor associated with a reduction in T_b and MR, but are also supposed to be the fastest horizontally flying bird, requiring a huge energy expenditure, which together with its diet of unpredictable flying insects may explain its need to use torpor.

The minimum T_b of swifts during torpor ranges from 17 to 28 °C, with the lowest T_b in *A. saxatilis*. The measured TMR was about 40% of BMR, and TBD was around 5–10 h (Ruf and Geiser 2015). Thermal biology data on free-ranging swifts are currently only available on juvenile Alpine swifts (*Apus melba*, ~65 g) which entered torpor during bad weather (Bize et al. 2007). Torpor during development and growth is used by several other birds to deal with energetic bottlenecks (see Chap. 8).

Hummingbirds, Trochiliformes

Hummingbirds (Fig. 3.4) are diurnal, restricted to the Americas, and many migrate from North America to middle or South America. The order contains some of the smallest endotherms (~2 g) and even the largest species, the giant hummingbird

Fig. 3.4 A coppery-headed emerald hummingbird (*Microchera cupreiceps*, ~3 g) from middle-America. Hummingbirds are restricted to the Americas, contain the smallest bird species and many use nocturnal torpor (photo and copyright F. Geiser)

(*Patagona gigas*), weighs only ~24 g (Krüger et al. 1982; Hiebert 1993a, b; Shankar et al. 2020; Wolf et al. 2020). Considering their small size and ephemeral diet of largely nectar and pollen and some insects, it is of little surprise that many species are heterothermic (Bartholomew et al. 1957; Lasiewski and Lasiewski 1967; Hainsworth and Wolf 1970; Krüger et al. 1982; Hiebert 1993a, b; Bucher and Chappell 1992; Bech et al. 1997; McKechnie and Lovegrove 2002; Schleucher 2004; Shankar et al. 2020; Spence and Tingley 2021).

Nocturnal torpor expression in these diurnal birds is common and this has been known to occur for some time and for many species (see Dawson and Hudson 1970). Hummingbird torpor appears to be restricted to the nighttime, often commences about 2 h after dusk and lasts for most of the night up to about 11 h. Rewarming occurs before dawn (Hiebert 1990). The T_b of some hummingbirds decreases by the greatest extent known for daily heterotherms, with a T_b as low as 6.5 °C measured via an artificial egg under an incubating bird in the Andean hillstar (*Oreotrochilus estella*, 6.5 g), and wild broad-tailed hummingbirds (*Selasphorus platycercus*, 3.5 g) (Calder and Booser 1973; Carpenter 1974). During the wet spring at ~3800 m elevation in Peru all five hummingbird species investigated, ranging in body mass from 5.4 to 24 g, displayed torpor (Wolf et al. 2020). The T_b was measured using a thermocouple inserted into the cloaca and secured to the tail (Wolf et al. 2020). Some hummingbird species seemed to thermoconform during torpor at low T_a, whereas others maintained a large $T_b - T_a$ differential (Wolf et al. 2020). The lowest T_b value in these hummingbirds was 3.3 °C in the black metal tail (*Metallura phoebe*, 6.1 g) and even the rather large giant hummingbird (*Patagona gigas*, 24.3 g) entered torpor with a minimum measured T_b of around 10 °C (Wolf et al. 2020). Nevertheless, in most hummingbirds investigated, T_b minima of 10 to 22 °C have been found and, as in other daily heterotherms, the TMR of torpid hummingbirds is typically 10–30% of BMR (McKechnie and Lovegrove 2002; Ruf and Geiser 2015).

Cuckoos, Cuculiformes

Cuckoos are diurnal, eat insects, small vertebrates and fruits, and occur all over the world except for extreme northern and southern latitudes. Many, but not all cuckoos are brood parasites and many are migratory (Scott et al. 1974). Shallow torpor has been observed in greater roadrunners (*Geococcyx californicus*, ~350 g), a sedentary species from southern north America and Mexico. A non-breeding male roadrunner in California reduced T_b from ~41 °C to a minimum of 33 °C and a breeding female lowered T_b to 34 °C (Vehrenkamp 1982). Roadrunners bask and expose their dark dorsal skin to solar radiation to aid in thermoregulation (Ohmart and Lasiewski 1971). Another cuckoo reported to be heterothermic is the smooth-billed ani (*Crotophaga ani,* 110 g) from Panama. Individuals were held in captivity for 2 days and, after refusing to eat food, reduced T_b from ~41 °C to 32.6 °C on the second night (Warren 1960).

Pigeons, Columbiformes

Pigeons are a diverse group of often medium-sized, diurnal birds with either a frugivorous or granivorous diet (Schleucher 2004). Their distribution is world-wide with the exception of extreme northern and southern latitudes and some oceanic islands. Nocturnal torpor lasting for several hours has been observed in several species. The granivorous Inca dove (*Scardafella inca*, 44 g) from Arizona reduced T_b from ~40 to 30 °C when food was withheld at T_a 20 °C; birds with lower T_bs became hypothermic and were unable to rewarm (MacMillen and Trost 1967). Collared doves (*Streptopelia* sp. 150 g) entered shallow nocturnal torpor in captivity with a reduction of T_b from 38.5 to 32 °C and torpor entry appeared to lie on a metabolic continuum with sleep (Walker et al. 1983). Captive fruit doves (*Drepanoptila holosericea*, 200 g) from New Caledonia lowered T_b at night from ~40 °C to a minimum of about 25 °C at T_a 12 °C and TMR was ~40% of BMR when food was withheld (Schleucher 2004). In African Namaqua doves (*Oena capensis*, 36 g), the nocturnal T_b reduction when food was withheld was about 6 °C with a minimum MR just slightly below the BMR (Schleucher 2004). Similarly in Australian diamond doves (*Geopelia cuneata*, 38 g), T_b was reduced by about 5 °C at night (Schleucher 2001).

Raptors, Ciconiiformes

Shallow torpor, with a reduction of T_b from 37.5 to 31 °C during cold Kalahari Desert nights, has been reported for African pygmy-falcons (*Polihierax semitorquatus*, 60 g; McKechnie and Mzilikazi 2011). However, this could not be confirmed in a more recent study of free-ranging birds, which regulated $T_b > 36$ °C (Lund et al. 2020). Turkey vultures (*Cathartes aura*, 2.2 kg) may also be heterothermic (McKechnie and Lovegrove 2002) and this is addressed below in the large species expressing shallow heterothermy section.

Penguins, Sphenisciformes

Penguins are rather large (1–35 kg), diurnal flightless birds found mainly in Antarctica, far southern islands and along the south coast of the southern continents, and the Galapagos Islands. Despite prolonged fasts and their exposure to extremely cold and windy conditions in Antarctica, penguins are generally considered to be homeothermic, but do reduce heat loss by huddling (Gilbert et al. 2010). Torpor has not been observed in any adult penguin, but torpor it has been documented in the wild on Possession Island in the southern Indian Ocean in large king penguin chicks (*Aptenodytes patagonicus*, ~8 kg; Eichhorn et al. 2011) (Chap. 8).

Petrels, Procellariformes

Petrels are mostly diurnal pelagic sea birds with a world-wide distribution that eat small crustaceans and fish. The small storm-petrels are nocturnal, likely to avoid predators (Scott et al. 1974). Although torpor has not been observed in any adults of this avian order, torpor has been recorded in fork-tailed storm-petrel chicks (*Oceanodroma furcata*, 60 g) (Boersma 1986) (see also Chap. 8).

Owls, Strigiformes

Owls are nocturnal and predatory and have a world-wide distribution except for some oceanic islands and Antarctica (Scott et al. 1974). Torpor is known to occur in only two owls, the large northern snowy owl (*Nyctea scandiaca*, 2 kg) and the African scops-owl (*Otus senegalensis*, 60 g). The snowy owls, held in a large outdoor aviary at Barrow, Alaska, reduced T_b by 0.5 to 8.4 °C from a mean of 41 °C (although it is not clear whether core T_b or T_{skin} was measured). The time of T_b reduction occurred two to nine times/day and lasted for <3 h (Gessaman and Folk 1969). Scops owls in the Kalahari Desert of South Africa, reduced T_b, measured as T_{skin}, from about 36 °C to a minimum of 29 °C. The lowest T_{skin} was usually maintained for only short periods and for the rest of the 3–4 h torpor bout, T_{skin} was >30 °C (Smit and McKechnie 2010). In other small owls from the northern hemisphere, reductions in T_b are less pronounced (Hohtola et al. 1994).

Mouse Birds, Coliiformes

Mouse birds are diurnal, largely frugivorous and are distributed in Africa south of the Sahara. Several species (*Colius* spp. 35–51 g; *Urocolius* spp. ~50 g) are known to display nocturnal torpor in captivity (Prinzinger et al. 1981; Hoffmann and Prinzinger 1984; McKechnie and Lovegrove 2001, 2002). Mouse birds remained torpid for up to 10 h, during which time the T_b decreased from 36 to 39 °C during normothermia to 18–26 °C during torpor. TMR was 10–30% of BMR. In free-ranging clustering white-backed mouse bird (*Colius colius*), which use huddling extensively, torpor was only rarely observed (McKechnie et al. 2004).

Kingfishers, Coraciiformes

Kingfishers are diurnal, have a world-wide distribution with the exception of extreme latitudes and some deserts and oceanic islands. Two species are known to be heterothermic. A small largely insectivorous species, the Puerto Rican tody

Fig. 3.5 The largest kingfisher, the kookaburra (*Dacelo novaeguinae*, 350 g), uses nocturnal torpor in eastern Australia in winter (photo and copyright F. Geiser)

(*Todus mexicanus*, 6 g), reduced T_b from a rather low 37 °C to about 23.5 °C during torpor in captivity (Merola-Zwatjes and Ligon 2000). The largest kingfisher, the Australian laughing kookaburra (*Dacelo novaeguineae*, 350 g; Fig. 3.5) is a social and sedentary species, which eats invertebrates and small vertebrates, and also uses torpor. Free-ranging kookaburras in an open forest in montane eastern Australia lived in family groups of up to around six birds that formed huddles on winter nights (Cooper et al. 2008). They reduced T_b from ~39.5 °C during the day to a minimum of 28.5 °C during nocturnal torpor and, on cold winter days, exhibited bouts of torpor that lasted on average for 9 h (Cooper et al. 2008). In contrast, captive kookaburras displayed less pronounced heterothermy, however T_b did fall from about 37 °C to near 32 °C at night when exposed to low T_a (Buttemer et al. 2003). Considering the large difference in body mass between the two known heterothermic kingfishers, it seems highly likely that more species in this order are heterothermic.

Songbirds, Passeriformes

Passerines are the largest order of birds containing more than half (>6500) of all avian species. It now appears likely that they first evolved in eastern Gondwana (i.e. Australia and New Guinea) about 71–60 Mya (Edwards and Boles 2002). Passerines are diurnal, most of them are small, eat high energy food and they are found all over the world except for Antarctica and some oceanic islands. In the past it was assumed that passerines are homeothermic or do not reduce T_b below 30 °C (Lyman et al. 1982). More recent work (see McKechnie and Lovegrove 2002; McKechnie and Mzilikazi 2011) has revealed shallow torpor with minimum T_bs of about 23–29 °C in an ever increasing number of species. The species known to use torpor include New Zealand rifleman (*Acanthisitta chloris*, 7 g), fairy wrens (*Malurus cyaneus*, 9 g), Redpolls (*Carduelis flammea*, 11 g), manakins (*Manacus vitellinus*, 15 g), sunbirds (*Nectarinia famosa*, 17 g, *Nectarinia* spp. 7–11 g), great tits (*Parus major*, 17 g), house martins (*Delichon urbicum*, 22 g), honey eaters (*Lichenostomus virescens*, 25 g), dusky woodswallows (*Artamus cyanopterus*, 35 g), red crossbill (*Loxia curvirostra* 37 g) and noisy miners (*Manorina melanocephala*, ~75 g) (Serventy 1970; Bartholomew et al. 1983; Reinertsen 1983; Collins and Briffa 1984; Reinertsen and Haftorn 1996; Prinzinger and Siedle 1988; Prinzinger et al. 1991; Maddocks and Geiser 1999; Downs and Brown 2002; McNab and Weston 2018; Geiser 2019; Romano et al. 2019). Interestingly, despite their small size, T_b <20 °C has not been reported for any passerine species to date (McKechnie and Lovegrove 2002). However, to my knowledge, the highest T_b ever measured in an endotherm was 49.1 °C for a passerine the red-billed quelea (*Quelea quelea*, 18 g), a South African weaver (Freeman et al. 2020).

A member of the honeyeater family (Meliphagidae), which eat nectar, pollen and insects and mainly live in Australia and New Guinea, expresses torpor in the wild. The medium-sized free-ranging honeyeater the noisy miner (*Manorina melanocephala*, 75 g; Fig. 3.6), is a social species with cooperative breeding (Ford 1989). Miners regularly used shallow nocturnal torpor (63% of days) during the cold season from autumn to spring (Geiser 2019). Birds were measured in an open woodland in eastern Australia where core T_b fluctuations were quantified over ~4.3 months. Torpor expression was highly predictable (Fig. 3.7), TBD was 6.5 h on average (maximum 13.5 h), T_b ranged from a maximum of 43.5 °C to a minimum of 33.0 °C, and often fell by 7 °C at night. Somewhat unexpectedly, and perhaps because they were huddling, minimum T_bs for noisy miners were not strongly affected by T_a, as is often the case in free-ranging daily heterotherms (e.g. Parker et al. 2019), but rather by day length, whereas TBD was affected by T_a (Geiser 2019).

Woodswallows (Artamidae), another passerine family, have an Australasian distribution, and feed mainly on flying insects on the wing (Simpson and Day 1993) and are known to huddle during cold spells (Fig. 3.8). Captive dusky woodswallows (*Artamus cyanopterus*, 35 g) exhibited predictable daily changes in T_b, which fell at dusk, even when food was available throughout the day. Woodswallows remained torpid throughout most of the night and rewarmed at

Fig. 3.6 The noisy miner (*Manorina melanocephala*, 75 g), a medium-sized honeyeater from eastern Australia, approaching a *Grevillea* flower for nectar. It frequently uses shallow nocturnal torpor from autumn to spring (photo and copyright F. Geiser)

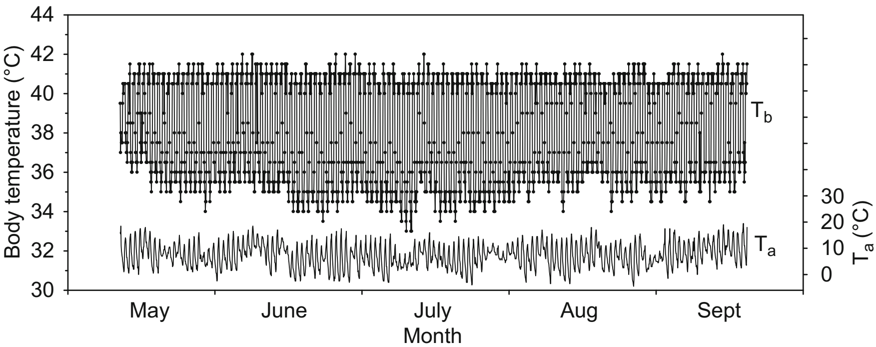

Fig. 3.7 Expression of nocturnal torpor in a noisy miner (*Manorina melanocephala*, 75 g) throughout the cold season in eastern Australia. Note the substantial drop of core body temperature (T_b dots and line, measured in 90-min intervals, left axis) essentially on every night with the lowest values observed in mid-winter in July and the gap between normothermic T_b of around 41 °C during the day, and torpor $T_b < 36$°C at night. The ambient or air temperatures (T_a, line, right axis) are shown on the bottom of the graph (data from Geiser 2019)

dawn. Especially in late autumn/winter when T_a was low, T_b regularly fell from ~41 °C to ~30 °C and on some occasions to 29 °C (Maddocks and Geiser 2007).

Data are also available for the small passerine, the Australian superb fairy wren (*Malurus cyaneus*, 9 g; Fig. 3.9). These birds entered torpor in the wild in winter and

Fig. 3.8 Dusky woodswallows (*Artamus cyanopterus*, 35 g) of south-eastern Australia not only enter nocturnal torpor, they also form large clusters to huddle as in this picture during a cold spell in southeast Queensland (photo and copyright, Ken Cross)

Fig. 3.9 A male superb fairy-wren (*Malurus cyaneus*, 8.5 g) from eastern Australia. The species routinely uses nocturnal torpor in winter (photo and copyright F. Geiser)

routinely reduced T_{skin} from maxima of ~42 °C to nocturnal minima of 27.4 °C on average; the individual minimum was 26.1 °C (Romano et al. 2019). The calculated reduction in resting energy expenditure, achieved by the lowering of the $T_b - T_a$ differential at low T_a, was about 42% (Romano et al. 2019).

There is also considerable and interesting anecdotal evidence about torpor use in passerines. Perhaps the most extreme report with regard to heterothermy is for mistletoe birds (*Dicaeum hirundinaceum*) as it claims that six birds, while in transit from Australia to America, froze close to death and were resurrected four times (Heumann 1926). The author also observed that captive mistletoe birds regularly became cold in winter in an aviary, but no quantitative measurements were made and none are currently available. Another report claims that welcome swallows (*Hirundo neoxena*) show 'semi hibernation' and huddled in rock crevices in winter and emerged to forage only on warm days (Dove 1923). This report implies that the birds remained in the crevices for several days. However, detailed data are not available and it is not clear whether birds simply huddled or were torpid.

Observations on torpor in white-backed swallows (*Cheramoeca leucosterna*) made near Perth, Western Australia describe a group of about 20 torpid birds found in a burrow. These birds did not move and were cold to touch when removed for examination, but the birds had disappeared a week later (Serventy 1970). As this observation was made during the daytime on a cold winter's day, it is not an example of nocturnal torpor common in diurnal birds, but suggests the use of multiday torpor. Independent observations of four white-backed swallows, support this interpretation (Congreve 1972). The swallows were detected north of Perth in Western Australia during collection of sand at the end of a tunnel (Congreve 1972). At 13:15, when first discovered, the swallows were cold to touch, they were shivering from 13:35, and at 14:00 they were able to fly Congreve (1972). The author suggests that white-backed swallows may spend some of the winter in a state of torpor (Congreve 1972), however, this interpretation needs confirmation.

Behavioural observations on several other Australian arid-zone birds suggest torpor use (Ives 1973). This report claims that adult captive banded whitefaces (*Aphelocephala nigricincta*) entered torpor each night and rewarmed when T_a rose in the morning. Nocturnal torpor was also reported to occur in red-capped robins (*Petroica goodenovii*) and white-fronted honeyeaters (*Phylidonyris albifrons*) (Ives 1973), but no further details were provided. Young crimson chats (*Epthianura tricolor*) disperse from the nest early during development and spend the night on the ground (Ives 1973). These young birds appear to enter a torpid state during the night and when handled on the following morning they remained inert, but did revive after passive rewarming. In a recent paper on New Zealand rock wrens (*Xenicus gilviventris*) it was suggested that they may hibernate (McNab and Weston 2018). However, this claim seems unjustified because the data presented barely qualify for shallow torpor as T_b fell only by about 3 °C (Geiser et al. 2020), so further work is needed to determine the pattern of heterothermy expressed in this species. Overall, more quantitative work on passerine thermal biology and that of other birds is needed to better establish patterns of heterothermy, especially in free-ranging individuals.

Mammals

Mammals range in body mass from ~2 g seen in Etruscan shrews (*Suncus etruscus*) and bumblebee bats (*Craseonycteris thonglongyai*) to about 190,000,000 g in blue whales (*Balaenoptera musculus*). Nevertheless on average, mammals like birds are also small with a median body mass of just over 100 g. About 56% of mammals weigh 200 g or less and ~84% of mammals weigh less than 10 kg (Smith et al. 2003; Withers et al. 2016). Moreover, the largest mammalian orders, the rodents and bats, contain mainly small species and these two orders combined make up about two thirds of all mammalian species. Most mammals are quadrupedal and move on land, which, in comparison to flight, is energetically expensive and slow, especially in small species (Fig. 1.5). Therefore most small mammals cannot migrate over long distances for temporal and energetic reasons and must deal with seasonal and/or unpredictable changes in weather and food availability by using behavioural and physiological adaptations. Bats are the only mammalian order capable of true flight and some migrate often over long distances (Baerwald and Barclay 2011; Weller et al. 2016; Dechmann et al. 2017). However, a very large number of bats, especially the small insectivorous species, can be sedentary or migrate only short distances and use torpor extensively. Similar to birds, torpor and migration in bats are not mutually exclusive as torpor is used during stopovers (McGuire et al. 2014).

Torpor is used by many species of all three mammalian subclasses (Fig. 3.10; Table 3.1): the egg-laying mammals (Monotremata or Prototheria), the pouched mammals (Marsupialia or Metatheria), and the placental mammals (Placentalia or Eutheria) (Merritt 2010; McKechnie and Mzilikazi 2011; Ruf and Geiser 2015; Nowack et al. 2020). Hibernation and daily torpor are used by many representative species of at least 15 mammalian orders or nearly 60% of all mammalian orders (Tables 3.1 and 3.2). There are many more known mammalian than avian heterotherms although the diversity of mammals is less (around 5500 species) than that of birds (over 10,000 species) (Pough and Janis 2019).

Egg-laying mammals, Monotremata

Monotremes are an ancient mammalian group, with roots reaching back to the beginning of mammalian evolution at almost 200 Mya (O'Leary et al. 2013). They comprise the echidnas and platypus and live in Australia and New Guinea. Unique to the monotremes, they reproduce by laying leathery eggs (Fig. 3.11). In the past it was assumed that both Australian egg-laying mammals, the amphibious platypus (*Ornithorhynchus anatinus,* ~1.5 kg), which is distributed along the Australian east coast and ranges, and the short-beaked echidna (*Tachyglossus aculeatus*, ~2–7 kg; Fig. 3.12) display torpor. However, detailed fieldwork revealed that free-ranging platypus are homeothermic with a low but stable T_b of around 32 °C (Grigg et al. 1992a).

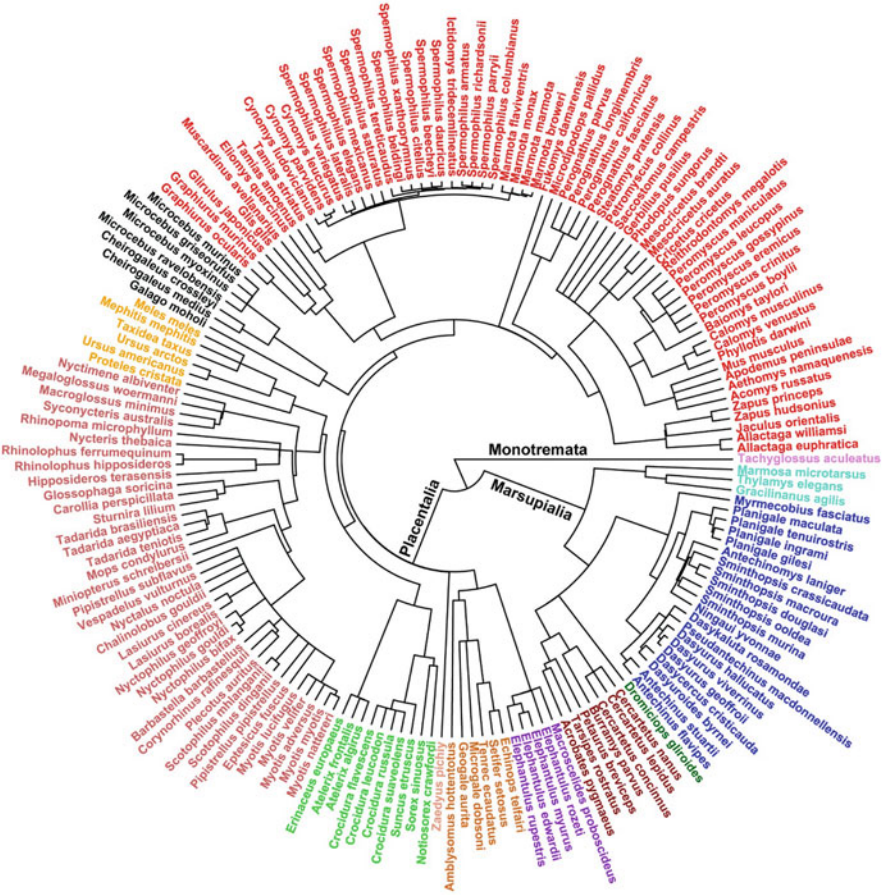

Fig. 3.10 The mammalian phylogenetic tree showing the three sub-classes and heterothermic species for which physiological measurements are available. Related taxa are shown in the same colours. Some of the genus names have changed recently especially for North-American ground squirrels. For example, *Spermophilus* is now *Callospermophilus*, *Ictidomys* or *Urocitellus* (figure from Ruf and Geiser 2015, with permission)

In contrast, the echidna, or spiny anteater, *T. aculeatus*, which feeds on termites, ants, beetle larvae and other soil invertebrates hibernates in many areas (Grigg et al. 1992b; Nicol and Andersen 1996). Echidnas, which superficially look similar to hedgehogs, but are much larger (up to tenfold) and unrelated, are found all over the Australian continent and New Guinea. In cold climates, including high areas of the Australian Alps or in Tasmania, echidnas show a prolonged hibernation season beginning in late summer and lasting until spring in non-reproductive individuals. Echidnas are among the largest mammalian deep hibernators with an adult body mass of 2–7 kg, their bouts of torpor last for up to 30 days and the minimum T_b is ~4

Fig. 3.11 An echidna (*Tachyglossus aculeatus*) egg in comparison to an Australian 5-cent coin. Echidna egg dimensions are ~15 × 13 mm, weigh ~1.4 g and have a leathery shell similar to reptile eggs (photo and copyright F. Geiser)

Fig. 3.12 The short-beaked echidna (*Tachyglossus aculeatus*, 2–7 kg), an egg-laying mammal, is among the largest hibernators. Is it distributed all over the Australian continent and in parts of New Guinea, hibernates in cool areas and expresses short bouts of torpor in warm areas including in summer (photo and copyright F. Geiser)

°C, reduced from a low and rather unstable normothermic T_b of ~32 °C (Grigg et al. 1992b; Nicol and Andersen 2002). During torpor, hibernating Tasmanian echidnas reduce TMR to minima that are similar to those of other hibernators of that size (Ruf and Geiser 2015), but because of their low BMR the TMR is relatively high at about 20% of BMR. Captive *T. aculeatus* are reluctant to express torpor (Nicol et al. 1992). Torpor in free ranging echidnas in warmer regions, such as Idalia National Park in SW Queensland, a hot area with high daily fluctuations in T_a, was not as deep and of shorter duration, but even there was expressed during summer (Brice et al. 2002). Reproductive echidnas terminate hibernation in mid-winter for mating (Morrow and Nicol 2009). Torpor also has been observed in captive long-beaked echidnas (*Zaglossus bartoni*, 10 kg) from New Guinea, which reduced T_b to a minimum of 24.2 °C, but did not display multiday torpor (Grigg et al. 2003).

Pouched Mammals, Marsupialia

Marsupials are another old mammalian group, diverging from the placentals around 140 Mya (O'Leary et al. 2013). Marsupials differ from placentals in their reproductive biology. They give birth to very small neonates weighing between ~10 and 900 mg (<1% of maternal body mass) after a brief period of gestation, and have a long developmental period usually in a pouch while relying on the mother's milk for nutrition and energy (Tyndale-Biscoe and Renfree 1987; Tyndale-Biscoe 1973). However, marsupials do have a placenta, which is a primary site for feto-maternal exchange before birth (Renfree 2010). There are a total of ~335 extant marsupial species, most of which (~225) are found in Australia and New Guinea and the rest (~100) mainly in South and Central America. Currently marsupials are classified as belonging to seven orders and five of these are known to contain heterothermic species (Fig. 9.2) and a sixth, the shrew opossums (Paucituberculata), are likely to be heterothermic.

Opossums, Didelphimorphia

Opossums (Didelphimorphia), not to be confused with the Australian possums (Diprotodontia, see below), occur in South and Central America and one in North America. Opossums are now considered to be the oldest extant marsupial group (Bininda-Edmonds et al. 2007) and are largely insectivorous/carnivorous or omnivorous (Hume 1999). Carnivorous opossums tend to be small and it is therefore not surprising that several display either daily torpor or short-term hibernation. The insectivorous murine opossum (*Gracilinanus microtarsus*, 13 g) lowered T_b to ~16 °C during bouts of daily torpor lasting for up to ~8 h, and similar torpor patterns have been recorded in *G. agilis* (30 g) and *Thylamys elegans* (30 g) (Morrison and McNab 1962; Opazo et al. 1999; Cooper et al. 2009). Daily torpor has also been observed in

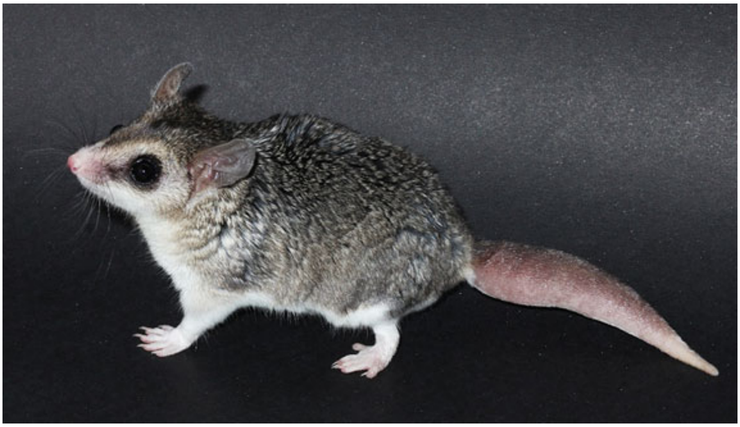

Fig. 3.13 The Patagonian opossum (*Lestodelphys halli*, 50 g) a carnivorous marsupial mammal from southern Argentina. The species stores fat in its tail and can remain torpid for up to ~2 days (photo and copyright F. Geiser)

the slightly larger (~100 g) omnivorous opossums, the Robinson' mouse opossum (*Marmosa robinsoni*), the northern red-sided opossum (*Monodelphis brevicauda*) and the grey short-tailed opossum (*Monodelphis domestica*) with minimum T_bs around 25 °C (see Riek and Geiser 2014).

The opossum with the southernmost distribution and extreme caudal fat storage is the carnivorous Patagonian opossum (*Lestodelphys halli*, 50 g; Fig. 3.13). Its normothermic resting T_b was ~33–35 °C, but that was substantially reduced during bouts of torpor. The minimum measured T_b during torpor in captive Patagonian opossums was 7.7 °C and TBD was almost 2 days (Geiser and Martin 2013). As the $T_b - T_a$ differential during torpor was often <1 °C, even at low T_a, it appears that T_b was not defended during torpor at the T_a measured and it is probable that it can fall further. This opossum was extremely difficult to capture and only two males were caught in autumn at a time when it began to snow. It is therefore possible that the low capture rate (2 males in >4000 trap nights) was due to extensive torpor use during late autumn and the possibility that females were already hibernating or used torpor extensively (Geiser and Martin 2013).

Shrew Opossums, Paucituberculata

Currently there are no data on torpor for the shrew opossums (Paucituberculata) from South America. However, since they are small and largely insectivorous (Hume 1999), and the long-nosed caenolestid (*Rhyncholestes raphanurus*, ~40 g) seasonally stores fat in its tail, it is likely that they use torpor (Golzales et al. 2020).

Monito del Monte, Microbiotheria

The only extant species of the marsupial order Microbiotheria is the insectivorous Monito del Monte or 'monito' (*Dromiciops gliroides*, 30 g). It is found in the wet forests of southern Argentina and Chile. *Dromiciops* is interesting from an evolutionary point of view, because Australian marsupials are thought to be derived from its ancestor (O'Leary et al. 2013; Fig. 10.2). Therefore it is likely that all Australian marsupials, including the homeothermic kangaroos, koalas and wombats, are derived from the ancestor of a hibernating species. *Dromiciops* seems to differ from most didelphid opossums because it is capable of expressing multiday torpor bouts of up to 6 days. Similar to many placental hibernators, *Dromiciops* can lower TMR to only ~1% of normothermic RMR and T_b decreased to <10 °C (Bozinovic et al. 2004; Ruf and Geiser 2015). Water loss in torpid *Dromiciops* was as little as 21% of normothermic values (Withers et al. 2012). When held at a T_a of ~20 °C, *Dromiciops* entered short bouts of torpor especially when food was limited, although at T_a 10 °C food availability did not affect torpor expression (Nespolo et al. 2010). *Dromiciops* enter torpor during lactation (Nespolo et al. 2021) and in the wild fatten in autumn and disappear during winter, suggesting that they hibernate in the wild (Grant and Temple-Smith 1987).

Insectivorous/Carnivorous Marsupials, Dasyuromorphia

Dasyuromorph marsupials are a diverse group of insectivorous/carnivorous marsupials from Australia and New Guinea (Hume 1999). There are about 75 species, comprising 22% of all extant marsupial species. The order includes the families Dasyuridae (insectivorous/carnivorous marsupials), Myrmecobiidae (numbat), and also the extinct Tasmanian 'wolf' or Thylacine (Thylacinidae) (Withers et al. 2016).

Members of the Dasyuridae are largely nocturnal, but may be diurnal in winter (Körtner et al. 2010; Pavey et al. 2016). The normothermic resting T_b of dasyurids is often between 34 and 36 °C. Daily torpor has been observed in ~50% of Australian dasyurid species, which are especially successful in the arid center of the continent, likely because of their extensive use of torpor (Geiser and Körtner 2010). It is highly likely that all or most members of this family are daily heterotherms, as multiday torpor has not been recorded for any species to date. Torpor expression is known for species ranging in body mass from ~5 g in planigales (*Planigale* spp.) to ~1 kg in quolls (*Dasyurus* spp.) (Riek and Geiser 2014). Depending on the species and to some extent size, the minimum T_b during torpor ranges from 11 °C in kultarrs (*Antechinomys laniger*, 27 g) to ~28 °C in northern quolls (*Dasyurus hallucatus*, 500 g, Cooper and Withers 2010). Metabolic rates during torpor by captive dasyurids were ~10–60% of BMR, and TBD was up to 19.5 h, but TBDs of 2–8 h are more common (Riek and Geiser 2014). Water loss in torpid dunnarts (*Sminthopsis macroura*, 24 g) was reduced to ~1/3 of that in normothermic

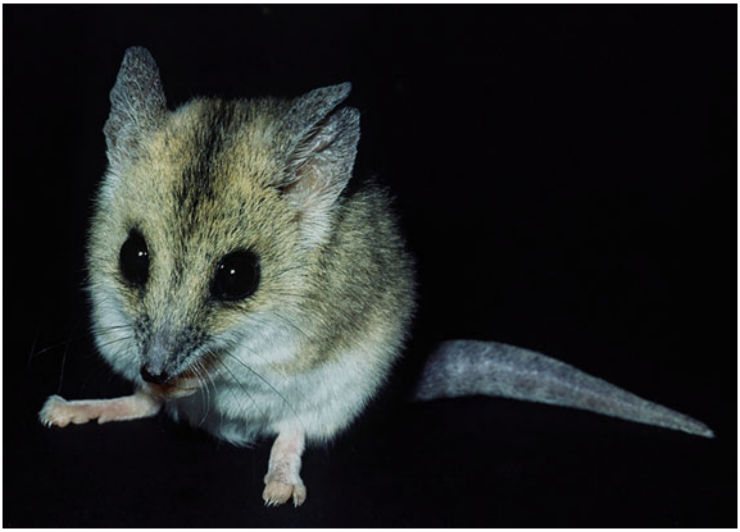

Fig. 3.14 A fat-tailed dunnart (*Sminthopsis crassicaudata*, 17 g) from arid/semi-arid southern Australia. It stores fat in its tail and in the wild uses daily torpor on every day in autumn/winter (photo and copyright F. Geiser)

individuals at the same T_a (Cooper et al. 2005). Daily torpor by free-ranging dasyurids is generally more pronounced and TBD is about twice as long as for individuals in captivity. Further, torpor in the wild may be used daily during winter to minimize foraging to a few hours/day or even eliminate foraging altogether for a few days (Warnecke et al. 2008; Körtner et al. 2008; Körtner and Geiser 2009).

In the Australian arid zone, torpor has been examined extensively in wild fat-tailed dunnarts (*Sminthopsis crassicaudata*, 17 g; Fig. 3.14) and stripe-faced dunnarts (*S. macroura*, 24 g). These species enter daily torpor essentially every day in autumn/winter (Warnecke et al. 2008; Körtner and Geiser 2009) with torpor bouts lasting for about half a day on average. Fat-tailed dunnarts, similar to arid zone fat-tailed antechinus (*Pseudantechinus macdonnellensis*, ~30 g) regularly use basking in the sun to lower the cost of rewarming from torpor (Chap. 7). In medium-sized arid zone mulgaras (*Dasycercus blythi*, *D. cristicauda*) in central Australia, torpor expression and duration are reduced when the proportion of vertebrates in their diet is increased likely because of the larger meal size and energy content of vertebrates (Pavey et al. 2009). Torpor patterns in mulgaras also depend on reproductive status (Chap. 8) and differs between sexes with more torpor in the smaller females (62 g) than the males (84 g). However, torpor expression was similar in different habitats and under different weather conditions (Körtner et al. 2016).

Torpor in dasyurids is not restricted to animals living in deserts. In cool-temperate forests, free-ranging brown antechinus (*Antechinus stuartii*, ~23 g; Fig. 3.15) and yellow-footed antechinus (*A. flavipes* ~30 g) also enter torpor frequently in winter (Hume et al. 2020; Parker et al. 2019). Antechinus have a most unusual reproductive

Fig. 3.15 A brown antechinus (*Antechinus stuartii*, 25 g) from mesic forests and rainforests in eastern Australia. It uses daily torpor frequently in winter (photo and copyright F. Geiser)

biology because males exhibit a complete post-mating mortality and live for only ~11 months and most females die after weaning of the young at an age of about 1.5 years (Woolley 1966; McAllan et al. 2006; Chap. 8). In free-ranging yellow-footed antechinus (*A. flavipes*), torpor expression was strongly affected by reproductive condition and sex, although minimum T_b was affected by T_a. Non-reproductive females in the wild used torpor on 60–90% of days, but pregnant females on only 28% of days. However, males before the mating period used torpor on 64% of days while during mating only on ~25% of days measured (Parker et al. 2019). The torpor use in *A. flavipes* is modified similarly by reproductive status as in the medium-sized arid zone mulgaras (*D. blythi*). In free-ranging female brown antechinus (*A. stuartii*) torpor occurred on >82% of days in winter. Torpor expression was strongly affected by weather, with torpor use and duration increasing with decreasing T_a on cold, dry days (Hume et al. 2020).

Torpor patterns in small dasyurids change with season, but daily torpor is typically expressed throughout most of the year (Chap. 6). Torpor expression in dunnarts (*S. macroura* and *S. crassicaudata*), held under outdoors conditions was observed throughout the year but reduced in summer (Geiser and Baudinette 1987). Thermal biology, torpor use and even morphology are also subject to developmental phenotypic flexibility in *S. crassicaudata* (Riek and Geiser 2012), and individuals reared at low T_a have more frequent and deeper torpor bouts than those raised at a relatively higher T_a. Torpor is used during the development and growth of dasyurids (Wacker et al. 2017), and is often more pronounced in juveniles than adults (Chap. 8).

Fig. 3.16 A numbat (*Myrmecobius fasciatus*, 500 g), a termite-eating diurnal marsupial uses nocturnal daily torpor. The species is now restricted to south-western Australia (photo and copyright F. Geiser)

Numbats (*Myrmecobius fasciatus*, 500 g; Fig. 3.16), sometimes called the marsupial ant-eater, eat exclusively termites in the wild (Cooper and Withers 2004). They were formerly distributed over much of arid and semi-arid southern Australia, however since European settlement they have become restricted to a few areas of open forest in the south-west of Western Australia and only remain there due to an extensive eradication program of feral cats and foxes. Numbats belong to the family Myrmecobiidae, and, unusual for marsupials, are diurnal. Both free-ranging and captive numbats used daily torpor with a maximum TBD of 15 h and a minimum T_b of 19 °C (Cooper and Withers 2004). In the wild they use fallen logs, tree hollows or burrows as night retreats and in winter express nocturnal torpor on 90% of days (Cooper and Withers 2004).

Marsupial Moles, Notoryctemorphia

Marsupial moles (*Notoryctes* spp.) include two species of insectivorous burrowers that live almost entirely underground in the sand dune deserts of inland Australia. The energy expenditure of marsupial moles during 'sand swimming' was similar to that of the morphologically convergent Namib golden mole (Seymour et al. 1998). Information about their thermal biology is limited, but captive *N. caurinus* have a low and labile T_b ranging from 22.7 to 30.8 °C (Withers et al. 2000).

Possums, Diprotodontia

Kangaroos, koalas, possums and relatives comprise the derived marsupial order of the diprotodont marsupials found in Australia and New Guinea. Torpor has been observed in four of the now eleven diprotodont 'possum' families, the pygmy-possums (Burramyidae), feathertail gliders (Acrobatidae), honey possums (Tarsipedidae), and the Petauridae containing small species of both gliding and non-gliding possums (see Riek and Geiser 2014; Chap. 10).

All five species of the insectivorous/nectarivorous pygmy-possums (Burramyidae) that have been investigated in some detail enter multiday torpor (Geiser and Körtner 2010). At low T_a, torpid pygmy-possums lower T_b to a minimum of ~2–6 °C, their minimum TMR is only ~2–4% of BMR, and they display torpor bouts lasting for up to 4 weeks. The eastern pygmy-possum (*Cercartetus nanus*, Fig. 3.17) is capable of extensive fattening prior to torpor (Bladon et al. 2002). Fat individuals weighing about 50 g, when maintained at low T_a of 7 °C and without access to food, can hibernate for up to an entire year relying on only stored fat for energy supply (Geiser 2007). *C. nanus* were able to do that despite frequent arousal early during the hibernation season, when mass loss was rapid, but mass loss stabilized when animals began to express multiday torpor bouts. Hibernation for more than the usually required ~6 months suggests that a large safety margin has been favoured by natural selection in *C. nanus* in response to the

Fig. 3.17 The eastern pygmy-possum (*Cercartetus nanus*, 20 g) from eastern Australia. It can more than double its body mass and hibernate for up to one year, relying entirely on stored body fat for energy (photo and copyright F. Geiser)

Fig. 3.18 A torpid western pygmy-possum (*Cercartetus concinnus*, 18 g) from southern Australia. Note the ball shape and that the animal has been turned on its back to show the face, curled up ears, appendages and tail, which are usually tugged under the body (photo and copyright F. Geiser)

unpredictability in rainfall and food availability of the Australian continent. Year-long hibernation also shows that torpor in the genus *Cercartetus* is not strongly seasonal. Prolonged torpor can be induced during any time of the year by exposure to low T_a in captivity. In the wild, in addition to long TBDs in winter, short bouts of torpor have been observed during summer (Turner et al. 2012a).

Free-ranging western pygmy-possums (*C. concinnus*, 18 g) in a Mediterranean climate in South Australia hibernated in winter expressing both brief and multiday torpor bouts of up to 8 days (Turner et al. 2012b). When hibernating at low T_b, all pygmy-possums, like many other hibernating mammals, adopt a ball-shape with appendages tugged under their body (*C. concinnus*, Fig. 3.18) and they retain the ball shape during the arousal process likely to minimize heat loss (Fig. 3.19). Western pygmy-possums have not been examined in summer in the field, but captive individuals as well as little pygmy-possums (*C. lepidus*, 12 g) expressed spontaneous torpor throughout the year. When held at a constant T_a of 20 °C and natural photoperiod, TBD was affected by photoperiod in both *C. nanus* and *C. concinnus* (Turner and Geiser 2017). Even at T_as of 26–30 °C, eastern, western and little pygmy-possums entered torpor, although at these T_as torpor lasted only for part of the day. In *C. nanus* near the TNZ, TMR was only ~50% of BMR despite a reduction in T_b by only ~2.5 °C (Song et al. 1997) (see Chap. 5). The tropical long-tailed pygmy-possum (*C. caudatus*, 30 g), which has not been examined in detail, also displays torpor (see Geiser and Körtner 2004). Torpor in *Cercartetus* spp. therefore

Fig. 3.19 Western pygmy-possum (*Cercartetus concinnus*, 18 g) rewarming from torpor (photo and copyright F. Geiser)

Fig. 3.20 The endangered mountain pygmy-possum (*Burramys parvus*, 50 g), the largest pygmy-possum. It shows seasonal hibernation in snow-covered glacial boulder fields in the Australian Alps (photo and copyright F. Geiser)

appears to be an adaptation to unpredictable adverse changes in the thermal environment and food availability during any time of the year rather than just a strategy for overwintering.

The endangered mountain pygmy-possum (*Burramys parvus*, 50 g; Fig. 3.20), which is the largest species in the family, is restricted to high elevations in the

Australian Alps. It used to have a much wider distribution range during the last Pleistocene glacial period (Archer et al. 2019), and the remnant population of ~2000 individuals now live on/near mountain tops in glacial boulder fields on 'sky islands'. The species was first discovered as a fossil jaw bone in 1895 and was considered to be extinct until re-discovered in 1966 in a ski hut in the Victorian Alps (Mansergh and Broome 1994). *Burramys* feeds predominantly on Bogong moths (*Agrotis infusa*) that migrate to the mountains to estivate during summer, and succulent fruits and seeds from the mountain plumb pine (*Podocarpus lawrencei*). In autumn captive *Burramys* can fatten substantially. All captive adults began hibernation when food was freely available, but began to hibernate about one month earlier than juveniles of the year (Geiser and Broome 1991). The hibernation season in captive adults was about 7 months and in juveniles 5–6 months. During winter hibernation *Burramys* feeds on little or nothing, and this independence from food for over half a year is probably the main reason why they have managed to survive in nature (Broome et al. 2012). Hibernacula in the wild are located under snow-covered boulder fields and torpor expression is more seasonal than that for other pygmy-possums (Geiser and Broome 1991; Körtner and Geiser 1998). The hibernation season in the wild is similar to that in captivity and lasts from late autumn until spring, but varies somewhat with the time of snow melt (Körtner and Geiser 1998). The torpor bouts of captive females tend to be deeper and longer (minimum T_b 2.0 °C, mean TBD 16 days) than those of males (minimum T_b 2.7 °C, mean TBD 12.5 days). Possibly this is a result of the spatial segregation of the sexes and exposure to different microclimates in the wild where similar observations on torpor expression have been made (Geiser and Broome 1991; Körtner and Geiser 1998).

Feathertail gliders (*Acrobates pygmaeus*, 12–14 g; Fig. 3.21) are insectivorous/ nectarivorous, and now belong to the family Acrobatidae. They have been split into two species and are found in Australia and New Guinea. Feathertail gliders use torpor in the wild and in captivity (Frey and Fleming 1984; Fleming and Frey 1984; Geiser and Ferguson 2001). In captivity, torpor in *A. pygmaeus* lasted for a maximum of 8 days, the minimum T_b was 2 °C, and the TMR was only about 1% of the RMR in normothermic animals at a T_a of 5 °C, and 6% of the BMR (Geiser and Ferguson 2001). Thus, there are some similarities between the pattern of torpor in feathertail gliders and the pygmy-possums (Burramyidae), the family they were part of in the past. However, similar to some bats, *A. pygmaeus* does not fatten extensively like the pygmy-possums and many other hibernators. Free-ranging feathertail gliders, living in cable junction boxes in Victoria and checked every two or four weeks, maintained their body mass at a mean of 13.5 g between autumn and spring and gliders aroused form torpor on a daily basis during that time (Fleming and Frey 1984; Frey and Fleming 1984). Captive-bred feathertail gliders showed less pronounced torpor (shorter TBD, higher minimum T_b) than wild-caught gliders suggesting that the species exhibits developmental phenotypic plasticity (Geiser and Ferguson 2001). Torpor expression in feathertail gliders also features regional differences with deeper torpor in montane than subtropical coastal areas, but this could also reflect different species at different sites. Torpor in *A. pygmaeus* is also

Fig. 3.21 The feathertail-glider (*Acrobates pygmaeus*, 12–14 g) a tiny arboreal marsupial from eastern Australia. It enters bouts of torpor that may last for over a week. The feather-like appearance of the tail is due to a fringe of stiff hair on either side of the tail, which is used for steering during glides (photo and copyright F. Geiser)

influenced by dietary lipid consumption. Individuals express deeper and longer torpor bouts when fed diets containing unsaturated oils (see Chap. 9).

The honey-possum (*Tarsipes rostratus*, 10 g, Tarsipedidae), is the only extant species in this family and is restricted to south-western Australia. The species has an extremely long muzzle and tongue for extracting nectar and pollen from flowers and is an important pollinator of *Banksia* flowers (Hume 1999). Honey possums use torpor in the wild mainly during the cold season between autumn and spring, but a few individuals were observed torpid during summer (Withers et al. 1990; Bradshaw et al. 2007; Bradshaw and Bradshaw 2012). In captivity, the species exhibited a T_b of ~5 °C, similar to that of hibernators and the minimum TMR was also similar to small hibernators, but TBD did not exceed 10 hours (Withers et al. 1990).

In the largely insectivorous/nectarivorous family the Petauridae, daily torpor has been observed in sugar gliders (*Petaurus breviceps*, 130 g), in the similar-sized non-gliding Leadbeater's possum (*Gymnobelideus leadbeateri*) and there are anecdotal reports about torpor use by the much larger yellow-bellied glider (*P. australis*, 600 g; Geiser and Körtner 2010) and unpublished observations on free-ranging squirrel gliders (*P. norfolcensis*, 200 g; Dausmann et al., unpublished). Sugar gliders reluctantly enter shallow and brief periods of torpor in captivity, and mainly when food is withheld (Fleming 1980). Minimum TMR of captive gliders was about 10% of that for normothermic and resting individuals (Fleming 1980). In the field, daily torpor, interrupted by arousal around dusk, was often observed over a sequence of several days during periods of cold and wet conditions. TBD was up to 23 h (mean 13 h), and T_b was as low as 10.4 °C during torpor (Körtner and Geiser 2000b). However, recently it was found that free-ranging sugar gliders expressed torpor during a subtropical cyclone when thermal conditions were mild likely to minimize the need to forage as well as to enhance survival during the storm (Nowack et al. 2015). Torpor expression in sugar gliders is strongly affected by captivity because free-ranging gliders in a cool-temperate area entered torpor more frequently than captive gliders even though the latter were held under outdoor conditions that were thermally similar to those in the wild, and the T_b in the wild decreased to a lower level as well (Geiser et al. 2007a).

Placental Mammals, Placentalia

Placentals (or Eutheria) are by far the largest mammalian subclass with around 5000 species (Pough and Janis 2019). They spend a large proportion of their development period as a fetus in the female uterus and are born in a much more developed state than marsupials. Although most placental species are altricial, small, naked and relatively undeveloped at birth, some, especially the ungulates, are precocial and are more or less fully developed at birth. Terrestrial placental neonates are much bigger than marsupial neonates and weigh from ~0.2 g in shrews (*Suncus etruscus*) to ~8 g (*Tamiasciurus hudsonicus*) in sciurid rodents to ~90 kg in elephants (*Elephas maximus*) (Eisenberg 1981).

Afrotheria

The Afrotherians are often considered to be basal placental mammals and together with the monotremes and marsupials, have roots that reach beyond the Cretaceous-Paleogene boundary (at about 65 Mya) (Bininda-Emonds 2007; Lovegrove 2019). Afrotherians are therefore of interest with regard to the evolution of endothermy and torpor (Lovegrove 2019). Heterothermic afrotherians include the tenrecs (Tenrecidae) and golden moles (Chrysochloridae), the elephant shrews (Macroscelidea) and even the large aardvark (Tubulidentata) (McKechnie and Mzilikazi 2011; Weyer et al. 2020).

Tenrecs and Golden Moles, Afrosoricida

Arguably one of the most unusual patterns of hibernation known is that of the tenrec (*Tenrec ecaudatus*, 1–2 kg) from subtropical Madagascar. Tenrecs hibernate underground without periodic arousals for up to 9 months, including during the summer, with T_bs > 22 °C and T_b tracking T_{soil} (Lovegrove et al. 2014). Currently this is the only hibernator (with the exception of bears hibernating at T_b ~ 34 °C for ~2.5 months, see below) for which periodic rewarming has not been observed, likely because of the rather high T_b during torpor. Hibernation in *T. ecaudatus* was disturbed after several months, so it is possible hibernation can last even longer.

The lesser hedgehog tenrecs (*Echinops telfairi*, 130 g) held in outdoor enclosures during mid-winter in southwestern Madacascar had a low 'normothermic' T_b (daily maximum T_b ~ 31 °C), and predominately expressed brief bouts of torpor with a mean minimum T_b of 18.4 °C and a minimum measured T_b of 12.5 °C. However on several occasions multiday torpor for 3–4 days was also recorded (Lovegrove and Genin 2008). Free-ranging large hedgehog tenrecs (*Setifer setosus*, ~300 g), exhibit substantial pre-hibernation fattening with an increase in body mass from about 150 to over 300 g in some individuals. *S. setosus* hibernated from autumn to spring (Levesque et al. 2013), the minimum T_b measured was 13 °C and the minimum TMR was ~4% of BMR (Ruf and Geiser 2015). Shrew tenrecs (*Microgale* spp., 40 g) and large-eared tenrecs (*Geogale aurita*, 7 g) from Madagascar enter daily torpor with minimum T_bs of 15 to 25 °C (Stephenson and Racey 1993; Nowack et al. 2020).

For the golden mole (*Amblysomus hottentotus longiceps,* ~70 g) in the Drakensberg Mountains of South Africa, data are available for only a single individual and these differ from the tenrecs. In spring the mole expressed multiday torpor bouts of ~5 days with T_b as low as 8.6 °C, interrupted by multiday normothermic periods (Scantlebury et al. 2008). Other golden moles such as the Namib desert golden mole (*Eremitalpa granti*, 26 g) burrow in loose shifting sand dunes during the day, but forage on top of dune surfaces at night. This species is heterothermic with a fluctuating T_b that follows the T_a of the surrounding sand (Fielden et al. 1990).

Elephant Shrews, Macroscelidea

Elephant shrews are often considered to be daily heterotherms. However, South African rock elephant shrews (*Elephantulus* spp.) seem to differ from the majority of heterothermic mammals in that they typically have TBDs that are of intermediate duration between daily heterotherms and hibernators, although their T_b and metabolic rates are low and are similar to those of hibernating mammals (Lovegrove et al. 2001; Geiser and Mzilikazi 2011). Captive *E. edwardii* (Fig. 3.22), a species previously described to be homeothermic (Leon et al. 1983), remained torpid for up to 44 h (Fig. 2.3) with a minimum T_b of 9.2 °C (Geiser and Mzilikazi 2011). The minimum TMR for the cogeners *E. myurus* (57 g) and *E. rozeti* (45 g) was between 2 and 7% of BMR (Lovegrove et al. 2001), similar to hibernators of similar size. Torpor bouts in *Elephantulus* spp. (~50 g) and also *Macroscelides proboscideus* (50 g) often lasted for 8–10 h with a maximum of 20 h in the laboratory (Lovegrove et al. 2001; McKechnie and Mzilikazi 2011).

In the wild, the temporal patterns of torpor in elephant shrews suggested mainly, but not exclusively, daily arousals (Mzilikazi and Lovegrove 2004). Free-ranging

Fig. 3.22 The South African rock elephant shrew (*Elephantulus edwardii*, 45 g) is primarily insectivorous and can remain torpid with a T_b <10 °C for up to almost 2 days (photo and copyright F. Geiser)

E. myurus, in KwaZulu Natal, South Africa, expressed torpor throughout the year, but torpor was most pronounced in winter and spring when TBD usually was ~8–14 h and T_b fell to ~15 °C (Mzilikazi and Lovegrove 2004). However, the maximum TBD of *E. myurus* was 39 h in spring and the minimum T_b was 7.5 °C in winter. Similar to dasyurid marsupials, elephant shrews appear to use basking to minimize re-warming costs during arousal from torpor (McKechnie and Mzilikazi 2011; Chap. 7).

Aardvark, Tubulidentata

Aardvarks (*Orycteropus afer*) are distributed over wide range in sub-Saharan Africa. They are a large (~35 kg) ant and termite eating nocturnal mammal. Aardvarks usually maintain a high and stable T_b (Weyer et al. 2020). During a summer drought animals increased daily T_b fluctuations and in the following winter showed substantial heterothermy with T_b falling from a maximum of 38.8 °C to a minimum of 24.7 °C. Aardvarks used passive rewarming to increase T_b (see Chap. 7), and shifted activity into the daytime and a number of individuals died during the drought (Weyer et al. 2020). Therefore, this is an example of torpor use during an emergency situation.

Xenarthra

The Xenartha (armadillos, sloths and anteaters) are another ancestral order of placental mammals, now restricted to the Americas. Some data are available on heterothermy in all three groups, but more work is required for clarification of the patterns of heterothermy expressed.

Armadillos, Cingulata

The pichi (*Zaedyus pichiy*, 1100 g) is an omnivorous armadillo from central and southern Argentina and Chile. Pichis hibernate with a TBD of nearly 5 days with a minimum measured T_b of 12.5 °C reported (Superina and Boily 2007). The hibernation season lasts from autumn to late winter, with short and shallow bouts of torpor also occurring during other times of the year (Superina and Boily 2007). It is likely that the small pichiciego (*Chlamyphorus truncatus*, ~120 g) from the deserts of central Argentina also uses torpor.

Sloths and Anteaters, Pilosa

Sloths are Neotropical folivores (Foley et al. 1995). Early observations of three-toed sloths (*Bradypus* sp. 2–6 kg; Fig. 3.23) with a minimum measured T_b of 23 °C suggested they are heterothermic (Morrison 1945). However, these observations may have reported data from hypothermic animals, because passive re-warming was required to raise T_b to normothermic levels (Morrison 1945). In a recent study on thermo-energetics of *Bradypus*, Cliffe et al. (2018) found that they have low BMRs and may use metabolic inhibition at high T_a without a change in T_b, similar to tropical bats (see below).

Anteaters are also found in Central and South America and expression of heterothermy has been reported for two species. Captive giant anteaters (*Myrmecophaga tridactlyla*, ~40 kg), and southern tamanduas (*Tamandua tetradactyla*, ~5 kg) lowered their tympanic temperature by up to 6.5 °C during sleep (Fernandez and Young 2008).

Insectivores, Lipotyphla

The insectivores occur worldwide, except for Australia and Antarctica. Well-known hibernators in this group (now Lipotyphla) are the hedgehogs. The European hedgehog (*Erinaceus europaeus,* ~700 g) has been investigated with regard to its

Fig. 3.23 The three-toed sloth (*Bradypus* sp.), a folivore from Middle America, appears to be heterothermic with a minimum T_b of 23 °C measured, but it needs to be confirmed whether this was torpor or hypothermia (photo and copyright F. Geiser)

hibernation physiology for decades (Kristoffersson and Soivio 1964; Warnecke 2017). Captive European hedgehogs have TBDs of up to 12 days, their T_b was reported to decrease to ~5 °C, and TMR is reduced to ~3% of BMR (Ruf and Geiser 2015). In Russia, minimum T_bs of <0 °C have been reported recently for *E. europaeus* and *E. roumanicus* held in outdoor enclosures (Rutovskaya et al. 2019). Danish *E. europaeus*, also kept in large outdoor pens, remained within their hibernacula continuously for up to 6 months from October to April (Walhovd 1979). Free-ranging English *E. europaeus* had lower FMRs in badger-inhabited sites and possibly use torpor for predator avoidance (Pettett et al. 2016). Algerian hedgehogs (*Atelerix algericus*, ~600 g) held individually in a room with open windows near the Mediterranean Sea, commenced the hibernation season with short bouts of torpor in November, expressed long TBDs of 6–7 days in January/February, and ended the hibernation season again with short bouts in March (Mouhoub-Sayah et al. 2008). The southern African hedgehog (*Atelerix frontalis,* ~400 g), held under semi-natural conditions in the Karoo, South Africa, hibernated for ~3 months. The minimum regulated T_b of *A. frontalis* was about 4 °C, with a minimum measured value of 1 °C for one individual, and TBD lasted for up to ~5 days (Hallam and Mzilikazi 2011).

In contrast to statements often given in the literature that all shrews are homeothermic, several small shrews (Soricidae, 2–30 g), both white-toothed (Crocidurinae) and red-toothed (Soricinae), express daily torpor lasting up to 8 h with minimum T_bs of 12–27 °C and minimum TMRs of around 10–40% of BMR (Vogel 1974; Newman and Rudd 1978; Frey 1979, 1980; Nagel 1985; Ruf and Geiser 2015).

Fig. 3.24 A European white-toothed shrew (*Crocidura russula*, ~11 g) a species which exhibits daily torpor (photo and copyright, Gerhard Körtner)

Known heterothermic shrews include: *Suncus etruscus*, *Crocidura* spp., *Sorex* sp. and *Notiosorex* sp. White-toothed shrews (*Crocidura russula*) also display daily torpor during development (Nagel 1977). The large Asian musk shrew (*Suncus murinus*, 30 g) uses spontaneous daily torpor independent of T_a or sex (Sato et al. 2016). To the best of my knowledge, multiday torpor has not been observed in shrews (Fig. 3.24).

Bats, Chiroptera

Bats are a large group of >1300 mostly small flying mammals found on all continents except far northern and southern latitudes (Wilson and Mittermeier 2019), but their diversity decreases substantially with increasing latitude and most are insectivorous (Willig and Selcer 1989). Bats have been estimated to be 'only' about 50–60 million years old (Hand et al. 2017), and traditionally were classified into the 'Megabats' (family Pteropodidae, 'Fruit' bats) and 'Microbats' with the rest of the families containing most species. Based on more recent molecular evidence, bats are now classified as Yinpterochiroptera and Yangochiroptera (Teeling et al. 2005).

Bats are small (body mass range ~2–1400 g) with a large surface area for heat exchange with the environment. Mean vespertilionid body mass is 11.2 g (n = 191 species), therefore T_as around 30 °C approximate the lower end or lower critical

Fig. 3.25 The lesser long-eared bat (*Nyctophilus geoffroyi*, 7 g). This insectivorous bat is distributed over much of the Australian continent. It hibernates in cool areas in winter, displays short bouts of torpor in summer including during reproduction, and also uses torpor in the tropics (photo and copyright, Gerhard Körtner)

T_a of the TNZ in these small bats (Geiser and Stawski 2011; Riek and Geiser 2013). The large relative surface area of bats results in a steep linear increase of heat loss below the TNZ (i.e. from ~T_a 30 °C) because the $T_b - T_a$ differential increases as T_a falls (Figs. 1.1 and 1.2). Although bats can reduce heat loss at rest when wings are vaso-constricted (Bartholomew et al. 1964), during flight heat loss is augmented by their large vascularized wings (Speakman and Thomas 2003; Fig. 3.25), which requires compensation through an increase in MR. Therefore, likely due to the combination of the high energetic cost of thermoregulation and flight, but also often fluctuating, unpredictable, or temperature-dependent food supply the order Chiroptera probably contains the largest proportion of heterothermic species of all mammalian orders.

Torpor is known to be used by many members of at least 12 out of the now recognized 21 chiropteran families (Stawski et al. 2014b; Czenze et al. 2017a, b, c; Wilson and Mittermeier 2019). Torpor occurs in all largely insectivorous families, but also in small frugivorous/nectarivorous, carnivorous and hematophagous bats. Many species in the families Rhinopomatidae (mouse-tailed bats), Hipposideridae (old world leaf-nosed bats), Rhinolophidae (horseshoe bats), Mystacinidae (New Zealand short-tailed bats), Molossidae (free-tailed bats), Miniopteridae (bent-wing bats), and Vespertilionidae (vesper bats) hibernate during winter and some species exhibit extremely long and deep torpor bouts (Jonasson and Willis 2012). Several members of other families are known to use daily torpor or brief bouts of torpor including the Pteropodidae (old world fruit and blossom bats), Rhinonycteridae (trident bats), Emballonuridae (sheath-tail bats), Phyllostomidae (new world leaf-nosed bats), and Natalidae (funnel-eared bats). Heterothermy with some substantial reduction in T_b has also been observed for the Megadermatidae (false vampires) and torpor or heterothermy are likely to occur in the remaining families that have not been studied in detail (see Stawski et al. 2014b; Geiser et al. 2019b).

Hibernation has been described in bats ranging from cold northern regions, temperate regions, tropical and subtropical regions and deserts (Ransome 1990; Stawski et al. 2014b; Geiser et al. 2019b). Hibernating bats often hibernate in caves, mines or buildings, but some tree-roosting bats from temperate and warm climates hibernate in trees (Ransome 1990; Turbill and Geiser 2008; Stawski et al. 2014b). Hibernating bats have low minimum regulated T_bs often between 0 and 5 °C, and an extreme minimum T_b of −2 °C has been recorded in long-eared bats, *Plecotus auritus* (Table 5.1). Hibernating bats exhibit a low TMR often between 2 and 5% of BMR, and heart rates that can be as low as 5 beats/min similar to that of larger hibernators (see Chap. 5), which have much lower heart rates during normothermia (Currie et al. 2014; Ruf and Geiser 2015).

During the hibernation season bats exhibit TBDs that may last >50 days as measured via telemetry (Jonasson and Willis 2012), and the TBD appears to be limited to some extent by evaporative water loss (Thomas and Geiser 1997; Ben-Hamo et al. 2013). Even during inter-bout arousal episodes, when most hibernators are normothermic, shallow bouts of torpor with T_b as low as 20 °C have been observed in little brown bats (*Myotis lucifugus*, 5 g) apparently to further minimize energy expenditure (Jonasson and Willis 2012). In cool-temperate Australia, tree-roosting long-eared bats (*Nyctophilus* spp., 7–10 g, Fig. 3.25) may display TBDs that last for up to 15 days in winter despite large daily fluctuations of T_b because of the fluctuating T_a (Turbill and Geiser 2008). In summer, TBD in *N. geoffroyi* usually lasted for less than 1 day, but during cool periods TBD was up to 2 days (Turbill et al. 2003b). Many other hibernating bats regularly use short bouts of torpor in summer (e.g. Otto et al. 2012), often in the second half of the night or the early morning, and forage in the following evening (see Stawski et al. 2014b; Geiser et al. 2019b). These short torpor bouts do not, however, resemble daily torpor by daily heterotherms (Geiser and Brigham 2000; Ruf and Geiser 2015). In foliage-roosting red bats (*Lasiurus borealis,* ~11 g) in Ohio short bouts of torpor of up to 31 h were also observed in spring/summer and torpor expression was affected by T_a and elevation in both sexes (Monarchino and Johnson 2020). Hoary bats (*L. cinereus*, ~30 g), another foliage-roosting bat hibernated in November in central Mexico in a shrub 1.2 m above the ground and remained torpid for up to 12.7 days (Marin et al. 2020). Counter to the long-held view that torpor and reproduction are not compatible, during spring and summer many bats use torpor during pregnancy and lactation, probably to increase reproductive success (see Chap. 8).

In warmer regions, short-tailed bats (*Mystacina tuberculata*) from the family Mystacinidae displayed torpor on both main islands and a subtropical offshore island of New Zealand. These bats displayed multiday torpor with $T_b < 10$ °C and TBD of up to 5 days in winter and short bouts of torpor in summer and all solitarily roosting bats expressed torpor (Czenze et al. 2017a, b, c). The mystacinids are an old family believed to be of Gondwanan origin and they used to occur in Australia but are now extinct (Hand et al. 2017). In other tropical and subtropical areas multiday torpor is regularly used by vespertiliond and hipposiderid bats in the wild and its function is not only for energy and water conservation (Liu and Karasov 2011), but also predator avoidance (Stawski et al. 2014b). Hibernation has also been recorded for bats in geothermally heated caves in Israel. Mouse-tailed bats (*Rhinopoma* spp.) hibernate in these warm caves at a T_a of around 20 °C and high humidity (Levin et al. 2015). It is likely that hibernation under these conditions enable the species to survive winter at the northern edge of their distribution.

In deserts, multiday torpor may also be expressed in winter and short bouts in summer. For example in a molossid, the inland free-tail bat, *Ozimops petersi* (Bondarenco et al. 2014, 2016) TBDs up to 8 days were observed in winter in an Australian desert. Even during a summer heat wave, when T_a exceeded 48 °C, the highest T_as recorded in four decades at the site bats were measured, *O. petersi* used torpor in the morning when T_a fell to below 25 °C and T_b to <30 °C. The T_b then slowly increased lagging by ~5 h behind T_a because the bats were roosting in well-insulated dead trees, and it appears that bats were thermoconforming for most of the time even when T_a approached 48 °C. The highest T_{skin} reached was 46 °C. This lag in T_b is crucial because it resulted in a delay of the time the T_b reached critically high values that would have required evaporative cooling. Extreme heat-tolerance in addition to expressing torpor has also been observed in Angolan free-tailed bats (*Mops condylurus*), which largely thermoconformed from low T_bs up to T_as of 40–45 °C with only a small increase in MR despite increased cooling requirements (Maloney et al. 1999). A record maximum core T_b of 46.5 °C has been measured in the flat-headed bats (*Sauromys petrophilus*) another molossid (Cory Toussaint and McKechnie 2012).

In contrast to the largely insectivorous bats addressed above, some tropical and subtropical bats appear to be daily heterotherms because multiday torpor has not been observed in these species. These include frugivorous/nectarivorous/hematophagous new world leaf-nosed bats (Phyllostomidae), old world blossom-bats and small fruit bats (Pteropodidae), but also funnel-eared bats (Natalidae), which appear to use daily torpor exclusively with minimum T_bs between 17 and 26 °C (Rasweiler IV 1973; Genoud 1993; Audet and Thomas 1997; Kelm and von Helversen 2007; Stawski et al. 2014b; Geiser et al. 2019b). Use of daily torpor has been confirmed for the Australian northern blossom bat (*Macroglossus minimus*, 16 g, Fig. 3.26) from tropical Queensland and the common blossom-bat, (*Syconycteris australis*, 18 g) from a subtropical area, but only in captive individuals (Bartels et al. 1998; Coburn and Geiser 1998). Seasonal expression of daily torpor in *S. australis* is strongly linked to food availability rather than seasonal change in T_a (see Chap. 6).

It is astonishing that apart from differences between the phyllostomids and pteropodids and perhaps a few other tropical families, which seem to be daily heterotherms, and hibernation in the other mainly insectivorous families from different regions, torpor patterns in bats are extremely similar. Torpor patterns

Fig. 3.26 The tropical northern blossom-bat (*Macroglossus minimus*, 16 g) a nectar feeder from northern Australia, but also south-east Asia. It is a pteropodid bat that enters daily torpor (photo and copyright F. Geiser)

seem to reflect differences in T_a to a large extent and when T_a is similar torpor expression is also similar. One wonders whether this is because most species are small and, to deal with high energy demand and limited energy and nutrient resources, there are limited options for expression of thermal biology characteristics that ensure survival.

Pangolins, Pholidota

Pangolins are covered in scales, made from agglutinated hair. They are ant and termite eaters found in Africa and southern Asia, and many populations are threatened by illegal trafficking. Although to my knowledge torpor has not been described in pangolins, fasted captive pangolins in West Africa reduced T_b with T_a from about

34 to 26.5 °C (*Manis gigantea*, ~30 kg), and about 35 to 27 °C (*M. tricuspis*, ~1.5 kg). However, active rewarming was not described (Jones 1973). One *M. tricuspis* died after T_b fell to 16 °C (Jones 1973). In captive Chinese pangolins (*M. pentadactyla*, ~4.5 kg), T_b was regulated between 33.4 and 35.5 °C, over a large T_a range (Heath and Hammel 1986).

Carnivora

As the name implies, the Carnivora to a large extent, but not exclusively, eat meat. Carnivores are distributed worldwide and include medium-sized to large mammals. Torpor is known only in the terrestrial, but not marine carnivores and appears to be largely restricted to bears (Ursidae), some badgers (Mustelidae), skunks (Mephitidae) and aardwolf (*Proteles cristata*, Hyaenidae). T_b during carnivore torpor is relatively high in all species that have been described (Harlow 1981; Anderson 2004; Hwang et al. 2007; Tøien et al. 2011). Dogs (Canidae), including the raccoon dog (*Nyctereutes procyonoides*), which is supposed to be heterothermic did not reduce T_b below 36 °C in a long-term captive study (Nieminen et al. 2005), and there are no reports of heterothermy in cats (Felidae).

Hibernating black bears (*Ursus americanus*, ~80 kg; Fig. 3.27) and brown bears (*Ursus arctos*, ~100 kg) show prolonged periods of dormancy in winter and,

Fig. 3.27 The North American black bear (*Ursus americanus*, ~80 kg or more) hibernates for several months with a rather high T_b of around 30 °C (photo and copyright F. Geiser)

surprisingly, give birth and suckle young during their hibernation season (Tøien et al. 2011). Bears do not eat, drink, defecate, or urinate during the 3 to 6-month hibernation period. Although it is widespread knowledge that bears hibernate, unlike in many small hibernators, the core T_b of bears decreases to only ~30 °C (Tøien et al. 2011). However, the TMR of hibernating *U. americanus* is similar to that of many other hibernators (Tøien et al. 2011), to some extent because of their large size and therefore low normothermic mass-specific RMR and also physiological inhibition (Tøien et al. 2011). Therefore considerable energetic savings are achieved during the course of the winter. Because of the high T_b animals remain conscious and capable of moving throughout hibernation. Free-ranging brown bears (*U. arctos*) in Sweden reduced activity, T_b and heart rate weeks before they began denning (Evans et al. 2016). Bears entered dens in October/November when T_a was ~0 °C and snow had fallen. They finished denning in early April. During hibernation T_b fell from ~38 to 33 °C and heart rate by ~80%. Captive brown bears (*U. arctos*, ~100 kg) in Finland reduced T_b from 37.5 to 32.5 °C during hibernation, bears denned from late November/early December to late February/early March and T_b remained <35 °C for about 70 days (Hissa 1997). However, not all bears den as *U. americanus* have been observed on the ground with newly fallen snow melted off the back (Svihla and Bowman 1954).

Other carnivores do not seem to display multiday torpor bouts regularly. European badgers (*Meles meles,* 13 kg, Mustelidae) did so once for around 42 days in winter, with T_b falling from ~37 °C to about 29 °C (Fowler and Racey 1988). In North American badgers (*Taxidea taxus*, 9 kg, Mustelidae) and skunks (*Mephitis mephitis*, 3 kg, Mephitidae) the minimum T_bs during torpor were also rather high, at 26 to 28 °C, with bouts of torpor shorter than one day (Harlow 1981; Ruf and Geiser 2015). South African aardwolfs (*Proteles cristata*, 9 kg, Hyaenidae), which are small nocturnal mammals that mainly eat termites, reduced T_b from about 36.5 to a minimum of 31 °C in winter when termites are largely unavailable (Anderson 2004)

Primates

Torpor in primates has been observed in Madagascar, southern Africa and south-east Asia, but not to my knowledge, in South American primates. However, some South American marmosets are small (~100 g) and they likely arrived in America 40 Mya via rafting from Africa and somehow must have survived that journey (see below). Most information on primate torpor is from Madagascar. The island of Madagascar broke away from what used to be Gondwanan India, about 88 Mya, at a time when no placental mammals were present on the island (Nowack and Dausmann 2015). Therefore, Madagascar must have been colonized. As the closest relatives of Malagasy mammals occur in Africa, they must have moved across the sea over a long distance between the two land masses (Nowack and Dausmann 2015). Bats could fly to Madagascar from Africa or Asia, but this is not possible for non-flying mammals.

Several hypotheses have been proposed on how mammals could have colonized Madagascar, but rafting from Africa seems the most plausible. One obvious problem with this argument is the long distance of >400 km that had to be bridged, meaning the rafting animals had to survive for many days. Because this is not possible for small homeothermic mammals, which die after a few days (Fig. 7.13), it has been proposed that torpor use would have enabled the mammals to survive the long journey and thus colonize the island (Nowack and Dausmann 2015). The primates rafting to South America, also had to survive the journey somehow and homeothermy would have been a hindrance in that.

Torpor is widely used by the extant mammals of Madagascar, as for example in tenrecs, bats and primates. Eleven primate species belonging to four genera in the Malagasy lemur family Cheirogaleidae are known to use torpor (Dausmann and Warnecke 2016), but the taxonomy is not fully resolved. The most detailed information is available for the fat-tailed dwarf lemur (*Cheirogaleus medius*, 250 g). This species has a prolonged hibernation season lasting up to 7 months during the dry and cool Malagasy winter. However, unlike most other hibernators the T_b of individuals in poorly insulated tree-hole hibernacula passively fluctuates daily between about 12 and 30 °C with the daily variations in T_a and there are no obvious periodic arousal episodes. If individuals hibernate in well-insulated tree stumps with a constant T_a of about 22 °C, they do show periodic arousals approximately every 7 days similar to other hibernators, but from a higher minimum T_b (Fig. 3.28). The torpor patterns described for *C. medius* are reminiscent of those of the only known avian hibernator the poorwill (see above). Three other dwarf lemurs (*Cheirogaleus* spp.) also hibernate, and of these *C. sibreei* hibernates underground (Blanco et al. 2013).

Mouse lemurs (*Microcebus* spp.) also use torpor extensively. Some species appear to use daily torpor (e. g. *M. berthae*, 30 g), whereas others (e.g. *M. griseorufus*, 50 g) display a hibernation patterns similar to that of *Cheirogaleus* spp. (Dausmann and Warnecke 2016). Deep torpor bouts lasting for almost 4 days in the wild have been observed in the 70-g *M. murinus* (Schmid and Ganzhorn 2009), and minimum measured T_b was 7.8 °C (Schmid 2000). Other heterothermic lemurs from Madagascar belong to the genera *Allocebus* and *Mirza* (Dausmann and Warnecke 2016). However, although low T_bs have been measured in some species, it has not been confirmed whether and at what minimum they physiologically defend T_b when exposed to low T_a.

In contrast to the Malagasy lemurs, the South African lesser bushbaby (*Galago moholi*, 180 g) of the family Galagidae uses daily torpor only rarely, and apparently only as an emergency measure (Nowack et al. 2010). Torpid bushbabies reduce T_b to a minimum of 22 °C, TMR to 10% of BMR, and torpor bouts last for about 5 h.

For the south-east Asian loris (Lorisidae), recent data show that the pygmy slow loris (*Nycticebus pygmaeus*, 450 g) is capable of short-term hibernation, with TBDs up to 3 days and T_b approaching T_a of 10–15 °C in winter (Ruf et al. 2015). There is also some anecdotal evidence that the slender loris (*Loris tardigradus*, ~200 g) and slow loris (*Nycticebus* javanicus ~600 g) are heterothermic (Dausmann and Warnecke 2016).

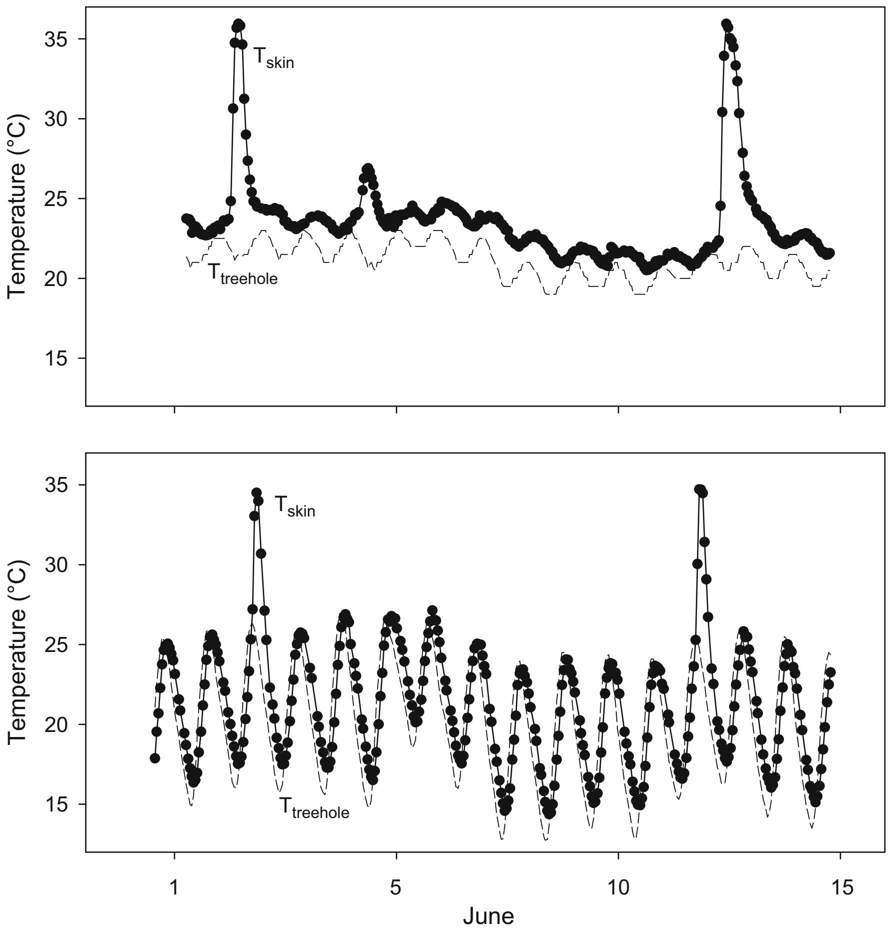

Fig. 3.28 Patterns of skin temperature fluctuations (T_{skin} filled circles) in free-ranging fat-tailed dwarf lemurs (*Cheirogaleus medius*, ~250 g) in Madagascar during the dry season in the austral winter. The top graph shows a lemur in a well-insulated tree hollow with a stable tree-hole temperature ($T_{treehole}$ thin broken line) and stable T_{skin} with periodic arousals. The bottom individual was in a less well insulated tree hole, its T_{skin} fluctuated to a large extent with that of the hollow, but with some endothermic arousals. However, endothermic arousals can entirely vanish when animals are exposed to even more extreme $T_{treehole}$ fluctuations (Dausmann and Warnecke 2016; data from Nowack et al. 2020)

Rodents, Rodentia

The Rodentia are the largest mammalian order with >2200 species or >40% of all mammalian species. Rodents are distributed worldwide and most are small. Rodents are a relatively new mammalian order with an approximately 70 Myr history (Swanson et al. 2019). Torpor has been studied extensively in many species of the group and many important principles about the ecology, physiology and biochemistry of torpor have been derived from these studies. One reason for the extensive data on rodents is the relative large size of sciurids, which permits attachment of electronic devices for measuring physiological variables. Because so much detailed information is available for rodents, both from captive studies and from the field, different important heterothermic families will be treated separately.

Squirrels, Sciuridae

Some of the best and most frequently studied rodent hibernators are members of the family Sciuridae, which include many hibernating ground squirrel genera including *Spermophilus, Citellus, Urocitellus, Callospermophilus* and *Ictidomys* (body mass ~100–700 g), marmots (*Marmota* spp., ~3–5 kg), prairie dogs (*Cynomys* spp., ~1 kg) and chipmunks (*Tamias* spp., ~30–130 g). Also in this family are the flying squirrels (*Glaucomys* spp., ~70 g), which appear to be daily heterotherms, whereas tree squirrels (e.g. *Sciurus, Tamiasciurus*) appear to be homeotherms.

Captive ground squirrels have been extensively studied with regard to the physiology of hibernation and it was in this group in which the nervous control of thermoregulation during hibernating was first examined (Heller and Hammel 1972). Moreover, the classic pattern of hibernation in free-ranging mammals was first quantified using temperature-telemetry for Richardson's ground squirrels (*Urocitellus richardsonii*, 400 g; Fig. 3.29) near Edmonton, Canada (Wang 1978). The hibernation season in most *U. richardsonii* in the wild commenced in mid-July in adults, two months later in juveniles and was terminated by all in mid-March. Torpor in *U. richardsonii* is characterised by minimum T_bs of ~2 °C and TBDs of 10–20 days in mid-winter in the wild, but TBD was shorter in captive individuals (Wang 1978). Michener (1992) provided more specific data, especially on sex differences of hibernation and these confirm that in this ground squirrel hibernation in the wild lasts from summer until spring. Similar patterns of seasonal torpor expression have been observed in North American golden-mantled ground squirrels (*Callospermophilus lateralis*; Fig. 3.30, and *C. saturatus*) (Kenagy et al. 1989; Healy et al. 2012), Columbian ground squirrels (*Urocitellus columbianus*) (Young 1990), but also for Anatolian ground squirrels (*Spermophilus xanthoprymnus*) from Turkey (Kart Gür et al. 2009). In other northern ground squirrels, the thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) in Michigan and Daurian ground squirrels (*Spermophilus dauricus*) in northern China, the hibernation season lasts for 6–7 months (Yang et al. 2011; Kisser and Goodwin 2012) and their TBD, TMR and T_b during torpor are similar to the other ground squirrel species (Ruf and Geiser 2015), but *S. dauricus* is one of the species that reduces T_b below 0 °C (Yang et al. 2011).

Arctic ground squirrels (*Urocitellus parryii,* ~700 g) occur in the far north of Alaska and Siberia. They undergo an extremely long hibernation season, lasting for up to 9 months and exhibit extremely low T_bs with minimum regulated T_bs of −2.9

Fig. 3.29 The Richardson's ground squirrel (*Urocitellus richardsonii*, 400 g) from North-American grasslands, hibernates from late summer to spring (photo and copyright F. Geiser)

°C (Barnes 1989; Richter et al. 2015). Because their hibernacula are situated above permafrost, where T_a is about −6 °C on average, they have to maintain a large $T_b - T_a$ differential during torpor (Barnes 1989). In comparison to females, male *U. parryii* enter torpor later in summer and emerge earlier in spring to establish territories and prepare for mating (Barnes 1996). The end of hibernation in March/April is inflexible in reproductive males, resulting in a potentially disastrous phenological mismatch during spring snow storms. In contrast, non-reproductive males and reproductive females, after the end of the usual hibernation season, can re-enter hibernation with short TBDs of 1–6 days, emerge in May and thus delay reproduction although reducing the time available for growth of young and pre-hibernation fattening for the next winter (Williams et al. 2017).

Alpine marmots (*Marmota marmota*, ~3 kg), which are found in the European Alps use social hibernation. Periodic rewarming is highly synchronised among individuals with adult males sharing heat with juveniles and the degree of synchrony affects mass loss during winter (Arnold 1988, 1993; Ruf and Arnold 2000). North American solitary woodchucks (*Marmota monax,* ~3.5 kg) have a very wide distribution and their hibernation season differs according to latitude and drought (Zervanos et al. 2010). During a severe drought in Pennsylvania, free-ranging *M. monax* entered short bouts of torpor in August with T_b fluctuating between ~25

Fig. 3.30 The golden-mantled ground squirrel (*Callospermophilus lateralis*, 200 g) from mountainous areas in western North America has been investigated extensively with regard to hibernation, as has the similar-looking Cascade golden-mantled ground squirrel (*C. saturatus*) (photo and copyright F. Geiser)

and 38 °C when T_a ranged from 20 to 30 °C. After rainfall some individuals remained normothermic, whereas others continued to exhibit torpor (Zervanos and Salsbury 2003).

North American prairie dogs (*Cynomys* spp.), especially black-tailed prairie dogs (*Cynomys ludovicianus,* ~1 kg), are considered to be 'facultative' hibernators (Harlow and Menkens 1986), but torpor expression differs somewhat among species. Captive white-tailed prairie dogs (*Cynomys leucurus,* ~1.5 kg), which had access to food, entered torpor at T_a 7 °C and expressed TBDs of only around 4 days interrupted by IBEs of 1.2 days. In contrast, only some *C. ludovicianus* entered torpor at T_a 7 °C, and did so only after food deprivation; TBD was brief at 2.1 days on average and was interrupted by long IBEs of ~ 1 week (Harlow and Menkens 1986). In the field in Colorado, TBD in *C. ludovicianus* was highly irregular and T_b was typically >15 °C even at high elevations. In contrast, in southern Canada the minimum T_b of *C. ludovicianus* was <10 °C and TBD often was around 10 days, similar to Utah prairie dogs (*C. parvidens,* ~800 g) (Gummer 2005; Lehmer and Biggins 2005). In *C. parvidens*, the hibernation season lasted from autumn to spring in high and mid-elevation populations, whereas low elevation populations terminated hibernation by late winter, when food became available (Lehmer and Biggins 2005).

Chipmunks, often confused with golden-mantled ground squirrels, are considerably smaller at around 30–120 g. Most live in North America, but the Siberian chipmunk (*Eutamias sibiricus*) is found in Asia. Chipmunks cache food for hibernation and because of this are often considered to be intermediate between food-storing and fat-storing rodent hibernators. Although it has been claimed they rely entirely on stored food during hibernation (Humphries et al. 2003), some species also store substantial amounts of fat, at least in captivity. In free-ranging Siberian chipmunks (*E. sibiricus*) measured in Hokkaido, Japan, hibernation commenced first in adults in September/October followed by juveniles about a month later. Spring emergence occurred around April for adult males and in May for females and the yearly variation in the timing of hibernation reflected snow cover (Kawamichi and Kawamichi 1993). Mortality during hibernation for all age classes was low (3.7–5.7%) whereas during the active period mortality in adults was around 50% (Kawamichi and Kawamichi 1993).

In North American western chipmunks, such as yellow-pine (*Tamias amoenus*, ~50 g) and Townsend chipmunks (*T. townsendi*, ~100 g) the hibernation season in the wild in Washington lasted from October/November to March, somewhat shorter than in sympatric ground squirrels (Kenagy and Barnes 1988). Hibernation in *T. amoenus* is rather predictable and, at least in the laboratory, is associated with substantial fattening (~45% increase in body mass) in autumn. Animals eat little or nothing when hibernating during mid-winter even if food is available (Geiser et al. 1990). On the other hand, free-ranging eastern chipmunks (*Tamias striatus*) from Quebec, Canada, differ from many other sciurids as their torpor expression in winter is variable and depends largely on food availability (Landry-Cuerrier et al. 2008). In good food years when many trees produce seeds, torpor in *T. striatus* was used in winter but was rather irregular and shallow (T_b often >10 °C). Whereas in low-food years hibernation was characterized by a regular expression of a sequence of deep ($T_b < 10$ °C) and multiday torpor bouts and lasted from ~November/December to May (Landry-Cuerrier et al. 2008), which is much shorter than that seen in most ground squirrels. Hudson (1978) suggested based on data for *T. striatus* that chipmunks in general may differ from 'classical' hibernators by having rather high minimum T_bs of 5–7 °C and because not all individuals expressed torpor in captivity. However, western chipmunks, *T. amoenus*, can have low minimum T_bs during torpor (minimum regulated T_b -1.0 °C, Geiser et al. 1994). All *T. amoenus* entered torpor in captivity despite access to food, but the TBD was generally somewhat shorter (~8 days) than in sympatric ground squirrels (*C. saturatus*, ~11 days) in mid-winter (Geiser et al. 1990; Chap. 5). Therefore, variables of torpor and torpor expression in *T. striatus* differ from many other hibernators in an interesting way, and should not be considered representative of other sciurids.

Unlike many other sciurid rodents, North American flying or gliding squirrels (*Glaucomys* spp. ~70 g), appear to daily heterotherms. Both northern (*G. sabrinus*) and southern (*G. volans*) flying squirrels expressed daily torpor in captivity with rather high minimum measured T_bs of around 26–28 °C (Olsen et al. 2017). Muul (1968) measured a T_b of 22 °C in a captive male *G. volans* without food for 36 h, but also observed torpor in the wild.

Other sciurids like Eurasian red squirrels (*Sciurus vulgaris,* ~300 g) and North American red squirrels (*Tamiasciurus hudsonicus* ~250 g) appear to be strictly homeothermic (Brigham and Geiser 2012; Dausmann et al. 2013). North American red squirrels assemble enormous larder hoards of conifer cones in autumn, which are stored underground within middens. Free-ranging *T. hudsonicus*, measured over three winters in the Cypress Hills of Saskatchewan, Canada, where the mean minimum T_a is below −10 °C in mid-winter with extremes of below −40 °C, never displayed torpor (Brigham and Geiser 2012). However T_b was slightly reduced, by about 2 °C in mid-winter and the lowest measured T_b was 34.5 °C.

Dormice, Gliridae

The dormice (Latin 'dormire', to sleep), family Gliridae, are one of the oldest extant rodent families (Swanson et al. 2019). There are ~30 species and they are found in Africa, Asia and Europe. Giant dormice, which were the size of small cats and lived on Mediterranean islands including Sicily during the Pleistocene are now extinct, but there is an extant population of giant garden dormice (*Eliomys quercinus*) in Formentera (Hennekam et al. 2020). The dormouse family contains many hibernators and apparently all members, unlike for the sciurids or cricetids, exhibit heterothermy (French 2008). It is possible that, similar to pygmy-possums (Burramyidae), all species in this family are hibernators or capable of displaying multiday torpor, because daily torpor has not been observed in any species of this family. Hibernating dormice include the edible dormice (*Glis glis*, ~100 g; Fig. 3.31), which are called 'edible' because they were held by the Romans in large dark ceramic pots, to fatten them up before consuming them as delicacies. Fattening is also extensively used by free-ranging *G. glis* before hibernation. Usually they increase body mass by 40-100% (Fietz et al. 2012; Bieber et al. 2014; Ruf and Bieber 2020). Hibernating captive *G. glis* were used in the first study demonstrating thermoregulation during deep torpor (Wyss 1932).

Captive non-reproductive *G. glis* in good body condition hibernated for up to 11 months of the year, and re-entered multiday torpor soon after the hibernation season terminated (Bieber and Ruf 2009). As these dormice had access to food and were in good condition, the prolonged underground hibernation was interpreted as a mechanism for predator avoidance in the wild (Bieber and Ruf 2009). The captive data replicate the situation in the wild, where non-reproductive *G. glis* can hibernate for ~11 months (Hoelzl et al. 2015). Free-ranging *G. glis* can start estivating as early as June, which can continue without transition into hibernation throughout winter, and therefore the animals may use multiday torpor for up to 11.4 months in total. This is the longest known hibernation season for any free-living mammal (Hoelzl et al. 2015).

Captive garden dormice (*Eliomys quercinus,* ~70 g), expressed multiday torpor throughout the year when held at T_a 12 °C (Daan 1973). Juvenile garden dormice use torpor during growth when food is restricted (Giroud et al. 2014). In addition to hibernation from autumn to spring when T_{skin} fell to a minimum of −2.9 °C (Pretzlaff and Dausmann 2012), hazel dormice (*Muscardinus avellanarius,* ~25 g)

Fig. 3.31 A hibernating edible dormouse (*Glis glis*) in its typical hibernation position with the tail wrapped over the back. These dormice can hibernate for up to 11 months in the wild (photo and copyright F. Geiser)

frequently expressed torpor during summer, although torpor bouts were generally brief (Pretzlaff et al. 2014). Adult male *M. avellanarius* enter torpor more frequently than females during the active season in summer in nest boxes in Lithuania, but reproductive individuals use torpor (Juškaitis 2005). Hibernation in captive woolly dormice (*Dryomys laniger* ~25 g) found in Turkey lasted for about 7 months (Kart Gür et al. 2014). Other hibernating dormice include the African dormice (*Graphiurus murinus* , ~30 g and *G. ocularis*, ~80 g) (Perrin and Ridgard 1999; Mzilikazi et al. 2012), the former of which also may express torpor throughout the year since torpid animals were observed both in summer and winter (Webb and Skinner 1996; Mzilikazi et al. 2012). Hibernation also occurs in the Japanese dormouse (*Glirulus japonicus* ~30 g), with T_b approximating 0 °C and TBDs up to 19 days and even T_bs below 0° have been measured, but the authors were uncertain about the precision of those readings (Iwabuchi et al. 2017). The desert dormouse (*Selevinia betpakdalaensis*, ~25 g) from Kazakhstan and *Roach's* dormouse (*Myomimus roachi*, ~30 g) a rare, small species found in Bulgaria and Turkey, also hibernate (French 2008).

Pocket Mice and Kangaroo Mice, Heteromyidae

Daily torpor or hibernation are common in many heteromyid species, many of which live in western North America. Captive little pocket mice (*Perognathus longimembris*, 8 g) hibernated with TBDs lasting between 1 and up to 5 days at a T_a of 8 °C, and the minimum measured T_b was 4 °C (Bartholomew and Cade 1957; French 1977). In the wild the hibernation season lasted for 8 months (Kenagy and Bartholomew 1985). In Great Basin pocket mice (*Perognathus parvus*, 24 g) the TBD was longer, lasting up to 8 days, with a minimum regulated T_b of 2 °C and a minimum TMR of about 3% of BMR (MacMillen 1983). Kangaroo mice (*Microdipodops pallidus*, 12 g) exhibited both brief and long torpor bouts with a maximum TBD of ~3.5 days and T_b fell to 6 °C (Brown and Bartholomew 1969). Other hibernating heteromyids include the desert pocket mouse (*C. penicillatus*, ~18 g), and the long-tailed pocket mouse (*Chaetodipus formosus*, ~20 g), which hibernated for 4–6 month in the wild (Kenagy and Bartholomew 1985; French 2008).

Free-ranging Ord's kangaroo rat (*Dipodomys ordi,* ~60 g) appear to enter daily torpor exclusively even at the northernmost extent of their range in Canada (Gummer 2005) similar to captive *D. merriami* (~40 g) and *D. panamintinus* (~80 g), which remain active throughout the year in the wild (Kenagy and Bartholomew 1985; French 2008). Torpor has been reported for several other heteromyid species (Cade 1964).

Jerboas, Jumping Mice, Birch Mice, Dipodidae

Many northern hemisphere dipodid rodents (*Allactaga, Dipus, Sicista, Zapus*) hibernate (Cade 1964; French 2008). Jerboas appear morphologically similar to kangaroo rats with their large hindlegs and small front legs, but these are convergent traits as they are not closely related to kangaroo rats diverging about 40 Mya (Swanson et al. 2019). Hibernation from winter to spring has been observed in captive Egyptian jerboa, (*Jaculus orientalis*, ~170 g) during which they reduced T_b to ~10 °C and remained torpid for up to 6.5 days (El Ouezzani et al. 2011). Turkish jerboas (*Allactaga euphratica*, ~90 g and *A. williamsi*, ~150 g) hibernate with TBDs of up to 14 and 6 days, respectively (Colak and Yigit 1998). Dwarf fat-tailed jerboas (*Alactagulus acontion,* ~30 g) are known to hibernate (Kalabukhov 1960) and Chinese three-toed jerboas (*Dipus sagitta*, ~80 g) from Inner Mongolia also hibernate in captivity (Chi et al., unpublished observations). In captivity, American western jumping mice (*Zapus princeps,* 35 g) hibernated for over 300 days with torpor bouts lasting up to 27 days (Cranford 1978; French 1985), and in the field the hibernation season lasted just under 300 days (September to early July) at >2000 m elevation Utah (Cranford 1978). The minimum T_b of *Z. princeps* is about 5 °C and the TMR 2% of BMR (Ruf and Geiser 2015). Captive meadow jumping mice (*Z. hudsonicus*, ~23 g) also expressed long torpor bouts of ~19 days and a minimum

TMR of 3% of BMR (Muchlinski and Ryback 1978). The tiny northern birch mice (*Sicista betulina,* ~8 g) hibernate for 6–8 months (Eisentraut 1956) and so do several other species of this family not described above (Cade 1964). It is possible that dipodids are yet another family that consists mainly or entirely of hibernators.

Hamsters, Cricetidae

The hamster family (Cricetidae) occurs in Eurasia and the Americas, and includes medium to large hibernators, but also small species many of which are daily heterotherms. Hamsters, as for example common Eurasian hamsters (*Cricetus cricetus*, ~400 g), store large amounts of food in the form of seeds rather than mainly body fat for the hibernation season, unlike many other hibernators (Herter 1956; Wendt 1989; Wassmer 2004; Siutz et al. 2016). Because hamsters rely on food, the digestive tract is not reduced but rather needs to be maintained during winter (Humphries et al. 2003; Tissier et al. 2019). The hibernation season is similar or shorter than that of many other rodent hibernators lasting for about 4 to 6 months (Siutz et al. 2016). The T_b of *C. cricetus* falls to 3–4 °C, however, the TBD is somewhat shorter at ~5 days and IBEs are longer (~29 h) than in many other hibernators (Siutz et al. 2012; Giroud et al. 2021), for which TBD is often 8–20 days (Chap. 4). The usual sexual differences in the hibernation season, with males typically terminating hibernation before females is reversed, as adult male *C. cricetus* hibernate for longer than females (Siutz et al. 2016).

Laboratory populations of golden hamsters (*Mesocricetus auratus* ~90 g) are widely used in hibernation research. They appear to be descendants of a single brother–sister pairing originating from near Aleppo, Syria, in 1930, although more recently additional wild caught individuals have been added (Gattermann et al. 2001). Golden hamsters were the subject of the seminal study by Lyman (1948), which established that when torpid hamsters were hibernating at T_a 3–5 °C, their TMR was ~6% of BMR and the $T_b - T_a$ differential was 1 °C or less. If however, hamster were cooled to 0 °C the animals were likely to rewarm demonstrating the precise control of thermoregulation even at these low T_bs during hibernation (Lyman 1948). Therefore, the minimum T_b of ~4 °C measured at T_a 3 °C represents a value that is or is close to the regulated minimum. Captive golden hamster have rather brief torpor bouts, which on average last for about 4–5 days (Pohl 1961). The Turkish hamster (*M. brandti*, ~150 g) is another slightly larger species widely used for hibernation studies in captivity. This species expressed multiday torpor bouts of up to 6 days (Goldman 1989; Batavia et al. 2013). These data suggest the TBD in large hibernating hamsters is generally rather short, which was emphasized in the early study on *M. auratus* by Pohl (1961).

Available data suggest that small hamsters mainly express daily torpor. Djungarian or Siberian hamsters (*Phodopus sungorus*, ~25 g) originate from Asian steppes with large populations in Kazakhstan (Flint 1966). *P. sungorus* change their fur color from grey/brown in summer to white in winter (Fig. 3.32). Captive

Fig. 3.32 The Djungarian hamster (*Phodopus sungorus*, 25 g) from Asian steppes is reproductive in summer when its fur is grey/brown (left). Its fur turns to a large extent white (right) and it reduces its body mass over autumn and enters spontaneous daily torpor mainly in winter. The seasonal change in appearance and physiology is to a large extent induced by the change in photoperiod (photo and copyright F. Geiser)

P. sungorus express spontaneous daily torpor in outdoor enclosures from autumn to spring when they are white, in summer they remain normothermic (Heldmaier and Steinlechner 1981b). During torpor in *P. sungorus*, T_b fell from ~35 °C to a minimum regulated T_b of 12.3 °C and the minimum TMR was ~ 35% of BMR (Ruf et al. 1993; Geiser et al. 2016). Captive *P. sungorus* bask when given a heat lamp during torpor and normothermia (Geiser et al. 2016). Daily torpor after food restriction has been recorded in the desert hamster (*P. roborovskii*, 20 g) from Inner Mongolia, but spontaneous torpor expression was not investigated (Chi et al. 2016).

The thermal energetics of torpor have been extensively studied in north-American ‘mice’ (*Peromyscus* spp., Cricetidae). Early work by MacMillen (1965) on captive cactus mice (*Peromyscus eremicus*, 17 g) and Morhardt (1970) on several species including deer mice (*P. maniculatus*, 18 g), white-footed mice (*P. leucopus*, 20 g) and canyon mice (*P. crinitus*, 20 g) established that members of this genus use daily torpor. Typically the T_b fell to T_b minima ranging from about 13 °C in *P. maniculatus* to about 18 °C for the other species, from which animals were able to rewarm. These T_b minima were regulated as the $T_b - T_a$ differentials increased from about 3–5 °C when animals were exposed to T_as above 20 °C to >6 °C at $T_a <$ 15 °C (Morhardt 1970). At T_as around 10 °C, *P. eremicus* became hypothermic (MacMillen 1965). The minimum TMR in *Peromyscus* spp. is usually around 20–30% of BMR (MacMillen 1965; Ruf and Geiser 2015). Spontaneous torpor in *P. leucopus* was observed in all seasons, or in all seasons except summer (Lynch et al. 1978; Tannenbaum and Pivorun 1988). Daily torpor has also been observed in pygmy-mice (*Baiomys taylori*, 6 g) and harvest mice (*Reithrodontomys megalotus*, 11g) (Hudson 1965; Thompson 1985) from North America, and leaf-eared mice (*Phyllotis darwini,* 35 g) and vesper mice (*Calomys venustus*, 50 g) from South

America (Caviedes-Vidal et al. 1990; Bozinovic and Marquet 1991). It now also appears that microtine voles (*Microtus* spp.), widely considered to be homeothermic, also express at least shallow torpor, because a minimum T_b of 26 °C was recorded in *M. lusitanicus* (17 g) in Portugal (Monarca et al. 2019).

Fat and Pouched Mice, Nesomyidae

The pouched mouse (*Saccostomus campestris*, 70 g), fat mice (*Steatomys pratensis*, 30 g) and rock mice (*Petromyscus* sp. 19 g) belong to the African family Nesomyidae. Pouched mice express daily torpor lasting for up to ~6.5 h with an average of 2.8 h for both males and females (Mzilikazi and Lovegrove 2002). During torpor, the T_b of pouched mice fell to a minimum regulated value of ~28 °C at T_a 20 °C, at lower and higher T_as, T_b during torpor increased slightly; the minimum TMR was ~56% of BMR (Mzilikazi and Lovegrove 2002). Captive fat mice entered daily torpor for up to ~20 h, reduced T_b to 16.4 °C and TMR to ~22% of BMR (Ellison 1995). Rock mice in the Namib Desert entered torpor in traps and reduced T_b to 18 °C (Withers et al. 1980).

Mice, Muridae

Murids are a large family of rodents with several hundred species, now distributed almost worldwide because of the human vectored introductions of mice (*Mus musculus*) and rats (*Rattus* spp.). In the past, murids were believed to be homeothermic (Cade 1964), however, more recent work has shown that the family appears to contain mainly daily heterotherms and homeotherms. The species that are known to express daily torpor include house mice (*Mus musculus*, ~30 g), wood mice (*Apodemus* spp., 20–40 g) and gerbils (*Gerbillus pusillus*, 13 g) (Hudson and Scott 1979; Buffenstein 1985; Eto et al. 2014; Ruf and Geiser 2015).

Most research has been conducted on captive individuals, but recent work on yellow-necked mice (*A. flavicollis*, 32 g) shows that they display daily torpor in the wild when T_a is low during autumn and winter (Boratyński et al. 2018). Japanese field mice (*A. speciosus*, 40 g) use torpor in combination with huddling and even when food is overabundant (Eto et al. 2014, 2015). A Namaqua rock mouse (*Aethomys namaquensis*, 46 g) entered torpor in a trap in the Namib Desert, reduced T_b to 19.8 °C and survived as it was recaptured later (Withers et al. 1980). Although native Australian rats (*Rattus fuscipes*, ~120 g) appeared to be homeothermic in a captive study (Glanville and Seebacher 2010), one individual displayed torpor after restricted foraging in the field and reduced T_b to about 24 °C (Nowack et al. 2020). Feral house mice (*M. musculus domesticus*) have been observed to use torpor in the wild in Australia while sharing nests, apparently for thermal comfort, with a potential predator, the marsupial dunnart (*S. crassicaudata*) (Morton 1978). One study compared torpor use by wild caught but captive *M. musculus* and a native Australian murid (*Pseudomys hermannsburgensis*, 11 g). *Mus* entered torpor, whereas *Pseudomys* became hypothermic and were unable to rewarm endogenously, but survived (Tomlinson et al. 2007). *Mus musculus* is often used in biomedical research especially with regard to cardiac function at low T_bs during daily torpor and neural control of torpor (Swoap and Gutilla 2009; Hrvatin et al. 2020).

In contrast to the other murids mentioned above, which expressed daily torpor exclusively, captive spiny mice (*Acomys russatus*, 60 g) remained torpid for 57 h when flooded during a storm (Barak et al. 2018), but this observation needs to be confirmed in the wild. *A. russatus* also expresses torpor in the TNZ (Grimpo et al. 2013).

Mole Rat, Heterocephalidae

The naked mole rat (*Heterocephalus glaber*, ~45 g) is an unusual rodent species, with respect to both social and thermal biology. This subterranean species lives in large colonies in thermally constant underground burrows found in the tropical semiarid areas of northeastern Africa. The species appears to be largely poikilothermic because its T_b in captivity is a direct function of T_a, and MR shows a thermal response similar to that in ectotherms at T_a below 29 °C, although at T_a above 29 °C, the MR shows a typical endothermic response (Buffenstein and Yahav 1991). However in the wild, naked mole rats live in groups at a T_a of 30–34 °C, and thus they maintain a more or less constant T_b (Bennett et al. 1988; Buffenstein and Yahav 1991), demonstrating that homeothermy without high heat production can be maintained under suitable thermal conditions.

Heterothermy in Large Mammals and Birds

Heterothermy is not only restricted to small mammals and birds, but also occurs in larger species (Arnold et al. 2006; Hetem et al. 2016). However, large species, unlike small species, have the ability to use substantial regional heterothermy with a reduction in surface temperature or T_{skin}, which reduces heat loss at low T_a, although core T_b may remain high (Withers et al. 2016). In some other large species core T_b may fall somewhat (Hetem et al. 2016). Perhaps the best-known example of large core T_b fluctuations are camels (*Camelus dromedarius*, ~450 kg, Schmidt-Nielsen et al. 1957). Camels exposed to heat substantially increased daily T_b fluctuations from ~2 °C when water was available to up to ~7 °C when water was restricted. Importantly, to achieve this increased T_b fluctuation, they reduced T_b below normal levels in the morning as a predictive response to delay passive heating of the body by the afternoon heat to minimize evaporative cooling (Schmidt-Nielsen et al. 1957). As for spontaneous torpor, which is not a response to food shortage, this T_b

reduction in camels is an example of Rheostasis or a predictive change in physiology (Mrosovsky 1990). This predictable T_b-reduction saves the camel about 5 l of water/day because evaporative cooling can be minimized. Although the T_b of camels may show daily fluctuations of up to 7 °C, this includes both a fall below the normothermic T_b in the morning and a rise above the normothermic T_b in the afternoon. Therefore, it is not a reduction by >5 °C below the normal resting T_b, as used for defining torpor here.

Hetem et al. (2016) summarized use of heterothermy by seventeen large mammals that were mostly from Africa. These ranged in size from sand gazelles (*Gazella s. marica*, 15 kg) to elephants (*Loxodonta africana* 4000 kg), but also included American Pronghorn (*Antilocapra americana*, 45 kg) and Australian western grey kangaroos (*Macropus fuliginosus*, 50 kg) (Hetem et al. 2016). The data show that even these large mammals do not have a 'constant' core T_b. The observed daily T_b amplitude ranged from 0.8 °C in black wildebeest (*Connochaetes gnou*, 130 kg) to 3.7 °C in Arabian oryx (*Oryx leucoryx*, 70 kg). Above a body mass of 10 kg, the mean 24-h core T_b amplitude decreased by on average ~1.3 °C for each tenfold increase in body mass. An extrapolation of these amplitudes to <10 kg results in small T_b amplitudes of less than 5 °C compared to the T_b amplitudes of up to 40 °C that have been observed in some of the small heterothermic species (Fig. 5.7), emphasizing the pronounced differences in thermal biology between small hibernators and large heterothermic mammals.

Other large mammals that show interesting T_b fluctuations are Alpine ibex (*Capra ibex*, ~50–100 kg). Free-ranging ibex at high elevations in the European Alps showed daily fluctuations in average rumen temperature from about 38.5 to 39.5 °C and this was paralleled by changes in heart rate from about 40 beats/min to 100 beat/min (Signer et al. 2011). During rewarming from the daily minimum T_{rumen} in the morning, the heart rate showed a phase delay in relation to T_{rumen}, suggesting the ibex moved into the sun to bask to passively rewarm and thereby minimize energetic costs of rewarming (Signer et al. 2011; see also Chap. 7). Heterothermy also has been observed in the large red deer (*Cervus elaphus*, ~140 kg), Przewalski horses (*Equus ferus przewalski* ~300 kg), and llamas (*Lama galma* ~120 kg) (Arnold et al. 2006; Turbill et al. 2011b; Riek et al. 2019).

In birds, pronounced T_b fluctuations have been observed in free-ranging barnacle geese (*Branta leucopsis*, ~2 kg) in Spitsbergen, Norway. Barnacle geese reduced T_b by ~4 °C below the normothermic resting T_b during pre-migration in autumn for energy conservation despite availability of food (Butler and Woakes 2001). Captive large Eurasian griffon vultures (*Gyps fulvus*, ~6.5 kg), held in the Zoological Garden at the Tel-Aviv University in Israel, showed small daily T_b fluctuations measured via transmitters of around 1.8 °C. After food had been withheld for 10 days T_b fell from maxima of around 39.5 °C to about 36.5 °C in the early morning (Bahat et al. 1998). Similarly, a captive new world turkey vulture (*Cathartes aura*, 2.2 kg), on loan from the San Diego Zoological Society, and with access to food, reduced T_b (measured in the cloaca) from 38 to 34 °C and this daily cycle was maintained for eight nights (Heath 1962).

Hibernating Humans?

Speculations about hibernation in humans have a long history and are highly popular in the media. These are often related to medical interests, spaceflight, and survival of indigenous humans with limited shelter, during recent glaciation periods, or of humans during immergence into cold water or under avalanches. Torpor use in other primates is typically used to argue that torpor in humans may be possible or even likely, however, the large size difference between humans (~80,000 g) and those primates that are known to express torpor (<600 g) and the long evolutionary separation (~50 Mya) of heterothermic primates from the branch leading to humans are often not considered. Bears, which typically serve as the other angle of the argument have been separated from primates for >60 Myr. Although pronounced hypothermia has been observed regularly, for example during burying under avalanches where minimum T_bs as low as 19 °C have been recorded, these humans required substantial medical intervention such as intubation and ventilation for recovery (Oberhammer et al. 2008).

Physiological measurements provide little evidence for torpor expression in extant humans. Indigenous humans living in the Australian desert barely reduced T_b overnight despite exposure to cold, although T_{skin} was reduced somewhat (Morrison 1965) and similar observations were made for indigenous North Americans exposed to T_a 0 °C and with insufficient covering (Irving et al. 1960). Somewhat greater fluctuations, especially in MR, have been measured in an Indian yogi, who are supposed to be able to reduce MR during a meditative state (Heller et al. 1987). An experienced yogi, asked to display his abilities in an underground chamber, indeed reduced MR by about 40% over a 4-h period of meditation. Some of this may have simply been due to the transition from activity to the resting state as T_b only fell by ~0.4 °C, however T_{skin} increased by 2–4 °C suggesting there was some control (Heller et al. 1987). Recent assumptions of extinct hominins hibernating in Spain during a period of glaciation around 450,000 years ago are based on bone morphology revealing bone disorders supposedly due to seasonal hibernation (Bartsiokas and Arsuaga 2020). However, these could just as easily be due to severe seasonal starvation or uncontrolled hypothermia during prolonged cold exposure.

Important in the context of possible human hibernation is that all species for which pronounced reductions in T_b (>10 °C) have been observed are small and weigh less than ~10 kg. Bears, which are of similar mass of humans, reduce T_b only by ~5 °C and they can reduce MR by physiological inhibition (Tøien et al. 2011), which requires specific physiological adaptations (Storey 2010). The extreme thermoregulatory patterns expressed during daily torpor and hibernation in small endotherms have been selected for over thousands or millions of years. Although some small reduction of MR may possibly occur in humans, and neonates have some thermal tolerance of low T_bs (T_b ~32 °C, Kumar et al. 2009), it seems unlikely that a mammals the size of adult humans can express deep torpor naturally simply because of their body mass. Humans may be induced into hypothermia perhaps via some chemical intervention. However, considering the many complex and different changes that occur for example for micro RNAs during torpor (see Chap. 5), it seems unlikely that a simple administration of a chemical or chemicals can produce 'natural' torpor. On the other hand, there is little doubt that other groups or species, both small and large are heterothermic to some extent. More likely candidates than humans for pronounced heterothermy include many birds, including swifts on the wing, tree-shrews, small mustelids, small cats, many unstudied bats, small South American primates, a large number of unstudied rodents, and perhaps small lagomorphs. It would be surprising if there were not many others.

How many heterothermic Species are there and why do Patterns of Torpor differ among Taxa?

As we have seen in this chapter, torpor is used by many birds and mammals. Although detailed data on which species use it are far from complete, enough information is available to make an educated guess on how many heterotherms there might be, especially for mammals. In terrestrial Australian mammals it has been estimated, based on information on families, that torpor is likely to be used by 43% of species (Geiser and Körtner 2010). Because Australia is a continent with on average low rainfall and low quality soils and with a different composition of mammalian species than on other continents this may not be representative. However, if we assume that 90% of all bats and 50% of all rodents are heterothermic without considering any of the other heterothermic orders we arrive at about 50% of the ~5500 species of mammals worldwide being heterothermic. The estimate for rodents may appear to be overly generous, but if we assume that only 20% rodent species are heterothermic and add the 90% for bats, which does not seem an overestimate, we still end up with heterothermy in around 30% of all extant mammals, a large proportion.

For birds, such estimations are more difficult to make because so little is known. However, it is likely that the largest order the passerines contains many more heterotherms than is currently known. Further, there are other groups with many species such as hummingbirds, which seem to be entirely heterothermic, and caprimulgiforms many of whom are known to be heterothermic. Therefore, a considerable proportion, likely more that 10% of the ~10,000 avian species are probably heterothermic. Of course these numbers are only rough estimates and it is probable that the real numbers, if ever revealed, differ. But it is clear that homeothermy is not a generic characteristic of birds and mammals as many text books claim.

With regard to patterns of torpor expressed, the biggest known groups of largely heterothermic species are the hummingbirds and bats, both of which are capable of flight. Hummingbirds are diurnal and all seem to display nocturnal daily torpor whereas bats are nocturnal and most species seem to display multiday torpor. Both groups rely on fluctuating food so why is their torpor expression so different? A possible explanation seems to be related to foraging behaviour, diurnal vs nocturnal. Perhaps during the day even in winter, T_a rises far enough to allow adequate foraging in the hummingbirds. In contrast in nocturnal bats, this is often not possible at least not for many species in winter.

Other differences in thermoregulation within groups are also not so easily explained. Why are some species of the hamster and squirrel families homeotherms, while others in the same family are daily heterotherms and still others hibernators? Size appears to be one possible explanation between the two heterothermic hamster groups, with the larger species being hibernators and the small species daily heterotherms, but for many small hamsters we do not know their pattern of heterothermy, and therefore this interpretation may be incorrect. For the sciurids there is no obvious difference in size between homeothermic tree squirrels, hibernating ground squirrels, and gliding squirrels expressing daily torpor. In glirid rodents, despite their different sizes, all appear to be hibernators. In contrast in some other taxa, there seem to be clear differences in torpor patterns between families, such as the dasyurid marsupials which all seem to be daily heterotherms, and the similar-sized burramyid marsupials, which all seem to be hibernators. In the marsupial example it could be argued that the difference is perhaps due to phylogeny and diet, but this does not appear to be the case for the hamsters and ground squirrels. Thus to be able to understand why such differences may have evolved, there seems to be no alternative but to systematically gather more data on the diversity of heterothermy.

Chapter 4
Patterns and Expression of Torpor

Patterns of Torpor

Torpor is used by many birds and mammals. However, despite the number and diversity of species, it seems only two major patterns have been favoured by natural selection. In most heterothermic endotherms torpor is characterized by either a daily occurrence (‘daily torpor’ in the ‘daily heterotherms’), which often use torpor throughout the year, or multiday torpor in the ‘hibernators’ with often a seasonal occurrence (Fig. 1.7). In many species these two patterns of torpor differ ecologically and functionally. Only a few species appear to display intermediate torpor patterns. However, the comparison between the two torpor patterns is complicated by the strong temperature-dependence of most physiological variables of torpor, which therefore may overlap especially at high T_as (see below). Moreover, long-term studies that have reliably characterised patterns of torpor of species are not always available.

Hibernation

Mammalian hibernation has been the subject of scientific investigation for nearly two centuries (Hall 1832). The expression of hibernation is often seasonal, usually occurring from autumn to spring and is known to be used by many mammals, but only one species of bird (McKechnie and Lovegrove 2002, Ruf and Geiser 2015; Chap. 3). Although the hibernation season may last for many months, most hibernators do not remain torpid throughout, but display a sequence of multiday torpor bouts interrupted by periodic rewarming (Fig. 1.7). The average torpor bout duration (TBD) of hibernators is 8.3 days and the mean maximum TBD 16.3 days (Fig. 4.1) and during these torpor bouts T_b is typically low and bodily functions are reduced to a minimum. Periodic rewarming is usually achieved by an increase of internal heat

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_4

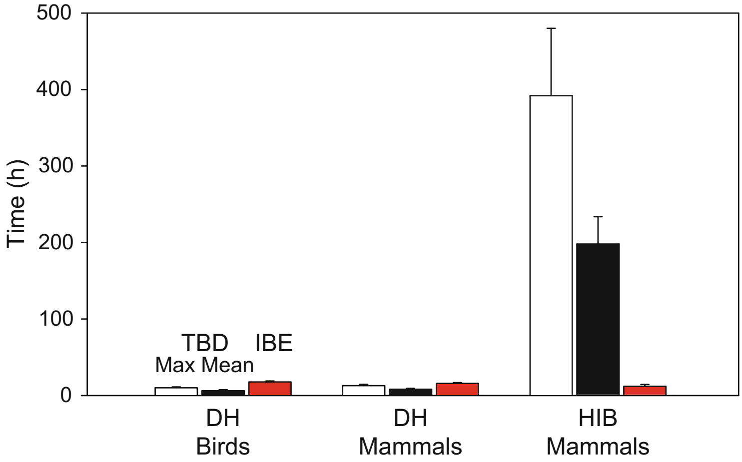

Fig. 4.1 The mean maximum torpor bout duration (TBD white) and mean average torpor bout duration (TBD black), and the mean duration of interbout euthermias (IBE red) of avian and mammalian daily heterotherms (DH) and mammalian hibernators (HIB. Data from Ruf and Geiser (2015)

production to raise T_b to normothermic values. Rewarming is followed by a brief normothermic/euthermic resting period called inter bout euthermia (IBE, usually 2–25 h, mean 12 h, Figs. 1.7 and 4.1), before the animal re-enters torpor (Ruf and Geiser 2015). Periodic rewarming is energetically expensive. However, it seems to be a physiological requirement for most species even though overly frequent arousals during the hibernation season can result in depletion of energy stores and death due to starvation before the end of winter. Only a few hibernators, the tenrec, *Tenrec ecaudatus*, which hibernates at high T_bs for months in subtropical Madagascar and some bears (e.g. *Ursus arctos*), which have an even higher T_b during hibernation, are known to not rewarm periodically (Hissa 1997; Lovegrove et al. 2014).

Most hibernating mammals are small (<10,000 g), with many weighing between 10 g and 1000 g, and the median mass is 68 g (Ruf and Geiser 2015), somewhat below the median for all mammals of around 100 g (Fig. 4.2). The only known avian hibernator the poorwill, *Phalaenoptilus nuttallii*, weighs around 45 g (Brigham et al. 2012). Bears often weigh around 100 kg or more and their pattern of hibernation differs somewhat from the small <10 kg hibernators. Hibernators often, but not always, fatten extensively before the hibernation season and rely to a large extent on stored fat and fewer on stored seeds as an energy source during winter (Humphries et al. 2003). Torpid hibernating mammals often adopt a ball-shape (Fig. 3.18), perhaps to minimize heat loss during torpor and rewarming, and possibly to prevent frost bites on appendages at low T_a.

Hibernating species typically reduce their T_b from normothermic T_bs of around 33–40 °C to below 10 °C, with many T_b minima maintained between 0 and 10 °C

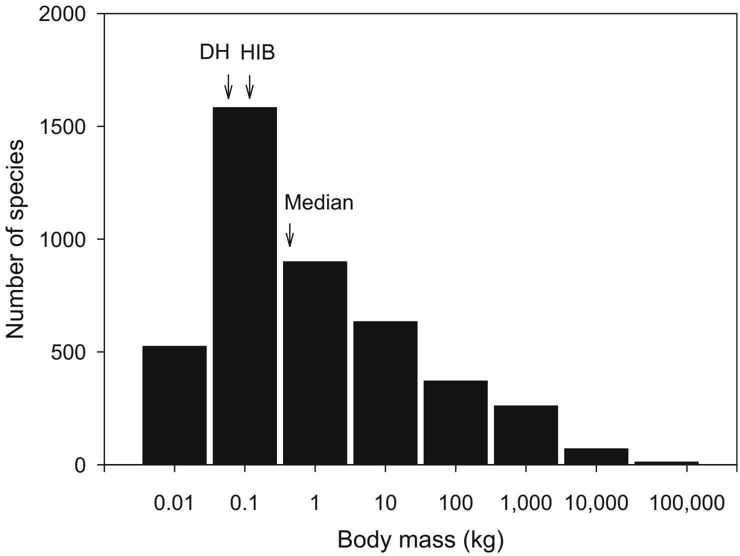

Fig. 4.2 The distribution of body masses of extant mammals. The arrows indicate the median for daily heterotherms (DH), hibernators (HIB) in comparison to all mammals (Median). The values on the x-axis represent the maxima for the respective column. Data from Smith et al. (2003), Ruf and Geiser (2015)

(Barnes 1989; Ruf and Geiser 2015). The minimum T_bs for species capable of expressing multiday torpor ranges from −2.9 °C in arctic ground squirrels (*U. parryii*) to 29.4 °C in black bears (*U. americanus*) and the T_b is affected by body mass (Fig. 5.8). However, most species have minimum T_bs around 5 °C with a median of 5 °C and a mean of 6.2 °C (Fig. 4.3) (Barnes 1989; Tøien et al. 2011; Ruf and Geiser 2015). The minimum T_b-T_a differential during steady-state torpor in thermoconforming hibernators is usually 0.5–2 °C. The MR in torpid hibernators (TMR) is on average reduced to 4% of the BMR (Fig. 4.3) and can be less than 1% of that of active individuals or in resting individuals at low T_a. Even if the high cost of periodic arousals is considered, energy expenditure during the mammalian hibernation season is still reduced to about 4–15% of that of an animal that would have remained normothermic throughout winter (Wang 1978; Geiser 2007). Energy expenditure is only 13–17% of the annual energy expenditure in ground squirrels although the hibernation season lasts for nearly 2/3 of the year (Kenagy et al. 1989). This enormous reduction in energy expenditure is perhaps best illustrated by the fact that many hibernating mammals can survive for 5–7 months entirely on body fat that has been stored prior to the hibernation season. In the most extreme cases, hibernators can survive for up to 12 months on stored fat (Chap. 6). However, some hibernators such as chipmunks (*Tamias* spp.) store food in addition to body fat. Hamsters (*Cricetus cricetus*) rely largely on stored seeds for food through the winter (Humphries et al. 2003; Wassmer 2004; Siutz et al. 2016; Tissier et al. 2019).

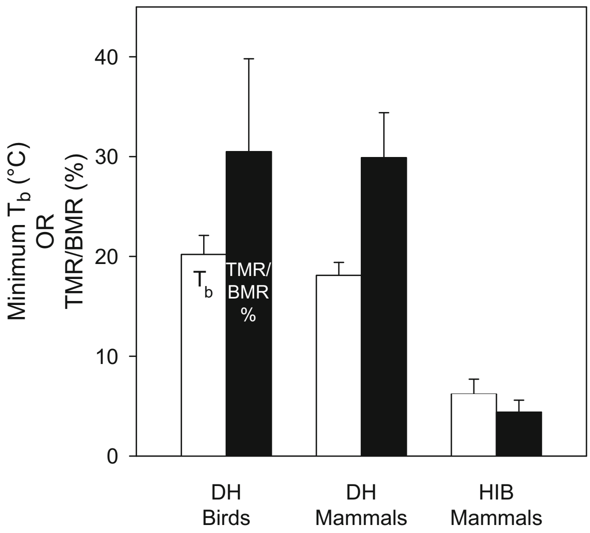

Fig. 4.3 The mean minimum regulated body temperature (T_b white bars) and the TMR/BMR% (back bars) for avian and mammalian daily heterotherms (DH) and mammalian hibernators (HIB). Data from Ruf and Geiser (2015)

Daily Torpor

Daily torpor in the daily heterotherms is the other widely used pattern of torpor in mammals and, unlike hibernation, is also widely used by birds. In diurnal birds, daily torpor occurs at night and is therefore often referred to as nocturnal torpor or shallow nocturnal torpor, especially in passerines. Daily torpor, unlike hibernation, is a more recent discovery (e.g. Bartholomew et al. 1957; MacMillen 1965; Morhardt and Hudson 1966; Dawson and Fisher 1969) because it is not as obvious as hibernation since animals often forage between bouts of torpor. On average, daily heterotherms are even smaller than hibernators and most weigh between 10 and 50 g with a median of 26 g for both mammals and birds (Ruf and Geiser 2015) or around ¼ of the median body mass for mammals (Fig. 4.2). Daily torpor is usually not as deep as hibernation, lasts only for hours rather than days or weeks, and is usually, but not always, interrupted by daily foraging and feeding. Importantly, unlike the hibernators, daily heterotherms appear to be unable express multiday torpor even when exposed to low T_a and food is withheld. These animals have been observed to die if they remain torpid too long. However, small extensions beyond 24 h, but with high T_bs a few degrees below normothermic values have been reported in the wild (Körtner and Geiser 2009). In many species, such as small carnivorous marsupials (*Sminthopsis* spp.), and white-footed mice (*Peromyscus leucopus*), daily torpor is less seasonal than hibernation, and even spontaneous torpor (when food is available) can occur throughout the year (Chap. 6). The regular use of spontaneous daily torpor in some species shows that one of its functions is the balance of energy budgets even when environmental conditions appear favourable. In contrast, in some daily heterotherms from strongly seasonal climates spontaneous torpor only used in the cold season (Heldmaier and Steinlechner 1981b). However, when food is restricted (induced torpor), daily torpor in many captive daily heterotherms is expressed during most of the year and often on about 80% of days (see below). In the wild the expression of daily torpor occurs up to 100% of days in autumn and winter (Warnecke et al. 2008; Körtner and Geiser 2009).

In daily heterotherms, the T_bs fall to average minima of 18.1 °C in mammals and 20.2 °C in birds (Fig. 4.3). However, in some hummingbirds values below 10 °C have been reported, whereas in other, mainly large species, such as tawny frogmouths (*Podargus strigoides*), T_bs during torpor are maintained around 30 °C (Körtner et al. 2000). The minimum T_b-T_a differential during steady-state torpor in thermoconforming adult daily heterotherms is often 2–6 °C. The average minimum TMR (Fig. 4.3) during daily torpor is about 30% of the BMR in both birds and mammals (i.e. ~ eightfold higher than that of hibernators), although this percentage ranges from less than 10% to around 80% of BMR and is strongly affected by body mass and other factors. While the mean values for minimum T_b, TMR and TBD are rather similar in avian and mammalian daily heterotherms (Figs. 4.1 and 4.3), the variance in birds is somewhat higher (Ruf and Geiser 2015) and that reflects the low T_bs measured especially in hummingbirds, and the high T_bs measured in passerine birds. When the normothermic energy expenditure or resting metabolic rate (RMR) at low T_a is used as point of reference, reductions of MR during daily torpor to about 10–20% of that in normothermic individuals at the same T_a are common. Overall, daily energy expenditure is usually reduced by 10–80% on days when daily torpor is employed in comparison to days when no torpor is used, primarily depending on the species, the duration of the torpor bout, torpor depth and whether or not the animals is rewarming endogenously or passively (see Chap. 7).

Two Patterns of Torpor or a Continuum of Variables?

Most species seem to conform to these two patterns of daily torpor and hibernation. When variables reflecting the physiological capabilities of species are compared in statistical analyses, the frequency distribution of the minimum TMR, minimum T_b, the mean and maximum TBD (Ruf and Geiser 2015) is clearly bimodal. Of these variables, TBD and TMR provided the strongest difference with no or little overlap between daily heterotherms and hibernators. This is reflected in substantial differences in survival times without food between the daily heterotherms and hibernators, which are manyfold (Fig. 7.13). For the minimum T_b, the weakest variable for differentiating the groups, some overlap was observed although the means differed.

Nevertheless, based on the heterothermy index (HI) derived from T_b measurements for heterotherms and homeotherms, it has been proposed that the two patterns of torpor described actually form a continuum (Boyles et al. 2011, 2013). Unlike the interpretation of Ruf and Geiser (2015), who aimed to compare single physiological minima and maxima for each species, Boyles et al. (2013) compared HI values of species under different thermal conditions and included multiple measurements for several species. The calculated HI ranged from 0.3 in homeothermic springbok, *Antidorcas marsupialis* to 35.5 in the arctic ground squirrel, *Urocitellus parryii*, a hibernator (Boyles et al. 2013), i.e. HI increases with increasing expression of heterothermy. For heterotherms HI values were calculated from winter data for long-eared bats (*Nyctophilus* spp.) (Boyles et al. 2013). The HI used for subtropical *N. bifax* (HI 20.6) was similar to that of cool-temperate *N. geoffroyi* (HI 21.6) despite substantial differences in the manner in which torpor was used, and the minimum regulated T_b used in the comparison by Ruf and Geiser (2015) differed by 5 °C between the species. Clearly many these HI values reported by Boyles et al. (2013), apart from the homeotherms, do not reflect the physiological capabilities of the species, but rather prevailing thermal conditions. The data presented therefore are more representative of the T_a the heterothermic animals experienced than their thermal biology. One could argue that using the HI this way provides an ecological approach that is trying to integrate what animals do in the wild. Others may question whether comparing the T_b of thermoregulating homeothermic with in part thermoconforming torpid individuals is meaningful because the latter reflect the T_a the animal was experiencing to a large extent.

Thus the analysis and interpretation of such relationships in heterotherms is complicated by the strong temperature-dependence of many variables of torpor. To further illustrate that point, the TBD, the variable best suited for distinguishing between the two heterothermic groups (Fig. 4.1), is compared between a hibernator and a daily heterotherm (Fig. 4.4). The examples shown are a hibernating pygmy-possum (*Cercartetus nanus*), which exhibits some of the longest known torpor bouts of hibernators of up to 35 days, and the daily heterotherm the dunnart (*Sminthopsis crassicaudata*) exhibiting an average TBD of about 5 h in captivity. The longest TBDs of both species as a function of T_a, within the T_a-range each thermoconform, are well described by a single linear regression on a logarithmic scale. The regression line describes the measured values well, with an r^2 of 0.91 (i.e. 91% of the variance of TBD is explained by T_a) (Fig. 4.4a). If however, the two species are regressed separately (Fig. 4.4b), an even better fit is obtained as the r^2 are increased to 0.93 and 0.98, respectively (1.0 is a perfect fit). Moreover, in the T_a range (15–20 °C) in which both species express torpor and thermoconform, the difference in TBD between the two is almost fivefold. When the maximum and mean TBDs of the two species are compared (Fig. 4.4c) the difference between the two species is about 35-fold, despite seemingly forming a single relationship when compared as a function of T_a, and at first glance may give the impression of a continuum or a single pattern of torpor (Fig. 4.4a).

Temperature-dependence of variables of torpor also explains the classifications and conclusions by Nowack et al. (2020) on non-holarctic, mainly tropical and subtropical, ‘weird’ heterotherms to some extent. Nevertheless, there are some species that seem to exhibit a pattern somewhere between the two patterns, these include hummingbirds (*Calypte anna*), honey possums (*Tarsipes rostatus*) and elephant shrews (*Elephantulus* spp.) which expressed bouts of torpor typically lasting less than a day, but TMRs that were similar to those of hibernators (Lasiewski

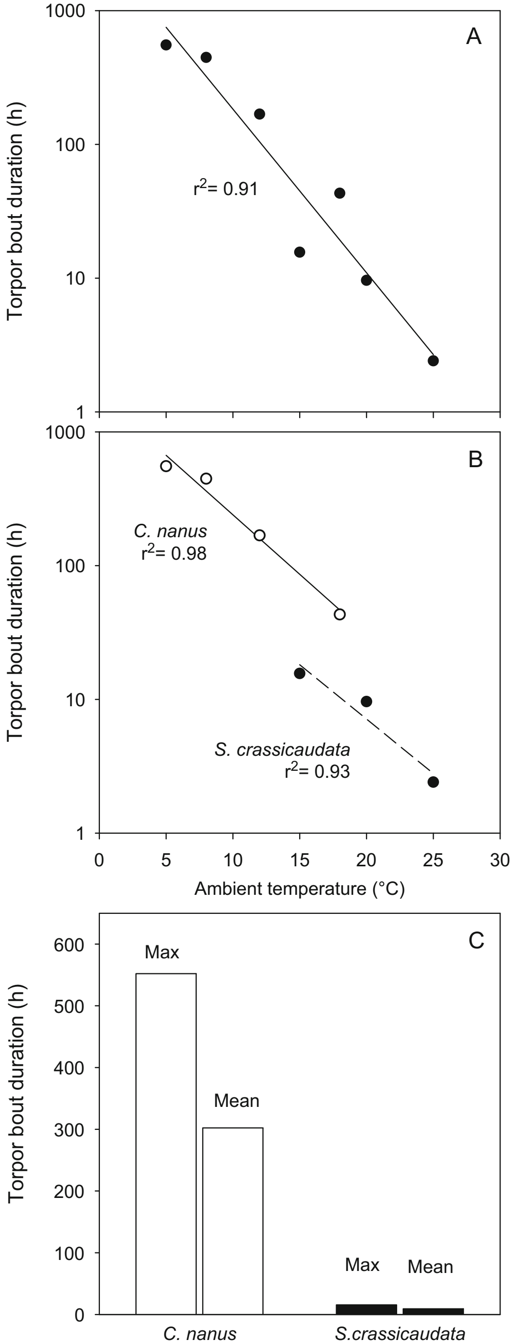

Fig. 4.4 The duration of torpor bouts (TBD) as a function of ambient temperature in a hibernator (*Cercartetus nanus*) and a daily heterotherm (*Sminthopsis crassicaudata*) of similar-size and thermoconforming in the respective T_a range. On the top graph (**a**) TBDs of both species are fitted with a single regression, suggesting they form a continuum, whereas on the middle graph (**b**) TBDs for each species are regressed separately. The bottom graph (**c**) shows the mean values for the same data differ enormously, although they are well described by a single regression line (**a**)

1963; Withers et al. 1990; Lovegrove et al. 2001). It will be interesting to see whether new long-term studies on more species, especially on those from low latitudes (Nowack et al. 2020), will reveal more intermediate species or mainly species that physiologically belong to either the daily heterotherms or hibernators.

Are Short Torpor Bouts in Hibernators Daily Torpor?

Some hibernators such as pygmy-possums, bats, primates and rodents enter torpor both in summer and winter. Typically, the torpor bouts expressed in summer last for less than a day and the question arises whether these resemble 'daily torpor' as they are often called in the literature or brief bouts of hibernation. Thermo-energetic data seem to support the latter and the best data are available on pygmy-possums, bats and dormice.

As described above, pygmy-possums (*C. nanus*, ~35 g) enter multiday torpor at low T_a and short bouts of torpor often lasting less than a day at high T_a. Even during short bouts at high T_a their TMR is well below that of daily heterotherms at the same T_b and/or T_a and similar to that predicted by hibernators (Song et al. 1997; Ruf and Geiser 2015). Non-reproductive *Nyctophilus* bats (~10 g), from temperate, subtropical and tropical habitats, did not significantly change TMR with season. Their steady-state TMR was reached within ~4 hours and the TMR was as predicted for hibernators even if they aroused daily, and about 15% of that for daily heterotherms at the same body mass (Geiser and Brigham 2000; Stawski and Geiser 2011; Currie 2015; Ruf and Geiser 2015). Even for reproductive *Nyctophilus* bats, TMR during short torpor bouts was as predicted for deep hibernators of the same body mass (Turbill and Geiser 2006; Ruf and Geiser 2015). Although interpreted to show the opposite, dormice (*Glis glis*, ~140 g) a much larger species (Wilz and Heldmaier 2000), support the view that short bouts of torpor in hibernators are not the pattern expressed by daily heterotherms. During short torpor bouts called 'daily torpor' by the authors, dormice with an on average TBD of 12 h did not reach the steady-state minimum TMR, which was only reached after 35 h (Wilz and Heldmaier 2000). However, even after 12 h the TMR of the dormice was less than 1/3 of that predicted for a daily heterotherm at that body mass (Wilz and Heldmaier 2000). This suggests that the observed pattern was not daily torpor, but rather a short bout of hibernation during which steady state TMR was not reached because of the short bout duration (Ruf and Geiser 2015). As TBD is strongly temperature-dependent (Fig. 4.4; Fig. 5.22), the short and shallow torpor bouts expressed by many small free-ranging hibernating bats at high T_a in summer seem to largely reflect ambient thermal conditions, rather than a change in physiology from hibernation to daily torpor.

Further support for this argument comes from field observations on poorwills (*Phalaenoptilus nuttallii*) and fat-tailed lemurs (*Cheirogaleus medius*) (Dausmann et al. 2004; Woods et al. 2019). Poorwills when exposed to cold nights and sunshine during the day show large daily T_{skin} fluctuations and rewarm daily. In contrast, when shaded they express multiday torpor with periodic arousals (Woods et al.

2019). Fat-tailed lemurs in poorly insulated tree hollows rewarm daily with T_a, which superficially may appear to be daily torpor. However, when hibernating in well-insulated tree-hollows they express multiday torpor bouts with periodic arousals (Dausmann et al. 2004), and the same is the case in captive individuals hibernating at T_as of 10–15 °C with maximum TBDs of 8–11.5 days (Blanco et al. 2021). In both these species the change in torpor patterns is due to the environment, not due to a difference or change in physiology. Thus, from a thermal energetics point of view, the brief and shallow torpor bouts expressed by some hibernators in summer, when T_a, is high T_a or fluctuating seem to be short bouts of torpor, rather than the pattern of daily torpor as expressed by daily heterotherms, which have much higher TMRs (Geiser and Brigham 2000; Stawski and Geiser 2011; MacCannell and Staples 2021). It therefore appears prudent not to call short bouts of torpor in hibernators 'daily torpor' because functionally they do not appear to be.

Aestivation

In contrast to hibernation and daily torpor, the term 'aestivation' is used to describe periods of torpor in summer or at high T_as. Torpor under these conditions is likely used for both water and energy conservation, but in some species it is also important in limiting the rise of T_b to dangerously high level during heat exposure (Bondarenco et al. 2014; Reher and Dausmann 2021). In some ground squirrels, the hibernation season begins in the hottest part of the year (Young 1990; Michener 1992) and therefore qualifies as aestivation and the transition from aestivation to hibernation seems to a large extent due to the seasonal fall of T_a in autumn. The physiological differences between aestivation and hibernation or daily torpor, apart from the typically higher T_bs and MRs during aestivation due to the relative high T_as, are generally small. However, in several species physiological differences have been observed between summer ('aestivation') and winter torpor patterns (daily torpor or hibernation) and physiological variables expressed under the same thermal conditions suggesting that some seasonal physiological changes do occur (Geiser 2020).

Torpor Expression in Response to Food and Water Availability

Both daily torpor and hibernation are crucial adaptations for survival of predictable or unpredictable shortages of food and water. Torpor is also used to increase the probability of survival under many other challenging conditions, even when circumstances appear benign and when food is available. Expression of torpor has thus evolved to deal with various nutritional, hygric and thermal conditions.

Spontaneous torpor (Food *ad libitum*)

Although it is widely assumed that restriction of food intake or limited energy stores are the main reason or signal for torpor expression, torpor is frequently not a last resort strategy for survival of energetic bottlenecks. Many species use torpor in the presence of food in captivity or without obvious energy restraints in the field. In captivity this is referred to 'spontaneous torpor' (MacMillen 1965; Gaertner et al. 1973; Hill 1975). Spontaneous torpor, both daily and multiday torpor, can be viewed as a form of 'rheostasis' or a predictive rather than a reactive homeostatic physiological adjustment that is acutely dealing with a reduced access to energy (Mrosovsky 1990). It seems that many species, especially daily heterotherms, use spontaneous torpor regularly as a part of their daily routine for balancing energy supply and demand, especially, but not exclusively, in species living in resource-poor environments such as desert. Many daily heterotherms enter torpor in captivity when food is abundant, or even overabundant. Spontaneous daily torpor has been observed in diverse birds and mammals.

For birds, expression of spontaneous daily torpor can be pronounced. Rufous hummingbirds (*Selasphorus rufus*) use spontaneous daily torpor on ~85% of days during pre-migration, higher than in many other species, and also use torpor during other seasons (Hiebert 1993a, b). Fruit doves (*Drepanoptila holosericea*) regularly enter spontaneous daily torpor at T_as between 12 and 27 °C, with the lowest T_bs and TMRs recorded below T_a 15 °C (Schleucher 2001).

For mammals, spontaneous daily torpor has been observed for several species of carnivorous marsupials (Fig. 4.5). Captive insectivorous/carnivorous marsupials (*Sminthopsis* spp. and *Dasyuroides byrnei*) from arid zone Australia held in outdoor enclosures used daily torpor throughout the year (Geiser and Baudinette 1987).

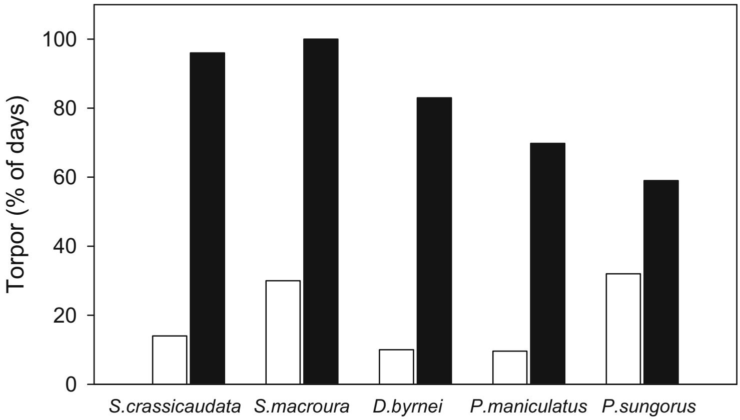

Fig. 4.5 Spontaneous torpor (white bars) vs induced torpor (black bars) in five mammals expressing daily torpor. Dunnarts (*Sminthopsis crassicaudata* and *S. macroura*), kowaris (*Dasyuroides byrnei*), deer mice (*Peromyscus maniculatus)* and hamsters (*Phodopus sungorus*). Data from Geiser and Baudinette (1987), Tannenbaum and Pivorun (1988), and Ruf et al. (1993)

Captive planigales (*Planigale gilesi*) from a semi-arid area entered spontaneous torpor on 32% of days when held at T_a 19 °C. Similar observations were made for the sympatric marsupial ningauis (*Ningaui yvonneae*), which increased spontaneous torpor expression from 29% at T_a 19 °C to 56% at T_a 16 °C, showing that at lower T_a use of spontaneous torpor typically increases (Geiser and Baudinette 1988). Related brown antechinus (*Antechinus stuartii*) and yellow-footed antechinus (*A. flavipes*) in outdoor cages only rarely expressed spontaneous torpor.

The use of spontaneous daily torpor has been extensively studied in rodents (Hill 1975; Fig. 4.5). The Djungarian hamster (*Phodopus sungorus*) expressed spontaneous daily torpor in outdoor enclosures in all seasons except for summer (Heldmaier and Steinlechner 1981b). Similarly, when held under short photoperiod *P. sungorus* expressed spontaneous torpor (28% of days) even at T_a 18 °C, but not when acclimated to long photoperiod (Geiser et al. 2013). At different T_as of 15, 10, and 5 °C, use of spontaneous torpor in *P. sungorus* increased from 20, to 33, to 40%, respectively (Ruf et al. 1993). North-American white-footed mice (*Peromyscus leucopus*) held in outdoor cages used spontaneous daily torpor in all seasons (Lynch et al. 1978), whereas deer mice (*P. maniculatus*) used spontaneous daily torpor only in autumn and winter (Tannenbaum and Pivorun 1988).

Captive hibernators, when they are physiologically ready to hibernate in autumn or early winter, may begin hibernation at high T_a and when food is provided. For example, thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), begin to hibernate even when food is freely available and T_a is as high as 25 °C (e.g. MacCannell and Staples 2021). Other hibernators that are known to use spontaneous torpor, often on ~100% of days in winter, include pygmy-possums (*Burramys parvus*), chipmunks (*Tamias amoenus*), ground squirrels (*Callospermophilus saturatus*), hamsters (*Cricetus cricetus*) and dormice (*Glis glis*) and many others (Geiser and Broome 1991; Geiser et al. 1990; Bieber and Ruf 2009; Siutz et al. 2018).

In the wild, use of spontaneous torpor is harder to verify because food availability is often difficult to assess. However, in tropical and subtropical bats (*Vespadelus pumilus* and *Nyctophilus bifax*) torpor has been observed in summer when food seemed abundant (Turbill et al. 2003a; Stawski et al. 2009). North American chipmunks (*Tamias striatus*, Landry-Cuerrier et al. 2008), which store large amounts of seeds and use less torpor when food is abundant, still express torpor in winter, so it could be classified as spontaneous. In the field torpor expression in hibernators is often near 100% in winter (Wang 1978; Kenagy and Barnes 1988; Young 1990; Hoelzl et al. 2015). Moreover, the hibernation season often commences when food seems abundant, and some species do have access to food during the hibernation season (Humphries et al. 2003). For example, male Richardson's ground squirrels (*Urocitellus richardsonii*) have larger hibernacula than females and to some extent to store food. Cached food allows males to be normothermic for longer during the hibernation season than females (Michener 1992), but they hibernate nevertheless and their torpor expression therefore appears to be spontaneous.

Overabundant Food

A rather unexpected observation was reported for Japanese field mice (*Apodemus speciosus*), a food-hoarding species expressing daily torpor (Eto et al. 2015). The absolute quantity of overabundant seeds, 2.4-fold vs 24-fold of food normally consumed by mice, did not affect torpor expression, although TBD changed somewhat. However, a reduction in overabundant food despite remaining well above that required to meet the energetic/nutritional needs of mice did affect frequency of torpor use. In the wild the mice have food stores that can be pilfered, and *Apodemus* mice seem to recognise changing food availability and respond by changing torpor expression accordingly (Eto et al. 2015).

Induced Daily Torpor (Food Restricted)

Occurrence of induced torpor by withdrawal or restriction of food is typically higher (often two to eight-fold) than when food is available (Fig. 4.5). In a number of captive birds, such as nightjars (*Caprimulgus europaeus*), swifts (*Apus apus*) and cuckoos (*Crotophaga ani*), daily torpor in captivity only occurs after severe food restriction. In Gerbils (*Gerbillus pusillus*) torpor was also recoded only after food restriction (Buffenstein 1985) and similar observations were made on vesper mice (*Calomys venustus*; Caviedes-Vidal et al. 1990).

Captive marsupial dunnarts (*Sminthopsis* spp.) increased daily torpor use from <30% of days with access to food, to 70–100% of days when food was restricted (Fig. 4.5). A high frequency of torpor expression, often around 100% of days, also occurs in free-ranging dunnarts as well as arid zone kalutas (*Dasykaluta rosamondae*) in autumn and winter (Warnecke et al. 2008; Körtner and Geiser 2009; Körtner et al. 2010), suggesting a shortage of food is at least partially the reason. In captive adult antechinus (*Antechinus stuartii*) held in outdoor cages from autumn to spring, food withdrawal increased daily torpor expression from rarely to about 30–80% of days (Geiser 1988a).

In rodents, food restriction also increases torpor use. Daily torpor in *Peromyscus leucopus* held in outdoor cages increased substantially to >30% of days after food withdrawal in all seasons. Similarly, torpor expression by *P. maniculatus* increased from <10% of days (food available) to 70-78% of days (food restricted) (Tannenbaum and Pivorun 1989). Torpor occurrence was about 70% of days when deer mice were acclimated to short photoperiod in the laboratory and food was restricted (Geiser et al. 2007b). In *Phodopus sungorus*, torpor occurrence increased by almost twofold when animals were food restricted (Fig. 4.5), and during 60% food restriction torpor use increased by 1.8 to 2.6-fold when exposed to T_as between 15 and 5 °C (Ruf et al. 1993). These data underscore the interactions between low T_a and food restriction increasing torpor expression. Torpor also could be induced by food restriction in a summer-acclimated desert hamsters (*Phodopus roborovskii*), which did not appear to express spontaneous torpor at that time (Chi et al. 2016).

Although spontaneous and induced torpor may appear to be functionally similar, detailed comparisons to verify this are rare. *Phodopus sungorus* acclimated to short photoperiod expressed spontaneous daily torpor as expected for the species, but these spontaneous torpor bouts were longer and the minimum TMRs were lower than those of long photoperiod-acclimated hamsters after food restriction (Diedrich et al. 2012). However, these observed differences also may reflect physiological differences that are directly due to photoperiod acclimation.

Unpredictable Food Availability

The unpredictability of food availability on torpor expression and patterns has been investigated in marsupial dunnarts (*Sminthopsis crassicaudata*) and great tits (*Parus major*). In *S. crassicaudata*, maintained on three food regimes: 150% *ad libitum* food, restricted with 70% of *ad libitum* food, and unpredictable food with food rations ranging from 0 to 120% of *ad libitum*, but at the same total amount of that offered to the food-restricted group over the same time period, torpor expression differed (Munn et al. 2010). Not surprisingly, torpor use increased from about 35% of days (*ad libitum* food) to about 65% of days (food restricted). However, unpredictable food resulted in a further increase in torpor use to >80% of days (Munn et al. 2010). Moreover, TBD increased from about 2.5 h (*ad libitum* food) to 3.5 h (food restriction), to 4.5 h (unpredictable food).

In tits (*P. major*) two groups of birds, one provided with a constant food supply via feeding stations, the other without, were studied in the wild (Nilsson et al. 2020). Nocturnal T_b of males measured in nest boxes was not affected by the treatment, whereas females on the 'unpredictable' food supply reduced T_b by about 1 °C in comparison to the food supplemented group. This may have resulted in a reduction in energy expenditure for females.

Water Conservation and Restriction and Torpor Use

Although a reduction in energy expenditure is generally considered to be the most important function of torpor, it also appears to be crucial for water conservation, especially when water is limited (see Chap. 7). Marsupial dunnart (*Sminthopsis macroura*) evaporative water loss declined during daily torpor to about 20–40% of that in normothermic individuals (Cooper et al. 2005). Evaporative water loss in torpid cactus mice (*Peromyscus eremicus*) was about 37% of that of normothermic individuals at the same T_a (MacMillen 1965) and similar values have been recorded for gerbils (*Gerbillus pusillus*; Buffenstein 1985). More extreme reductions in evaporative water loss were observed in torpid wattled bats (*Chalinolobus gouldii*)

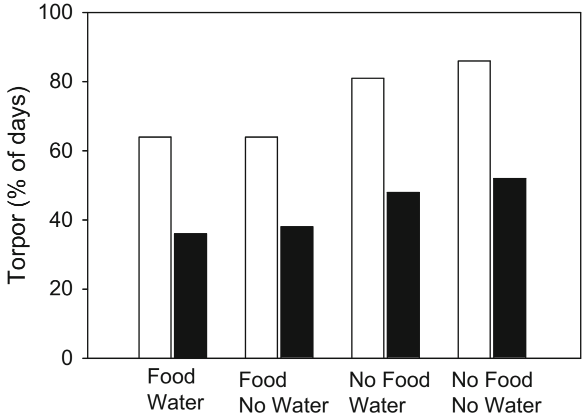

Fig. 4.6 Effect of ambient temperature (T_a white bars 18 °C, black bars 28 °C), and water and food availability on torpor expression in dunnarts (*Sminthopsis macroura*). For all treatments T_a had a stronger effect on torpor expression than food and/or water availability. Data from Song and Geiser (1997)

capable of hibernation (Stawski and Currie 2016). These bats were able to reduce evaporative water loss by almost 90% in comparison to normothermic individuals (Hosken and Withers 1997). Even greater reductions in evaporative water loss were reported for hibernating big brown bats (*Eptesicus fuscus*) which, when exposed to a humid environment, reduced water loss by about 98% in comparison to water loss during normothermia (Klug-Baerwald and Brigham 2017). In torpid honey possums (*Tarsipes rostratus*) evaporative water loss during torpor was so low as to be undetectable with the available equipment (Withers et al. 1990). Water conservation by using torpor has also been demonstrated in the field. Free-ranging mouse-lemurs (*Microcebus murinus*) using torpor had lower rates of water turnover than those remaining normothermic (Schmid and Speakman 2009). Mouse-tailed bats (*Rhinopoma* spp.) close their nostrils when not breathing during multiday torpor to further minimise pulmonary water loss (Levin et al. 2015). Thus, water conservation appears to be an important function of torpor in these bats beyond just a by-product of reduced energy turnover.

Desert organisms must be conservative with water use and since torpor reduces MR and water loss (MacMillen 1965; Cooper et al. 2005), water restriction would be expected to experimentally induce torpor. However, the reduced metabolic water production (i.e. the production of water H_2O from the oxidation of hydrogen) during torpor may make water restriction a less persuasive cue. This consideration is supported by studies on desert mammals, which suggest that short-term restriction of water typically does not greatly increase expression of daily torpor (MacMillen 1972; Buffenstein 1985).

In birds, shallow nocturnal torpor was observed in Inca doves (*Scardafella inca*) with access to food, but deprived of water, whereas combined withdrawal of food and water resulted in deeper torpor (MacMillen and Trost 1967). In desert marsupials (*Sminthopsis macroura*), which reduce water loss during torpor by about 70% (Cooper et al. 2005), daily torpor was expressed at T_a 18 (63% of days) and 28 °C (35% of days) when food and water were available. When both food and water were withheld from *S. macroura*, torpor use increased (Fig. 4.6), whereas withdrawal of water in the presence of moist food had no effect (Song and Geiser 1997). However, when dry food was offered, withdrawal of water resulted in an increase of torpor use in comparison to animals with access to food and water, although this may have reflected limited uptake of dry food by the animals without access to water rather than the lack of water *per se* (Song and Geiser 1997). Under all experimental conditions, occurrence of daily torpor in *S. macroura* was higher at T_a 18 than at 28 °C and the effect of T_a stronger than that of food and water availability.

Cactus mice (*Peromyscus eremicus*) that were water deprived in mid-winter, did not enter torpor, lost mass and, although they had free access to mixed bird seeds, died after 6–11 days (MacMillen 1965). In contrast, food restriction resulted in daily torpor use (MacMillen 1965). In summer, similar results after water deprivation were obtained for eight of ten *P. eremicus*. However, the two individuals that regularly expressed torpor did survive, suggesting that torpor use due to water deprivation allows some individuals to survive water shortages (MacMillen 1965). In gerbils (*G. pusillus*), 20% of individuals supplied with dry food and without access to water entered torpor, but when both food and water were withheld use of daily torpor increased to ~90% (Buffenstein 1985).

In contrast, in captive hibernating hamsters (*Mesocricetus auratus*), originating from the Syrian desert, water restriction clearly increased torpor expression. Hamsters with unpredictable water restriction began to hibernate earlier, spent more time in torpor and hibernated for longer than non-restricted control hamsters (Ibuka and Fukumura 1997).

Thus, the patterns of torpor differ substantially among species. The cues responsible for its use are complex, but seem to reflect ecological factors to a large extent.

Chapter 5
Physiology and Thermal Biology

Torpor is a complex phenomenon and involves a large number of physiological adjustments beginning with torpor entry and ending with the completion of the arousal process (Boyer and Barnes 1999; Carey et al. 2003; Bouma et al. 2011). During bouts of torpor, the most obvious physiological changes at the organismal level, apart from MR and T_b, include reductions of heart rate and breathing rate and breathing patterns.

While the neural or endocrinological signals that control the transition from normothermia to torpor at entry into torpor are not fully understood, it is known that the central sites for regulation of torpor include the hippocampus, hypothalamus of the brain, and nuclei of the autonomic nervous system (Drew et al. 2007; Cubuk et al. 2016; Jastroch et al. 2016; Hrvatin et al. 2020; Takahashi et al. 2020). The hypothalamus is involved in altered thermoregulation during torpor, but also the neuroendocrine control and timing of torpor (Drew et al. 2007). Cooling the preoptic anterior hypothalamus initiates an increase in thermoregulatory heat production when brain temperature falls below the set-point temperature (T_{set}) (Heller et al. 1977; Drew et al. 2007). The suprachiasmatic nucleus (SCN) situated in the hypothalamus above the optic chiasm, remains more active than other brain structures during deep torpor (Kilduff et al. 1982). Lesions of the SCN interfere with the circannual cycle in ground squirrels and hibernation in lesioned individuals may continue into spring and summer (Ruby et al. 1998). The SCN also contains receptors for melatonin a hormone that plays a role in the seasonal regulation of torpor (Cubuk et al. 2016).

The autonomic nervous system regulates metabolic rate, heart rate and cerebral blood flow at torpor entry (Drew et al. 2007). Before T_b falls at torpor entry in hibernators, the heart rate is reduced by parasympathetic activation, whereas an increase in sympathetic activation that elevates heart rate before T_b increases seems to be a major signal for arousal from hibernation in ground squirrels (Milsom et al. 1999). Similarly, for induced daily torpor in mice (*M. musculus*) via food restriction the autonomic nervous system also plays a central role in coordinating the reduction in T_b during torpor (Swoap et al. 2006).

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_5

Even before entry into the first bout of torpor at the beginning of the hibernation season or a period of daily torpor, mean normothermic T_b may slowly decline. In free-ranging arctic ground squirrels (*Urocitellus parryii*), T_b declined by ~4 °C on average from 45 days before the first torpor bout was used (Sheriff et al. 2012). Bears (*Ursus arctos*) reduce activity, T_b and heart rate weeks before they begin denning (Evans et al. 2016) and a similar decline in normothermic T_b prior to torpor expression also may occur in some daily heterotherms. In sugar gliders (*Petaurus breviceps*), a species that typically uses daily torpor during bad weather in winter (Körtner and Geiser 2000b), the normothermic resting T_b fell by on average 1.2 °C over 3 days before torpor entry, in comparison to individuals that did not enter torpor (Christian and Geiser 2007). These observations support the hypothesis that there is a physiological preparation for torpor, which seems more pronounced in hibernators than in daily heterotherms, or at least an attempt to minimise energy expenditure even before using torpor, perhaps because of decreased foraging success.

In some species, such as California ground squirrels (*Otospermophilus beecheyi*), entry into hibernation may involve a number of short torpor bouts with relatively high T_b (Strumwasser 1959). These 'test drops' used to be considered to be an essential part of the preparation for function at low T_b. However, is has subsequently been shown that test drops are not a prerequisite for hibernation. Some hibernators, such as ground squirrels (*Urocitellus columbianus*; *U. parryii*) and pygmy-possums (*Burramys parvus*), can express long and deep bouts from the beginning of the hibernation season (Young 1990; Körtner and Geiser 1998; Williams et al. 2017). Nevertheless, T_b and metabolic rate typically are lowest not at the beginning, but rather in the middle of the hibernation season, when torpor bouts are longest (see below).

Cooling and Rewarming

At torpor entry, when the animal is thermoconforming, the decline of T_b usually follows a Newtonian cooling curve (Nicol and Andersen 2007), and consequently the cooling rate slows as T_b approaches T_a (Figs. 5.1 and 5.4). Initially during torpor entry, the MR, falls precipitously from active values to below BMR, with ~75% of the MR reduction possible within 12 min (Fig. 5.4). Therefore heat production by the animal during the entry stage is minimal. The fall of T_b is slower than that of MR due to thermal inertia of the body. However, the maximum cooling rate, the steepest part of the curve, which is more or less linear when measured over ~10–20 min (Figs. 2.2, 2.3, 5.1, and 5.4) is also substantial. The maximum cooling rate is more easily compared than the overall cooling rate and therefore regularly used as a variable for interspecific comparisons.

To a large extent because of surface area/volume relationships, the maximum rate of cooling is strongly affected by T_a and body mass (Fig. 5.2). This maximum rate of cooling is about 0.5 °C/min for both mammals and birds with a body mass of around 5 g (Fig. 5.2). At a body mass of 500 g, predicted maximum cooling rates are much reduced and mammals cool at 0.05 °C/min and birds at about 0.08 °C/min. Consequently, and because cooling slows later during torpor entry, the time required for

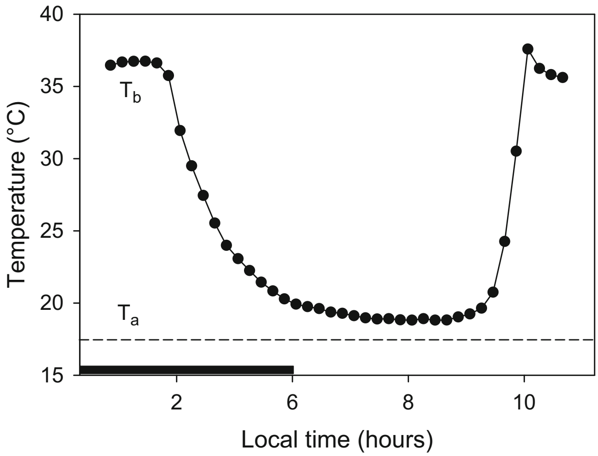

Fig. 5.1 Change of T_b during entry and rewarming from daily torpor in a dunnart (*Sminthopsis macroura*). Note the curvilinear decline during torpor entry with a fast initial near linear fall and the slowing of the fall of T_b as it approaches T_a. The increase of T_b during rewarming is also curvilinear, it is slow initially at low T_b and maximal and near linear as it approaches normothermic T_b. The dark bar indicates night. Unpublished data by the author

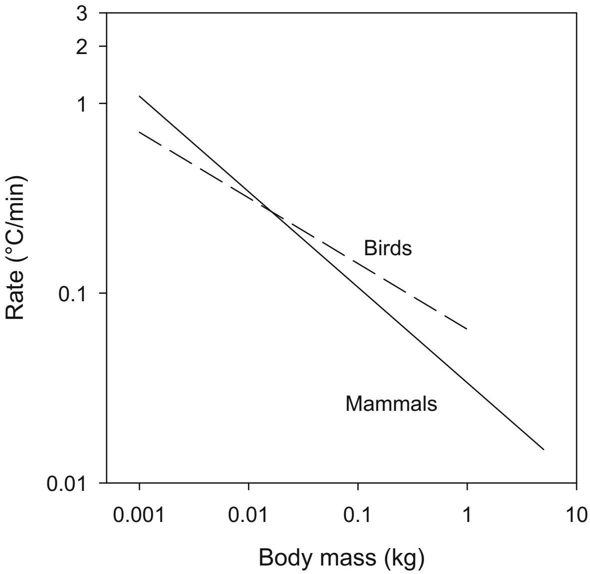

Fig. 5.2 Regression lines for maximum cooling rates measured over 10–20 min for six avian species ranging from 4 to 500 g (data from Lasiewski and Lasiewski 1967; Körtner et al. 2000; Brigham et al. 2000) and seven mammalian species ranging from 8 to 3100 g (data from Arnold 1988; Geiser et al. 2014, 2016; Körtner and Geiser 2000b; Turbill et al. 2003a, b; Yang et al. 2011). Data were fitted with least squares regressions. Equations: birds: $\log y = -1.19\text{–}0.346 \log x$, $r^2 = 0.85$; mammals $\log y = -1.46\text{-}0.5 \log y$, $r^2 = 0.94$

the reduction of T_b from normothermic to deep torpor ranges from ~3 to 4 h in small species like bats (*Nyctophilus* spp.) and up to >1–2 days in large hibernators such as echidnas (*T. aculeatus*) and marmots (*M. marmota*) (Nicol and Andersen 2007; Ruf and Arnold 2000).

At the end of a torpor bout, torpid animals can rewarm endogenously and the overall rate of rewarming is much faster than the rate of cooling (Menzies et al. 2016; Haase et al. 2019). When endogenous rewarming is used, heat is generated by shivering and/or non-shivering thermogenesis as during normothermic thermoregulation. Although it was believed in the past that brown adipose tissue (BAT) is more or less exclusively responsible for rewarming from torpor, this view is no longer supported, because monotremes, birds, and marsupials, which do not possess functional BAT can nevertheless rewarm from torpor (Nicol et al. 1997) and at a similar rate (Geiser and Baudinette 1990). These species rely heavily on shivering thermogenesis and likely non-shivering thermogenesis from other tissues, such as muscle, for heat production (Nowack et al. 2017b).

The increase in T_b at the end of a torpor bout is also curvilinear (Figs. 5.1 and 5.4; Nicol et al. 2009) and associated with a sharp increase in MR. The MR increases from low TMRs to a MR overshoot, which is typically similar to that of the MR during activity, and occurs at a time when rewarming rate is maximal (Fig. 5.4). When normothermic T_b is reached, the MR typically returns to RMR (Fig. 5.4). Initially at low T_bs warming is slow, but then accelerates to a maximum rate at a T_b that is slightly below the normothermic T_b (Nicol et al. 2009; Utz and van Breukelen 2013). In pocket mice (*Perognathus/Chaetodipus hispidus*) the rate of maximum

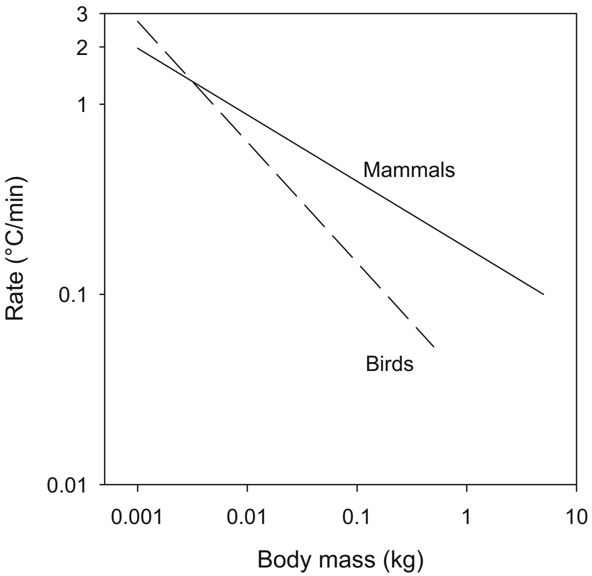

Fig. 5.3 Maximum rewarming rates for birds and mammals. Regression lines from Geiser and Baudinette (1990) and McKechnie and Wolf (2004)

rewarming is associated with intensive shivering or high MR, more so than during early during arousal (Wang and Hudson 1970).

The maximum rate of rewarming over 10–20 min is generally also close to linear (Figs. 5.1 and 5.4) and a function of body mass. At a body mass of 5 g, the predicted maximum rate of rewarming is just above 1 °C/min in mammals and just below 1 °C/min in birds (Fig. 5.3), i.e. about twice as fast as the rate of cooling. The fastest rewarming rates have been observed in some small hummingbirds (1.2–1.35 °C/min at 3.3–6.8 g; Lasiewski and Lasiewski 1967; Heinrich and Bartholomew 1971) and insectivorous bats at 2.7 °C/min in silver-haired bats (*Lasionycteris noctivagans*, 10.5 g), 1.8 °C/min eastern red bats (*Lasiurus borealis*, 13 g) (Menzies et al. 2016) and 2.5 °C over 1 min in long-eared bats, *Nyctophilus gouldi* (10.5 g; Currie et al. 2015a). However, endothermic insects exceed even these values. Bees (*Apis mellifica*, 0.1 g) warm at 8 °C/min and bumblebees (*Bombus impatiens*, 0.2 g) at 4.5 °C/min. Importantly, in these insects, mainly the thorax and not the entire body is warmed (Heinrich and Bartholomew 1971). At larger body masses of 500 g, the predicted maximum rate of rewarming is about 0.2 °C/min for mammals and only ~0.05 °C/min for birds (Fig. 5.3). At even higher masses rewarming is very slow, (~0.1 °C/min at 5000 g) and one likely reason as to why larger species such as carnivores do not substantially reduce core T_b during hibernation.

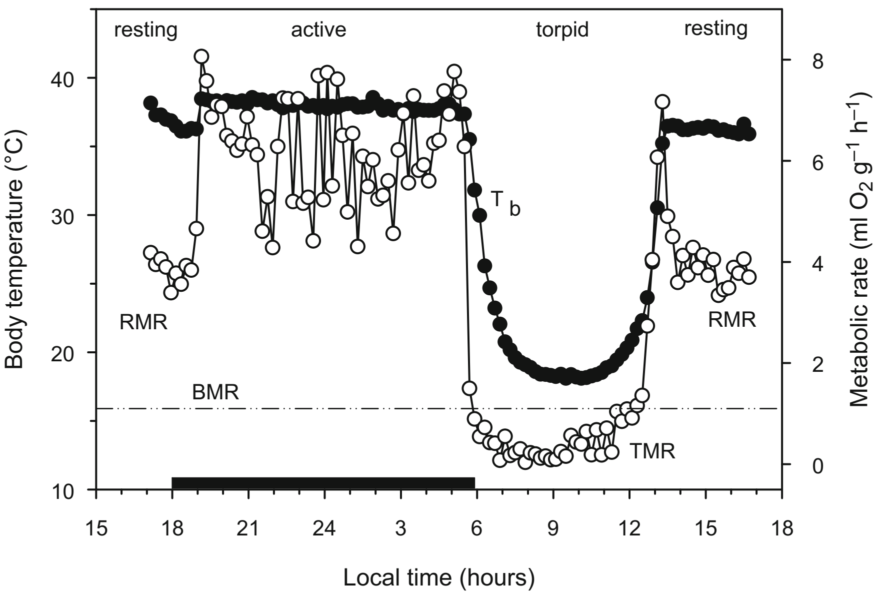

Fig. 5.4 Metabolic rate (ml O_2 g^{-1} h^{-1}, circles measured in 12-minute intervals) and body temperature (T_b, filled circles) of a dunnart (*Sminthopsis macroura*) measured over a day at T_a 15 °C. The times the dunnart was resting, active and torpid is shown at the top of the graph, times when the animal displayed resting metabolism (RMR) is show at the beginning and end of the measurement, the time it displayed torpor metabolic rates (TMR) is shows at the bottom of the graph. Basal metabolic rate (BMR), the horizontal dash-dotted line, is shown for reference. The dark horizontal bar indicates night. Unpublished data by the author

As expected from heat loss relationships, the rate of rewarming is also affected by T_a and is slowed at low T_a (Heinrich and Bartholomew 1971; Geiser and Baudinette 1990; Utz and van Breukelen 2013). Moreover, induced arousal via disturbance of torpid individuals is faster than spontaneous arousal in a number of species (Wang and Hudson 1970; Utz and van Breukelen 2013), suggesting that animals during spontaneous rewarming do not use the maximum heating capacity. Further and perhaps not unexpectedly, the BMR of mammalian species and their rates of rewarming are correlated (Geiser and Baudinette 1990; Careau 2013; Menzies et al. 2016).

Thermoregulation During Torpor

Although the reduction of MR and T_b during torpor in heterothermic endotherms may be reminiscent to that of ectotherms (Figs. 1.1 and 1.2), and result in energy savings in both, two features clearly distinguish the two. The first difference, as just discussed is that at the end of a torpor bout, heterothermic endotherms can rewarm from low T_bs using endogenous heat production, whereas ectotherms must rely on uptake of external heat. The second difference is that T_b during torpor by endotherms is regulated at or above a species-specific or population-specific minimum, or the T_{set}, by a proportional increase in heat production (Wyss 1932; Hainsworth and Wolf 1970; Heller and Hammel 1972; Heller et al. 1977; Florant and Heller 1977).

The first observation on thermoregulation during torpor was made for dormice (*Glis glis*) by Wyss (1932) from the University of Zürich. Wyss (1932) summarises: At T_as above 0 °C, the torpid dormouse thermoconforms (he describes it as 'poikilothermic'). Heat production was not measurable with the described equipment. At T_as below 0 °C the torpid animal commences a special thermoregulation, which is associated by a substantial increase in breathing frequency. The dormouse is able to maintain a constant T_b of $<+1$ °C, during which the heat production increases proportionally with the decrease of T_a below 0 °C. After a rise of T_a above 0 °C the hibernating organism returns to a thermoconforming state.

One reason why animals defend T_b during torpor is to prevent tissue damage. Although often stated otherwise in the literature this not only serves to avoid freezing because T_b is typically regulated at intermediate T_bs often well above 0 °C and the minimum T_b can be as high as 30 °C. Of course, in species exposed to subzero T_as, freezing is avoided by regulating the T_b typically near 0 °C. With regard to maintaining the ability to rewarm from torpor, regulation of T_b during torpor is crucial because if the T_b during torpor is forced below the minimum regulated T_b by, for example, excessive cold exposure or low energy reserves, the animal may become hypothermic (MacMillen 1965; Tucker 1966; MacMillen and Trost 1967; Geiser and Baudinette 1987) (Fig. 1.8). The T_b of a hypothermic individual is no longer controlled and endothermic rewarming is no longer possible. However, the animal may survive if it is passively rewarmed and if T_b has not fallen too far below the normally regulated value. Thus, hypothermia can be induced during both normothermia and torpor.

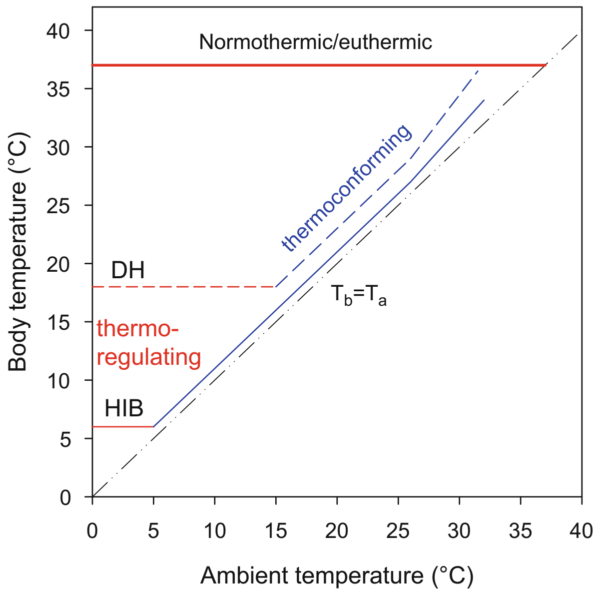

Fig. 5.5 Steady-state body temperature (T_b) of an average daily heterotherm (DH) and hibernator (HIB) as a function of T_a. The T_b in thermoconforming animals is shown in blue (broken DH, solid HIB) indicating that T_b falls with T_a in that range, but these animals are not ectothermic and retain the ability to activate thermoregulation at any point. The T_b of thermoregulating torpid animals is shown in red (broken DH, solid HIB). The normothermic/euthermic T_b is show as thick horizontal red line. The diagonal line is $T_b = T_a$. Values from Ruf and Geiser (2015), modified from Geiser (2011)

As reported above, the normothermic T_b of mammals is around 37 °C on average, achieved by a linear increase of RMR below the BMR (Figs. 5.5 and 5.6). At torpor entry, the T_b falls and, over the range of T_a a torpid animal is thermoconforming, T_b during steady-state torpor remains just above the T_a. The T_b-T_a differential is typically about 3 °C or more in daily heterotherms and about 1 °C in hibernators although at very high T_as the T_b-T_a differential may slightly increase in both (Fig. 5.5). When the torpid animal reaches its minimum regulated T_b, the T_b stabilizes, on average at about 18 °C in daily heterotherms and 6 °C in hibernators (Fig. 5.5), although these values vary with body mass (see below). The regulation of T_b at these minima during torpor is achieved by an increase of TMR (Fig. 5.6).

This T_b-pattern is reflected in the animal's metabolic rate (Fig. 5.6). Assuming no physiological inhibition over the T_a range the T_b-T_a differential is more or less stable (Fig. 5.5), the TMR in thermoconforming daily heterotherms in steady-state torpor declines curvilinearly with T_a, suggesting a temperature effect (Fig. 5.6). Below around T_a 15 °C (or T_b 18 °C, the TMR of the daily heterotherm increases in parallel to the RMR (Fig. 5.6) to regulate T_b at 18 °C despite increasing heat loss due to the increasing T_b-T_a differential (Fig. 5.5). In the hibernator in steady-state torpor in the T_a range it is thermoconforming, the TMR is lower than in the daily heterotherm

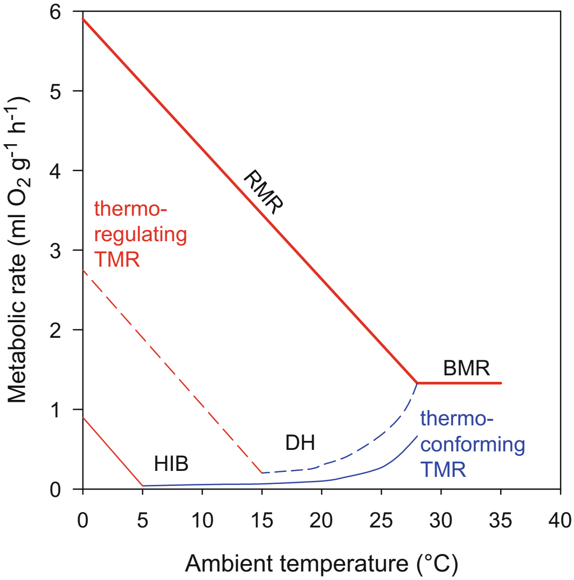

Fig. 5.6 Steady-state MR of an average daily heterotherm (DH) and hibernator (HIB) function of T_a. A body mass of 25 g was used for both to be able to directly compare the mass-specific MR. Thermoconforming is shown in blue (broken DH, solid HIB) indicating that T_b falls with T_a in this T_a range, but these animals are not ectothermic and retain the ability to activate thermoregulation at any point. Thermoregulation during torpor is show in red (broken DH, solid HIB). The RMR and BMR during normothermia are shown as thick red lines. Values from Bradley and Deavers (1980), Riek and Geiser (2013), Ruf and Geiser (2015) modified from Geiser (2011)

because of physiological inhibition, and the T_a-range over which thermoconformation is observed is much wider than in the daily heterotherm (Fig. 5.5). However, at around T_a 5 °C (Fig. 5.5) the TMR also increases to regulate T_b at 6 °C at even lower T_as (Fig. 5.6). In some species the T_b that is regulated during torpor is increased somewhat at very low T_as. For birds similar relationships are observed, but the normothermic T_b and BMR are somewhat higher.

The Range of Body Temperatures During Torpor and the Effect of Body Mass

As the T_b typically falls substantially at torpor entry, the minimum T_b during torpor is well below the normothermic T_b, on average falling to around 18–20 °C in daily heterotherms, and to 6 °C in hibernators (Figs. 4.3 and 5.5). However, the minimum T_bs for all heterotherms examined, range from about −3 °C to around 30 °C. Importantly, many of these reported values are species-specific regulated T_b minima, not just a T_b measured at any T_a above the T_{set}. At the lower end of T_bs measured,

Table 5.1 Minimum body temperatures below 0 °C in hibernators

Species	Body mass (g)	Minimum T_b (°C)	Source
European hedgehog, *Erinaceus europaeus*	700	−0.57	Rutovskaya et al. (2019)
Romanian hedgehog, *Erinaceus roumanicus*	700	−1.3	Rutovskaya et al. (2019)
Long-eared bat, *Plecotus auritus*	10	−2	Eisentraut (1956)
Gould's wattled bat, *Chalinolobus gouldii*	15	−0.2[a]	Stawski and Currie (2016)
Arctic ground squirrel, *Urocitellus parryii*	650	−2.9	Barnes (1989)
European ground squirrel, *Spermophilus citellus*	250	−0.9	Hut et al. (2002)
Daurian ground squirrel, *Spermophilus dauricus*	350	−2.4	Yang et al. (2011)
Golden-mantled ground squirrel, *Callospermophilus lateralis*	200	−1.0	Healy et al. (2012)
Yellow-pine chipmunk, *Tamias amoenus*	50	−1.0	Geiser et al. (1994)
Hazel dormouse, *Muscardinus avellanarius*	25	−2.9[a]	Pretzlaff and Dausmann (2012)

[a]T_{skin}

reductions of T_b below the freezing point of water have been observed, which are possible because of solutes in body fluids and supercooling (Barnes 1989). A T_b below 0 °C used to be considered exceptional during torpor. However, the number of species known to reach T_bs below the freezing point of water is steadily growing and now includes at least ten mammalian hibernators, insectivores, bats and rodents; but as yet no birds (Table 5.1).

Whereas homeothermic mammals have a narrow range of T_b (Hetem et al. 2016), the range of T_b from the minimum T_b to maximum T_b in hetrotherms can be enormous. In the most extreme cases the T_b range approaches or even exceeds 40 °C in hibernating desert bats (*O. petersi*) and arctic ground squirrels (*U. parryii*) (Fig. 5.7), which is similar to some terrestrial ectotherms (Tattersall et al. 2012). The average T_b range for hibernators is around 32 °C, between about 37 °C during normothermia to 5 °C during torpor (Ruf and Geiser 2015). In daily heterotherms the most extreme T_b ranges are not far from these in hummingbirds with a difference between the minimum and maximum T_b of around 37 °C for the black metaltail (*M. phoebe*) (Wolf et al. 2020) or a range of ~34 °C for freckled nightjars (*C. tristigmata*) (Smit et al. 2011). However, for average daily heterotherms the T_b range is ~20 °C for birds and ~19 °C for mammals (Fig. 5.7), because the T_b minima are around 18–20 °C (Ruf and Geiser 2015).

The minimum T_b is a function of body mass in avian and mammalian daily heterotherms and, at much lower T_bs, in mammalian hibernators (Fig. 5.8). Birds expressing daily torpor have a predicted minimum T_b of just under 20 °C at a body mass of 10 g, whereas at a body mass of 500 g, the body mass of the largest bird known to express torpor, the minimum T_b is just under 30 °C. Mammals using daily

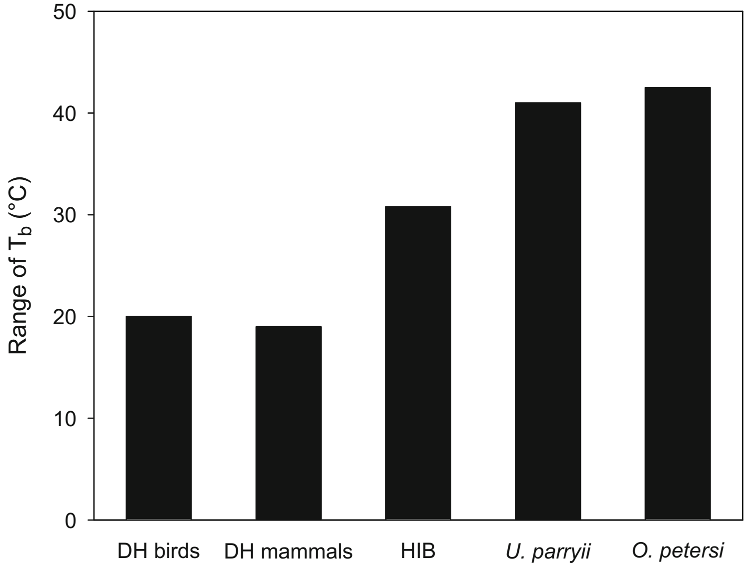

Fig. 5.7 The range of T_b for average avian and mammalian daily heterotherms (DH), mammalian hibernators (HIB) and two extreme values for arctic ground squirrels (*Urocitellus parryii*) and a desert bat (*Ozimops petersi*). Data from Barnes (1989), Bondarenco et al. (2014), Ruf and Geiser (2015)

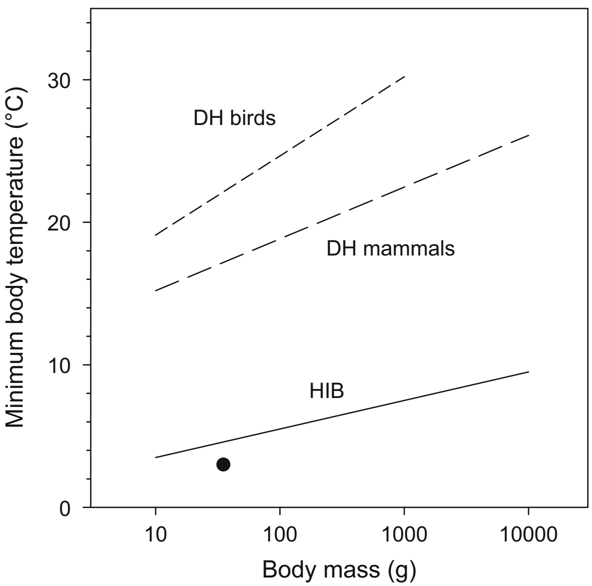

Fig. 5.8 The regression lines for the minimum body temperature (T_b) as a function of body mass in avian and mammalian daily heterotherms (DH) and in mammalian hibernators (HIB) with a $T_b < 20$ °C, i.e. essentially excluding large carnivores. If the species with $T_b > 20$ °C are included, the HIB line has a steeper slope, but the relationship remains the same otherwise. The only avian hibernator the poorwill (filled circle) falls near the value predicted for body mass of mammals. Data from Ruf and Geiser 2015

torpor have somewhat lower predicted minimum T_bs than birds at the same body mass, with around 15 °C at a body mass of 10 g and around 26 °C at 10 kg. In mammalian hibernators over the same body mass range, a further reduction by about 10 °C is observed, in comparison to daily heterotherms. This excludes minimum T_bs of >20 °C for mainly large carnivores, which are well above the regression line (Ruf and Geiser 2015). The predicted minimum T_b of hibernators is ~4 °C at a body mass of 10 g, whereas at 10 kg the minimum T_b is about 10 °C; the single known avian hibernator (minimum T_b 3 °C at 45 g) falls near the regression for mammals. If hibernators with a T_b of >20 °C are included in the regression, the body mass range increases, but the relationship is similar with a somewhat steeper slope (Ruf and Geiser 2015). Overall, the greater reduction of the minimum regulated T_b with decreasing body size in all groups compared (Fig. 5.8) suggests that a lower T_b is selected in the smaller species, which have relatively smaller energy stores. This will minimise TMR and the need of thermoregulation during torpor. The differences in T_b between hibernators and daily heterotherms even in the same habitat may be due to the rather short duration of torpor and the need for frequent arousal for foraging in the latter.

The reasons for differences in the minimum regulated T_b among species with the same pattern of torpor and beyond those due to size is likely due to phenotypic plasticity or selection, because regulation of T_b much above the T_a the animal is exposed to is costly and should not be selected for. The reasons why not all animals have an extremely low minimum regulated T_b are more difficult to explain, and perhaps are related to indirect costs such as reduced response times or shortening of telomere length during torpor at low T_b (Humphries et al. 2003; Nowack et al. 2019).

Metabolic Rate and its Reduction during Torpor

The temporal changes of MR and T_b at torpor entry and their interrelations have been closely examined and, despite their transient nature, reveal some underlying mechanisms.

The change of MR during torpor in comparison to that during normothermia can be astonishing. In homeothermic endotherms (Fig. 5.9) the average increase of MR from BMR to the maximum MR during cold exposure, or aerobic metabolic scope, is around 5.5-fold in birds and up to eight-fold for mammals (Hinds et al. 1993). During running, in comparison to BMR, the metabolic scope can be around 17-fold (Hinds et al. 1993) and during hovering flight in hummingbirds it is about 15 to 18-fold (Bartholomew and Lighton 1986; Powers and Nagy 1988). Although rarely discussed with regard to the energetic capabilities of endothermic species, the metabolic scopes from the minimum TMR during torpor to the MR during activity are many-fold higher (Fig. 5.9). Often the scope from TMR to active MR is in the order of 100 or 200-fold, but some extreme examples include bats with a metabolic scope of ~230-fold (*Myotis veliger*; 13 g), ~600-fold (*Nyctophilus gouldi*; 9 g), and

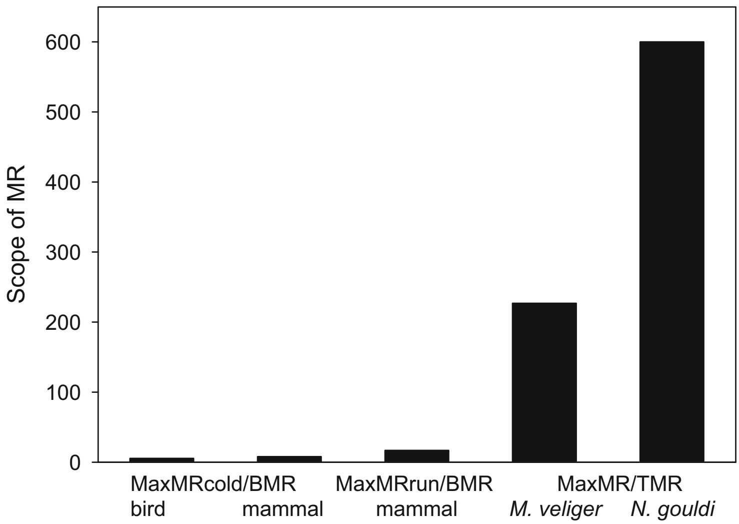

Fig. 5.9 The scope of aerobic metabolic rate (MR) during cold exposure in comparison to BMR (MaxMRcold/BMR) in birds and mammals, the maximum MR during locomotion in comparison to BMR (MaxMRrun/BMR) in mammals (Hinds et al. 1993), and examples for the maximum MR during activity in comparison to the minimum TMR (MaxMR/TMR) in two bats, *Myotis veliger* (13 g, Riedesel and Williams 1976) and *Nyctophilus gouldi* (9 g, Currie et al. 2014). Reptiles would be barely visible on this scale

exceeding 1000-fold (*Vespadelus vulturnus*; 4 g) (Riedesel and Williams 1976; Willis et al. 2005b; Currie et al. 2014).

Thus, few would argue against the fact that the MR is substantially reduced during torpor. What continues to be a topic of debate is about how the MR reduction is achieved. The original view was that (1) because the MR during torpor entry often falls in parallel with the T_b, the low TMRs during steady-state torpor are due to temperature effects slowing metabolic processes because of the typically large reduction of T_b (Hammel et al. 1968; Snapp and Heller 1981). As the TMR in some species is extremely low and lower than expected due to temperature effects alone, it has been proposed that (2) a physiological inhibition must be involved to explain the very low values (Malan 1986; Milsom 1993; Song et al. 1997). In some studies animals were examined at low T_a in the T_a-range below the T_{set} when they were thermoregulating during torpor (e.g. Heldmaier and Steinlechner 1981b). The data from these suggested that, (3) as during normothermia, the TMR during torpor is a function of the T_b-T_a differential (Heldmaier and Ruf 1992). Finally, (4) it has been suggested that the low TMR may be due to a low apparent thermal conductance of torpid individuals (Snyder and Nestler 1990).

Although these proposed mechanisms of MR reduction during torpor are often presented as being mutually exclusive, I argue that they are in fact all correct to some extent. However, their relative contribution to MR reduction depends primarily on whether torpor is entered at T_as near or below the TNZ, the T_a range the torpid

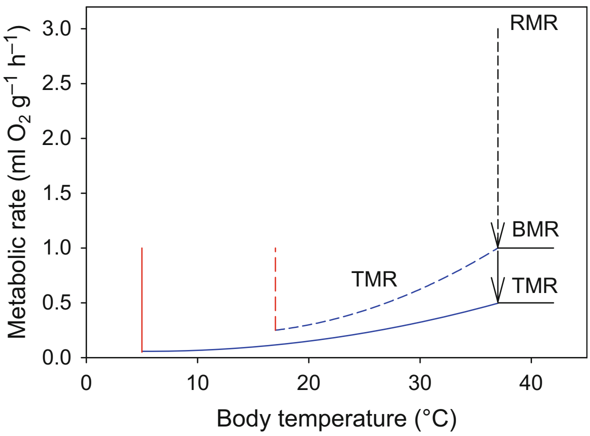

Fig. 5.10 Theoretical model of reduction of metabolic rate (MR) with and without physiological inhibition. The de-activation of normothermic thermoregulation (vertical broken arrow, indicates fall of MR from RMR to BMR without change of T_b), the reduction of TMR from BMR with a reduction in T_b in a thermoconforming animals in steady-state torpor without physiological inhibition (upper blue broken curve), and the transition from BMR to TMR due to physiological inhibition (vertical solid arrow) followed by the reduction of TMR due to the fall of T_b (lower blue solid curve). The red vertical lines indicate the increase in TMR for thermoregulation during torpor

animal is exposed to below the TNZ (thermoconforming at T_as above the T_{set} or thermoregulating at T_as below the T_{set}), the pattern of torpor (daily torpor vs hibernation) and the size of the animal.

Torpor entry appears to entail three major steps: The first of these, observed at low T_as, is a de-activation of heat production for normothermic thermoregulation, or the maintenance of a high T_a-T_a differential. At this time, the T_{set} falls below the previously maintained normothermic T_b but T_{set} is reduced faster than the T_b, because cooling is slowed by thermal inertia (Heller et al. 1977). Perhaps easier to understand is the analogy of switching off an electric heater of a house that instantly reduces energy consumption, but does not immediately result in the cooling of the house. Of course the consumption of electricity does not fall to zero at that point because other appliances and lights in the house are still on, which is analogous to BMR. The generality of the T_{set} model for thermoregulation has been criticised because, unlike for the heater, there appears to be no single temperature controller, but rather an independent thermoeffector loop. Therefore, the term ‘balance point’ has been suggested as alternative to set point (Romanovsky 2007). However, since the MR response observed at the organismal level remains the same, the T_{set} term is still widely used and remains a useful concept in T_b regulation (Tan and Knight 2018). The T_{set} concept is especially useful in explaining torpor entry and other aspects of MR reduction. Therefore, when T_{set} falls at the beginning of torpor entry, the neural signal that maintains a large T_b-T_a differential via heat production ceases. Thus theoretically, as is shown in Fig. 5.10, the MR should fall from RMR to near BMR (i.e. MR without thermoregulatory heat production) without a fall of T_b.

Second, as this reduced MR near BMR after de-activation of normothermic thermoregulation is insufficient for maintenance of a high T_b-T_a differential or a thermal gradient between the body and the surroundings, T_b must decline (Figs. 2.2 and 5.4). This fall in T_b and the resulting temperature effects will cause a curvilinear reduction of TMR (Fig. 5.10). These two metabolic processes appear to be major reasons for the substantial fall in the metabolic rate first below the RMR and then even below the BMR during torpor in daily heterotherms exposed to a T_a below the T_{lc} (Malan 1993; Geiser 2004; Bech et al. 2006). The TMR falls with T_b until the minimum T_b is reached, below which TMR increases for thermoregulation (Fig. 5.10).

However a third mechanism is involved, which is especially obvious in hibernators and during torpor at high T_a. This comprises a physiological inhibition of metabolism employed to reduce TMR to a minimum (Fig. 5.10). Instead of falling with T_b from the BMR, the MR is further reduced via physiological inhibition to TMR, and only then the effects of cooling the T_b reduce TMR to a minimum. Thus usually, physiological inhibition appears to be employed together with temperature effects to lower TMR to the values observed, but again TMR increases for thermoregulation at the T_{set} (Fig. 5.10). At low T_as in thermoconforming animals, the extent of this physiological inhibition seems to be the major reason, in addition to the higher T_bs, why daily heterotherms have almost ten-fold higher minimum TMRs than hibernators (Ruf and Geiser 2015), which, as for the minimum T_b, is likely related to daily foraging.

The above sequence of events is only possible if, at the prevailing T_a, the animal is small enough to have a RMR that is well above the BMR at the time of torpor entry (see Figs. 1.2 and 1.3). If an animal is large, >5 kg, its RMR will not be much above the BMR unless it is very cold, so de-activating normothermic thermoregulation will have little or no effect. Consequently, expressing torpor near the TNZ, which is at low T_as large species, whereas in small species it is at high T_as (Fig. 1.4), requires metabolic inhibition to some extent.

If physiological inhibition is activated immediately upon torpor entry it will form part of the fast initial decline of MR. In this possible scenario, the fall of MR is due to both de-activation of normothermic thermoregulation plus physiological inhibition, but both occur before or during the fall of T_b. Thus, as torpor entry is a transient state, the exact contribution of de-activation of heat production for normothermic thermoregulation, physiological inhibition, and fall of T_b during which stage of the torpor entry phase is hard to untangle, but the available evidence suggests they are all involved.

Evidence for Inactivation of Normothermic Thermoregulation at Torpor Entry

The evidence for de-activation of normothermic thermoregulation comes from two major sources: The first of these is the above mentioned and quantified rapid reduction of the hypothalamic T_{set} during torpor entry, well ahead of the falling T_b, resulting in cessation of normothermic thermoregulation (Heller et al. 1977). Second at torpor entry, MR often falls precipitously before T_b declines, and much faster than T_b (Figs. 2.2 and 5.4). One could argue that this discrepancy is support for the view that physiological inhibition is involved from early in the torpor cycle. While this is possible, it is not the only explanation because similar fast, but transient reductions of RMR to near BMR (a drop of MR by ~80%) have been observed between the activity phase and the resting phase in sugar gliders (*P. breviceps*), which involved a fall of T_b by only ~3 °C without torpor expression (Geiser 2004). This transient fall of RMR without torpor entry supports the interpretation that the fall of T_{set} causing a de-activation of normothermic thermoregulation at torpor entry must be responsible to a large extent for the initial fall of MR at low T_a (Florant and Heller 1977; Heller et al. 1977).

Evidence for the Temperature Effect on MR during Torpor

In multiple taxa and for most studies from which detailed data are available, steady-state TMR is a curvilinear function of T_b or T_a in thermoconforming individuals, which is a characteristic of temperature effects (Schmidt-Nielsen 1997; Hill et al. 2016). These data support the view that temperature is responsible for the reduction of MR during torpor to a large extent. The curvilinear decline of TMR with T_b during torpor is similar to the effect of temperature on SMR of ectotherms (Fig. 1.2). It reflects temperature-dependence of biochemical reaction rates, which typically change by ~two-fold over a 10 °C increment and are referred to as the Q_{10} effect (i.e. $Q_{10} = 2$ means there is a two-fold increase in rate when temperature increases by 10 °C, or a reduction to 1/2 when temperature decreases by 10 °C).

Data showing temperature effects on TMR are available for many avian and mammalian species. Obvious examples of curvilinear falls of steady-state TMR with T_b or T_a include hummingbirds (Lasiewski and Lasiewski 1967; Bech et al. 2006), marsupials (Song et al. 1995, 1997), elephant shrews (Lovegrove et al. 2001, Fig. 5.11), bats (Hock 1951; Willis et al. 2005c; Currie et al. 2014) and rodents (Snapp and Heller 1981; Buffenstein 1985; Zimmer and Milsom 2001). In a few instances, although a temperature-dependence of TMR was observed at high T_as, only small changes of TMR occurred at low T_as (e.g. Buck and Barnes 2000). However, this involved rather small temperature intervals (TMR was ~constant from T_a 4–8 °C) and is likely explained by a contribution of physiological inhibition at the higher T_a and onset of thermoregulation at the lower T_a. In other studies limited

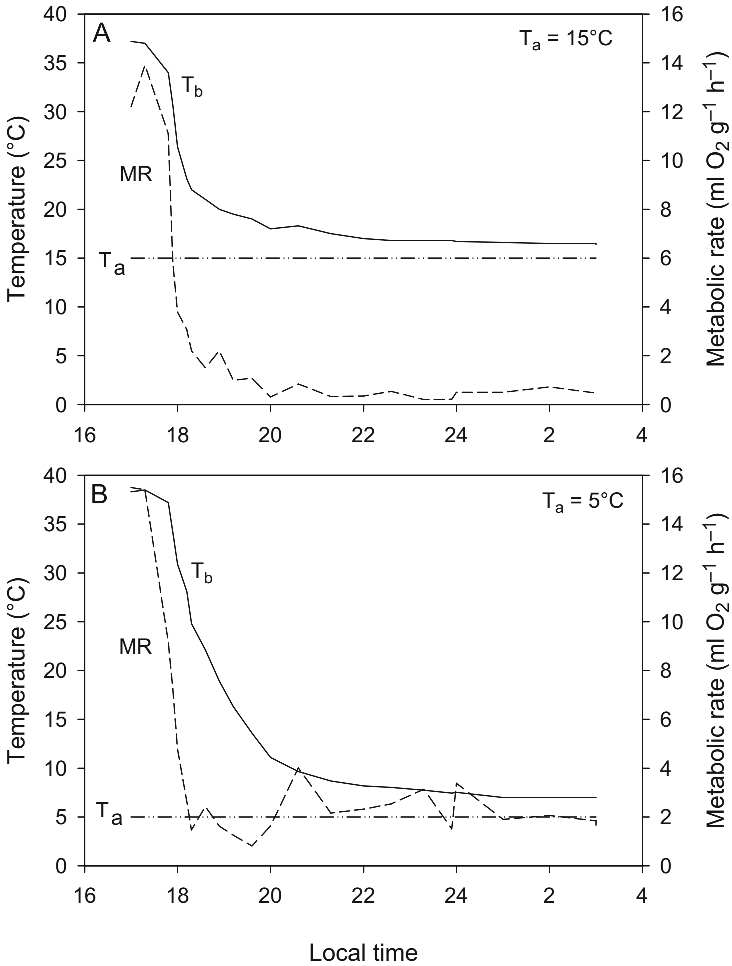

Fig. 5.11 The reduction of body temperature (T_b) and metabolic rate (MR) in an elephant shrew (*Elephantulus rozeti,* 45 g) vs time. The top graph (A) shows an animal that is thermoconforming during torpor entry at an ambient temperature (T_a) of 15 °C. The bottom graph (B) shows an animal that is exposed to T_a 5 °C, which is below the T_{set} and will require thermoregulation after torpor entry. Initially the animal in B shows an MR undershoot at a time T_b is still falling, but then the MR increases for regulation of the T_b during torpor, which commences before the minimum T_b is reached. Note that the TMR after torpor entry is about 8-times higher in the thermoregulating animal at T_a 5 °C than that in the thermoconforming animal at T_a 15 °C. Data from Lovegrove et al. (2001)

temperature-dependence of TMR was observed, but only O_2 consumption minima were used for the analyses, without integrating periodic breathing events, as is required for measuring MR via indirect calorimetry (see Chap. 2).

Further evidence of the temperature effect on MR is observed during torpor entry. When the T_b and MR are examined as a function of time from torpor entry, generally

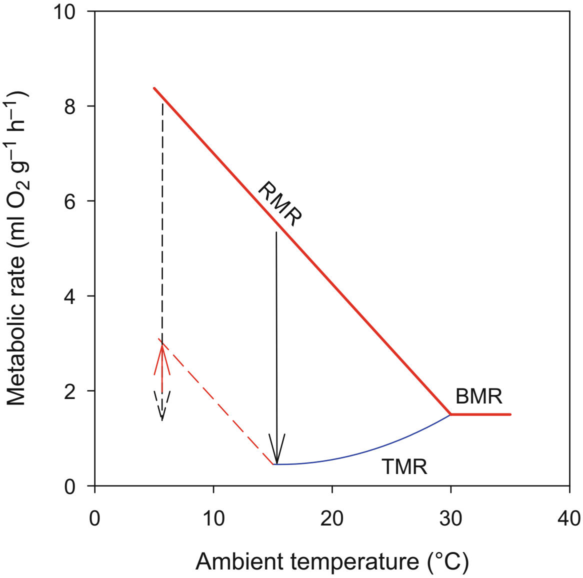

Fig. 5.12 Schematic diagram of metabolic rate (MR) reduction at T_as above and below the T_{set}. When torpor entry occurs at a T_a the animal is not required to thermoregulate during torpor the decline in MR is steady (curvilinear when plotted as a function of time, Figs. 2.2 and 5.4) until it reaches its minimum (black solid arrow at T_a 15 °C). If torpor entry occurs at a T_a the animal will have to thermoregulate once it T_b approaches the minimum, MR can show an initial undershoot below the values required for thermoregulation during torpor (black broken arrow at T_a 5 °C), which can occur because of thermal inertia during cooling of the body. Once T_b approaches the regulated minimum, TMR is again raised (red upward arrow) to prevent a fall of T_b below the T_{set}. Experimental data show that this thermoregulatory response is predictive and that the heat production is activated slightly before the T_{set} is reached (e.g. Fig. 5.11)

a smooth reduction of MR with falling T_b is observed, but as explained above, the fall in T_b is slower because of thermal inertia and therefore, unlike MR, T_b cannot change abruptly by a lowering of T_{set}. The decline of both T_b and MR at torpor entry further supports the view that a temperature effect is involved in the MR reduction and is typically observed at T_as above the T_{set} of the species examined (Figs. 2.2 and 5.11).

However, in the T_a-range below T_{set} in which the animal must eventually thermoregulate during torpor, the pattern of torpor entry differs and appears to contradict the interpretation that temperature effects are involved in the MR reduction. When the T_b during torpor entry is still declining because cooling is slow, the MR may show an undershoot below the values required for regulation of T_b during torpor, but MR then increases again when T_{set} is approached and thermoregulation is activated (Figs. 5.10, 5.11, and 5.12). This phenomenon is more obvious in large species because they cool slowly. The MR undershoot at torpor entry has been observed in marsupials (*Sminthopsis macroura*), elephant shrews (*Elephantulus rozeti,* Fig. 5.11), hamsters (*Phodopus sungorus*) and marmots (*Marmota marmota*)

(Song et al. 2000; Lovegrove et al. 2001; Heldmaier et al. 2004; Jastroch et al. 2016). Dunnarts, *S. macroura*, a daily heterotherm with a minimum T_b or T_{set} of about 15 °C, showed a steady decline of MR and T_b during torpor entry at T_a 18 °C (Song et al. 1996). In contrast at T_a 10 °C, below the T_{set}, a MR undershoot was observed initially during torpor entry, after which the animals regulated a T_b-T_a differential of around 11 °C by an increase of TMR, in comparison to the T_b-T_a differential of about 2 °C during steady-state torpor at T_a 18 °C where they were thermoconforming (Song et al. 1996). *P. sungorus* exhibits a MR undershoot early in the torpor bout when measured at T_a 5 °C. This T_a is well below their T_{set} and their minimum T_b-T_a differential was ~9 °C (Jastroch et al. 2016), about twice that of thermoconforming individuals during steady-state torpor at T_a 15 or 23 °C, which had T_b-T_a differentials of 4–5 °C (Ruf et al. 1993; Geiser et al. 2016).

The decline of T_b and MR in elephant shrew, *R. rozeti* (Lovegrove et al. 2001) at torpor entry shows similar relationships. At T_a 15 °C, *E. rozeti* thermoconformed during torpor entry and the decline of T_b and MR were curvilinear and steady and there was no evidence of thermoregulation during torpor because the T_b was ~16.5 °C and well above the species' T_{set} (Fig. 5.11a). At T_a 5 °C, below the T_{set} of the species, the MR showed an initial undershoot between 18:00 and 20:00, but MR then increased and the steady-state TMR was about 8-times higher than at T_a 15 °C because regulation of T_b during torpor entry commenced when T_b approached the minimum of about 7 °C after the cooling phase (Fig. 5.11b). For large, hibernating *M. marmota*, an initial MR undershoot occurred at torpor entry, but TMR increased later in the torpor bout to maintain a large T_b-T_a differential of around 4 °C throughout the torpor bout of several days (Heldmaier et al. 2004). This T_b-T_a differential of 4 °C is well above the ~1 °C typically observed in thermoconforming hibernators in steady-state torpor. As detailed above, this reflects that initially when T_b and MR fell together, de-activation of normothermic thermoregulation, temperature effects and metabolic inhibition are all involved in reducing MR during the MR undershoot (Figs. 5.11 and 5.12), but as soon as the animal approached minimum T_b, TMR was increased for thermoregulation to slow the fall of T_b although T_b still declined somewhat.

Evidence for physiological inhibition

Although the concept of physiological inhibition of MR during torpor in endotherms has received little support in the past, more recently, data have emerged that do demonstrate its existence (Withers and Cooper 2010). As discussed above, these come from diverse heterotherms, including small heterothermic mammals expressing torpor at low T_a or high T_a in or even above the TNZ and for very large hibernators especially bears, which are also near the TNZ when expressing torpor at T_a around or below 0 °C. In bears (*U. americanus*) the reduction of MR cannot be explained by temperature effects as these would reduce MR by only about 30% assuming a Q_{10} of ~2 for TMR, rather than the observed 75% (Tøien et al.

2011). Therefore physiological inhibition must be responsible for the large reduction in TMR.

Although at much higher T_as than for bears, torpor expression within/near the TNZ, has been observed in several small species, a pygmy-possum (*Cercartetus nanus*), gerbil (*Gerbillus pusillus*) spiny mouse (*Acomys russatus*), and a bat (*Macronycteris commersoni*) (Buffenstein 1985; Song et al. 1997; Grimpo et al. 2013; Reher and Dausmann 2021). For the small species expressing torpor at high T_a, it is impossible to reduce T_b substantially without increasing energy expenditure for evaporative cooling, which would be counterproductive and is known only for those species that use evaporative cooling to prevent a rise of T_b. Therefore small species near the TNZ must employ physiological inhibition to reduce MR and T_b, or MR can fall even without a reduction in T_b (Fig. 5.10). It is likely that the function of physiological inhibition at high T_as is not only to save of energy, but is also to limit an increase of T_b to pathologically high levels without using energy to cool. However, the MR reduction due to physiological inhibition is not instant, requires ~1 h (Reher and Dausmann 2021) and likely requires biochemical changes (Storey 2010). In contrast, the rapid initial MR reduction that can occur at a T_a below the TNZ, largely due to de-activation of normothermic thermoregulation, can take <30 min (Fig. 5.4). Importantly, the reduction of MR near the TNZ is only around 50% of BMR, well above the values observed at low T_b.

At the other extreme, at very low T_a or T_b, the TMRs in small hibernators are reduced more than those of large hibernators and TMRs are also well below those predicted by temperature effects alone with Q_{10} values well above 2 (Fig. 5.16). Therefore, a plausible explanation is that a combination of de-activation of normothermic thermoregulation, temperature effects plus physiological inhibition are collectively causing these low TMRs. Further support for physiological inhibition comes from the observation that the MR reduction from BMR to TMR at high T_b during steady-torpor in hibernators is more pronounced (steeper, $Q_{10} \sim 4$) than at low T_b (shallower, $Q_{10} \sim 2$; Geiser 1988b); if temperature effects were entirely responsible the fall of MR, they should be the same over different temperature ranges. In contrast, in daily heterotherms the Q_{10} remains slightly above 2 over the entire temperature range suggesting that mainly temperature effects are responsive for the fall from BMR to TMR in this group of heterotherms.

Biochemical and molecular evidence also supports the concept of physiological inhibition during torpor (Storey and Storey 1990). Biochemical effects involve suppression of energetically expensive transcription and translation, but also modification of proteins via reversible phosphorylation or differential expression of microRNAs (Storey 2010; Yuan et al. 2015). It also involves suppression of protein synthesis and specifically its initiation and prolongation early during hibernation (Frerichs et al. 1998; van Breukelen et al. 2012). Further, mitochondrial respiration is suppressed during torpor (Staples 2014). Interestingly, the reduction in enzyme inhibition via reversible phosphorylation, as for example for glycolytic enzymes such as pyruvate dehydrogenase, often show a reduction by roughly 50% (Storey 2012), rather similar to the values observed for the physiological inhibition of the whole organism MR.

Evidence for the Effect of the T_b-T_a Differential on TMR

As we have seen above, when torpid animals are exposed to a T_a below their minimum T_b endogenous thermoregulation is activated. The increase in steady-state TMR, in response to a falling T_a for maintenance of a constant or sometimes slightly elevated T_b, is roughly parallel to the RMR (Hainsworth and Wolf 1970; Figs. 5.6 and 5.12). This means the thermal conductance, or the slope of the increase in MR as a function of falling T_a and an indirect measure of heat loss (Fig. 1.3), is about the same during normothermia at high T_b and torpor at low T_b. The relationship described above for the MR undershoot at torpor entry may not appear to support the view of an involvement of the T_b-T_a differential in the regulation of TMR. However, because of the thermal inertia during the cooling phase, T_b requires more time to reach its minimum and will approach it well after TMR, which is reduced quickly because of the de-activation of normothermic thermoregulation, temperature effects and often physiological inhibition, has approached its nadir. Once T_b falls low enough during torpor entry, TMR is raised to slow or prevent a further decline, or, in other words, increased TMR maintains an increased T_b-T_a differential. During steady-state torpor in thermoregulating individuals, this is reflected by the negative relationship between TMR and T_a at T_as below the T_{set}, supporting the view that the T_b-T_a differential determines the TMR, or more precisely the TMR regulates the T_b-T_a differential.

One could argue that the larger steady-state T_b-T_a differential of thermoconforming daily heterotherms (~2 to 6 °C) when compared to hibernators (~0.5 to 2 °C) could explain the differences in TMR between the two groups. However, I argue in thermoconforming individuals it is not the T_b-T_a differential that determines the TMR, but rather the reverse. When a torpid thermoconforming animal is slowly warmed, the T_b-T_a differential decreases because of thermal inertia, which affects both cooling and warming, but the TMR increases with T_b (Currie et al. 2015b). A major influence on the T_b-T_a differential during a normal torpor cycle in thermoconforming individuals is the time since torpor entry, which can be much longer in hibernators than in daily heterotherms. The larger T_b-T_a differential in daily heterotherms seems to be caused mainly by thermal inertia and their relatively high TMR, preventing small differentials during short torpor bouts.

Evidence for the Influence of Thermal Conductance on TMR

Although thermal conductance may appear to be a compelling candidate for MR reduction, it seems to have little effect on TMR. When a thermoconforming animal during steady-state torpor was subjected to a change in thermal conductance as can be done by exposing them to an atmosphere of HeO_2 (79% Helium, 21% Oxygen) which about doubles thermal conductance in comparison to air (79% Nitrogen, 21% Oxygen), TMR was not affected (Geiser et al. 1996b). This observation is similar to the BMR of normothermic animals in the TNZ, also without physiological thermoregulation as in thermoconforming torpid animals. The value of BMR in HeO_2 in comparison to air did not change, but the TNZ shifted to higher T_as by about 3 °C (Holloway and Geiser 2001). However, thermal conductance may be important for MR reduction at torpor entry during the cooling process, and a somewhat reduced conductance has also been observed in thermoconforming torpid individuals, but the reduction of conductance was only a small fraction of that observed for TMR (Geiser 2004).

Effects of Body Mass on Metabolism

Torpor Entry

Many physiological variables of torpor are affected by body mass. These include the T_b discussed above, and steady-state metabolic rate and torpor bout duration

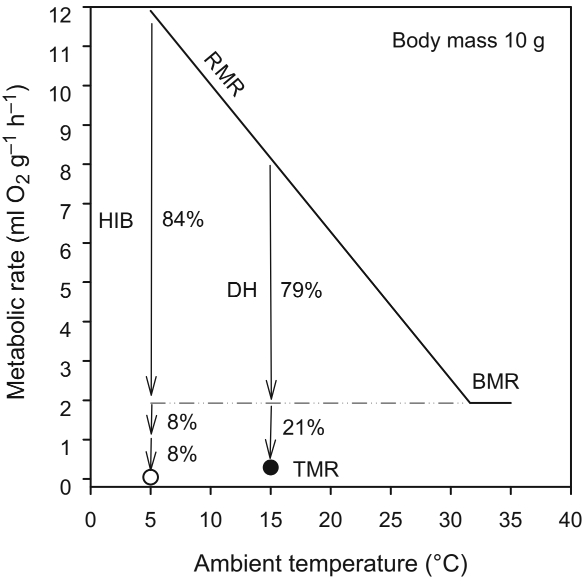

Fig. 5.13 Metabolic rate (MR) reduction during torpor entry vs ambient temperature (T_a) for a 10-g hibernator (HIB) and daily heterotherm (DH). The arrows indicate the fall due to de-activation of normothermic thermoregulation (RMR to BMR) near the T_a below which thermoregulation is activated during torpor, the % values show by how much the MR is reduced from RMR to BMR (84% HIB, 79%DH). For DH (filled circle) it is assumed that the fall of MR below BMR to TMR is entirely due to the fall of T_b (DH 21%), for HIB (circle) it is assumed that the fall of MR below BMR is due to half physiological inhibition and half the fall of T_b (8% and 8% each). Data from Bradley and Deavers (1980), Riek and Geiser (2013), Ruf and Geiser (2015)

discussed below. Body mass also has implications for the transition of MR from RMR during normothermia to TMR during torpor.

Small endotherms exposed to a low T_a, must elevate their RMR to maintain a high and stable T_b (Fig. 5.13). For a 10-g hibernator at T_a 5 °C, which is near its average minimum T_b (Figs. 5.5 and 5.6), the RMR needs to be about six-fold BMR (Fig. 5.13 and heading). In contrast for a 10-g daily heterotherm, with a higher average minimum T_b of around 15 °C the RMR at T_a 15 °C needs to be only about four-fold BMR. At torpor entry, when its normothermic thermoregulation is de-activated, the MR in the 10-g hibernator theoretically can fall by 84% to BMR (MR without physiological thermoregulation) and contributes most to the energy savings during torpor, simply due to the lack of normothermic thermoregulation. The fall of MR due to T_b and metabolic inhibition, assuming they contribute the same, are rather small at about 8% each in the overall reduction of RMR to TMR. The difference in the relative contribution to MR reduction above and below the BMR is simply because the RMR increases more above BMR at the low T_a than it falls below BMR at the same T_a. In the daily heterotherm because it enters torpor from a lower RMR at T_a 15 °C, not T_a 5 °C, the initial reduction of MR due de-activating normothermic thermoregulation is somewhat less at 79%, and,

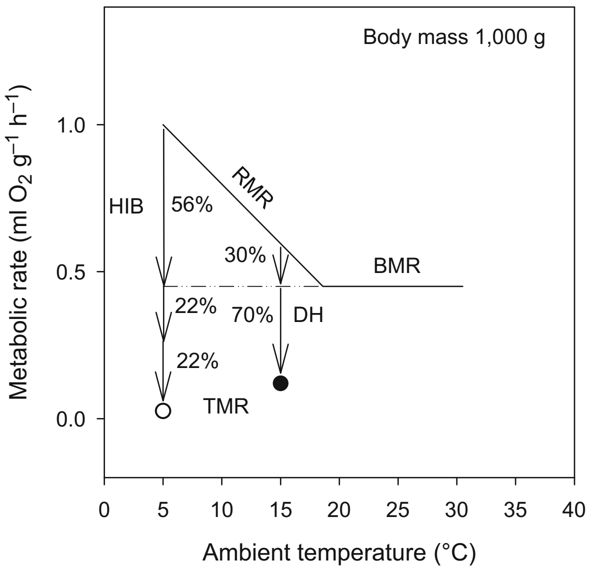

Fig. 5.14 MR reduction during torpor entry vs T_a for a 1000-g hibernator (HIB) and daily heterotherm (DH). The arrows indicate the fall due to de-activation of normothermic thermoregulation (RMR to BMR) near the T_a below thermoregulation is activated during torpor, the % values show by how much the MR is reduced from RMR to BMR (56% HIB, 30% DH). For the daily heterotherm it is assumed that the fall of MR below BMR is entirely due to the fall of T_b (filled circle 70%) for the hibernator (circle) it is assumed that the fall of MR below BMR is due to half physiological inhibition and half the fall of T_b (22% and 22% each). Data from Bradley and Deavers (1980), Riek and Geiser (2013), Ruf and Geiser (2015)

assuming no physiological inhibition is involved, the fall of T_b is responsible for the remaining 21% of the MR reduction (Fig. 5.13 and heading).

At a body mass of 1000 g, the situation is entirely different. For the hibernator at T_a 5 °C near its minimum T_b, RMR needs to increase only by ~two-fold in comparison to BMR (Fig. 5.14 and heading). Consequently, the fall of MR due to de-activation of normothermic thermoregulation is only about 56%, whereas the fall of T_b and physiological inhibition contribute 22% each for the overall reduction from RMR to TMR. In the 1000-g daily heterotherm at T_a 15 °C near its minimum T_b, the reduction of MR due to de-activation of normothermic thermoregulation is only ~30% because of the small increase of RMR above BMR, and therefore the bulk of the MR-reduction is due to the fall of T_b, assuming no physiological inhibition is involved. So even at a body mass of 1 kg, de-activation of normothermic thermoregulation still contributes substantially to energy savings during torpor at low T_a, and the reduction of MR is not entirely caused by metabolic inhibition as it is often stated. However, at even larger masses as for example 80–100 kg for bears, the TNZ extends to below 5 °C (Scholander et al. 1950), and therefore, as pointed out above, de-activation of normothermic thermoregulation will have no effect at all on metabolism at T_as around 5 °C and physiological inhibition must be responsible to some extent for MR reduction.

Steady-State Torpor

Body mass also strongly affects the steady-state BMR and TMR (Ruf and Geiser 2015). The mass-specific BMR of heterothermic endotherms, when plotted on double-log axes, shows the well-known negative function with body mass. For heterothermic mammals the slope for mass-specific BMR vs body mass is −0.31, and therefore +0.69 for the total BMR, which is in the expected range of 0.67–0.75 (Kleiber 1961; White and Seymour 2005; Glazier 2005), and nearer to 2/3 rather than 1, for a directly proportional relationship (Fig. 5.15). The slope of the mass-specific TMR-body mass relationship in daily heterotherms is −0.19, about 62% of that for BMR, and the slope for the total MR is 0.81 (Fig. 5.15). In hibernators the slope of the mass-specific TMR-body mass relationship is reduced even further to −0.12, or only about 38% of the slope for BMR. The slope for the total TMR of hibernators therefore is almost 0.9, well above 0.75 and approximating 1 (Kayser 1961; Geiser 1988b). The reduced slope for TMR in hibernators as a function of body mass is perhaps the best example for a relationship approximating a constant mass-specific MR over a wide range of body masses (i.e. the metabolic rate of each unit of mass is about the same and does not change much with body mass). It supports the view that the slope of MR vs body mass is not governed by a law nor a 3/4 rule (Hulbert 2014), contrary to what is often proposed. Different slopes during different physiological states in heterotherms reflect different energy demands and availability at different body masses.

When compared with the BMR of mammals (important to note here is that the comparison is with BMR, not with the RMR below the TNZ as above in Figs. 5.12,

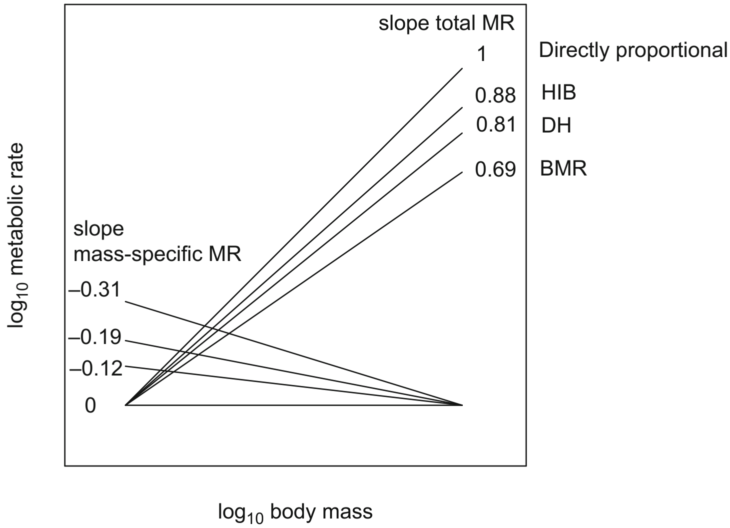

Fig. 5.15 The slopes of total metabolic rate (MR) and mass-specific metabolic rate for heterothermic mammals as a function of body mass on a double-log graph. The theoretical directly proportional relationship of 1 is indicated for comparison for total MR, which is equivalent of a slope of 0 for mass-specific MR (i.e. a unit of body mass of animals of all sizes is equal). Note that the slopes for hibernators (HIB 0.88 total and −0.12 mass-specific) and daily heterotherms (DH 0.81 and −0.19) are closer to 1 or 0, than the slopes for the BMR (0.69 and −0.31). Data from Ruf and Geiser (2015)

5.13, and 5.14), the minimum TMR of daily heterotherms is substantially reduced (Fig. 5.16). However, the MR reduction from BMR (at 100%) to TMR is more pronounced at a body mass of 10 g (a ~81% fall to 19%) than at 10,000 g (a ~62% fall to 38%) (Fig. 5.16). While the reduction of MR by ~60 to 80% will provide substantial energy savings for daily heterotherms, it pales in comparison to that the hibernators. In a 10-g hibernator the TMR is reduced by ~97% in comparison to BMR whereas in the 10,000-g hibernator it is reduced by ~90% (Fig. 5.16). Interestingly when compared with ectotherms, the calculated SMR for reptiles at T_b 10 °C (Fig. 5.16), assuming a Q_{10} of 2, the difference between SMR and TMR in small hibernators (10 g) is minor, whereas the TMR of the large hibernator (10,000 g) is about twice that of the reptile SMR at that body mass. Consequently, the slope for the reptile SMR at T_b 10 °C is similar to that of the BMR of mammals, but this is only correct if the real Q_{10} for reptiles is 2. For birds relationships are similar to mammals and the TMR of the single avian hibernator falls near the mammalian regression line (Ruf and Geiser 2015).

Thus the overall reduction of MR is much higher in hibernators than in daily heterotherms and the relative reduction in MR in comparison to the BMR in both is more pronounced in small than in large species. Probably this has been selected to maximise energy savings in small species. On the large size extreme and not shown on the graph are the bears. For comparison in an 80-kg bear (*Ursus armericanus*) the

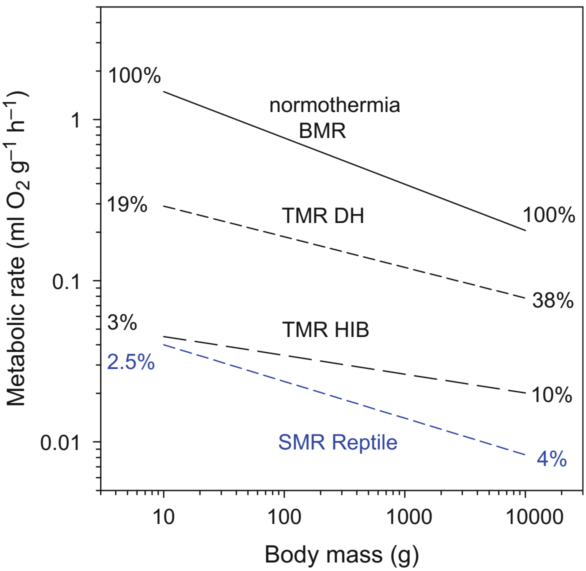

Fig. 5.16 The regression lines for the minimum metabolic rate during normothermia (BMR) and torpor (TMR) in mammals expressing daily torpor (DH) and hibernation (HIB) as a function of body mass on a double log graph. The percentage values are given in comparison to BMR=100% at a body mass between 10 g and 10,000 g. Note that the MR reduction is relatively more pronounced in small than in large species, that the minimum TMR in hibernators (TMR HIB) is only a fraction of those expressing daily torpor (TMR DH) and that the slope for the relationship for hibernators is less steep than that for BMR (see also Fig. 5.15). The SMR for reptiles at a T_b of 10 °C is shown for comparison. It is similar to the TMR HIB at a low mass, but lower at high masses and therefore the slope for SMR is similar to that of BMR. Birds are not shown for clarity and because they are similar to mammals. SMRs calculated from Bennett and Dawson (1976) assuming a Q_{10} of 2, the other values from Ruf and Geiser (2015)

reduction in TMR when expressed as a percentage of BMR is ~75% (Tøien et al. 2011), substantially less than in small hibernators.

The differences in TMR between daily heterotherms and hibernators (Fig. 5.16) might be assumed to be due to the differences in the minimum T_b (Fig. 5.8). However, this is not the case because the ~10 °C difference in minimum T_b between hibernators and daily heterotherms is not sufficient to explain the almost ten-fold difference in minimum TMR between the two, because temperature effects would predict only an ~two-fold difference (Schmidt-Nielsen 1997; Hill et al. 2016).

Torpor Versus Hypothermia

As we have seen above torpor is a precisely controlled physiological state that involves a coordination between thermoregulation, temperature effects, physiological inhibition and other processes during a torpor cycle. In a schematic diagram

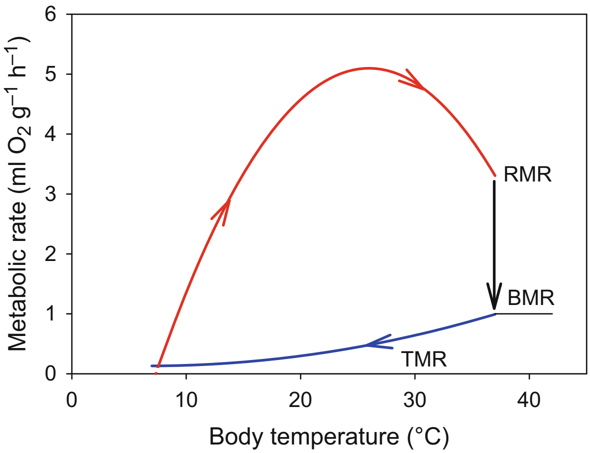

Fig. 5.17 Schematic diagram of interrelations between T_b and MR during entry into torpor without metabolic inhibition and arousal from torpor. The vertical black down arrow from RMR to BMR indicates the de-activation of normothermic thermoregulation. The blue curve (arrow pointing left) shows the decline of TMR due to the fall of T_b. The red curve (arrows pointing right) shows the MR increase during endothermic rewarming; it is limited initially by the low T_b, reaches the maximum MR when T_b approaches 30 °C, and then falls again as the normothermic T_b is approached. Values are approximate from Geiser et al. (2014)

from torpor entry to the end of arousal (Fig. 5.17), the MR is shown as a function of T_b. As described (Fig. 5.10), the transition from RMR to BMR can occur without a fall in T_b. However after this initial step, cooling of the body and its effect on TMR begins, which may involve an additional physiological inhibition to further reduce TMR. The TMRs during torpor entry remain low and decline curvilinearly with T_b to a minimum, in this example to T_b 7 °C. During rewarming from torpor from this T_b, the MR increases immediately and remains well above the MR during entry. However, the highest possible MR is limited initially by the low T_b and the maximum MR is only reached when T_b approaches about 30 °C, and then falls again as the normothermic T_b is approached (Figs. 5.4 and 5.17). All of these physiological changes during a bout of torpor can occur at a constant T_a below the TNZ.

The schematic diagram of a torpor cycle can be compared with that for cold-induced hypothermia and the associated rewarming process from hypothermia (Fig. 5.18). In contrast to torpor entry, induction of cold-induced hypothermia is characterised by an unsuccessful attempt by the animal to maintain a high T_b via a high MR. However, because heat loss exceeds heat production, MR falls with T_b, first gradually but then more steeply at T_bs below ~20 °C. Again in contrast to torpor, the animal cannot rewarm from low T_b at low T_a and, if it survives the cooling process, requires an external heat source to do so. The rewarming process from hypothermia is passive and occurs after exposure to a high T_a after which MR slowly rises with an increase in T_b. The MR during the rewarming phase remains below that

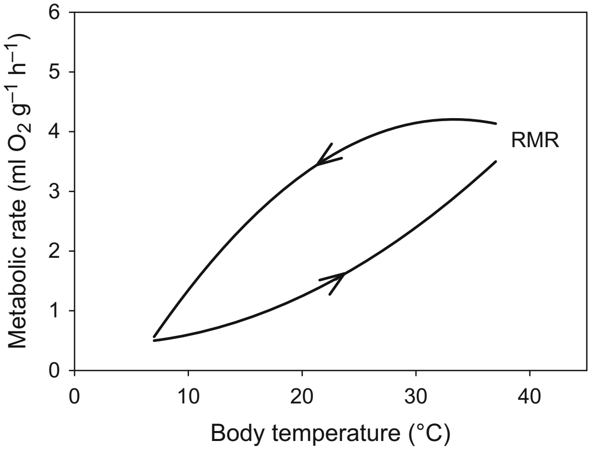

Fig. 5.18 Schematic scheme of the interactions between T_b and MR during cold-induced hypothermia. In contrast to torpor entry, entry into hypothermia is characterised by the animal unsuccessfully attempting to maintain a high T_b via a high MR which falls (arrow pointing left) as the T_a falls because heat loss exceeds heat production. Again in contrast to torpor during rewarming (arrow pointing right), the rewarming process from hypothermia is passive and lower than the MR during the T_b decline. Values are approximate from Geiser et al. (2014)

during the cooling phase, the opposite from the torpor cycle. Animals also may become hypothermic during a torpor bout if the T_a is too far below the T_{set} or energy stores are depleted and some individuals may die (MacMillen 1965; Tucker 1966; MacMillen and Trost 1967).

The differences in thermal energetics seem substantial enough to warrant the use of different terms for the two states, one physiological the other pathological (see also Morhardt 1970; Lyman et al. 1982). However, despite these differences, torpor is often called hypothermia and vice versa in the literature (see Geiser et al. 2014). Indeed, one of the early hibernation symposia recognised and specifically emphasised the differences in its title: 'Hibernation-Hypothermia: perspectives and challenges'. The differences were outlined in the Foreword (South et al. 1972).

In an attempt to address this problem with terminology the terms 'nocturnal' or 'natural' hypothermia have been used to describe the usually shallow bouts of torpor in birds. However, as mentioned in Chap. 3, the question arises whether these terms best describe torpor or whether natural hypothermia is in fact what is observed in juvenile altricial birds and mammals, which during development when only partially endothermic become cold at night and rewarm on the next day apparently passively and survive (see also Chap. 7).

Cold-induced hypothermia can differ from hypothermia induced by exposure to chemicals. Such chemicals often interfere with heat production. For example, hydrogen sulfide (H_2S), when applied at pharmacological dose, causes metabolic depression by inhibiting cytochrome c oxidase, induces a 'torpor-like' state in mice (*Mus musculus*) (Blackstone et al. 2005). In mice exposed to H_2S, MR fell before T_b

because heat production was inhibited. However, this was not a controlled response as observed during torpor, because mice only rewarmed passively after the chemical was metabolised or excreted and individuals were exposed to high T_a. At physiological levels, however, H_2S is a signalling molecule (Kimura 2015; Giroud et al. 2021). Other chemicals that induced a torpor-like state are the glucose inhibitor 2-deoxy-D-glucose (2DG), a non-metabolisable glucose analogue, or mercaptoacetate (MA) which causes fatty acid deprivation (Dark et al. 1994; Westman and Geiser 2004). Especially for 2DG the physiological variables during the torpor-like state differed substantially from natural torpor, whereas for MA values for the variables were similar, but animals were only measured above the T_{set} (Westman and Geiser 2004). It is not really surprising that application of a single chemical does not satisfactorily mimic the complex processes that occur during torpor. Nevertheless, more work in this area should help improve our understanding of the physiology of torpor.

Heart Function

As metabolism continues during torpor, O_2 and nutrients must be suppled and CO_2 removed from cells. Cardiac function of heterotherms is possible at low T_b, often well below the 'critical' temperature of around 20 °C where hearts of large homeotherms suffer circulatory arrest and ventricular fibrillation (Johansson 1996; Oberhammer et al. 2008). The heart of heterotherms, especially those of hibernators are resistant to ventricular fibrillation and continue to function at low T_b. The continued function at low T_b is perhaps due to different adrenergic innervation in hibernators, different enzyme temperature relationships, lower melting points of cardiac lipids and effective handling of intracellular calcium by muscle cells (Johansson 1996). However, even isolated perfused hearts of daily heterotherms, which typically do not lower T_b below 10 °C, continue to function at around or below 10 °C, well below those of homeotherms (Lyman and Blinks 1959; Geiser et al. 1989). The minimum T_b of heterotherms and the temperature of cardiac arrest of isolated hearts are positively correlated, suggesting a functional link (Geiser et al. 1989). Though, the temperature of cardiac arrest is lower than the minimum T_b (Fig. 5.19) especially in species with a high T_b during torpor.

Cardiac function is crucial during a torpor cycle to enable gas exchange and nutrient supply (Milsom et al. 1999). Similar to MR, at torpor entry heart rate is reduced before T_b falls. In rodent hibernators, heart rate is reduced by parasympathetic activation and the appearance of skipped beats on an electrocardiogram seem to signal the onset of torpor. However, lengthening the time between evenly spaced beats also contributes to slowing of the heart (Lyman 1982; Milsom et al. 1999; Zimmer and Milsom 2001). Arousal is associated with an increase in sympathetic activation that elevates heart rate before T_b increases and this sympathetic activity seems to be a major signal for arousal from hibernation (Milsom et al. 1999). The decrease and increase of heart rate during a torpor cycle is usually described as a

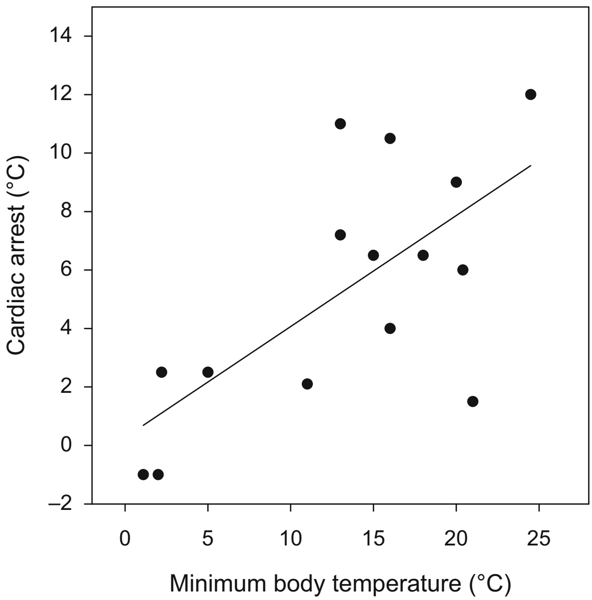

Fig. 5.19 Cardiac arrest as a function of the minimum body temperature (T_b) of heterothermic mammals. The cardiac arrest is lower than the minimum T_b, especially in daily heterotherms with a high minimum T_b. Data from Geiser et al. (1989)

hysteresis, however it is more complex in endotherms than in ectotherms because, as for MR, the initial reduction in heart rate typically follows the de-activation of normothermic thermoregulation and heart rate can fall well ahead of T_b. During torpor, heart rate is reduced substantially. However, low heart rates are compensated for by an increase in stroke volume. There is also an increased peripheral resistance because of increased blood viscosity and reduced venous return to the heart. Although the cardiac output can fall as much as 98% during deep torpor, the blood pressure usually falls only by about 20–40% because of the increase in blood viscosity and peripheral resistance with decreasing temperature (Milsom et al. 1999; Currie et al. 2014).

The reductions in heart rate during torpor can be large. For example in small hibernating long-eared bats (*Nyctophilus gouldi*, 9 g), which may have heart rates approaching 1000 beats/min during activity or ~800 beats/min at rest like other small endotherms, the minimum heart rate during deep torpor at a T_a of 0 °C was as low as 5 beats/min or 8 beat/min on average, a 99% reduction (Currie et al. 2014). These heat rates are well below those reported in the past for small hibernating bats suggesting these animals were not in steady-state torpor (Currie et al. 2014). In both resting and torpid *N. gouldi*, heart rate was strongly correlated with MR, but the relationship differed between normothermia and torpor, and there was a clear lack of association for the values measured the between physiological states (Currie et al. 2014). Further, the waveforms of the electrocardiogram in this bat were substantially prolonged at low T_b (Currie 2018).

In the slightly larger pygmy-possum (*Cercartetus nanus*, 35 g), the maximum resting heart rate was 630 beats/min. At a T_b of 8 °C, heart rate during torpor was reduced to a minimum of 8 beats/min, also well below previously reported values

(Swoap et al. 2017). During deep bouts of torpor, shivering, during which ventilation occurred was observed in regular intervals and heart rate increased to 40 beats/min. When the electrocardiogram of *C. nanus* was examined with regard to the duration of the electric signal responsible for cardiac contractions, it decreased by over 80% from ~12 ms during normothermia to ~70 ms during torpor, and this prolongation appeared to be due to temperature effects (Swoap et al. 2017).

In medium-sized ground squirrels (*Callopermophilus lateralis* ~200 g and *Urocitellus columbianus* ~500 g) heart rates decreased from around 300 beats/min during normothermia to 3–5 beats/min during deep hibernation (Milsom et al. 1999). It is somewhat surprising, and reminiscent of TMR, how similar the heart rate minima (about 5–8 beats/min) are between the small hibernators referenced above, considering the body mass range of 9 g to 500 g and the substantial differences in heart rates during normothermia (about 300–800 beats/min). In the much larger bears (*Ursus arctos,* most individuals >100 kg) heart rate fell from about 70 beats/min during normothermia to a minimum of around 15 beats/min (i.e. a reduction by 80%) with an fall of T_b by ~5 °C (Evans et al. 2016), a much less pronounced reduction than for the smaller hibernators.

In small daily heterotherms heart rates are reduced substantially less than for small hibernators. In blossom-bats, (*Syconycteris australis*, 18 g) heart rate during normothermia (T_b ~ 34 °C) was ~480 beats/min, which fell to ~70 beats/min during daily torpor at a T_b of ~23 °C (Currie 2015). A significant relationship was observed between MR and heart rate in *S. australis*, but the slope for this relationship was much steeper than that in hibernating *N. gouldi*. In hamsters, (*Phodopus sungorus*, 35 g) expressing daily torpor heart rate decreased from ~350 beats/min during normothermia (T_b ~ 36 °C) to ~70 beats/min (T_b ~ 21 °C) (Mertens et al. 2008). Similarly, in laboratory mice (*Mus musculus*, 22 g) heart rate fell from ~600 beats/min during normothermia (T_b 36.6 °C) to 158 beats/min during daily torpor (T_b 25.9 °C) and blood pressure fell as well (Swoap and Gutilla 2009).

Breathing Patterns

During torpor when both MR and heart rates are reduced and animals are in steady-state torpor, breathing continues but breathing rates also decline. During torpor cycles in hibernators lung tissue also undergoes substantial reversible changes in protein structure (Talaei et al. 2011). Breathing in many torpid hibernators is not steady, but episodic (Malan 1982). Other species show a prolongation between breaths, or the breathing patterns are temperature-dependent. During torpor entry, the breathing rate slows in parallel with the fall of MR rather than T_b (Zimmer and Milsom 2001). Episodic breathing typically is characterised by prolonged periods of no breathing (apnoea) lasting up to several hours, followed by a short period of rapid breathing (polypnoea), but at a slower rate than during normothermia. Species for which intermittent breathing has been observed include mainly hibernators, such as echidnas (*Tachyglossus aculeatus*), pygmy-possums (*Burramys parvus*), bats

(*Rhinopoma* spp.), hedgehogs (*Erinaceus europaeus*) and ground squirrels (*Callospermophilus* spp.), but also some daily heterotherms (Kristoffersson and Soivio 1964; Geiser and Kenagy 1988; Bech et al. 1992; Geiser and Broome 1991; Levin et al. 2015).

In echidnas (*T. aculeatus*) the breathing patterns during hibernation were irregular, but during torpor entry, respiration rate fell from about 6 breaths/min in thermoneutrality (Bech et al. 1992) often to <1 breath/min. Some torpid individuals were breathing regularly with one breath every 3–4 min, whereas others showed episodic breathing with apnoeas lasting for up to almost 2 h (Nicol et al. 1992). Pygmy-possums (*B. parvus*) exhibited periods of apnoea of about 20 min, which were interrupted by bursts of breathing at T_as when animals were thermoconforming. However, when possums were cooled below their T_{set} and began to increase TMR for thermoregulation, the breathing rate became regular (Geiser and Broome 1991, 1993) similar to ground squirrels (Fig. 5.20). In hedgehogs (*E. europaeus*) periods of apnea lasted for up to 150 min and were interrupted by 40–50 respirations over about 3–5 min (Kristoffersson and Soivio 1964). In big brown bats (*Eptesicus fuscus*) apnoeas lasted for 4–12 min at a T_b of 20 °C and increased to up to 150 min at T_b 10 °C. Apnoeas were associated with a significant decrease in arterial blood pH and PO_2 towards the end of the apnoeic cycle (Szewczak and Jackson 1992). Similarly, in mouse-tailed bats (*Rhinopoma* spp.), which hibernate in geothermally heated caves at a stable high T_a of around 20 °C, apnoeas were temperature-dependent and were longest at the T_a of their hibernaculum, where the apnoeas lasted for 15 min on average to a maximum of 28 min and these bats opened and closed their nostrils with their breathing cycle (Levin et al. 2015). In dormice (*Eliomys quercinus*) apnoeas lasted for up to 130 min and were interrupted by period of breathing of 1–8 min (Pajunen 1970).

Golden-mantled ground squirrels (*C. saturatus*), changed breathing patterns with T_a (Geiser and Kenagy 1988). At T_a 8 °C and 4 °C, thermoconforming animals in steady-state torpor used episodic breathing and this was reflected in a strongly fluctuating TMR as measured via O_2 consumption (Fig. 5.20). At T_a 2 °C, near the minimum regulated T_b, respiration became regular and TMR was steady. In contrast at T_a − 2 °C when torpid animals were thermoregulating, the TMR was increased by ~5.5-fold relative to TMR at T_a 2 and 4 °C. At a T_a of −2 °C, the TMR showed sinusoidal oscillations with a frequency of about 0.7 cycles/h (Fig. 5.20). The phase of TMR increase was accompanied by a ventilation rate of about 6 breath/min, whereas the phase of TMR decline coincided with ~3 breath/min. It appears that the change in breathing patterns and TMR reflect periods when thermoregulation during torpor was somewhat relaxed alternating with periods when it was re-activated, reminiscent of an oscillation around a set-point.

A transition between episodic breathing and more even breathing as temperature decreased has also been observed in *C. lateralis* (Hammel et al. 1968; Webb and Milsom 2017). However periodic breathing is not restricted to hibernators. Brief periods of apnea have been observed in daily heterotherms such as the marsupial kultarr (*Antechinomys laniger*, 27 g), which showed brief apnoeas lasting about 1 min, followed by polypnoeas (Geiser 1986). Interestingly, in hibernating

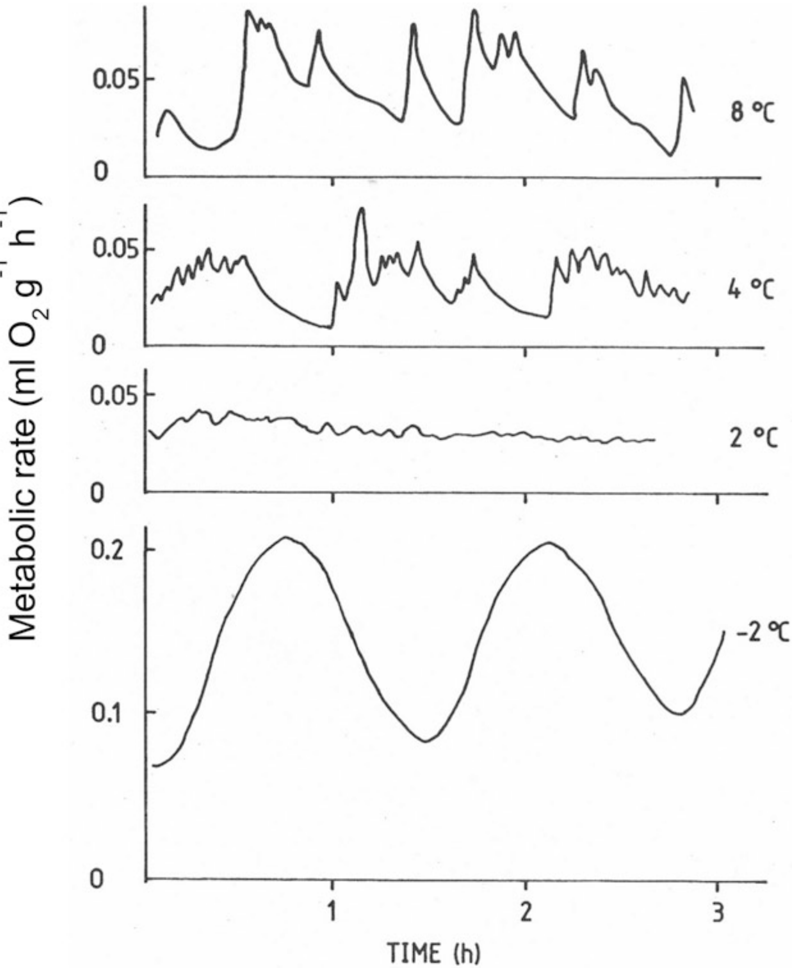

Fig. 5.20 Breathing patterns quantified via O_2 consumption a measure of metabolic rate during torpor in ground squirrels (*Callospermophilus saturatus*) at different ambient temperatures (T_a) as indicated on the right of each panel. At T_a 8 and 4 °C torpid animals were thermoconforming and showed periodic breathing as indicated by the fluctuating TMR (apnoeas indicated by TMR minima, polypnoeas by fluctuating TMR peaks). At T_a 2 °C when the torpid animal approached its minimum regulated T_b, breathing was steady and TMR stable, at T_a − 2 °C the TMR of the thermoregulating individual showed sinusoidal oscillations that were associated with a change in breathing frequency that was however not intermittent. Modified from Geiser and Kenagy (1988) with permission

chipmunks (*Tamias amoenus*) breathing is continuous, although the steady-state TMR is similar to that of ground squirrels (*C. saturatus*) at a similar T_b (Geiser et al. 1990). To my knowledge, the reasons for different breathing patterns are not understood.

The Duration of Torpor Bouts

As we have seen above physiological variables change substantially during bouts of torpor. The time an animal remains torpid is also not constant. It is affected by season and T_a, but also by latitude (Chap. 7). The seasonal change is characterised by brief torpor bouts at the beginning of the hibernation season, long and often more or less constant TBDs in the middle, and brief bouts again at the end. This pattern occurs in the field where T_a may contribute to some extent especially in autumn when T_a, T_{soil} or $T_{hibernaculum}$ are still declining from the high late summer values at a time animals begin to hibernate (Barnes 1989; Young 1990; Arnold 1993). The TBDs then shorten again towards the end of the hibernation season although the T_{soil} may be steady or still declining (Young 1990; Arnold 1993).

The seasonal change in TBD also occurs in the laboratory under constant thermal conditions (Fig. 5.21). The TBDs in ground squirrels (*C. saturatus*) were measured at T_a 2 °C for most of the hibernation season and lasted for ~2.5 days in September, ~8 days in October and 9–11 days on average from November to March (Fig. 5.21). The TBD then declined to ~7 days in April before the hibernation season was terminated. In chipmunks (*T. amoenus*) held under the same conditions, the hibernation season commenced 1 month later, and TBDs were somewhat shorter than in the ground squirrel at the same T_a. In October/November TBDs in chipmunks were 3–5 days on average, increased and remained at around 8.5 days from December to March and then declined to about 5 days in April. Similar seasonal changes have been observed other captive hibernators at constant or more or less constant T_a, including bats and marmots (French 1985) and dwarf lemurs (*Cheirogaleus medius*) (Blanco et al. 2021). Since these changes in TBD (Fig. 5.21) occurred under constant

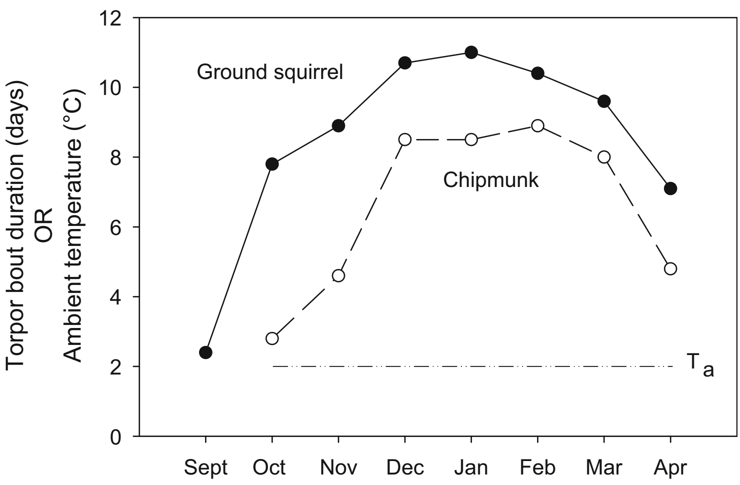

Fig. 5.21 The mean monthly duration of torpor bouts (TBD) in ground squirrels (*Callospermophilus saturatus*) and chipmunks (*Tamias amoenus*) as a function of season. The T_a was maintained at a constant 2 °C from October to April. Data from Geiser et al. (1990)

thermal and environmental conditions, and were associated with seasonal changes in TMR and minimum T_b, the seasonal change in TBD must have been due to a biological rhythm (Geiser et al. 1990).

Effects of Temperature on Torpor Bout Duration

The effect of season on TBD in hibernators can, to some extent, be influenced acutely by T_a (MacCannell and Staples 2021). For observed differences of TBD with latitude (Chap. 7) T_a also may be involved, but it is likely that longer bouts in hibernators at higher latitudes reflect long-term selection because long TBDs with low energy use are required for survival of a longer cold season.

Apart from acclimation effects, the direct effect of T_a on TBD is to a large extent acute. However, it is important that such thermal responses of TBD are examined at a time of year when TBD is near constant such as mid-winter for hibernators to exclude the intrinsic seasonal effects. In the past it was often assumed that TBD in hibernators is a continuous function of T_a or T_b, and forms either a linear or exponential relationship with temperature (Twente and Twente 1965; Willis 1982; French 1985). While this is correct over a wide T_a-range, it is, however, not the case over the entire T_a-range over which torpor is expressed by hibernators in the wild (Fig. 5.22). TBD is inversely related to T_a and T_b only over the T_a-range where torpid animals are thermoconforming, i.e. above the T_{set}. In this T_a-range, in which T_b and TMR decline with T_a and the T_b-T_a differential remains largely unchanged (Fig. 5.23), TBD increases substantially, often by two to four-fold (Fig. 5.22). For example in ground squirrels (*C. lateralis*), TBD at a T_b of 25 °C was just over 1 day, whereas at a T_b of 2 °C, following a curvilinear increase, TBD in the still thermoconforming animal was about 9 days (the T_b here is shown on a T_a axis because the T_b-T_a differential is typically constant and small, in this example ~1 °C during hibernation, Twente and Twente 1965). The thermal response of TBD in *C. saturatus* was similar to that of *C. lateralis* in the T_a-range in which both were thermoconforming (Fig. 5.22).

The TBD increase with decreasing T_b or T_a does not continue at low T_a (Pengelley and Kelly 1966). When torpid animals change from thermoconforming to thermoregulating during exposure to a T_a below T_{set}, the relationship changes (Fig. 5.22). Below this point, the TBDs become shorter with decreasing T_a. This response of TBD at T_as below 0 °C, is pronounced in arctic ground squirrels (*Urocitellus parryii*). Although *U. parryii* increased TBD from about 5 days to 15 days when thermoconforming between T_a 20 and 0 °C (Buck and Barnes 2000), this relationship was reversed once animals began to thermoregulate, and TBD declined from ~15 days at 0 °C to ~7 days at −16 °C. Other hibernating ground squirrels, such as *C. saturatus* show similar relationships (Figs. 5.22 and 5.23). Although the TBD of *C. saturatus* was shorter than in *U. parryii* at the same T_a, likely due to the effects of latitude (Chap. 7), the thermal response of TBD, although measured over a smaller T_a-range, was qualitatively similar. When *C. saturatus* was

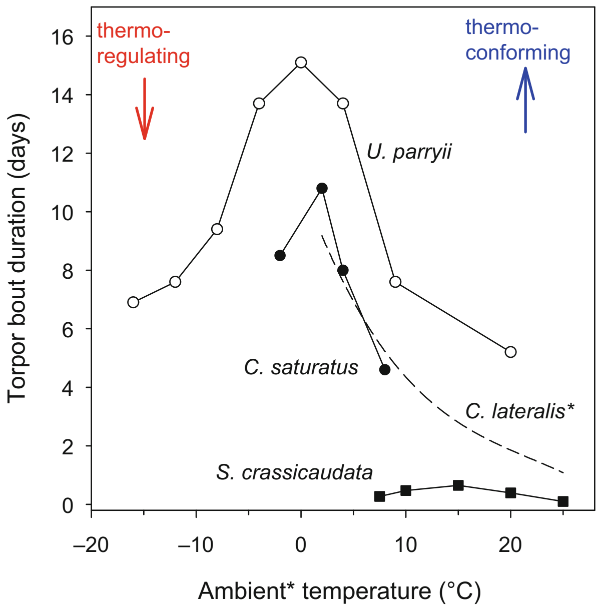

Fig. 5.22 Torpor bout duration (TBD) as a function of ambient temperature (T_a) in several ground squirrel hibernators (*Urocitellus parryii*, *Callospermophilus saturatus*, *C. lateralis*) and a daily heterotherm the dunnart (*Sminthopsis crassicaudata*) for comparison. For *C. lateralis**, which only was measured in the T_a range it was thermoconforming, TBD is shown as a broken regression line and TBD was measured as a function of T_b, but since the T_b-T_a differential in thermoconforming hibernators is small (~1 °C) the data are comparable. Note that TBD increases over the T_a range in which the species thermoconform (right blue arrow up), but decreases in the temperature range in which animals thermoregulate (left red arrow down). Although *C. lateralis* and *S. crassicaudata* express torpor at the same T_a, TBD is over ten-fold longer in the former. Data from Twente and Twente (1965), Geiser and Baudinette (1987), Geiser and Kenagy (1988), Buck and Barnes (2000)

thermoconforming between T_a 8 and 2 °C, TBD increased by more than two-fold from 4.6 to 10.8 days, however when exposed to T_a −2 °C, TBD was reduced by 20% (Figs. 5.22 and 5.23). In both *U. parryii* and *C. saturatus*, the decline in TBD in thermoregulating torpid individuals was associated with a substantial increase in TMR by 11-fold in *U. parryii* (Buck and Barnes 2000) and 5.5-fold in *C. saturatus* (Fig. 5.20). In both species this was accompanied by a doubling of the T_b-T_a differential, in *C. saturatus* from about 1.4 °C at T_a 2–8 °C, to 2.7 °C at T_a −2 °C (Fig. 5.23).

The TBD is similarly affected by T_a in daily heterotherms, but of course at different T_as and with very different TBDs. Although both *C. lateralis* and dunnarts (*Sminthopsis crassicaudata*) express torpor in the same T_a range, TBDs in *C. lateralis* at T_a or T_b 25 °C were greater than ten-fold of that in the dunnart (Fig. 5.22). This difference is not likely caused by a difference in latitude, but rather by an intrinsic difference due to different patterns of torpor expressed by the two species. However, dunnarts also increased maximum TBD by ~2.5-fold from T_a

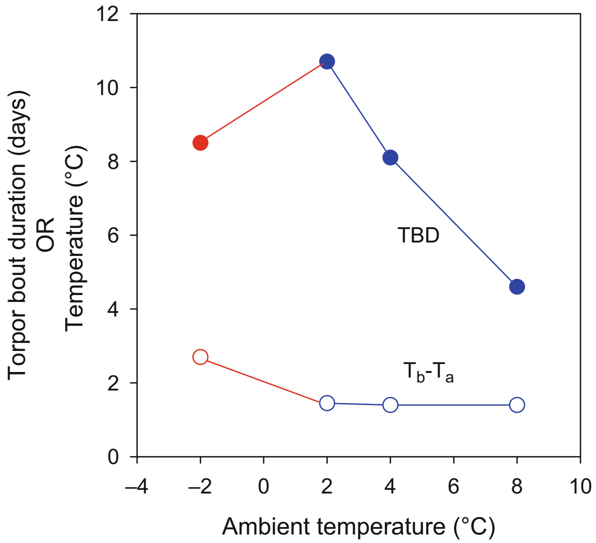

Fig. 5.23 The mean torpor bout duration (TBD) and the T_b-T_a differential as a function of T_a in ground squirrels, *C. saturatus*. Thermoconforming animals are shown in blue, thermoregulating animals in red. The doubling of the T_b-T_a differential from ~1.4 °C (blue, at T_a 2–8 °C) to ~2.7 °C (red at T_a −2 °C) was associated by a 5.5-fold increase in TMR (Fig. 5.20). Data from Geiser and Kenagy (1988)

25 to T_a 15 °C when they were thermoconforming, but reduced TBD when they had to thermoregulate at T_a 7.5 and 10 °C to maintain their T_b above the defended minimum. A similar decrease in TBD in thermoregulating torpid daily heterotherms has been observed in planigales (*Planigale gilesi*, 8 g). The reduction of TMR with T_a above T_a 15 °C in the tiny mammal was associated with a significant greater than two-fold increase in TBD, whereas the reduction of TBD below T_a 15 °C was accompanied by a ~ten-fold increase in TMR (Geiser 2003).

Interestingly, such relationships are often not observed in the wild where TBD may show a steady increase with decreasing T_a, especially when T_a remains above 5 °C (e.g. Bondarenco et al. 2014; Fig. 6.4). However, data from hibernators in cold climates show that TBD declines even in the wild when torpid animals are exposed to low T_as, as, for example, in free-ranging hibernating horseshoe bats (*Rhinolophus ferrumequinum*, Ransome 1990) and ground squirrels (*Urocitellus richardsonii*, Michener 1992). It is also often difficult to determine the exact T_a animals are exposed to in the wild, because it is usually not known whether they are in groups, in nests, or simply in a microclimate that is well buffered from outside thermal conditions. In animals in underground burrows the T_a is well buffered from that experienced outside and thermal buffering improves with rock or soil depth (Geiser and Pavey 2007; Körtner et al. 2008).

Why Do Animals Arouse from Torpor?

In daily heterotherms the normothermic periods between torpor bouts are for foraging and feeding (Körtner et al. 2008) and daily torpor is controlled by a circadian rhythm to a large extent. Therefore the control and function of arousals are clear (Körtner and Geiser 2000a; Ruf and Geiser 2015). As detailed above, hibernating mammals also arouse spontaneously from torpor at periodic intervals after TBDs of several days to several weeks and then remain normothermic typically for several hours. During the hibernation season TBDs show predictable changes and TBD is also strongly affected by T_b and T_a (Pengelley and Fisher 1961; Kristoffersson and Soivio 1964; Twente and Twente 1965; Wang 1978; Pajunen 1983; French 1982, 1986; Barnes et al. 1986; Pohl 1987; Geiser et al. 1990; Michener 1992; Figs. 5.21 and 5.22).

Arousals from deep torpor in hibernators are energetically expensive typically amounting to most of the energy used during hibernation (Wang 1978). Too frequent arousals can threaten winter survival in hibernators because of premature energy depletion and often a lack of foraging opportunities. Nevertheless, the reasons for periodic arousals remain unresolved. In hibernators, in contrast to daily heterotherms, circadian rhythms often do not persist throughout the hibernation season (Ruby et al. 1998; Wassmer and Wollnik 1997; Körtner and Geiser 2000a; Oklejewicz et al. 2001; Ruf and Geiser 2015) and the physiological drivers of periodic arousals to normothermic T_b and the associated IBEs appear highly complex.

A number of hypotheses have been proposed to explain the periodic occurrence of torpor bouts during hibernation. An early hypothesis, that is no longer widely supported, postulated that torpor bouts represent a prolongation of the sleep cycle or rest phase or the natural circadian cycle whose frequency is prolonged by the depression of T_b (Strumwasser 1959; Pohl 1961; Lyman et al. 1982).

An alternative hypothesis is related to metabolic processes. It proposes that the reduction of energy substrates or the accumulation of metabolic wastes forces animals to arouse to re-establish homeostatic conditions (Mrosovsky 1971; Galster and Morrison 1972; Zimmerman 1982; Jinka et al. 2012). Because MR decreases as T_a and T_b decline above the T_{set}, this theory predicts that the duration of torpor bouts should increase with declining T_a and T_b, consistent with observations (French 1982; Geiser and Kenagy 1988). Thus this hypothesis suggests that arousals are triggered by gradual, hourglass-like processes, such as accumulation of metabolic waste products that cannot be excreted at low T_b or by depletion of energy reserves that are temperature-dependent (Soivio et al. 1968; Mrosovsky 1971; Galster and Morrison 1972; Geiser and Kenagy 1988). Therefore, arousals may be linked to a restorative function to counteract a metabolic imbalance (Willis 1982; Geiser et al. 1990; Daan et al. 1991).

Another hypothesis is related to immune function. During torpor a number of species exhibit a reduced function of the immune system (Burton and Reichman 1999; Prendergast et al. 2002; Bouma et al. 2011). This can be associated with depletion of lymphocytes from the blood that are restored during periodic arousal (Bouma et al. 2011). Torpid ground squirrels (*C. lateralis*) did not produce an experimentally induced febrile response during torpor, but did so after arousal. Therefore the reduced immuno-competence that occurs at low T_b during torpor may be the reason why animals have to rewarm periodically to normothermia

(Prendergast et al. 2002; Bouma et al. 2011). Periodic arousals may activate a dormant immune system and combat pathogens during IBEs (Prendergast et al. 2002).

Yet another hypothesis concerns brain function. The ultrastructure of synapses in the frontal cortex of ground squirrels (*Spermophilus citellus*) shows changes during the torpor arousal cycle (Ruediger et al. 2007). Similarly, neural connectivity is reduced during hibernation, but the synaptic regression during torpor is followed by reconnection of synaptic contacts during arousals (Popov et al. 1992; Arendt and Bullmann 2013). If such changes were temperature-dependent they may contribute to explaining the temperature-dependence of TBD.

Periodic arousals also may be a result of a temperature-dependent deprivation of non-rapid eye movement (non-REM) sleep while in deep daily torpor or hibernation. Non-REM sleep is not observed at low T_b, but is expressed for much of the IBEs (Daan et al. 1991; Trachsel et al. 1991; Deboer and Tobler 1994; Strijkstra and Daan 1997). The 'sleep hypothesis' suggests that torpor at low T_b inhibits the restorative function of sleep. The sleep hypothesis is supported to some extent by data suggesting that periodic rewarming from hibernation is related to the low T_b experienced during deep torpor because a few species that hibernate at high T_b that do not show periodic rewarming (Hissa 1997; Lovegrove et al. 2014). However, the reduction of TBD in thermoregulating torpid animals at low T_a, where T_b remains more or less constant, does not appear to support it.

A water balance hypothesis argues that hibernators progressively lose body water through evaporative water loss until some critical threshold is crossed, forcing animals to arouse (Thomas and Cloutier 1992). Because the T_b of thermoconforming hibernators closely follows T_a and water vapour pressure at the body surface is temperature-dependent, evaporative water loss should decline with a lowering of T_b. Therefore as a result, TBD should increase as T_a and T_b decline (Thomas and Geiser 1997). Related to this hypothesis is the finding that ground squirrels (*Ictidomys tridecemlineatus*) remain hydrated during torpor by depleting osmolytes from extra-cellular fluids (Feng et al. 2019). The osmolarity levels are restored during IBEs but thirst remains suppressed permitting water retention by the kidney (Feng et al. 2019).

Another hypothesis for regulation of TBD involves the loss of potassium ions from muscle during hibernation (Willis et al. 1971). An increase in potassium ion concentration outside of the membrane of excitable tissues should lead to depolarization and increased excitability. Irritability during hibernation increases with bout duration (Twente and Twente 1968). The potassium ion hypothesis is supported by the observation of increased arousal frequency following injection of an isotonic mixture of KCI and NaCl that increased extracellular potassium concentration by about 20% (Fisher and Mrosovsky 1970).

All these hypotheses are based on scientific evidence and while all have their merits they are not easy to integrate especially since they may be more or less relevant among species. However, the thermal relationships of TBD as well as the duration of the IBEs may provide some general insights or a working model as to why hibernators arouse periodically (French 1985). If a metabolic imbalance does occur during multiday bouts of torpor that has to be rectified during IBEs, the duration of IBEs should increase with an increase in TBD (French 1985). However, this is not the case as IBEs show a positive relationship with body mass, whereas TBD does not (Ruf and Geiser 2015). Another complication for seeking a direct relationship between TBD and energy metabolism is the deviation from a constant thermal relationship in torpid thermoregulating individuals at low T_b, which also complicates the sleep hypotheses. MR only partially accounts for changes in TBD that occur at different T_as, and T_b is a better predictor of torpor bout duration than TMR (Geiser and Kenagy 1988). This suggests that both T_b and TMR may be involved in determining arousals. Therefore, a reduction in neural sensitivity to build-up of metabolites or depletion of nutrients at low T_b could be responsible for later arousals.

However, this relationship also could be explained by increased sympathetic activity associated with thermoregulation in animals exposed to a T_a below their T_{set} which increases the sensitivity or irritability of the animal. These phenomena may operate at very low T_as, whereas temperature-sensitive timing mechanisms may operate at the higher T_as. Therefore the reduction of TBDs below the T_{set} may reflect a switching of regulatory mechanisms for timing of arousals from above to below the T_{set}. An inadequacy of this hypothesis however, is that seasonal changes in torpor bout duration occur at a constant T_a.

Consequently, an explanation of both seasonal and temperature-dependent changes of TBD and how they can occur together is required. We need to know, which of the observed effects are causal and which are not. With modern molecular techniques it should be possible to resolve these questions if they are examined against the background of the known physiological responses.

Chapter 6
Seasonality of Daily Torpor and Hibernation

The weather of most geographical regions changes substantially with the seasons. Therefore, alterations in the thermal environment, rainfall and other environmental variables require a responsive adjustment of the physiology of animals to enable survival. However, geographic regions of the world differ substantially in their seasonal challenges. Whereas temperate and high latitude/altitude regions are characterised by warm T_as in summer and often high primary productivity, T_as in winter are low resulting in little or no primary productivity. Untimely, this low T_a and low productivity occur in the season when energy expenditure of animals often is high. In contrast, tropical areas may remain rather warm in winter, but often show strong seasonal changes in rainfall with almost all precipitation in summer and none in winter (Dausmann and Warnecke 2016). In subtropical areas the high summer heat may limit plant productivity. During the mild subtropical winter nectar production can be much higher than in summer (Ford 1989). In deserts T_as are often too hot, evaporation too high and/or precipitation too low in summer for significant plant growth, whereas winters can be rather mild during the day, at least in deserts not too far from the equator, as for example in the Australian deserts. The seasonal change in photoperiod, a reliable environmental signal for seasonal change in physiology, also differs enormously between high and low latitudes. Such regional differences are reflected in the seasonal expression of torpor.

Preparation for the Torpor Season

Shortening of photoperiod in late summer or autumn initiates physiological and behavioural changes of many species in preparation for hibernation. In other species, for example ground squirrels, a strong innate circannual rhythm controls the seasons of activity and torpor use is largely non-responsive to the prevailing photoperiod. In contrast other species, for example, those from unpredictable habitats, may show opportunistic hibernation and are able to enter multiday torpor irrespective of season

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_6

or photoperiod. For these species multiday torpor can be used at any time of the year when environmental conditions deteriorate, or as a strategy to avoid predation.

As many daily heterotherms can enter torpor throughout the year, they have to be able to do so without major physiological preparation. In those daily heterotherms that express seasonal changes in torpor use, torpor expression is often affected by photoperiod, food availability and quality, and T_a. However, all species need to select appropriate sites where they can safely express torpor.

Hibernacula and Torpor Sites

Of crucial importance for successful survival of the hibernation season is the selection of an appropriate hibernaculum or torpor site. The selection of thermally appropriate sites where torpor is expressed is important, because at T_a close to the minimum T_b that is defended during torpor, TMR is lowest and arousals are least frequent and therefore energy expenditure is minimal. Selection of a hibernaculum with a T_a below the minimum T_b for much of the hibernation season can be detrimental for small and solitary species because of the increased thermoregulatory energy expenditure and more frequent arousals. However, beyond possible behavioural adjustments it is likely that the minimum T_b is subject to strong selective pressure for evolution of minimum T_b to approximate the minimum T_a experienced.

Hibernators often use underground burrows, cellars, caves, mines, boulder fields, piles of wood or leaves, peeling bark, or tree hollows (Kayser 1961; Nagel and Nagel 1991; Webb et al. 1996). Hibernacula buffer the animal not only from temperature extremes and possible desiccation, but also often provide shelter from potential predators. Many hibernacula show temperatures a few degrees above 0 °C even when outside T_a are well below freezing. However, hibernacula are warmer than is often assumed and the common T_as for bat hibernacula are between 0 and 10 °C although higher and lower values have also been observed (Webb et al. 1996; Brack 2007). Snow often acts as additional thermal blanket in species hibernating in boulder fields, such as the mountain pygmy-possum (*Burramys parvus*) (Körtner and Geiser 1998), or in red bats (*Lasiurus borealis*) hibernating in leaf-litter (Dunbar and Tomasi 2006). Artic hibernators, such as arctic ground squirrels (*Urocitellus parryii*) (Barnes 1989) and others (Table 5.1) hibernate at T_as well below or near 0 °C. In these species nests and endogenous heat production during torpor maintain a large T_b-T_a differential and prevent freezing in most individuals (Barnes 1989; Buck and Barnes 2000; Richter et al. 2015). Some species like marmots (*Marmota marmota*) may reduce thermoregulatory energy expenditure via social hibernation (Arnold 1993).

There is also some evidence that the selection of hibernacula may change during winter during periodic arousals. Such changes occur when the thermal conditions change due to, for example, rainfall or a seasonal change of T_a in caves. The phenomenon is well known for bats, which select appropriate hibernacula sites along the thermal gradients in caves, which often change with season (Henshaw and Folk 1966; Brack 2007). Bats change the position within caves and select warmer areas in autumn in comparison to winter. In winter bats that are exposed to warm T_as use a trial and error system to select cooler places (Twente 1955). Mountain pygmy possums (*B. parvus*) select different hibernacula sites after rain, which causes a decrease in T_a in subnivean spaces where they hibernate (Körtner and Geiser 1998).

In hibernators from less-extreme climates, the selection of hibernacula can be more flexible. Some species, such as bats or fat-tailed lemurs, enter torpor under bark, in trees hollows, or even in foliage with little physical protection. Foliage-roosting individual hoary bats (*Lasiurus cinereus*) avoid extremely cold conditions by migrating, but they may be exposed to low T_as during cold snaps is spring when returning to their summer range (Willis et al. 2006). In foliage-roosting blossom-bats (*Syconycteris australis*), roost selection changes with season. In summer individually roosting blossom-bats select forest centres apparently to avoid heat exposure, in winter they select forest edges likely to allow bats minimize energy expenditure for thermoregulation during torpor (Law 1993; Coburn and Geiser 1998). Foliage-roosting bats seem to be able to roost like that because they are inconspicuous and well above the ground and thus avoid predation. Long-eared bats (*Nyctophilus* spp.) enter torpor under bark that will be exposed to sun on the following morning, which allows them to rewarm passively (Turbill et al. 2008; Chap. 7). Desert birds and mammals, in addition to tree roosts, often enter torpor in soil cracks and rock crevices. There are also species that have been recorded to enter torpor in the open on the ground such as poorwills (*Phalaenoptilus nuttallii*) and other nightjars, and bears may also hibernate in the open (Brigham 1992; French 1993; Svihla and Bowman 1954).

Body Mass, Fattening and Food Storage

Hibernators

Preparation for the hibernation season often involves fattening and/or hoarding of food. As fat is energy rich, it is well suited for energy storage. Therefore, the majority of mammalian hibernators undertake substantial pre-hibernation fatting, although a few cache food in the form of seeds (Humphries et al. 2003). Pre-hibernation fattening is common in many hibernators and often is achieved by a combination of hyperphagy and a reduction in activity to promote fat deposition (Kenagy et al. 1989; Körtner and Geiser 1995; Florant and Healy 2012). Fattening in pygmy-possums can be extreme. Eastern pygmy-possums (*Cercartetus nanus*), in captivity have a lean body mass of ~20 g and this increased to 90 g (Bartholomew and Hudson 1962), a 4.5-fold increase, although it is not clear whether this was a seasonal event. Mountain pygmy-possums (*B. parvus*) caught in the wild in autumn about doubled their body mass from ~45 g to 80 g during pre-hibernation (Geiser and Broome 1991). In sciurid and glirid hibernators pre-hibernation fattening is often characterised by a 30–60% increase in body mass and may be up to 100% and a large proportion of that is stored fat (Humphries et al. 2003; Dark 2005; Sheriff et al. 2013; Bieber et al. 2014; Fietz et al. 2005; Ruf and Bieber 2020). Fat stores are important quantitatively because in many species they are the main source of energy throughout the prolonged hibernation season (Dark 2005). During the hibernation season, which often lasts for around 5–9 months, many hibernators are aphagic irrespective of the access to food (Florant and Healy 2012).

However, not all hibernating species fatten or store food. Unlike rodent hibernators, bats are limited by how much fat they can carry because of the consequences for manoeuvrability during flight (Aldridge and Brigham 1988). The same is the case for birds, and apparently the feathertail glider (*A. pygmaeus*, Chap. 3), and therefore fat storage in flying/gliding hibernators is often less extreme than in non-flying hibernators. Data on the only avian hibernator the poorwill (*Phalaenoptilus nuttallii*) show that individuals can increase body mass to 55 g in autumn and reduce it to 35 g in spring (Woods 2002). In bats, substantial seasonal changes in body mass (~45%) have been observed in high-latitude northern bats such as Eurasian horseshoe bats (*Rhinolophus ferrumequinum*). These bats weighed 21.3 g (16% fat reserves) in late autumn and 14.6 g (4% fat reserves) in spring (Ransome 1990). At lower latitudes fattening has also been observed in the Australian little forest bat (*Vespadelus vulturnus*), which showed a clear change in the amount of lipid stored (relative to dry carcass mass) ranging from about 10−20% in summer to about 50−65% in winter in south-eastern Australia (Tidemann 1993). The body mass of *N. gouldi* in south-eastern Australia also increased in early winter (Phillips and Inwards 1985). Cave-roosting bent-wing bats (*Miniopterus schreibersii oceanensis*), increased body mass from ~14 to 18 g in cool-temperate area of south-eastern Australia, whereas coastal individuals from a subtropical area exhibited little or no autumnal fattening (Dwyer 1964). Similarly, long-eared bats (*N. geoffroyi*) in a cool-temperature area of south-eastern Australia, did not show obvious autumnal fattening with bats weighing about 7−8 g in all seasons captured (Turbill et al. 2003b, 2008; Turbill and Geiser 2008). Similar observations have been made in coastal, subtropical *N. bifax* (Stawski and Geiser 2010b) and for Natal long-fingered bats, *Miniopterus natalensis* (Pretorius et al. 2021). Thus in some Australian and South African bats seasonal changes in body mass are much smaller than those recorded for hibernating rodents or northern hemisphere bats. The small seasonal changes in body mass is probably because these bats can successfully forage to some extent even in winter (Turbill et al. 2003b, 2008), in contrast to many cold climate bats (Brigham 1987; Lausen and Barclay 2006). This may also explain why the patterns of torpor of hibernating bats in mild climates, apart from the effect of T_a on TBD, are not as predictable as those typical of cold climate hibernators in winter.

Hibernating hamsters (e.g. *C. cricetus* and *M. auratus*) store predominately seeds (Humphries et al. 2003; Wassmer 2004; Siutz et al. 2016; Tissier et al. 2019), whereas chipmunks and some male ground squirrels do both. Eurasian hamsters (*C. cricetus*), store large amounts of seeds for the hibernation season (Wassmer 2004; Siutz et al. 2016). Caches can be extreme with reports on up to 15−34 kg of barley or peas, but ~2.5 kg are more typical. The biggest food stores have been measured for males (Herter 1956; Wendt 1989).

Daily Heterotherms

In contrast to fat storing hibernators, daily heterotherms often either fatten little or may lose body mass in winter. Djungarian hamsters (*P. sungorus*) decrease body mass substantially from summer to winter. The mass loss is to some extent due to a reduction in gut and reproductive organ size, and muscle (Heldmaier and Steinlechner 1981b; Geiser et al. 2013). A seasonal reduction in body size, including the skeleton occurs mainly in small mammals. This body shrinkage is referred to as the Dehnel phenomenon and was originally described in shrews (Dehnel 1949; McNab 2002; Lazaro et al. 2019). The seasonal reduction in body mass means that overall less energy is needed to maintain the organism, although mass-specific MR is increased.

Little or no seasonal change in body mass has been observed in Australian arid-zone dunnarts (*Sminthopsis crassicaudata*), kowaris (*Dasyuroides byrnei*), and North American white footed mice (*Peromyscus leucopus*) (Geiser and Baudinette 1987; Tannenbaum and Pivorun 1988). Subtropical blossom-bats (*S. australis*) males captured in the wild weighed 18.0 g in summer and 17.5 g in winter (Coburn and Geiser 1998). This lack of a seasonal change in body mass it consistent with other observations that many daily heterotherms do not substantially change mass with season likely because they forage often daily even during the season they use torpor most.

However, in some daily heterotherms including the rufous hummingbird (*Selasphorus rufus*), tawny frogmouths (*Podargus strigoides*) and in marsupial mulgaras (*Dasycercus* sp.), fattening has been observed at the time torpor is expressed. In hummingbirds this occurs during the period of migration (Carpenter and Hixon 1988; Hiebert 1993a). Fattening occurs at a time food is available and it seems logical that hummingbirds would use nocturnal torpor to accumulate fat for use during migration. In frogmouths, substantial fattening has been observed in captive birds during the season when free-ranging birds express nocturnal torpor (Stulberg et al. 2018). To my knowledge data on seasonal body mass cycles of frogmouths in wild are not available. However, because frogmouths are rather large for daily heterotherms, foraging is energetically cheap, and their food is scarce during the season they use torpor, fattening in this species appears appropriate. Female mulgaras express daily torpor during the winter reproductive period in the wild (Körtner et al. 2016). In captivity females fatten extensively during pregnancy when they frequently use spontaneous torpor. Torpor use will promote fat stores for the energetically more demanding period of lactation, when they do not appear to use torpor (Chap. 8). Thus in daily heterotherms seasonal fatting can be used for special functions, related to activities such as flight or reproduction, but apparently also may be used in large species.

Fat Tails

Although *Sminthopsis* spp. may not change body mass substantially with season or photoperiod acclimation, they do change their tail width (McAllan et al. 2012). In *S. macroura*, tail width increases in both males and females acclimated to short winter photoperiod and the effect was especially obvious (a ~ 30% increase) in males treated with testosterone (McAllan et al. 2012). Morton (1980) reviewed the occurrence of caudal fat storage in small mammals. Both hibernators and daily heterotherms may store fat in the tail and also some large homeotherms, but it seems to be restricted to non-flying mammals. Caudal fat storage is found in South American marsupials (opossums and *Dromiciops*), Australian marsupials (dasyurids and pygmy-possums), afrosoricida (tenrecs), lipotyphla (moles), primates (dwarf lemurs) and rodents (heteromyids and dipodids) (Morton 1980). The conclusion from the comparison was that caudal fat storage is common in desert dwelling insectivores, species with a variable food availability and species expressing torpor. The advantage of storing fat in the tails is that is does not affect the bulk of the body and will not unduly interfere with manoeuverability. Although the energy content in fat tails of dunnarts (*S. crassicaudata* Fig. 3.14) is small (Morton 1980), it can be substantial in other species. For example, heterothermic Patagonian opossums (*Lestodelphys halli*) change the tail from a flat beaver tail-shape to a plump carrot-shaped tail in autumn (Fig. 3.13. Geiser and Martin 2013). Hibernating dwarf lemurs (*Cheirogaleus medius*), more than double tail volume to over 30 ml in autumn (Fietz et al. 2003) a substantial part of a 250-g animal.

Ghrelin and Leptin

Seasonal fattening is to some extent controlled by the intestine-produced peptide hormone ghrelin the ‘hunger hormone’ which stimulates food intake when the stomach is empty (Healy et al. 2010). In golden-mantled ground-squirrels (*C. lateralis*) peripherally administered ghrelin increased food intake in summer and plasma ghrelin concentrations increased during fasts (Healy et al. 2010). In mice (*M. musculus*), fasting elevates circulating ghrelin and induces torpor, and administration of ghrelin deepens torpor (Gluck et al. 2006).

Leptin, on the other hand, is a steroid hormone that is produced by fat cells and is considered to be an adipostatic signal that coordinates energy expenditure and food uptake (Klingenspor et al. 1996). Leptin signals abundant energy stores and acts as a satiety signal (Florant and Healy 2012). With regard to torpor, winter acclimatization and acclimation of hamsters (*P. sungorus*) to short photoperiod reduced leptin gene expression in depot fat and BAT (Klingenspor et al. 1996), at a time when the species expresses spontaneous daily torpor and decreases body mass (Heldmaier and Steinlechner 1981b; Ruf et al. 1993; Geiser and Heldmaier 1995). Administration of leptin reduced daily torpor expression by *P. sungorus*, whereas short photoperiod reduced body mass and resulted in a reduction of serum leptin concentration in hamsters expressing torpor (Freeman et al. 2004). In marsupial dunnarts (*S. macroura*), leptin administration significantly reduced daily torpor occurrence from 94 to 75%, raised the minimum T_b by almost 5 °C and the minimum TMR by ~two-fold, however, body mass was not affected (Geiser et al. 1998).

Use of torpor in small hibernating species such as bats (*M. lucifugus*) seems to differ from small daily heterotherms in response to circulating leptin. Small hibernators show a dissociation between circulating leptin and fat mass, because they enter torpor during fattening when leptin levels are high, possibly to maximise fat storage in autumn (Kronfeld-Schor et al. 2000; Florant and Healy 2012). In the small hibernating pygmy-possums (*C. nanus*) leptin administration affected torpor expression much less than in the daily heterotherm, *S. macroura* (Goldzieher 2004). In medium-sized hibernators, leptin increases during autumnal fattening and then falls during hibernation (Florant and Healy 2012).

Seasonal Control of Torpor

Photoperiod acclimation or specifically acclimation (or acclimatization in the wild) to short photoperiod is a strong signal for the preparation for hibernation or the expression of daily torpor in many species. Extensive work on photoperiodism and torpor use has been conducted on daily heterotherms such as hamsters, *P. sungorus*, or deer mice, *P. maniculatus*. Both species tend to be highly photoperiodic and respond strongly to exposure to short photoperiod by expressing torpor, with low T_a amplifying or accelerating the photoperiodic response in *P. sungorus* (Lynch et al. 1978; Steinlechner et al. 1986; Ruf et al. 1993; Geiser and Heldmaier 1995; Tannenbaum and Pivorun 1988; Hiebert et al. 2003a).

Day length is perceived via the lateral eyes in mammals, transferred via neural connections to the suprachiasmatic nucleus (SCN) of the hypothalamus, which controls release of the hormone melatonin from the pineal gland during darkness. Consequently in short photoperiod circulating melatonin levels are increased and this in turn increases the use of spontaneous daily torpor in *P. sungorus* (Cubuk et al. 2016). However, pelage colour, morphology, thermal and reproductive physiology, and tissue fatty acid composition also change in response to photoperiod acclimation in *P. sungorus*. Pelage colour seem to be linked to circulating prolactin levels, which decrease in autumn at the beginning of the torpor season (Cubuk et al. 2016). With regard to of daily torpor in *P. sungorus*, it is especially the expression spontaneous torpor that is strongly seasonal (Chap. 4).

Torpor expression in some hibernators such as dormice, *G. glis*, and European hamsters, *C. cricetus*, is also under photoperiodic control (Morrison 1964; Canguilhem et al. 1988). Dormice, *G. glis*, both when kept under natural and reversed photoperiods change torpor expression with day length and increase torpor use under short photoperiod (Morrison 1964).

In contrast, thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) held under the same environmental conditions as dormice, did not change torpor expression when exposed to different photoperiods (Morrison 1964). This is also the case in many other ground squirrels, which are often viewed as 'obligate' hibernators. In these sciurids torpor expression is strongly seasonal, governed by a circannual rhythm and highly predictable (Mrosovsky 1971). In ground squirrels (*I. tridecemlineatus*) hibernation occurs in winter irrespective of T_a and food availability (MacCannell and Staples 2021). In golden-mantled ground squirrels (*C. lateralis*) the hibernation season is also governed by a circannual rhythm, the circannual period was less than 365 days and not affected by light (Pengelley and Asmundson 1970; Pengelley et al. 1976). Thus in these and other sciurids, the seasonal use of torpor can be more or less independent of photoperiod and even from T_a and is controlled principally by a biological clock (Morrison 1964; Wang 1978; Kenagy and Barnes 1988; Barnes 1996; Geiser et al. 1990; Michener 1992; Arnold 1993; Körtner and Geiser 2000a; French 2008; Williams et al. 2017; MacCannell and Staples 2021).

In species from low latitudes (~30° S), such as the subtropical blossom-bat (*S. australis*), photoperiod acclimation did not show a strong effect on torpor expression in captive individuals (Geiser et al. 2005a). As blossom-bats captured in the wild change torpor patterns with season, other seasonal cues than photoperiod must be used in the wild. Similarly, in the mountain pygmy-possum (*B. parvus*), which shows seasonal hibernation in the wild (Körtner and Geiser 1998), yearly activity and body mass cycles were maintained only within the first winter in captivity (Körtner and Geiser 1995). Despite maintenance under a mimicked 'natural' yearly T_a and photoperiod cycle, this seasonal rhythmicity was lost and became more or less random in the second year in captivity. As *B. parvus* are highly seasonal in the wild, other seasonal signals than photoperiod and T_a must be used to coordinate seasonal rhythmicity in the wild. Therefore, as for other aspect of seasonal torpor use, the control of its seasonal expression differs among species and revealing the responsible cues will require further work.

Seasonal Occurrence of Torpor

The seasonal occurrence of hibernation is especially obvious in diurnal sciurid rodents, such as ground squirrels, chipmunks and marmots, which disappear into burrows around autumn and re-appear in spring and their seasonal use of torpor can be quantified to a large extent by observation or trapping. It is therefore of little surprise that the widely held view of seasonal expression of torpor, or specifically hibernation is one of torpor use in late autumn, winter and early spring, unlike the rest of the year, which is supposed to be devoted to activity and reproduction. The term hibernation has a seasonal connotation implying that it only occurs in winter. However, as we will see below, hibernation is only rarely restricted to winter and

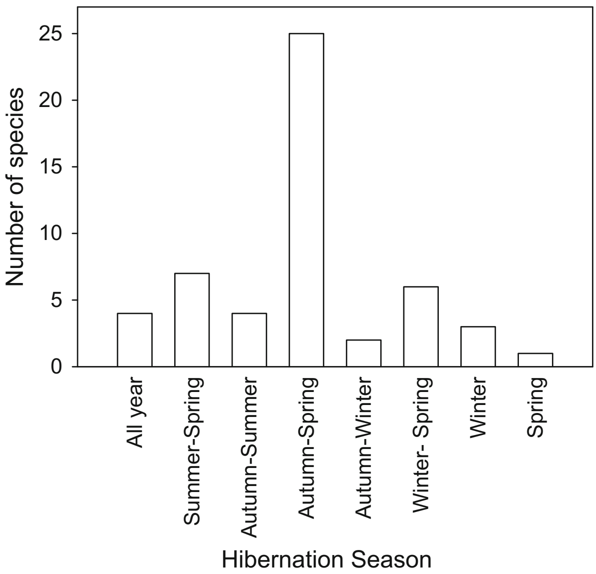

Fig. 6.1 The duration of the hibernation season and the number of species expressing multiday torpor during each season (from Geiser 2020)

may in fact last for much of the year in some species and under certain circumstances (Fig. 6.1).

Hibernators

Yearlong Hibernation

The most extreme expression of hibernation is known for three unrelated mammals, a marsupial and two rodents, phylogenetically separated for >140 Million years. These are the marsupial pygmy-possum (*C. nanus*) and the dormice (*G. glis* and *E. quercinus*). These species are opportunistic hibernators that do not only hibernate in winter, but, under laboratory conditions, continue to hibernate for an entire year (Fig. 6.1). In captivity the pygmy-possums hibernated at T_a 7 °C for over 12 months, relying entirely on stored body fat for energy expenditure (Geiser 2007). The climate within the distribution range of *C. nanus* is not cold enough to result in yearlong hibernation in the wild, but demonstrates the great potential for prolonged hibernation in the species. Edible dormice (*G. glis*) hibernated at T_a 5 °C for up to a year (Mrosovsky 1977). Similarly, captive non-reproductive *G. glis* hibernated for up to 11 months/year (Bieber and Ruf 2009) and, unlike for *C. nanus*, free-ranging non-reproductive dormice also can hibernate for up to 11 months (Hoelzl et al. 2015). Captive garden dormice (*E. quercinus*) expressed multiday torpor throughout the year when held at T_a 12 °C, but the TBD was shorter in summer than in winter (Daan 1973). It could be argued that yearlong hibernation or at least the yearlong use of torpor also occurs in long-eared bats (*Nyctophilus* spp.) and perhaps other mammals (see below) as they can display multiday torpor throughout the year in the wild.

Hibernation from Summer to Spring

Expression of hibernation from late summer to spring (i.e. for about 8–9 months) is a common seasonal pattern (Fig. 6.1). It occurs in medium-sized to large sciurid rodents such as ground squirrels, chipmunks and marmots (Sciuridae) and dormice (Gliridae). However, it also occurs in the large egg-laying mammals, the echidna (*T. aculeatus*), which, when not reproductive, hibernate from late summer to spring (Grigg et al. 1992b; Nicol and Andersen 2002). Rodents that hibernate from summer to spring include Richardson's ground squirrels (*U. richardsonii*) (Wang 1978; Michener 1992) golden-mantled ground squirrels (*C. lateralis* and *C. saturatus*) (Kenagy et al. 1989; Healy et al. 2012), Columbian ground squirrels (*U. columbianus*) (Young 1990), Anatolian ground squirrels (*Spermophilus xanthoprymnus*) (Kart Gür et al. 2009), arctic ground squirrels (*U. parryii*) (Barnes 1989) and woodchucks (*Marmota monax*) following drought (Zervanos et al. 2010). Although in many of these sciurids the hibernation season is controlled by a circannual rhythm and terminated in spring, in the laboratory the season can be extended by continued food withdrawal, when, however, the TBD is substantially shorter than in mid-winter (French 1985).

Hibernation from Autumn to Summer

A hibernation season of similar ~8–9 month duration, but commencing later and lasting from autumn to summer, has been observed in small species including bats and jumping mice. Little brown bats (*M. lucifugus*) hibernate from about October/November to March/April and express torpor also in summer when reproductive (Jonasson and Willis 2012; Johnson et al. 2019). Brand's bat (*Myotis brandtii*) hibernate from late September until the middle of June in Siberia (Podlutsky et al. 2005). Even in warmer regions, Hodgson's bats (*Myotis formosus*) hibernated in abandoned mines in southern Korea from October to June and, because of the high T_a, they were able to do that with a high T_{skin} of >11 °C (Kim et al. 2013). In the field at >2000 m elevation in Utah, jumping mice (*Zapus princeps*) hibernate just under 300 days (September to early July) (Cranford 1978).

Hibernation from Autumn to Spring

The most common hibernation season lasts for ~5–7 months from autumn to spring (Fig. 6.1). Species expressing this pattern of seasonal hibernation include free-ranging Australian mountain pygmy-possums (*B. parvus*) (Körtner and Geiser 1998), and European hedgehogs (*E. europaeus*) in outdoor enclosures (Walhovd 1979). Even near the Mediterranean Sea, Algerian hedgehogs (*Atelerix algericus*) commenced the hibernation season with short bouts of torpor in November, expressed long TBDs of 6–7 days in January/February, and ended the torpor season again with short bouts in March (Mouhoub-Sayah et al. 2008). Hibernation from autumn to spring has also been observed in small hibernating bats, including cave-roosting horseshoe bats (*Rhinolophus ferrumequinum*) in southern England (Park et al. 2000), but also in bats roosting an entirely different thermal environment, such as mouse-tailed bats (*Rhinopoma microphillum* and *R. cystops*). Mouse-tailed bats fatten in August on winged ants and hibernate in geothermally heated caves at T_a ~ 20 °C in cliffs at the Sea of Galilee. They hibernate with T_{skin} of ~23 °C and partial arousals from late October for 5 months (Levin et al. 2015). In Sweden, free-ranging brown bears (*U. arctos*) entered dens around October/November when T_a was ~0 °C and snow fell; bears finished denning in early April. Bears reduced activity weeks before they began denning (Evans et al. 2016). Hibernation from autumn to spring has been observed in several primates that hibernate during the cool dry winter in Madagascar (Dausmann 2014; Dausmann and Warnecke 2016). These include the fat-tailed dwarf lemur, *Cheirogaleus medius*, and the dwarf lemur, *C. crossleyi* (Dausmann and Warnecke 2016).

Many rodents hibernate from autumn to spring. These include woolly dormice (*Dryomys laniger*) (Kart Gür et al. 2014) and hazel dormice (*Muscardinus avellanarius*) which, however, also expressed brief bouts of torpor during summer (Pretzlaff et al. 2014). Other rodents hibernating from autumn to spring include thirteen-lined ground squirrels (*I. tridecemlineatus*) in Michigan, Daurian ground squirrels (*Spermopilus dauricus*) in northern China, (Yang et al. 2011; Kisser and Goodwin 2012) and European alpine marmots (*M. marmota*) (Arnold 1988, 1993; Ruf and Arnold 2000). Woodchucks (*Marmota monax*) typically hibernate from autumn to spring in Pennsylvania (Zervanos et al. 2010), but their hibernation season is affected by latitude (Chap. 7). Prairie dogs (*Cynomys parvidens*), also hibernated from autumn to spring in high and mid-elevation populations, however low elevation populations terminated hibernation already in late winter, when food became available (Lehmer and Biggins 2005). Siberian chipmunks (*Eutamias sibiricus*) in Hokkaido, Japan, hibernate from autumn to spring, and so do yellow-pine (*Tamias amoenus*) and Townsend chipmunks (*T. townsendi*) in the State of Washington, USA (Kenagy and Barnes 1988). Food-storing European hamsters (*Cricetus cricetus*) also hibernate from autumn to spring (Wassmer 2004; Siutz et al. 2016).

Hibernation from Autumn to Winter

A shorter hibernation seasons from autumn to winter has been recorded in only two species (Fig. 6.1). The pygmy armadillo (*Zaedius pichiy*) held in outdoor pens in Argentina, exhibited this seasonal pattern, but after the hibernation season, pichis continued to show large daily variation in T_b until spring (Superina and Boily 2007). Similarly, the southern African hedgehog (*Atelerix frontalis*), held under semi-natural conditions, hibernated from autumn to winter (Hallam and Mzilikazi 2011).

Hibernation from Winter to Spring

Hibernation from winter to spring occurs in several species (Fig. 6.1). These include European free-tailed bats, *Tadarida teniotis* (Arlettaz et al. 2000), Formosan leaf-nosed bats (*Hipposideros terasensis*), which hibernate in abandoned tunnels in Central Taiwan (Liu and Karasov 2011), and captive pygmy slow loris (*Nycticebus pygmaeus*) held outdoors in tropical Vietnam (Ruf et al. 2015). Black bears (*U. americanus*) maintained under outdoor conditions also hibernated from winter to spring (Tøien et al. 2011) and the same has been observed in the Egyptian jerboa, *Jaculus orientalis* (El Ouezzani et al. 2011). For eastern chipmunks (*Tamias striatus*) in Quebec, hibernation was characterised by a regular expression of a sequence of deep and multiday torpor bouts and lasted from winter to spring during years when food availability was low (Landry-Cuerrier et al. 2008).

Hibernation in Winter

Hibernation is rarely restricted to winter (Fig. 6.1). It occurs in species living in warm climates, migrating species and large species. Hibernation in migratory poorwills (*P. nuttallii*) in the southern USA and Mexico is restricted to winter (Brigham 1992; Woods et al. 2019). Data on free-ranging western pygmy-possums (*C. concinnus*) (Turner et al. 2012b) and European badgers (*M. meles*), suggest that multiday torpor is limited to winter (Fowler and Racey 1988).

Hibernation in Spring

Hibernation restricted to spring is known only for one species the South African golden mole (*A. hottentottus longiceps*). Data are available only on a single individual in spring when the mole expressed multiday bouts of torpor (Scantlebury et al. 2008).

Hibernation in the Cold Season and Short Bouts of Torpor in the Warm Season

Many of the species described above hibernate for the periods described and are homeothermic fort the rest of the year when they typically reproduce. However, other species continue to use torpor for the remainder of the year. In addition to hibernation in winter, free-ranging Canadian long-eared myotis (*Myotis evotis*), use typical short bouts of torpor on every day between May and August and even when reproductively active (Nagorsen and Brigham 1993; Chruszcz and Barclay 2002). Daubenton's bat (*Myotis daubentoni*) hibernate (Ransome 1990), and in late summer in central Germany reproductive males and females enter torpor (Dietz and Kalko 2006). Subtropical fishing bats (*Myotis vivesi*) hibernated on desert islands in the Gulf of California and expressed torpor in summer when T_as were extremely hot (Salinas-Ramos et al. 2014).

Despite partial passive rewarming each day long-eared bats (*Nyctophilus geoffroyi* and *N. gouldi*) expressed multiday TBDs in mid-winter. In a cool-temperate area in summer *N. geoffoyi* used short bouts of torpor on warm days on every day and on cool days TBDs up to 2 days were observed and TMRs in captive individuals were as predicted for hibernators (Turbill et al. 2003b). For tree-roosting hibernating long-eared bat *N. bifax* in the subtropics, torpor was observed on 100% of days in winter and 85% of days in summer, TBD lasted for up to 5 days in winter and <1 day in summer (Stawski and Geiser 2010a). It is likely that some of these species could hibernate for much of the year at low T_as in the laboratory, if they were capable of storing sufficient fat.

Daily Heterotherms

The expression of daily torpor is often not as obvious as hibernation because animals typically forage daily. Thus without physiological measurements it is difficult to ascertain whether an animal is torpid or whether it is simply resting or asleep. Therefore, data on seasonal torpor expression especially in free-ranging daily heterotherms in comparison to hibernators are rare, whereas data on captive animals are readily available.

Yearlong Daily Torpor

It appears that torpor expression throughout the year is common in daily heterotherms. Andean Hillstars (*Oreotrochilus estella*) living in the Peruvian Andes at ~4000 m elevation used nocturnal torpor both in winter and summer, suggesting they use torpor for large parts of the year (Carpenter 1974). Captive

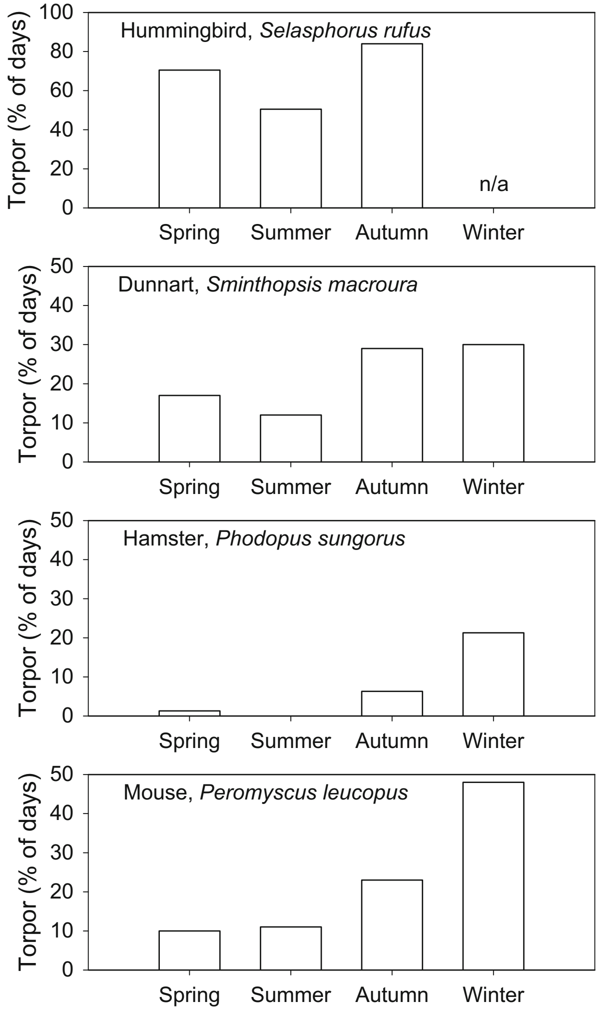

Fig. 6.2 Spontaneous torpor (food available *ad libitum*) expression (% of observation days) as a function of season in daily heterotherms. n/a = data are not available for this season (data from Lynch et al. (1978; Heldmaier and Steinlechner 1981b; Geiser and Baudinette 1987; Hiebert 1993a)

rufous hummingbirds (*Selasphorus rufus*) used torpor from spring to the time of pre-migratory fattening in autumn when torpor was most pronounced (Hiebert 1993a; Fig. 6.2). Although winter data are not available, it is likely that they express torpor throughout the year. Alaskan black-capped chickadees (*Poecile atricapilla*) reduced MR during nocturnal torpor to a similar extent in both summer and winter in captivity (Sharbaugh 2001), suggesting that it is used throughout the year, and captive South African sunbirds (*N. famosa*) entered nocturnal torpor in summer at low T_a (Downs and Brown 2002) suggesting that torpor may also be used at other times of the year.

Captive arid zone insectivorous/carnivorous marsupials (*Sminthopsis* spp. and *Dasyuroides byrnei*) held in outdoor enclosures also displayed daily torpor

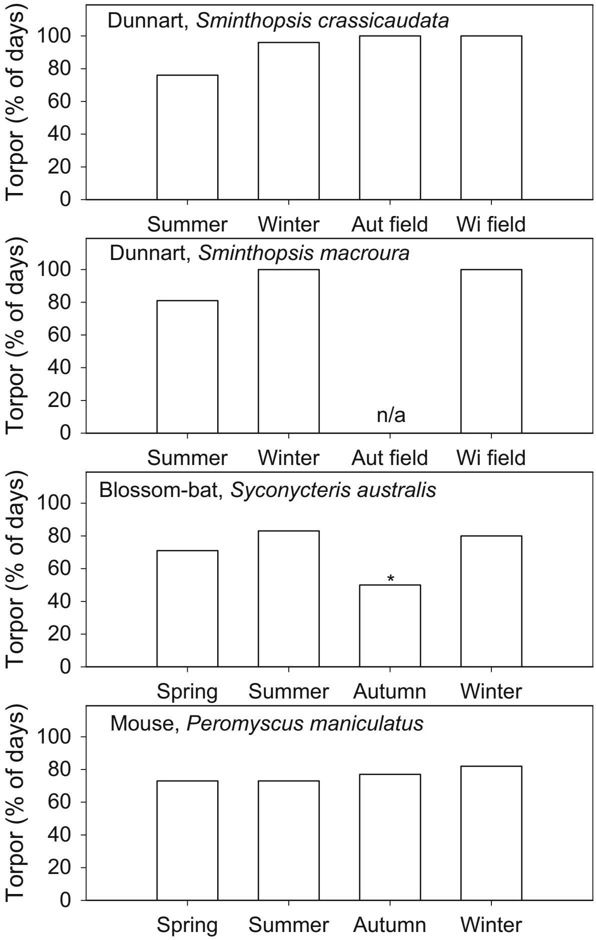

Fig. 6.3 Induced torpor (food restricted) expression (% of observation days) in captive and natural torpor in free-ranging (field) daily heterotherms as a function of season. In blossom-bats it is known that they use torpor in autumn, but the % torpor is not available, therefore 50% (*) is assumed. For *S. macroura* field data in autumn are not available (data from Geiser and Baudinette 1987; Tannenbaum and Pivorun 1989; Geiser 2020)

throughout the year (Geiser and Baudinette 1987). The use of spontaneous (food *ad libitum*) torpor was reduced in summer (Fig. 6.2), but occurrence of induced torpor by withdrawal of food and water showed small seasonal changes in *Sminthopsis* spp. with torpor use increasing from ~75% in summer to 100% of days in winter (Fig. 6.3). Torpor expression for free-ranging individuals in autumn and winter is also often around 100% (Warnecke et al. 2008; Körtner and Geiser 2009). Although captive *Sminthopsis* spp. did show seasonal changes in thermal energetics with a 2–3 °C reduction in the minimum regulated T_b and a 30–40% reduction of the minimum TMR from summer to winter (Geiser and Baudinette 1987; Geiser 2003), they nevertheless expressed torpor in all seasons. Free-ranging South African elephant shrews, *Elephantulus myurus*, also expressed torpor throughout the year. However, torpor use was most pronounced in winter and spring (Mzilikazi and Lovegrove 2004).

In north-American deer mice and white-footed mice (*Peromyscus* spp.), the seasonal expression of torpor was investigated in outdoor cages (Lynch et al. 1978; Tannenbaum and Pivorun 1988). Spontaneous torpor (Fig. 6.2) in *P. leucopus* was recorded for all seasons (Lynch et al. 1978), or in all seasons except summer (Tannenbaum and Pivorun 1988). The torpor incidence in *P. leucopus* increased substantially to >30% of days for all seasons after food withdrawal (Fig. 6.3). Similarly, *P. maniculatus* expressed spontaneous torpor in autumn (~4% of days) and winter (~10% of days) but not in spring. However, food withdrawal increased the torpor incidence to 70–78% of days for all four seasons (Tannenbaum and Pivorun 1989). Torpor duration and depth for *P. maniculatus* were also similar for all seasons investigated (Tannenbaum and Pivorun 1988), suggesting little or no seasonal functional change.

Seasonal Daily Torpor

In several free-ranging daily heterotherms torpor appears to occur from autumn to spring. In the large tawny frogmouths (*Podargus strigoides*), nocturnal torpor was mainly observed on cold winter nights and mornings, and rarely in autumn and spring, summer data are not available (Körtner et al. 2000, 2001). In owlet-nightjars (*Aegotheles cristatus*) torpor was used between late autumn and early spring, but not during other times of the year (Brigham et al. 2000). Whip-poorwills (*Caprimulgus vociferous*) rarely used torpor in spring or autumn and not in summer (Lane et al. 2004), and it is uncertain what they do during migrating to the south. Free-ranging noisy miner (*Manorina melanocephala*) expressed frequent, shallow nocturnal torpor from autumn to early spring (Geiser 2019).

Captive brown antechinus (*Antechinus stuartii*) and yellow-footed antechinus (*A. flavipes*) did not express spontaneous torpor in summer, and rarely did so in winter. However, food withdrawal increased daily torpor expression to about 30–80% from autumn to spring when juveniles are excluded, which did express torpor in summer (Geiser 1988a). In the field, daily torpor in *A. stuartii* in winter was strongly affected by weather (Hume et al. 2020). Daily torpor in free-ranging sugar gliders (*Petaurus breviceps*) was observed between autumn and spring and mainly on cold, wet winter days (Körtner and Geiser 2000b). However, sugar gliders also expressed daily torpor during a category one cyclone with heavy rainfall in a subtropical area in spring (Nowack et al. 2015; Chap. 6).

The seasonality of daily torpor has been investigated in detail in captive hamsters, *Phodopus sungorus* (Heldmaier and Steinlechner 1981b), and the data suggested that their expression of torpor is strongly seasonal. Spontaneous torpor (food *ad libitum*) in outdoor enclosures was used on ~21% of days in winter, less in autumn and spring, but not in summer (Fig. 6.2). However, as discussed above, torpor could be induced by food restriction in long photoperiod acclimated *P. sungorus* (Diedrich et al. 2012) and also in in summer acclimated *P. roborovskii* (Chi et al. 2016).

More Pronounced Torpor in Summer than in Winter

Even if torpor is used for much of the year, torpor expression is typically deepest and longest in winter. However, several species, two bats and a rodent, exhibit more pronounced torpor in summer. Nectarivorous blossom-bats *S. australis* from the subtropical south-eastern Australia, are one of these. Induced torpor occurrence in captive individuals was similar in summer and winter (Fig. 6.3). However, average TBD of *S. australis* captured in winter was short (5.5 h) and torpor was shallow with a minimum T_b of ~23 °C, whereas in bats captured in summer torpor was deep (minimum T_b ~ 19 °C) and long at 7.3 h on average (Coburn and Geiser 1998). The unusual seasonal response seems to be explained by the T_a, different day length and food availability. In winter, T_a on the subtropical east coast is relatively mild and bats can forage for prolonged periods during long nights and have access to an abundance of flowering plants (Armstrong 1991). In summer, nights and thus foraging times are brief and the availability of nectar is substantially reduced (Coburn and Geiser 1998). Thus, the unusual seasonal pattern of torpor use in *S. australis* appears to be an appropriate physiological adaptation to ecological constraints imposed by their subtropical habitat and specialised diet of nectar and pollen, and it does suggest a seasonal change in physiology.

The other observations on more pronounced torpor in summer than in winter seem to be related to water availability. The inland free-tail bat *Ozimops petersi* is, to a large extent, restricted to arid and semi-arid regions of Australia. The bat entered multiday torpor for up to 8 days in winter (Bondarenco et al. 2013, 2014), but even on cool days in summer, TBDs up to 2 days have been reported (Bondarenco et al. 2013). In both summer and winter, TBD of *O. petersi* was strongly affected by T_a, but the nature of the relationship differed significantly between seasons (Fig. 6.4). 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 summer. The seasonal change suggest a seasonal acclimatization to minimise water loss in summer.

Similar observations have been made for an unrelated heterothermic rodent from the Dead Sea desert region in Israel. Spiny mice (*A. russatus*), held in outdoor enclosures under natural food availability, expressed about twice as many torpor bouts and, on average spent about twice the time in torpor in summer (~780 min) than in winter (~370 min). It is likely that the mice did this to conserve water (Levy et al. 2011a, b). Even when food was offered *ad libitum*, summer torpor was more frequent and longer than winter torpor (Levy et al. 2011a, b).

Seasonal Change in Torpor Expression and Torpor Patterns

The seasonal change of torpor use in hibernators and daily heterotherms is summarised in Fig. 6.5. As we have seen in this chapter, both daily heterotherms and hibernators express torpor throughout the year. However, although daily

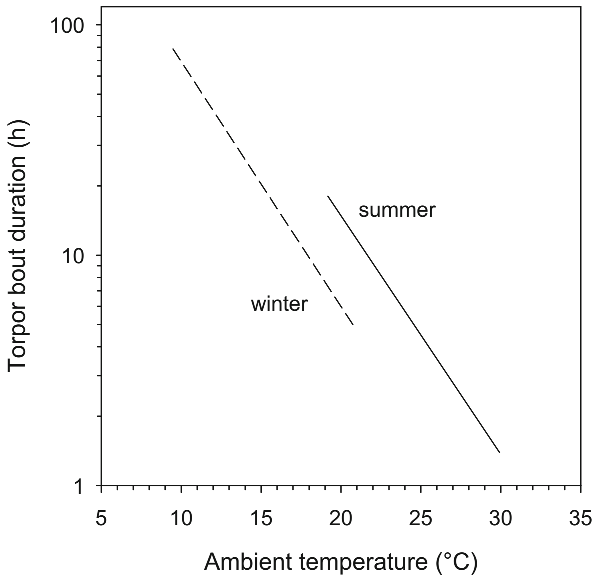

Fig. 6.4 Regressions lines for torpor bout duration (TBD) on a log scale as a function of ambient temperature (T_a) in free-ranging inland free-tail bats (*Ozimops petersi*) in an Australian desert in summer and winter. At $T_a < 15$ °C bats expressed multiday torpor, at $T_a > 15$ °C TBD was <1 day. 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 from Bondarenco 2014; Geiser et al. 2019b)

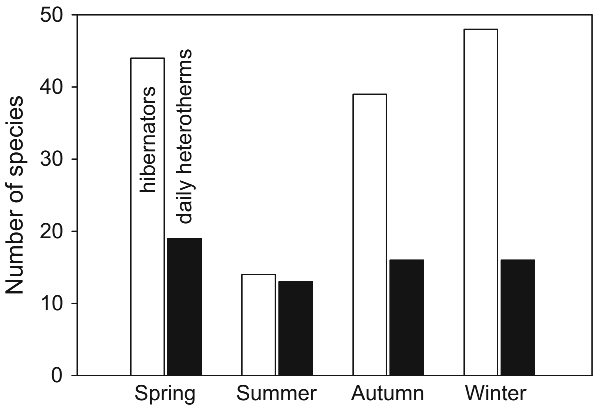

Fig. 6.5 Number of species known to express torpor during different seasons of the year. In hibernators (white bars), although summer torpor was used, the number of species using torpor changed significantly with season. In daily heterotherms (black bars) there was no significant change of species number using torpor with season (from Geiser 2020)

heterotherms show a slight reduction of torpor use in summer, torpor expression did not differ among seasons. In contrast, the number of hibernators using torpor in different seasons changed significantly with more species expressing torpor in winter (Fig. 6.5).

The available data show that the seasonal expression is not characterised by a simple change from homeothermy summer to heterothermy in winter. Often torpor is used for much of the year and in some species torpor can be more pronounced in summer than in winter. Clearly, the seasonal expression of torpor is affected by a multitude of ecological and physiological factors and it will require consideration of these and examination of different species if the underlying mechanisms are to be unravelled.

Chapter 7
Ecological and Behavioural Aspects of Torpor

Torpor and Geographic Distribution of Heterothermic Endotherms

Torpor is not only highly diverse in the manner it is used and found in many birds and mammals, it is also expressed by animals all over the world under different climatic conditions. Animals living in different regions will be exposed to the prevailing thermal conditions and therefore, to some extent, torpor expression should reflect their distribution. On average, hibernators are distributed at higher latitudes (~35°) than are daily heterotherms (25°) (Ruf and Geiser 2015). Both the maximum and mean TBD of hibernators are significantly affected by latitude, with the shorter bouts observed at lower latitudes (Fig. 7.1). The predicted mean TBD for hibernators from the regression line (Fig. 7.1) is ~32 hours at 0° latitude and ~ 680 hours at 70°, or an increase by ~108 hours for every 10° increase in distance away from the equator. To a large extent the longer TBDs at higher latitudes may simply reflect exposure to lower T_as (Chap. 5), but it is probable that the colder winters further north result in selection for deeper and longer torpor bouts. In contrast, TBDs in daily heterotherms are not affected by latitude. The average maximum TBD is 10.1 hours in birds and 12.9 hours in mammals, whereas the mean TBD is 6.3 hours in birds and 8.2 hours in mammals (Ruf and Geiser 2015). This suggests that because of their largely daily foraging, the time daily heterotherms allocate to torpor is not affected by latitude, although their TBD is affected by T_a.

The climate of geographical regions is not constant and distribution ranges of species are affected by climate change. Recently, substantial range extensions have been observed for heterothermic hummingbirds and insectivorous bats. In the past two decades, Anna's hummingbird (*Calypte anna*, ~4 g) from western North America has extended its range northwards by more than 700 km. Its northern most range extension used to be southern California, however it now winters near the Canadian border (Greig et al. 2017). The range extension has been correlated

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_7

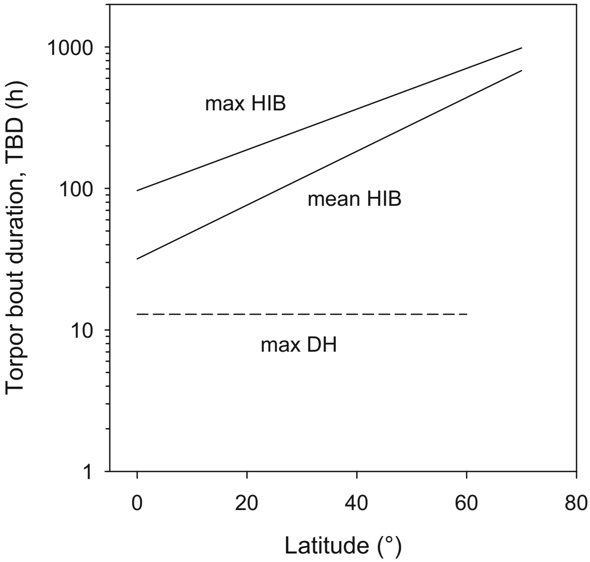

Fig. 7.1 Regression lines for torpor bout duration (TBD maximum and mean) as a function of latitude in hibernators (HIB). In daily heterotherms (DH) the relationship was not significant and the maximum TBD was 10.1 hours in birds and 12.9 hours in mammals (broken horizontal line), mean TBD was 6.3 hours in birds and 8.2 hours in mammals. Note that at 0° the difference in max TBD between HIB and DH is about ten-fold, whereas at 60° it is about 70-fold. Data from Ruf and Geiser (2015)

with the number of nectar feeders provided (Greig et al. 2017). However, these hummingbirds also eat insects and sap from trees and climate change seems involved. One crucial reason for survival of this diurnal bird during long and cold winter's nights is obviously their use of torpor, which for hummingbirds lasts for much of the night (Hiebert 1990; Wolf et al. 2020). Because of their small size and high BMR, during bouts of torpor the TMR of *C. anna* can fall to as low as ~5% of BMR (Lasiewski 1963) resulting in substantial energy savings, which together with the extra food provided by feeders and also introduced flowering plants seems a perfect combination permitting a range extension.

Kuhl's pipistrelle (*Pipistrellus kuhlii*) is a Eurasian bat that has expanded its geographical range. It used to be considered a Mediterranean species, but has expanded its range by about 394% in the last four decades since 1980, and now reaches northeast into Russia. The extension of this bat's range was best correlated with the rise of T_a during the coldest quarter of the year, and to a lesser extent increased urbanization (Ancilletto et al. 2016). However, it seems highly likely that the range extension, rather than a range shift, was made possible by the capability of hibernation in this 6-g bat (Wawrocka et al. 2012), which now is able to survive the shorter hibernation season further northeast because of the rise in T_a in winter (see Humphries et al. 2002). The bat is also likely less frequently exposed to T_as that require energy-expensive thermoregulation during torpor. It is currently not known whether the northward expansion of these two species resulted in more pronounced torpor due to selection or phenotypic plasticity.

Intraspecific Comparisons of Geographic Differences in Torpor Patterns

Some heterothermic species have large geographic ranges, are exposed to different climates and therefore patterns of torpor and variables of torpor may differ depending on the study location. It is interesting that at least in Australia, the only native mammals with distributions that span the entire continent can hibernate. Since the climate varies substantially among regions it is possible that torpor patterns have evolved to adjust for that. The native mammals distributed all over Australia are the echidna (*Tachyglossus aculeatus*) and two bats, a wattled bat (*Chalinolobus gouldii*) and a long-eared bat (*Nyctophilus geoffroyi*). While for the bats being able to fly has a major influence on their distribution range, this is clearly not the case for echidnas and flexible use of torpor likely contributes substantially to enabling these monotremes live under such diverse environmental conditions.

For echidnas no detailed quantitative regional comparisons about torpor patterns have been made, but it is known that individuals living in cold areas have a long hibernation season with prolonged torpor bouts, whereas those in deserts or in the subtropics show brief torpor bouts (Nicol and Andersen 1996; Brice et al. 2002). For *C. gouldii* no detailed regional comparative data are available.

Quantitative comparisons of torpor patterns between cool-temperate and tropical populations have been made for the long-eared bats (*N. geoffroyi*) (Stawski and Geiser 2012). As expected, torpor was deeper and longer in the colder area. However, when the regression line for TBD vs T_a from the cool-temperature area was extrapolated to the tropical area, it substantially underestimated the TBDs measured at the topical area, which was 2.8-fold higher than that predicted. This suggests that *N. geoffroyi* display regional phenotypic flexibility in torpor bout duration (Stawski and Geiser 2012). In another long-eared bat (*N. bifax*) restricted to the tropics and subtropics of eastern Australia, significant regional differences were observed for the minimum T_b during torpor (Stawski and Geiser 2011). Subtropical *N. bifax* defended T_b during torpor at 3.4 °C on average, tropical bats at 7.3 °C.

Similar regional differences have been observed for North American bats with large geographic ranges (Dunbar and Brigham 2010). Torpid big brown bats (*Eptesicus fuscus*) from Michigan (45.8°N) thermoconformed with a low TMR down to a T_a of 2 °C, whereas individuals from southern Alabama (31.3°N) thermoconformed only to T_a 5 °C and raised TMR for thermoregulation and consequently the T_b-T_a differential below that. In red bats (*L. borealis*) with a smaller geographic range, similar but less pronounced differences in the thermal response of TMR were recorded (Dunbar and Brigham 2010).

Another North American mammal with a large distribution range is the woodchuck or groundhog (*Marmota monax*), a solitary marmot. For this species it is the duration of the hibernation season varies with latitude (Zervanos et al. 2010). In Maine (~44° N) woodchucks hibernated on average from October to April (Fig. 7.2) whereas in Pennsylvania (~40° N) from November to March and in South Carolina

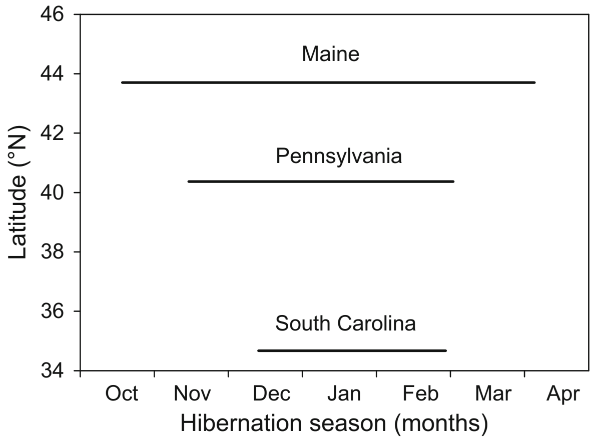

Fig. 7.2 The hibernation season as a function of latitude in American woodchucks (*Marmota monax*). Data from Zervanos et al. (2010)

(~35° N) from December to March (Zervanos et al. 2010), demonstrating that groundhog day (2 February) differs among populations.

Intraspecific differences in torpor expression have also been observed in a marsupial, the Australian feathertail gliders (*A. pygmaeus*). Differences were observed in morphology and behaviour between high elevation, montane versus subtropical, coastal individuals, but also for captive individuals. With regard to torpor expression, montane *A. pygmaeus* expressed the deepest (minimum regulated T_b 2.0 °C) and longest (mean maximum TBD ~5 days) torpor bouts. Subtropical individuals had shallower (minimum regulated T_b 4.2 °C) and shorter (mean maximum TBD ~0.5 days). Captive-bred individuals were the poorest performers with regard to torpor expression, as they expressed torpor less frequently in shorter and shallower bouts (Geiser and Ferguson 2001).

The data suggest that mammals from different continents and different phylogenetic backgrounds adjust their thermal physiology in an appropriate manner. This flexibility of torpor expression likely contributes to the ability of these species to live in vastly different habitats. The observed variability could be due to phenotypic plasticity but also to long term-selection.

Torpor Use and Migration

Flight and migration is an important difference in how small birds and bats deal with adverse conditions in comparison to non-flying terrestrial mammals. Because birds and bats can fly, they commonly employ the behavioural option of flight to deal with seasonal changes in weather and migrate to avoid cold conditions and food shortages. In contrast, small terrestrial mammals cannot migrate because of the slow speed and high energy expenditure of locomotion (Fig. 1.5). Therefore, they often opt for a physiological option and thus employ torpor to survive adverse conditions often during winter.

However, torpor and migration are not mutually exclusive processes. The first observation of torpor expression during migration was made on hummingbirds, which entered torpor to enhance fat storage at night to accumulate fuel for the next part of the journey (Carpenter and Hixon 1988). A free-ranging migratory rufous hummingbird (*Selasphorus rufus*) used torpor for most of the night while roosting, despite having more than enough stored fat to remain normothermic (Carpenter and Hixon 1988). Captive *S. rufus* enter the longest and most frequent bouts of spontaneous torpor during the autumnal migration period, the time of the year when they are at peak body mass and have amassed fat stores up to 50% of lean body mass (Hiebert 1993a, b). Such fat stores would easily allow for regulation of normothermic T_b in the cold (Hiebert 1993a, b). These observations clearly show that pre-migratory torpor use in these hummingbirds is not an acute response to an energetic challenge, but rather predictive anticipating a likely future energy challenge. Shallow torpor was also used during migration presumably to speed up fuel accumulation during stopovers in a passerine bird the blackcap (*Sylvia atricapilla*) (Wojciechowski and Pinshow 2009). Further, torpor is also used in migrating bats. During migration stopovers silver-haired bats (*L. noctivagans*) used torpor extensively, saved almost 90% of the energy they would have required for normothermic thermoregulation, and thereby maximised energy availability for the next flight (McGuire et al. 2014).

Torpor and Locomotion

While torpor is an effective means for energy conservation, a widely presumed downside of torpor is a limited ability to move (IUPS 2003; Boyles et al. 2020), and thus an increased vulnerability to predation. However, the available data show that small arid zone dasyurids (Marsupialia), elephant shrews (Macroscelidea) and other heterothermic species including bats that regularly use torpor in the wild, are capable of moving well enough while torpid at low T_b. Some of these mammals can move to basking sites and expose themselves to solar radiation to passively rewarm, which minimizes the energetic costs of raising T_b at the end of a torpor bout. However, basking while in torpor entails risks if the animals cannot move fast enough to avoid becoming prey.

To assess locomotor performance at low T_b, Rojas et al. (2012) quantified the running speed as a function of T_b of three small heterothermic marsupials (kalutas, *Dasykaluta rosamondae*, 35.1 g, dunnarts *Sminthopsis crassicaudata*, 17.5 g, planigales *Planigale gilesi*, 11.7 g). These mammals were compared with jacky lizards (*Amphibolurus muricatus*, 24.2 g), a reptile known to move when cold (Heatwole and Taylor 1987). All animals were able to begin to move at low T_b (kalutas from 17.9 °C, dunnarts from 15.3 °C, planigales from 14.8 °C, lizards from 8.4 °C) and their running speed increased in a sigmoid fashion with increasing T_b

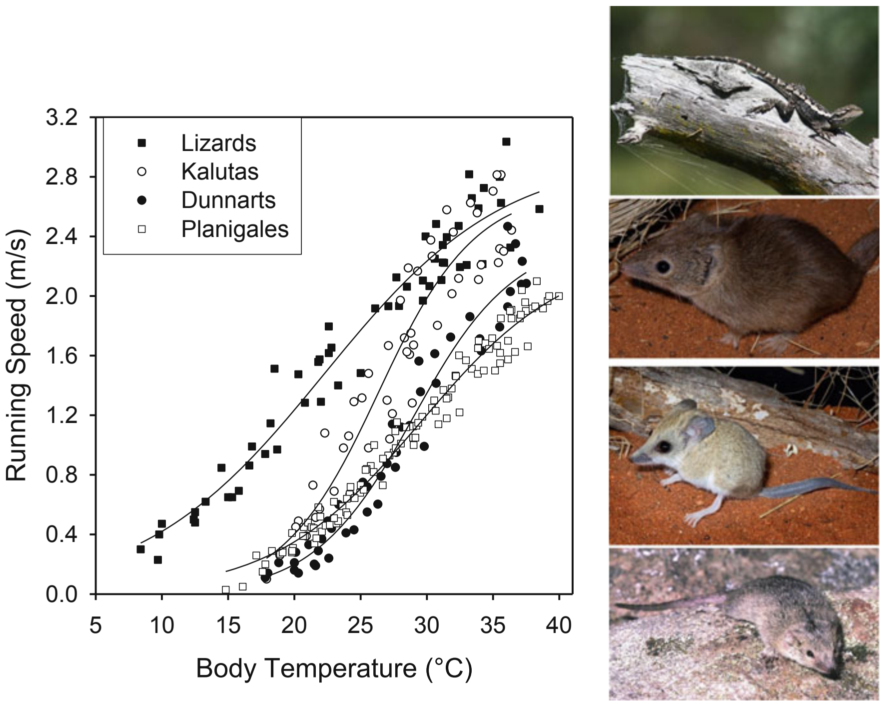

Fig. 7.3 Running speed as a function of body temperature in three mammals in comparison to a lizard. Following the order on the graph left and the pictures right the species are: jacky lizards (*Amphibolurus muricatus*, 24.2 g), kalutas (*Dasykaluta rosamondae*, 35.1 g), dunnarts (*Sminthopsis crassicaudata*, 17.5 g), and planigales (*Planigale gilesi*, 11.7 g). In all species running speed has a sigmoid relationship with body temperature. Line graph from Rojas et al. (2012) with permission, photos F. Geiser

(Fig. 7.3). Maximum running speed ranged from 2 to 3 m/s and occurred between T_b 35 and 40 °C in all species. Body mass did not strongly affect running speed in the size range investigated, but the effect of T_b on running speed differed among species. At T_b 20 °C, a T_b regularly experienced by dasyurids during daily torpor or during basking in the wild (Warnecke et al. 2008), running speed was around 0.3 m/s. This appears to be fast enough to avoid approaching predators when these mammals are basking near a burrow or rock crevice where they can hide. In the lizards running speed at T_b 20 °C was ~1.2 m/s.

Although torpid animals move more slowly than when normothermic, they obviously can move in a coordinated fashion and many mammals can move well enough above T_b 15 °C (Walhovd 1979; Rojas et al. 2012). This includes arboreal pygmy-possums (*Cercartetus nanus*), which can climb along a narrow branch when T_b is 15.6 °C (Nowack et al. 2016b). Hibernating bats can move slowly along a substrate at T_bs as low as 5–8 °C (Choi et al. 1998; Bartonička et al. 2017). Even flight is possible at low T_bs. Flight capability in birds has been observed from a minimum T_b of 28.5 °C in poorwills (*P. nuttallii*) (Austin and Bradley 1969). In bats minimum T_bs for initiation of flight range from 21.3 °C in *Myotis sodalis*, 28 °C in *Eptesicus fuscus*, to 32 or 33° in *Tadarida brasiliensis* and *Myotis yumanensis* (Studier and O'Farrell 1972; Willis and Brigham 2003).

Passive Rewarming from Torpor

Endothermic rewarming from torpor requires a substantial increase in energy expenditure and can compromise the energy savings gained from using torpor. It is therefore often seen as a major disadvantage of torpor. Although MR may be reduced by ~90% during a bout of daily torpor compared with the RMR for normothermic, resting individuals, daily energy savings by employing daily torpor are usually only ~20% to 50% because of the short duration of torpor bouts, high costs of activity and high costs of rewarming (Kenagy 1989; Holloway and Geiser 1995; Lovegrove et al. 1999). Even during multiday hibernation, when TMR may be reduced by more than 99% of that in normothermic individuals (Ruf and Geiser 2015), IBEs still require most of the total energy used during the hibernation season (Wang 1978; Thomas et al. 1990). This energy cost occurs despite endothermic arousals and IBEs last only for several hours, whereas the TBDs last for several days or even weeks. It has been estimated that endothermic rewarming and IBEs require between 85% and 95% of the energy used during the hibernation season (Wang 1978; Geiser 2007). However, more and more evidence is accumulating that rewarming by birds and mammals is not always fully endogenous often containing a passive component.

Estimates of energy expenditure during torpor have largely been based on laboratory data obtained under constant T_as. However, data from the field on both birds and mammals show that rewarming from torpor in many species is partially or entirely passive, which should reduce energy costs (Schmid 1996; Körtner et al. 2000; Brigham et al. 2000; Dausmann 2005; Geiser et al. 2002; Mzilikazi et al. 2002; Lane et al. 2004; McKechnie and Wolf 2004). Rewarming costs can be reduced significantly by passive rewarming associated with a rise in T_a (Schmid 1996; Lovegrove et al. 1999), by direct exposure to radiant heat (Geiser and Drury 2003), or by social thermoregulation (Arnold 1993). Therefore, the energetic costs of rewarming in animals measured at constant T_a or assuming all individuals were exposed to the same thermal conditions may not reflect the conditions for free-ranging animals.

Passive rewarming from torpor in birds is currently known only from the nightjar-relatives (Caprimulgiformes) and roadrunners (Cuculiformes). Most caprimulgiforms for which torpor in the wild has been observed seem to use passive rewarming to some extent. This includes poorwills (*Phalaenoptilus nuttallii*), owlet nightjars (*Aegotheles cristatus*) and frogmouths (*Podargus strigoides*). In most of these species arousal from torpor involves basking in the sun (Brigham et al. 2000; Körtner et al. 2000; Lane et al. 2004; Woods et al. 2019).

In mammals passive rewarming from torpor is used by members of all three mammalian subclasses. Passive rewarming has been observed in echidnas (*T. aculeatus*, Monotremata), many dasyurid marsupials and possums (reviewed in Geiser et al. 2004) and in placentals including hamsters (*Phodopus sungorus*), marmots (*Marmota marmota*), elephant shrews (*Elephantulus myurus*), Namib golden mole (*Eremitalpa granti*), primates (*Microcebus myoxinus*, *M. murinus* and *Cheirogaleus medius*), Ethiopian hedgehogs (*Paraechinus aethiopicus*) and many bats (including: *Eptesicus fuscus*, *Myotis evotis*, *M. lucifugus*, *Nyctophilus geoffroyi*, *N. gouldi* and *Vespadelus pumilus*) (Kurta 1990; Arnold 1993; Schmid 1996; Mzilikazi et al. 2002; Dausmann et al. 2013; Turbill et al. 2003a, b; Lausen and Barclay 2003; Willis and Brigham 2003; Abu Baker et al. 2016; Geiser et al. 2016).

Passive rewarming has been recorded at $T_b < 10$ °C in some hibernators. In many species it does not appear to involve movement although it may involve selection of an appropriate site to enter torpor with a high chance of an increase in T_a that will result in passive rewarming the following day (Turbill et al. 2003b). Since the roost T_a of bats under sun-exposed bark are warmed several degrees above T_a during the day (Turbill et al. 2003b) it seems likely that the roosts selected by long-eared bats (*Nyctophilus* spp.) play an important part in minimising energy expenditure. This allows them to exploit the energy saving benefits of torpor while minimising arousal costs (Turbill and Geiser 2006). The T_s of long-eared bats, *N. geoffroyi* and *N. gouldi* show large daily fluctuations while they remain in hibernation, but on the days bats rewarm, the increasing T_a helps passive rewarming initially, followed by endogenous rewarming later (Turbill and Geiser 2008). Partial passive rewarming also has been observed in the short-tailed bat, *Mystacina tuberculata*, in temperate New Zealand (Czenze et al. 2017c).

The selection of thermally appropriate roosts for minimising energy expenditure has been documented for captive long-eared bats, *N. gouldi*, held in outdoor aviaries in a temperate region. In winter *N. gouldi* selected black boxes, which absorb more heat from light and therefore are warmer, over colder white boxes (Doty et al. 2016b). Selection of black boxes was most obvious when food was restricted, apparently to facilitate passive rewarming, but also by maintaining a normothermic T_b for longer at reduced energetic costs because of the smaller T_b-T_a differentials (Doty et al. 2016b).

When captive long-eared bats, *N. geoffroyi*, were exposed to a summer T_a-cycle increasing from 13 °C at night to 27 °C during the day, the rewarming process consisted of two components. Bats rewarmed passively first, followed by endogenous rewarming as identified by an increase in MR and faster rise of T_b than T_a (Turbill et al. 2008). The critical T_a at which endothermic rewarming was initiated, after the initial passive rewarming phase, was a function of time of day suggesting an underlying circadian rhythm (Turbill et al. 2008). When the heating cycle commenced at 06:00, the average critical arousal T_a where endogenous rewarming began was ~25 °C, whereas when the heating cycle commenced at 12:00, the critical arousal T_a was only ~20 °C. This means that the timing of afternoon normothermia, the function of which remains obscure, is reached is not substantially delayed (Turbill et al. 2008). The critical T_b for endothermic arousal of around 20 °C in

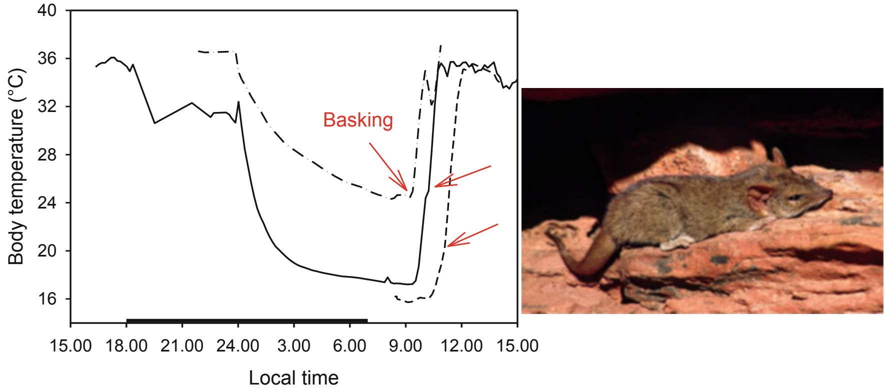

Fig. 7.4 Basking in free-ranging pseudantechinus (*Pseudantechinus macdonnellensis*). The graph shows three individuals on three different days. Animals entered torpor in the second half of the night in rock crevices, and were seen basking (red arrows) at low T_bs on rock ledges (picture right). The dark bar indicates night. Data from Geiser et al. (2002), photo F. Geiser

bats potentially is related to maximizing cardiac capacity from that T_b (Currie et al. 2015b). A fully functional cardiovascular system is crucial for endothermic arousal because adequate delivery of O_2 and fuel for metabolism are required for heat production (Currie et al. 2015b).

In some heterotherms, rewarming can be entirely passive. The most extreme examples for passive rewarming, with an increase of T_b with T_{roost} and without an endogenous component, has been observed in Australian arid-zone bats and Malagasy lemurs. Broad-nosed bats, *Scotorepens greyii*, relied on entirely passive rewarming from torpor on 45% of days in summer, whereas, *S. balstoni*, used it on 29% of days (Bondarenco et al. 2016). Entirely passive rewarming was also common in free-tail bats, *Ozimops petersi* (Bondarenco et al. 2014). Passive rewarming from torpor without an obvious metabolic component, as verified by MR measurements in the wild, also is used extensively by Malagasy lemurs, *Cheirogaleus medius*, when they are in poorly insulated roosts whose T_{roost} fluctuates over the day (Dausmann and Warnecke 2016).

The above mentioned species rewarm in roosts and do not need to move. However, active movement at low T_b from a torpor site to a favourable basking site, typically at T_bs of ~15 to 20 °C, has also been documented, mainly in daily heterotherms. For example, in central Australia, the marsupial rock-dwelling fat-tailed antechinus (*Pseudantechinus macdonnellensis*) at T_bs between 19 and 25 °C, emerged from rock crevices to move to a rock ledge where they exposed themselves to the morning sun (Fig. 7.4). Similar observations have been made for dunnarts (*Sminthopsis crassicaudata*) basking near the entrance of soil cracks while torpid with T_bs as low as 14.6 °C (Warnecke et al. 2008). An alternative to basking in the open is to use shallow burrows that are warmed by the sun and also afford protection from predators, but may involve some movement for selection of a thermally appropriate site (Körtner et al. 2016).

In species that socially thermoregulate, such as marmots and sugar gliders, passive rewarming may simply involve delayed arousal and absorbing heat from adjacent individuals. In the socially hibernating Alpine marmot (*Marmota marmota*), rewarming is highly synchronised among individuals (Arnold 1988; Ruf and Arnold 2000). Territorial males commence the rewarming process first and juveniles can use the heat generated to help with rewarming. In sugar gliders (*Petaurus breviceps*) mixed groups of torpid and normothermic individuals huddle meaning that torpid individuals should benefit from the heat released by normothermic individuals during the rewarming process (Nowack and Geiser 2016).

Most observations on passive rewarming have been made recently, reflecting the increasing use of small temperature transmitters and data loggers in the field. Thus it is likely that many other heterothermic species will be found to rewarm this way.

For those species (e.g. *Sminthopsis macroura*, *Microcebus myoxinus*, *M. murinus, Cheirogaleus medius*) for which MR measurements are available, MR remained low (below or near BMR), at least during the initial part of the rewarming process (Schmid 1996; Dausmann et al. 2004). It has been estimated that passive rewarming via an increase in T_a from 15 to 25 °C reduces the rewarming costs in dunnarts (*S. macroura*) by ~65% relative to active rewarming (Lovegrove et al. 1999) and savings will be even greater if most of the rewarming process is passive such as in fat-tailed lemurs (*C. medius*) (Dausmann et al. 2004).

Energy savings during radiant heat assisted passive rewarming in *S. macroura* basking under a heat lamp is also substantial (Geiser and Drury 2003). After torpor entry in the early morning when MR had approached its steady-state minimum at around 09:00, dunnarts were exposed to a heat lamp for about 1.5 hours. The torpid dunnarts stretched out under the lamp similar to the fat-tailed antechinus basking in the sun on a rock ledge (Fig. 7.4). Dunnarts rewarmed entirely passively when exposed to radiant heat with only a small rise of MR despite the large rise of T_b from about 19 °C to about 35 °C (Fig. 7.5). Although the artificial heat source provided much less radiant heat than the sun, endothermic heat production remained below BMR for most of the rewarming process. The dunnarts re-entered torpor after the heat lamp was switched off, and rewarmed endogenously from the second torpor bout (Fig. 7.5). In contrast to the first bout, the rewarming in the second bout saw a substantial increase in MR although the increase in T_b in the two torpor bouts was similar (Fig. 7.5). The use of radiant heat assisted passive rewarming by *S. macroura* reduced rewarming costs by ~85% on average of that required for endothermic rewarming at the same T_a (Geiser and Drury 2003). When torpid dunnarts have the option to move from a shelter to a basking site in captivity they always do so (Warnecke and Geiser 2010).

For dunnarts remaining normothermic and resting throughout the day at T_a 16 °C daily energy expenditure was 48 kJ/d on average (Fig. 7.6). When dunnarts used torpor and used endothermic arousal it was reduced to 30 kJ/d. However, when dunnarts used passive rewarming in the morning, and basked for most of the afternoon, daily energy expenditure was further reduced to 23 kJ/d or by 52% (Fig. 7.6). Basking during rewarming from torpor occurs in *S. macroura*, *S. crassicaudata* and *P. macdonnellensis* in the wild (Geiser et al. 2002; Warnecke et al. 2008; Körtner and Geiser 2009). The reduction in daily energy expenditure

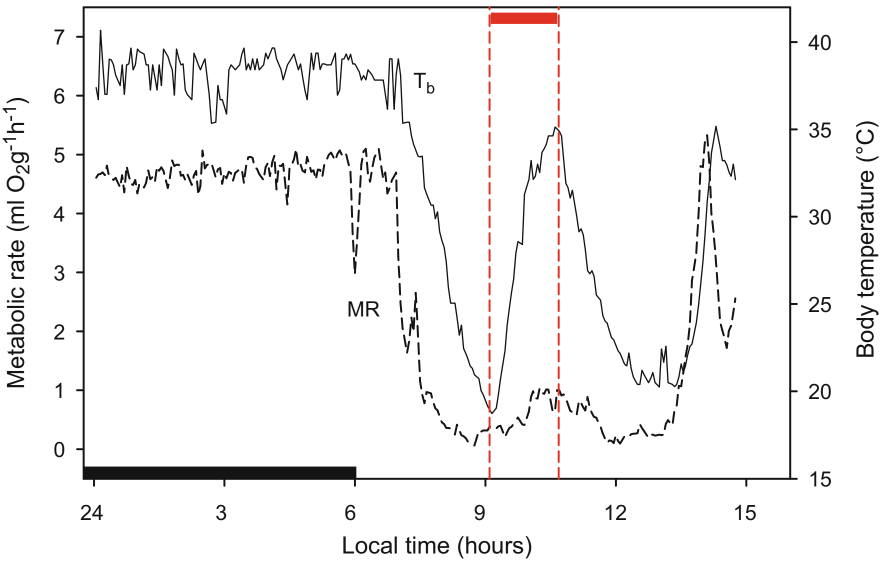

Fig. 7.5 The body temperature (T_b, solid line) and metabolic rate (MR, broken line) of a dunnart (*Sminthopsis macroura*) as a function of time of day at T_a 16 °C. The dunnart entered torpor in the morning and when MR approached its minimum it was exposed to a radiant heat source (red bar, time between vertical red broken lines). Although the T_b rose substantially during that exposure to radiant heat the MR rose only slightly. The dunnart re-entered torpor after the heat source was switched off and then rewarmed endogenously after about 13:00, this time the MR increased substantially to produce a similar increase of T_b. Data from Geiser and Drury (2003)

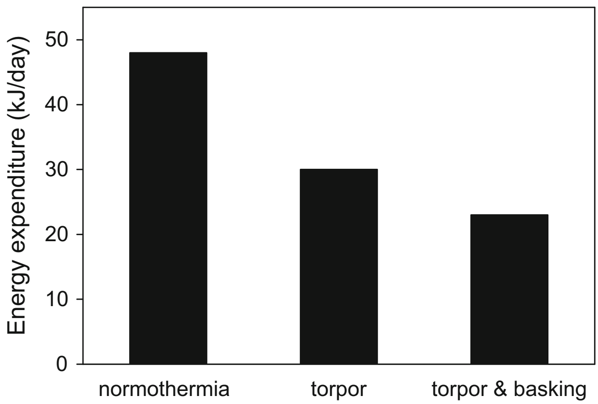

Fig. 7.6 Average daily energy expenditure of dunnarts (*Sminthopsis macroura*) remaining normothermic throughout the measurement period (left), expressing a bout of daily torpor of average duration (centre), or expressing a bout of daily torpor of average duration and basking during and after rewarming (right). Data from Geiser et al. (2004)

indicates that access to solar energy during passive rewarming from torpor and during the normothermic rest phase, combined with low TMR, enable animals to benefit even more substantially from torpor than is often assumed.

Passive rewarming also has implications for torpor use *per se*. Access to solar radiation and/or exposure to daily T_a fluctuations including daily T_a maxima that are well above T_b minima during torpor, may be important factors that determine whether or not a species uses torpor. This is in addition to unpredictable changes in climate and food availability that often are associated with daily torpor use (Lovegrove 2000). Many species known to use passive rewarming from torpor live in areas that receive substantial amounts of solar radiation or experience pronounced daily T_a fluctuations, such as deserts and high elevations. These areas may be limiting with regard to food availability, but provide an alternative source of energy in the form of sunshine.

Interactions Between Torpor Use and Huddling Behaviour

Huddling in groups is an effective way of reducing heat loss (Gilbert et al. 2010; Eppley et al. 2017; Chap. 1). In contrast to torpor, RMR during huddling remains at or above the BMR (Fig. 1.6), but it is lower than for a single animal at low T_a, as it reduces thermoregulatory energy expenditure. Therefore one could predict that the opportunity to huddle would reduce torpor use. This interpretation is supported by data for marsupial sugar gliders (*P. breviceps*). When groups of gliders had access to food, only a few individuals entered torpor whereas others remained normothermic. This resulted in mixed groups of torpid and normothermic individuals. A possible reason for this social thermoregulation is to maintain T_{nest} above the value requiring regulation of T_b by torpid individuals (Nowack and Geiser 2016). If, however, food was withheld, all individuals entered torpor. These findings suggest that, if food is available only a few individuals of a huddling group use torpor, which has been observed in the wild, resulting in an overall modest reduction in energy savings of the group, whereas when food is restricted, the energy conservation of the entire group is maximised by the use of communal torpor.

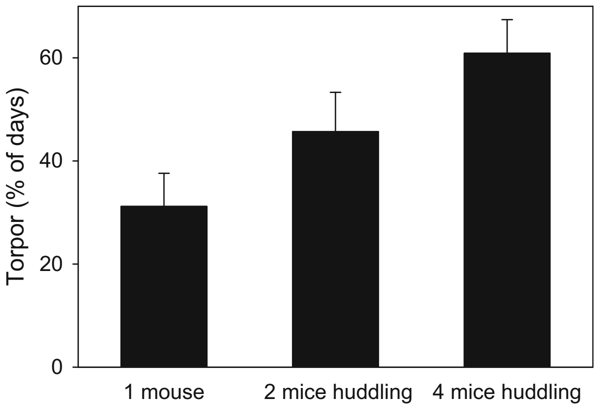

Fig. 7.7 Effect of group size on torpor expression in huddling Japanese field mice (*Apodemus speciosus*). Data from Eto et al. (2014)

Perhaps surprisingly, rather different data exist for Japanese field mice (*Apodemus speciosus*). Eto et al. (2014) found the number of huddling individuals had a positive effect on torpor use (Fig. 7.7). The frequency of torpor use of single individuals was ~31% of days, that of two huddling individuals ~46%, and that of 4 huddling individuals ~61%. Food consumption decreased with an increase in group size (Eto et al. 2014). Rewarming from torpor was slowed in large groups, suggesting that *A. speciosus* used partially passive rewarming by sharing heat to maximise energy savings (see above).

In the field, torpor in huddling mixed groups of mice (*Mus musculus domesticus*) and their potential predators, dunnarts (*S. crassicaudata*) has been observed in southern Australia in winter (Morton 1978). This suggests that under the prevailing environmental and social circumstances, sharing body heat and using communal torpor was more important for both species than predation or predator avoidance.

Temperature Selection and Torpor Use

Torpor expression is strongly temperature-dependent and therefore one would expect that selection of roosts and the microclimate within them would allow animals to adjust torpor patterns. In fat-tailed antechinus (*P. macdonnellensis*) living in rocky outcrops in central Australia, the thermal conditions at various crevice depths are rather constant throughout the year. In winter they could select warm nest sites to enter torpor or remain normothermic, but rather seem to use cool sites to enter torpor and save energy during torpor (Fig. 7.8), perhaps because they can bask to rewarm passively (Geiser and Pavey 2007). In cave-roosting bats selection of different microclimates within a cave is well known (Twente 1955; Nagel and Nagel 1991). As outlined above, cave roosting European bats tend to select T_as between −2.5 and 9 °C with a mean of around 5 °C (for *Myotis* spp., *Plecotus auritus* and *Pipistrellus pipistrellus*). The choice is thought to permit prolonged torpor bouts, but avoid thermoregulation requiring heat production at T_as well below 0 °C during torpor. As expected from temperature effects on TBD, big brown bats, *Eptesicus fuscus*, hibernating in a house in Indiana, expressed relative short torpor bouts (3.3 days on average) at a T_a of about 12 °C, whereas individuals of the same species hibernating in caves at much lower T_as remained torpid for 7–25 days (Hallsall et al. 2012). South African bent wing-bats (*Miniopterus* sp.) who roost in caves select much lower T_as when using torpor during winter than when normothermic in summer (Brown and Bernard 1994).

Using roosts with differing thermal properties and torpor expression is not restricted to mammals. Owlet-nightjars (*Aegotheles cristatus*), roost in both rock crevices and hollow trees in Central Australia. The T_a in rock crevices was warmer and more stable than tree hollows and torpor was expressed nearly twice as often in the tree roosts (Doucette et al. 2011). Nevertheless, owlet nightjars used tree roosts on about 2/3 of occasions, a choice likely made for predator avoidance as the cavity

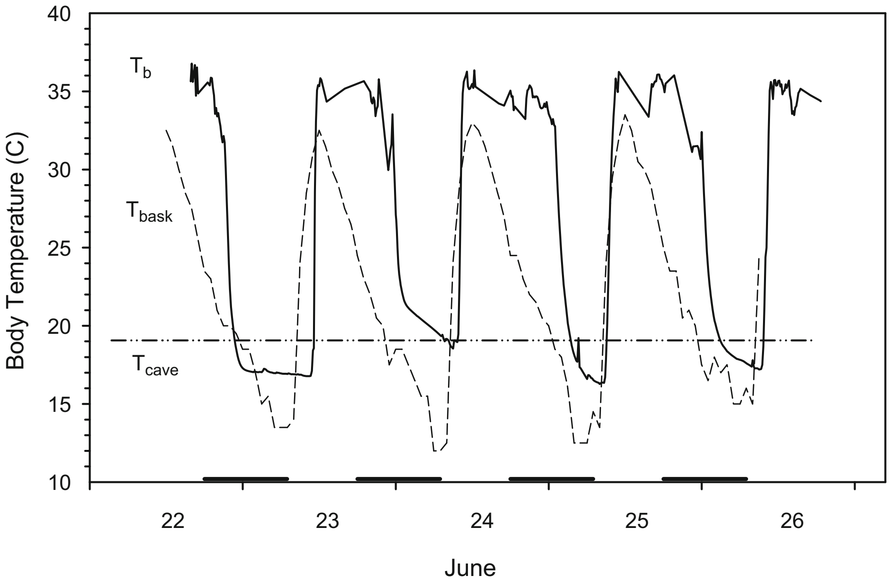

Fig. 7.8 Body temperature (T_b) of a fat-tailed antechinus (*Pseudantechinus macdonnellensis*) over 5 days in June, plotted with the temperature at the morning basking site (T_{bask}) and cave temperature (T_{cave}) near the torpor site. Note that the T_b fell below that of T_{cave} on most nights and the close match of T_{bask} and T_b in the morning. Black horizontal bars indicate night. Data from Geiser and Pavey (2007)

entrances were high above the ground. Moreover, owlet-nightjars roosting in trees likely had more opportunity to use passive rewarming (Doucette et al. 2011).

Other species select roost sites in more open areas. Solitary western long-eared bats (*Myotis evotus*) roost in rock crevices in Canada with different thermal conditions to accommodate different thermal preferences and to express different patterns of torpor (Chruszcz and Barclay 2002). Tree-roosting long-eared bats (*Nyctophilus geoffroyi* and *N. gouldi*) in Australia selected roosts under bark on the northern side of trees in summer and winter, but expressed torpor throughout the year and used the radiant heat from the sun warming their roost for partially passive rewarming (see above). In eastern red bats (*Lasiurus borealis*), a foliage-roosting species, torpor was common in summer and elevation of roost sites and T_a were the best predictors for its use (Monarchino and Johnson 2020). In winter, *L. borealis* hibernate in leaf litter with fluctuating T_as, which can however be buffered by snow (Dunbar and Tomasi 2006).

Torpor Use in Relation to Fires

Changes in global weather patterns are predicted to increase the frequency and intensity of severe events such as fires, droughts, storms, and floods (Diffenbaugh and Field 2013; IPCC 2014). Episodes of severe wildfires are increasing worldwide. In the past these have occurred mainly in the warm season, however, recent wildfires in Australia, California and Norway have occurred or began in winter. In other regions of the world the timing of the 'fire season' also has increased to well beyond 'summer' (Flannigan et al. 2009). However, wildfires are not the only fires animals are confronted with. In Australia and other regions 'fuel reduction burns', 'prescribed fires' or 'management burns', which are usually low on intensity, are mainly conducted during the cold season in an attempt to reduce the severity of wildfires in the following warm season. These prescribed burns during the cold season when heterothermic animals are often in deep torpor present different challenges for mammals compared with wildfires that usually occur in the warm season and often are severe.

The response of mammals to fire appears to differ among large mammals, small terrestrial quadrupedal mammals and small volant bats. Large mammals tend to avoid fires as they can quickly run away, and often their mortality rates are low (Singer et al. 1989). However, during extensive fires like those experienced in 2019/20 in Australia, many mammals were killed. For small mammals it is often assumed that most die during fires, but many actually survive the direct impact of the fire, because they can hide in underground burrows or crevices (Geiser et al. 2018). While some individuals die directly from burns, most die because of a decrease in cover and food availability that continue for a considerable time after the actual fire event (Lunney et al. 1987; Recher et al. 2009). Consequently, the longer-term limited availability of food and water in a post-fire landscape can present a severe challenge to small mammals because of their relatively high energy demands and foraging requirements, especially at low T_as. Moreover, reduction in cover may increase vulnerability to predation, exacerbated by predators invading the area in response to improved hunting conditions (Körtner et al. 2008; Stawski et al. 2015a; McGregor et al. 2016). Bats differ from other small non-flying mammals because of their ability to fly and to move long distances quickly and economically (Tucker 1975). Bats also have access to both aerial and ground-dwelling prey, so their response to fire is likely to differ from that of other small mammals.

One effective way to deal with the challenge of a post-fire landscape and reduced food availability would be to use torpor (Geiser and Körtner 2010), but first the animals must survive the fire. To be able to do this they require the ability to sense and react to fire cues, such as smoke and noise from fire, especially important in the context of management burns conducted during the cold season.

Recent evidence shows that torpid animals can respond to smoke if T_a and T_b are not too low. Dunnarts (*Sminthopsis crassicaudata*), pygmy-possums (*Cercartetus nanus*) and bats (*Lasiurus borealis* and *Nyctophilus gouldi*) can sense and respond to smoke, but the response is slowed by low T_a (Scesny 2006; Stawski et al. 2015b;

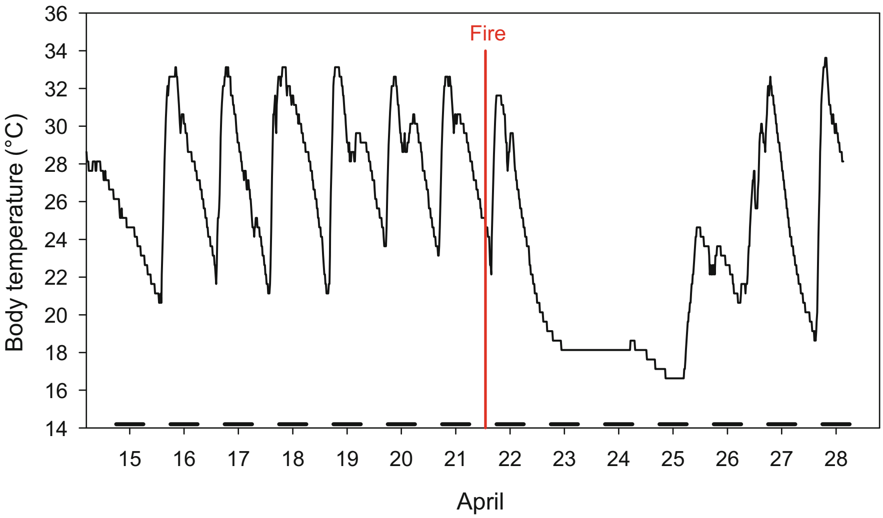

Fig. 7.9 Torpor expression of a free-ranging echidna (*Tachyglossus aculeatus*) before and after a management burn (fire). Before the fire torpor was shallow and brief, after the fire, torpor was deep and prolonged. Black horizontal bars indicate night. Data from Nowack et al. (2016a)

Nowack et al. 2016a, b; Doty et al. 2018). Dunnarts, *S. crassicaudata*, in shallow torpor with T_bs between ~18 and 25 °C rewarmed from torpor about 40 minutes after smoke exposure. At a T_a of 15 °C, torpid pygmy-possums, *C. nanus*, responded to smoke after 6–8 minutes by increasing metabolic rate and had aroused or partially aroused within ~30 min. In contrast, at a T_a of 10 °C and a T_b of ~13 °C only some individuals responded and only one aroused (Nowack et al. 2016b). Bats, *N. gouldi*, mostly responded within less than a minute to smoke, but the response was slowed at low T_a (Doty et al. 2018). However, not all torpid mammals detect fire cues and arouse in sufficient time to escape a fire. One of two free-ranging echidnas (*T. aculeatus*) in torpor in the same hollow tree log left the log and fled the fire whereas the other did not arouse and did not survive (Nowack et al. 2016a). Nevertheless, animals in protected burrows may still survive fires even if they do not respond to smoke cues.

If animals survive the fire they must then cope with reduced cover and food and often reduced access to water. Considering the energy and water savings that can be achieved, it seems only logical that torpor would be widely used by terrestrial mammals to deal with the post-fire environment. Echidnas, *T. aculeatus*, during a management burn in autumn displayed brief bouts of torpor daily before the fire, but after the fire they responded by increasing the depth and duration of torpor bouts (Fig. 7.9). Echidnas in unburnt control areas continued with the pre-fire torpor pattern and their T_bs were significantly higher than that of animas in the post-fire group (Nowack et al. 2016a). Interestingly, echidnas reduced their daily activity, but remained within their original home range after the fire, suggesting that animals can use the physiological option of torpor to minimise their energy needs sufficiently to

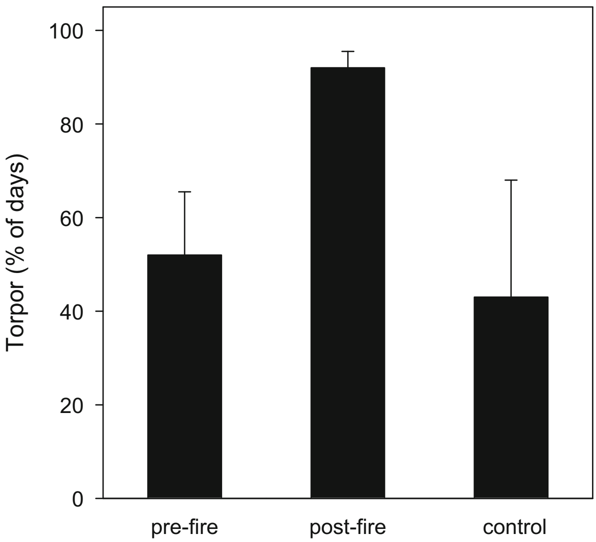

Fig. 7.10 Expression of torpor in free-ranging antechinus (*Antechinus stuartii*) before and after a management burn and relative to a control site. Post-fire torpor use was about twofold higher than pre-fire and controls. Data from Stawski et al. (2015a)

preclude the need to move to unburnt areas outside their familiar range. Ants and termites, their prey, also survive fires if they are underground and provide a food source post-fire.

Forest-dwelling antechinus also increased torpor expression and duration and decreased daily activity in a post-fire environment (Stawski et al. 2015a; Matthews et al. 2017). After a hazard reduction burn in late autumn, the brown antechinus (*A. stuartii*) increased post-fire torpor use and torpor duration by ~two-fold when compared to the torpor expression of animals measured immediately before the fire (Stawski et al. 2015a; Stawski and Rojas 2016). Post-fire antechinus also differed from animals measured at the same time in a nearby unburnt area (Fig. 7.10). Increased torpor use in post-fire antechinus was accompanied by a 50% decrease in activity. The reduction in activity was mainly achieved by reducing daytime activity, which likely reduced exposure to predators in a habitat now with little vegetative cover. Like the echidnas, antechinus remained in burned areas for weeks despite availability of unburned areas nearby and the population was still present 1 year after the fire, by which time the vegetation had recovered to a large extent and both torpor use and activity of antechinus had returned to pre-fire and control levels (Stawski et al. 2017a).

Some populations of the yellow-footed antechinus (*A. flavipes*) another forest dweller, survived an extremely hot wildfire in south-eastern Australia in late summer that caused the mortality of many other mammals (Stawski et al. 2014a). Males in autumn used torpor on almost 80% of days, much more frequently than in a control site in a similar habitat where torpor occurred on less than 50% of days (Matthews et al. 2017). In a female antechinus torpor was used on almost 90% of days. After the fire, a male antechinus rested in blackened hollow logs during the daytime, likely because reduced canopy cover permitted increased exposure to solar radiation (see

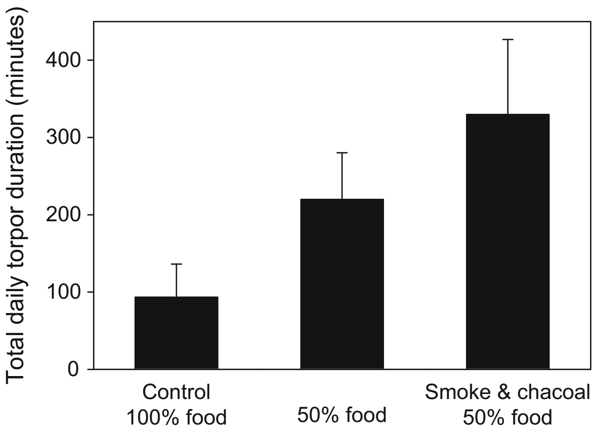

Fig. 7.11 Torpor duration in captive antechinus (*Antechinus flavipes*) females under different experimental conditions. Restricting food by 50% significantly increased torpor use. However, food restriction during charcoal substrate and smoke exposure further increased torpor use. Males showed a similar response to treatments, but torpor duration was less than half of that for females. Data from Stawski et al. (2017b)

above), resulting in the warming of logs and consequently a reduction in thermoregulatory energy expenditure (Matthews et al. 2017).

Much of the increase in post-fire torpor use is likely a consequence of a long-term decrease in food availability and lack of cover. However data for captive mammals indicate that the presence of charcoal-ash substrate and smoke increases torpor use beyond that induced by food restriction alone. These post-fire cues presumably signal a period of imminent food shortage and increased risk (Stawski et al. 2017b). In yellow-footed antechinus (*A. flavipes*) food restriction about doubled torpor use (Fig. 7.11). Exposure to smoke and a charcoal-ash substrate after withdrawal of food resulted in another almost two-fold increase in daily torpor duration and a more substantial T_b reduction (Fig. 7.11) in comparison to food restriction alone (Stawski et al. 2017b). For arboreal sugar gliders (*P. breviceps*) food reduction and a charcoal ash substrate resulted in a ~ 25% prolongation of torpor bouts in comparison to food restriction alone (Nowack et al. 2018).

Desert-dwelling dunnarts (*Sminthopsis crassicaudata*) respond differently to post-fire cues compared with small forest-dwelling mammals. When provided with food and exposed to a charcoal/ash substrate, minimum T_b increased and activity decreased. When food was withheld, torpor expression on a charcoal/ash substrate was similar to the control substrate (Stawski et al. 2015b).

Bats have an advantage over small terrestrial non-flying mammals because flight provides increased mobility at low cost (Tucker 1975; Withers et al. 2016). Bats likely escape threats such as fire more easily than other small non-flying mammals, but data on torpor by bats in relation to fire are scant. The tree-roosting long-eared bat (*N. geoffroyi*), modified its patterns of torpor use following an extensive wildfire (Doty et al. 2016a). Although *N. geoffroyi* used torpor on all measurement days and mean post-fire TBD was ~12 h, when trees had recovered 2 years later TBD was about twice as long. Individuals were also active or normothermic more often and for longer periods after the wildfire compared to 2 years later. The reasons for this may be largely due to the 20-fold greater insect abundance for months following the wildfire, which was extinguished by heavy rain. The large number of insects post-fire likely encouraged foraging by bats. Moreover, the landscape was denuded and uncluttered following the fire, allowing for easier foraging and more solar penetration for warming of roost sites compared to roosts used two 2 years after the fire (Doty et al. 2016a). However, even under these apparently favourable conditions, bats spent about half their time torpid (Doty et al. 2016a).

Torpor Use and Survival of Droughts

Primary productivity of plants is highly dependent on water. The unpredictability of food due to lack of water in environments such as deserts may be the reason for the extensive expression of torpor in these areas (Lovegrove 2000; Munn et al. 2010). Given that torpor expression also reduces water loss, its use for water conservation is also likely ecologically important (Serventy and Raymond 1973; Warnecke et al. 2008; Doucette et al. 2011, 2012; Levy et al. 2011a). It has been hypothesized that torpor is partially responsible for the diversity of small dasyurid marsupial species in the arid zone of Australia, all of whom appear to express daily torpor extensively (Warnecke et al. 2008; Körtner and Geiser 2009). Dasyurids are more diverse than those in mesic areas of the continent (Dickman 2003; Pavey et al. 2020), despite the arid environment, which is often subjected to droughts. Although direct evidence for the initiation of torpor with the removal or restriction of water is more equivocal than for food restriction (Chap. 4), more extensive use of torpor in summer than winter has been observed in desert spiny mice (*Acomys russatus*; Levy et al. 2011a). Possibly water limitation rather than energy shortage may be the major cue for torpor use in these animals in summer and thus the ultimate function of torpor may be for water rather than energy conservation. Desert bats also use relatively more pronounced torpor in summer than winter, and, during heat waves, the reduction of T_b during torpor in the morning delays the time when evaporative cooling is required to prevent lethally high T_b and thus saves water (Bondarenco et al. 2014).

Cold northern winters have the advantage of lasting about 6 months and this time period can be bridged by fat or food storage and/or by appropriate use of torpor. In contrast, El Niño events, which are known to cause droughts, may last for years, a period of time that is too long for survival on stored energy, at least in homeothermic endotherms. Torpor use provides an avenue to help animals survive prolonged periods with limited food and water. In free-ranging Australian owlet-nightjars (*A. cristatus*) the lack of rainfall in dry years substantially affected the use and patterns of torpor in central Australia (Doucette et al. 2012). In a dry year, owlet-nightjars used torpor more frequently than in a wet year (61% vs 27% of days). The TBD in the dry year was about twice as long as in the wet year and the minimum T_b

in the dry year was 3.3 °C lower than in the wet year (Doucette et al. 2012). The variation in torpor variables between years was not strongly related to differences in T_a, but was best explained by availability of insects, which were less than half in the dry year. However, availability of water *per se* also may have affected torpor use. Thus torpor seems to be an important adaptation to overcome droughts and allow animals to persist in areas that are subject to prolonged rather than seasonal shortages of food and water.

Torpor Use and Survival of Floods

Although lack of water is challenging to small mammals and birds, too much water can be instantly and catastrophically threatening. Flooding regularly occurs over wide areas of inland Australia and many other regions of the world. Flooding restricts the opportunities for foraging and often results in reduced food availability during or after floods that could be compensated for by the use of torpor. Further, wet fur (and like wet feathers) substantially reduces the insulation properties (Withers et al. 2016) and therefore increases heat loss and the need for thermoregulatory energy expenditure (Dawson and Fanning 1981). Although in ancient Greece, Aristotle proposed torpor in mud as a consequence of flooding as the avenue for winter survival by birds (Lincoln and Peterson 1979), quantitative information on torpor in relation to floods remains scarce. Direct evidence of flood-induced torpor is currently restricted to two observations, one on a captive bird, the dusky woodswallow (*Artamus cyanopterus*) and the other on a captive golden spiny mouse (*Acomys russatus*) (Maddocks and Geiser 2007; Barak et al. 2018). For both the flooding was accidental, but resulted in interesting, although seemingly appropriate physiological responses that may be important for survival in the wild.

When held in an outdoor aviary in late autumn and winter, woodswallows (*Artamus cyanopterus*), expressed regular nocturnal torpor with reduction in T_b from ~41 °C during the day to ~29 °C during the night (Chap. 3). On a winter's morning one bird was discovered in the aviary partially submerged in a water bath with a much lower T_b of ~22 °C (Maddocks and Geiser 2007). It appears that after a disturbance around midnight, perhaps due to a cat, the bird tried to escape, ended up in the water bath and reduced its T_b. The reduction of T_b from ~32 °C to 22 °C occurred within only 12 min. The bird was removed in the morning, dried and rewarmed in the laboratory and survived. However, although the bird did not entirely rewarm using endogenous heat production, it seems that it was torpid rather than hypothermic because it was able to maintain a T_b-T_a differential of >10 °C for about 10 hours despite being wet (Geiser et al. 2014), and despite expressing much deeper torpor in water than in air. As the T_b during torpor was controlled, it does not appear to be a 'diving reflex' during which homoeostatic regulatory responses are bypassed (Hill et al. 2016). While the observation of an unusually low T_b in woodswallows might be dismissed as an artefact of captivity, the rapid reduction of T_b during the immersion in water, is at least physiologically if not ecologically interesting and deserves further investigation.

Although the heterothermic spiny mice (*Acomys russatus*) occur over extremely arid and rocky regions of the Middle East, they are occasionally exposed to floods. In most of their habitat the average annual rainfall is <100 mm/year. However, spiny mice live in dry wadi beds around the Syrian African Rift Valley, receiving the run-off rain from the Hebron Mountains about 1000 m above sea level that flows to −400 m below sea level over less than 50 km. *A. russatus* typically use short bouts of torpor lasting for 7.5 hours on average year round with a reduction of T_b to about 25 °C (Gutman et al. 2006; Levy et al. 2011a, b, 2012).

Similar to the woodswallows, captive spiny mice were exposed to a flooding event (Barak et al. 2018). Before the flooding, spiny mice held in outdoor cages at a T_a of about 26.5 °C were fed *ad libitum* and none entered torpor with T_b remaining above a mean minimum of ~33 °C. Over one night heavy rain fell, leaked through the roof of two aviaries and T_a fell below 24 °C. One spiny mouse substantially reduced its T_b after its bedding material was soaked with water. During that night T_b fell from ~38 °C to below 30 °C within ~40 minutes. After entering torpor the animal maintained a T_b-T_a differential of >3 °C for most of the torpor bout. When discovered and the wet bedding material had been replaced, the dried mouse was placed back into its cage. Its arousal from torpor was endogenous because T_a did not exceed T_b during any part of the arousal process, but rewarming was slow with T_b increasing from 24.0 to 30 °C over 350 min (Barak et al. 2018). The torpor bout observed in this spiny mouse lasted for ~2.3 days, which is about seven-fold longer than the average TBD for the species. This prolonged torpor bout shows that *A. russatus* is physiologically capable of displaying multiday torpor, which may be one reason why they store fat (Gutman et al. 2006), a typical characteristic of seasonal hibernators (Boyer and Barnes 1999).

Torpor Use in Response to Storms

Storms are frequently experienced by animals, occur worldwide, can occur at any time of the year and animals are exposed to storms especially if roosting well above ground. However, evidence for torpor use during storms is rare, and to date has only been reported for two unrelated species, und under entirely different thermal conditions. Pregnant hoary bats (*Lasiurus cinereus*) a species roosting individually in foliage, migrate from south-western USA to Canada in spring where they may encounter cold-spells. Several of these bats used torpor during a snow storm in spring when T_a fell as low as 0 °C (Willis et al. 2006). Bats remained inactive for up to 9.1 days and displayed multiday torpor bouts with a minimum T_{skin} of 5.5 °C. When T_a increased at the end of the storm, bats became normothermic or expressed only brief bouts of torpor and gave birth within several days. In this instance torpor had two important functions: First it enabled the adult bats to survive the storm and

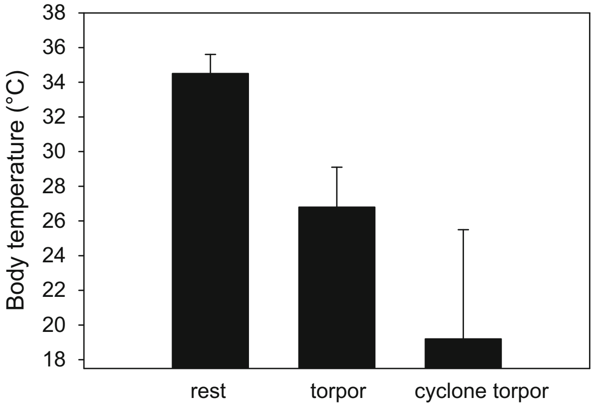

Fig. 7.12 Body temperatures of free-ranging sugar gliders (*Petaurus breviceps*) in a subtropical area in spring at rest, during torpor before the cyclone, and during torpor during a cyclone. The T_a during the cyclone did not differ from before the cyclone. Data from Nowack et al. (2015)

second, torpor prolonged the pregnancy until conditions were better, improving the chance of survival for neonates (Chap. 8).

The other example of torpor during a storm is for sugar gliders (*P. breviceps*), who experienced a subtropical cyclone. Sugar gliders are usually reluctant to enter daily torpor and mainly use it during cold and wet winter nights. In a warm subtropical area gliders also rarely used torpor (Nowack et al. 2015). However, during a storm in spring with category 1 cyclone wind speed and heavy rain, gliders remained inactive, even at night when they usually forage, and used highly synchronized torpor. Seven of the ten free-ranging individuals entered torpor with T_b falling to an average of 19.2 °C, about 7.6 °C lower than on the other few days torpor was observed (Fig. 7.12). During the storm, T_a was no lower than nights prior to it and therefore torpor use likely occurred in response to high wind speeds and rainfall. However, it also could have been in response to other environmental cues such as barometric pressure (Nowack et al. 2015). Hibernating little brown bats (*M. lucifugus*) and other bats appear to use changing barometric pressure as a cue for conditions outside their hibernacula and emerge from torpor when falling barometric pressure indicates favourable foraging conditions (Czenze and Willis 2015; Blomberg et al. 2021). Whatever the cue, the increase in torpor use and reduction in activity likely enhanced survival of the gliders during the cyclone.

Torpor Use and Inter-Specific Competition

Torpor also appears to be crucial in a social context where it may permit co-existence of competing species and reduces inter-specific competition. Common spiny mice (*Acomys cahirinus*) held in large outdoor enclosures in Israel, exclude their congener golden spiny mice (*A. russatus*) from nocturnal activity, forcing the latter to become diurnal (Levy et al. 2011b). This temporal partitioning allows the two species to co-exist on a diet of arthropods in summer. During winter, when arthropod levels are low, both species rely on a largely vegetarian diet. In winter, removal of the dominant *A. cahirinus* reduced the duration of daily torpor in *A. russatus*, both with and without food supplementation. These results suggest that torpor used in the presence of the dominant species was no longer required (Levy et al. 2011b). Further, torpor use and the concomitant energy savings may allow subordinate species to occupy areas dominated by larger competitors.

This is the case for hummingbirds in Arizona (Powers 2004). Dominant territorial blue-throated mountain gems (*Lampornis clemenciae*) had twice the fat store of their subordinate competitors the black-chinned hummingbird (*Archilochus alexandri*) and Rivoli's hummingbirds (*Eugenes fulgens*). Mountain gems stored enough fat to minimise nocturnal torpor use, whereas the two subordinate species with restricted access to food frequently expressed torpor, but all three species were able to live in the same area (Powers 2004).

Daily torpor may also be a key reason for the diversity of different-sized sympatric dasyurids in the Australian arid zone (Dickman 2003; Pavey et al. 2020). It also could play a role in explaining why other small desert mammals, such as the many rodent species in the Asian steppes, are so diverse despite the limited supply of food and water and the presence of predators.

Torpor Use and Fasting Endurance

When food is withheld from homeothermic mammals, small species survive for limited periods of time (Lindstedt and Boyce 1985). Under thermo-neutral conditions when energy expenditure in homeotherms is minimal, fasting endurance, or survival time, under conditions of acute starvation is short, ranging from 5 to 6 days in rats (*Rattus* sp.), 15 days in rabbits (*Oryctolagus cuniculus*) and 20 days in cats (*Felis catus*). When exposed to T_as below the TNZ, fasting endurance is shortened even further (Lindstedt and Boyce 1985). Survival time of homeotherms in the TNZ is a linear function of body mass on a double-log plot (Lindstedt and Boyce 1985; Fig. 7.13). At 10 g, fasting endurance is about 1 day, and, although endurance increases with mass, survival times remain short. At a body mass of 100 kg, survival of homeotherms is still only about 75 days (Fig. 7.13). In daily heterotherms survival times are better as they can survive without food for 2 to 2.5-fold longer than homeotherms of similar body mass (Fig. 7.13). The survival times of hibernating species in sharp contrast, often are around 300 days or more and they are many-fold longer, despite animals surviving, than those in homeotherms and daily heterotherms at comparable body masses (Fig. 7.13). Thus, there is no evidence of a continuum for survival times between homeotherms, daily heterotherms and hibernators (Chap. 4). For example in ~20 g big brown bats (*E. fuscus*), fasting endurance is ~180-fold that of a 20 g homeothermic mammal and ~ 65-fold that of the daily heterotherm, *S. crassicaudata* (Fig. 7.13). At a body mass of ~1 kg survival time of yellow-bellied marmots (*M. flaviventris*) is 32-fold longer than that in similar-sized homeotherms. And even at 100 kg, in the size range of bears, the difference is still

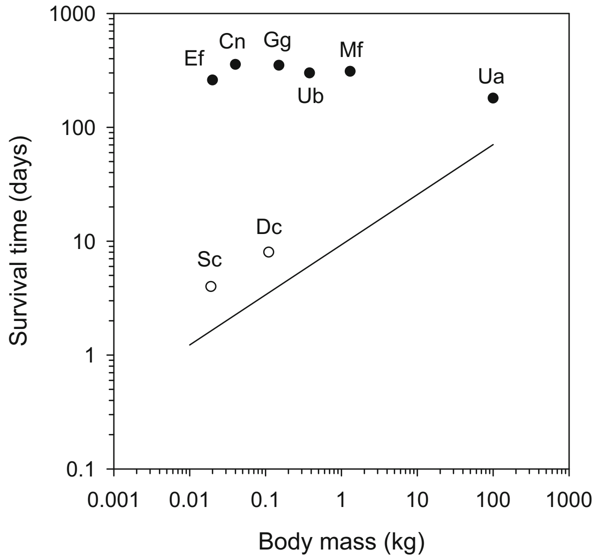

Fig. 7.13 Mammalian survival times (fasting endurance) without food. The regression line shows the survival time of homeothermic animals under thermo-neutral conditions (survival time (days) = 9.3 body mass (kg) $^{0.44}$, Lindstedt and Boyce 1985). The filled circles show survival times of hibernators without food: Ef *Eptesicus fuscus*, Cn *Cercartetus nanus*, Gg *Glis glis*, Ub *Urocitellus beldingi*, Mf *Marmota flaviventris*, Ua *Ursus americanus*, and daily heterotherms (circles): Sc *Sminthopsis crassicaudata*, Dc *Dasycercus cristicauda*. Data from: Kennedy and MacFarlane (1971); French (1985); Geiser (2007); Tøien et al. (2011); Hoelzl et al. (2015)

about 2.5-fold (Fig. 7.13). Clearly, prolonged survival without food, often approaching a year, would be a useful trait under a variety of challenging conditions.

Life Span

Hibernating animals have extremely long life spans. Whereas many non-flying small mammals live for only a year or two, small hibernating bats can live for decades, with records of over 30 years (Wilkinson and South 2002). An extreme example is Brand's bat (*Myotis brandtii*) a ~ 6-g hibernating bat, which holds the longevity record for small mammals at 41 years (Podlutsky et al. 2005). The average maximum longevity of hibernating bats is 3.5 times greater than in non-flying placental mammals of similar size (Wilkinson and South 2002). However, for bats the relationship is complicated by their ability to fly, which also increases longevity. Birds also have long life spans for their size on average (Wilkinson and South 2002). Nevertheless, long life spans have also been recorded for small non-flying hibernating mammals (Turbill et al. 2011a). For example, hibernating marsupial mountain pygmy-possums (*B. parvus*) can live for over 10 years and females may reproduce over that entire time (Mansergh and Broome 1994). These pygmy-possums can live that long despite that fact that marsupials are considered to be ‘short-lived’ (Lee and Cockburn 1985). The mean monthly survival rates in hibernators over winter are significantly higher than during the activity phase in summer, probably because many hibernators retreat to relatively inaccessible underground burrows, nests or other sheltered locations (Turbill et al. 2011a). Body odours during torpor use are reduced and hibernating individuals are largely motionless and quiet, therefore the likelihood of being detected by a predator is significantly reduced (French 1993; Turbill et al. 2011a; Woods et al. 2019). It appears that torpor use in some species allows for a “slow-paced” life history that is associated with increased survival rates during the hibernation season, retarded physiological aging, perhaps because of the reduced MR during torpor, increased maximum longevity and resulted in long generation times (Lyman et al. 1982; Turbill et al. 2011a).

Torpor and Mammalian Extinctions

An increase of the risk of predation during torpor due to immobility and inactivity is a traditional paradigm (Armitage 2004; Humphries et al. 2003; Estok et al. 2009). Predation is widely viewed as one of the major costs associated with torpor, which should result in selection pressure that reduces its use. Contrary to this, many heterothermic species use spontaneous torpor under thermal conditions without any obvious energetic stress. The use of spontaneous torpor has been widely observed in daily heterotherms, but also hibernators (Chap. 4). For example, non-reproductive captive dormice (*Glis glis*) in good condition and with access to food enter a sequence of short torpor bouts in summer often after brief periods of activity following the final arousal from hibernation in spring (Bieber and Ruf 2009). Perhaps in contrast to the traditional paradigm, dormice may use torpor to avoid predation in the wild when not reproductively active, thus increasing long-term survival. Field observations on subtropical bats support the interpretation of torpor use for predator avoidance. Long-eared bats (*N. bifax*), a hibernating species, enter torpor frequently during summer in a subtropical, coastal region (85% of observation days) and do so even on 38% of nights during their normal activity period (Stawski and Geiser 2010a, b). Counter to more traditional predictions, that torpor is only used during condition of negative energy balance, bats in good condition (high body condition index) entered torpor more frequently, displayed longer torpor bouts, were in torpor for a greater proportion of the day (Fig. 7.14) and had lower minimum T_bs than bats with a low body condition index. Thus it appears that these bats did not increase torpor use because of food shortages or low energy stores, but likely to avoid exposure to predators during foraging. It seems that bats could avoid foraging because of their high energy stores, further extended by using torpor. This interpretation is supported by data on captive mice (*M. musculus domesticus*), which, when faced with lower ground cover and consequently high perceived predation risk,

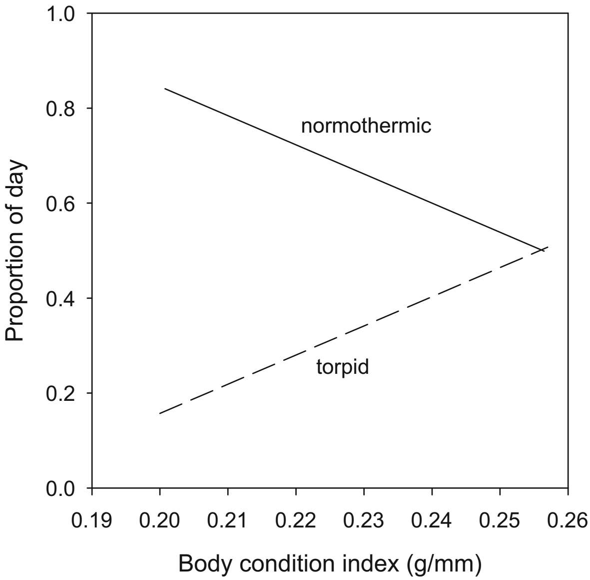

Fig. 7.14 Proportion of the day spent in torpor or normothermia by long-eared bats (*Nyctophilus bifax*), as a function of body condition index (body mass/forearm length, g/mm). A greater body condition index indicates increased fat storage. Data from Stawski and Geiser (2010b)

reduced daily food intake and compensated for that by a more pronounced reduction of T_b during torpor (Turbill and Stojanovski 2018).

Predator avoidance appears to be one of the reasons why opportunistically heterothermic mammals are less threatened with extinction (Liow et al. 2009) and have suffered fewer extinctions than their homeothermic relatives (Geiser and Turbill 2009; Hanna and Cardillo 2014). Of the 61 confirmed extinctions of mammal species worldwide over the past 500 years, only four (6.5% of species) were likely heterothermic. Considering that 2/3 of mammals are rodents and bats, many of which are heterothermic, the small proportion of extinct heterotherms is astonishing. Perhaps the reduced extinction risks in heterothermic mammals is due the enormous scope by which torpor can be employed to adjust energy requirements. Using torpor may allow long-term survival even during adverse conditions and the environmental challenges described above. Torpor use can also help individuals cope with habitat degradation and avoid or minimise contact with introduced or native predators (Geiser and Turbill 2009; Liow et al. 2009). Thus, the use of torpor and the typically prolonged life span of heterotherms (Turbill et al. 2011a) appear to have permitted opportunistically heterothermic mammals to better cope with anthropogenic disturbances responsible for extinctions than is the case for small homeothermic species (Geiser and Turbill 2009; Hanna and Cardillo 2014). However, some strongly seasonal hibernators, species living on sky islands, and species that have to deal with new diseases that are difficult to combat at low T_bs are likely adversely affected by anthropogenic influences (Inouye et al. 2000; Warnecke et al. 2012; Falvo et al. 2019).

The Advantages and Disadvantages of Torpor Use

As evident from above, torpor has many advantages. However, despite being highly effective in reducing energy and water use, it has been argued that that torpor should be minimised to reduce the risks associated with it (Humphries et al. 2003; Boyles et al. 2020). Potential risks include: (1) a metabolic imbalance perhaps due to accumulation of waste products at low T_b, (2) oxidative stress during periodic rewarming, (3) negative effects on neural tissues or memory, (4) reduced immuno-competence, (5) sleep deprivation (6) increased predation, (7) a nearly complete absence of behavioural responses during torpor, and (8) the increased likeliness of freezing during deep torpor.

It is important to examine these perceived risks in the context of the benefits summarised in this book. As evident from Chap. 5, it is correct that the reasons for periodic arousal from hibernation are still not fully understood but likely involves some physiological imbalance at low T_b. However, these seem to be regularly overcome by periodic rewarming and, although rewarming is energetically expensive, it adds up to only a fraction of that during normothermic thermoregulation. Moreover, in some species hibernating at high T_bs at around 20–25 °C such as tenrecs (Lovegrove et al. 2014), hibernation is possible for months without the need to rewarm. Fat-tailed lemurs rely on passive rewarming (Dausmann 2014) and bats and other species use passive or partially passive rewarming from torpor to minimise energy costs and perhaps also the associated oxidative stress (Currie et al. 2015a). If oxidative stress does occur in species that do not use passive rewarming, it does not seem to unduly interfere with their wellbeing because heterotherms tend to live longer than homeotherms (Turbill et al. 2011a). The memory loss reported for some species, as for example, during hibernation in ground squirrels (*Spermophilus citellus*) (Millesi et al. 2001), remains controversial because hibernating bats (*Myotis myotis*) do not suffer memory loss (Ruczynski and Siemers 2011).

Perhaps the greatest concern however, is the reduced immuno-competence during torpor (Prendergast et al. 2002; Bouma et al. 2011). Often this is counteracted by slowed bacterial growth at low T_b, but unfortunately, this is not the case for the new pathogen the fungus *Pseudogymnoascus destructans*, imported in 2008/09 to North America from Eurasia. This fungus has caused white-nose syndrome in hibernating North American bats, and resulted in catastrophic population declines in many regions (Warnecke et al. 2012). However, some surviving bats appear to have developed some immunity (Frick et al. 2017) like their Eurasian counterparts and survival rates are improving (Frank et al. 2019).

Sleep deprivation during deep torpor (Daan et al. 1991; Trachsel et al. 1991) can be counteracted by periodic rewarming and again the main costs seems to be energy expenditure, which, as is stated above, is much lower than in normothermic animals despite endogenous rewarming. The perceived increased predation risk during torpor is based on observations of predation of hibernating individuals such as marmots (*Marmota flaviventris*) killed by badgers (*Taxidea taxus*) (Armitage 2004) or bats (*Pipistrellus pipistrellus*) killed by great tits (*Parus major*) (Estok et al. 2009) or several species of insectivorous bats by wood mice (*Apodemus sylvaticus*) (Haarsma and Kaal 2016). However, even when badgers found the marmot colony, the predation rate was still $<5\%$ (Armitage 2004) and population studies show that hibernators have much better survival rates during winter hibernation than during the active season in summer (Kawamichi and Kawamichi 1993; Lebl et al. 2011a, b), at least for non-flying species. As detailed above (Fig. 7.3), although torpid animals are slower than they are during normothermia, they can move nevertheless, many from around T_b 15 °C (Walhovd 1979; Rojas et al. 2012).

Exposure to low T_a during torpor does have a negative effect on telomere length (Nowack et al. 2019). However, the likelihood of freezing during hibernation is rather low because of selection of appropriate hibernacula sites (Twente 1955) and many torpid hibernators show T_bs below 0 °C without freezing (Table 5.1). Even in arctic hibernators that hibernate well below 0 °C, endogenous heat production during torpor maintains a large T_b-T_a differential and prevents freezing in most individuals, again at a lower energetic cost than to remain normothermic (Barnes 1989; Buck and Barnes 2000; Richter et al. 2015). Obviously some individuals expressing torpor will be affected negatively by the risks summarised above. However, on balance it seems, the advantages of torpor outweigh the disadvantages and the fact that the trait persists speaks to this.

Chapter 8
Torpor During Reproduction and Development

Reproduction and development are energetically expensive and risky processes in most organisms. Animals typically must increase the acquisition of nutrients and energy, which results in high energy expenditure. This may result in increased predator exposure due to more foraging needed by the parents to obtain food for the growing young. In birds and mammals it also often includes an increase in T_b and MR during the mating period or during various stages of the reproductive cycle (Tyndale-Biscoe and Renfree 1987; Monaghan and Nager 1997; Speakman 2008). Generally in small placental mammals, energy expenditure increases with pregnancy, the increase is usually more pronounced after parturition and, during the period of lactation, may about double in comparison to energy expenditure without reproduction (Speakman 2008; Rödel et al. 2016). In monotremes and marsupials the change in energy expenditure during the typically long reproductive period is less pronounced, but it occurs over a longer time (Munks and Green 1995; Nicol 2017). In flying birds and bats extra costs arise from carrying an egg or growing foetus as well as allocating nutrients to the young. Mammalian reproduction is also associated with an increase in circulating reproductive hormones, such as steroids and specifically testosterone, which are known to inhibit torpor in at least some heterothermic species, especially sciurid and cricetid rodents (Goldman et al. 1986), and sperm production is negatively affected by deep torpor (Gagnon et al. 2020). All of these requirements and physiological changes seem to preclude the use of torpor of adults during the reproductive cycle and it is of little surprise that reproduction in birds and mammals and expression of torpor have been widely viewed as mutually incompatible (Landau and Dawe 1960; Wimsatt 1969). This tenet applies especially to areas at high latitudes with strong seasonal cycles of temperature and food availability and only a narrow window of time that is suitable for reproduction, growth and development.

Because reproduction is so different between birds, monotremes, marsupials and placentals, this chapter is ordered according to taxonomy.

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_8

Reproduction

To avoid both the energetic and hormonal incompatibilities, many heterothermic mammals and likely also birds use a sequence of torpor followed by reproduction during the yearly cycle (Kenagy 1989). In typical heterothermic rodents from climates with cold winters in the Northern Hemisphere, torpor is expressed from autumn to spring, after which reproduction commences and continues during summer (Kenagy 1989). This pattern is often observed in species that live in strongly seasonal environments with highly productive summers. During the summer, the young of many high latitude heterothermic rodents must grow fast and mature and, especially hibernating species, must fatten sufficiently to have enough energy stores for the impeding cold season. Some cricetid and sciurid rodents are known to resist torpor expression during the reproduction season, reduce the size of their gonads before the beginning of the torpor season and may remain homeothermic when reproductive hormones are administered (Landau and Dawe 1960; Goldman et al. 1986).

In incubating or brooding birds expression of torpor is also often reduced or avoided (Kissner and Brigham 1993). Many birds migrate to high latitudes to reproduce during productive summers (Ramenofsky and Wingfield 2006) and after reproduction migrate to more benign low latitudes or to high latitudes in the opposite hemisphere. Young birds must be developed enough to be able to make the long journey. Therefore many birds are selected for fast development as juveniles and thus the view that adults must avoid using torpor during reproduction.

Nevertheless, considering the diversity and geographical distribution of heterothermy, it is unsurprising to find that not all species are strictly homeothermic during reproduction. For example, species living in deserts and rely on fluctuating food sources, such as insects, may not be able to remain normothermic throughout reproduction which may commence in winter (Körtner et al. 2008). Because torpor conserves energy and nutrients, it also may be an avenue to permit reproduction in desert environments where resources are often limited.

However, in most regions of the world, even those with predictable climates, the weather is not always predictable. It may therefore be advantageous for species confronted with bad weather to use torpor to survive adverse conditions and food shortages and produce and raise their young rather than lose them.

Birds

Although heterothermy is used by many avian orders (Chap. 3), only three species from three orders are known use torpor during reproduction. These includes the only known avian hibernator, the poorwill, *Phalaenoptilus nuttallii* (Brigham 1992). Although poorwills regularly enter deep torpor in winter and reduce T_b to about 5 °C (Woods et al. 2019), when brooding or incubating, a few males became torpid and their T_b fell to a minimum of 11.5 °C, but apparently the eggs did not hatch (Kissner and Brigham 1993).

Another observation on torpor in reproductive birds is available for the broad-tailed hummingbirds, *Selasphorus platycercus*, in the Rocky Mountains. These birds were reproducing successfully in summer under the cold conditions at high elevations despite a marginal energy supply (Calder and Booser 1973). Hummingbirds displayed nocturnal torpor during cold nights while incubating eggs. Free-ranging hummingbirds were measured with an artificial egg containing a temperature logger and because the measured T_{egg} fell to 6.5 °C, it appears that torpor during incubation may be as pronounced in this species as in non-reproductive birds. The hatched chicks developed normally, even though the egg was exposed to low temperatures.

Shallow torpor has also been observed in a breeding female greater roadrunners (*Geococcyx californicus*). This breeding female lowered T_b from ~41 to 34 °C almost as low as in a non-breeding male (Vehrencamp 1982).

Mammals

Monotremes

Although echidnas (*Tachyglossus aculeatus*) hibernate in many areas of Australia and have a distinct seasonal biology, their hibernation and reproductive seasons do overlap. Non-reproductive individuals hibernate till spring, whereas reproductively active echidnas terminate hibernation in mid-winter to mate (Nicol and Andersen 2002). The first observation of torpor during reproduction was made for a captive female echidna, which used torpor during pregnancy 2 days before she laid her egg. The T_b of the female was 21 °C, but increased later during the day to >30 °C (Geiser and Seymour 1989). Initially, it not was not clear whether this observation was a laboratory artefact, however, torpor in reproductive echidnas has now been observed in the wild (Morrow and Nicol 2009). Reproductive males have been found with torpid females, or with recently mated pregnant females that re-entered hibernation after mating (Morrow and Nicol 2009). Unlike many other hibernators, which reduce testes size during hibernation, male echidnas continue to have enlarged testes during hibernation. However, not all echidnas mate each year, and those that are not involved in reproduction continue to hibernate for all winter (Morrow and Nicol 2009).

Marsupials

Daily torpor or hibernation are used by a diversity of marsupials for much of the year (Chap. 3). The Monito del Monte (*Dromiciops gliroides*), some insectivorous/

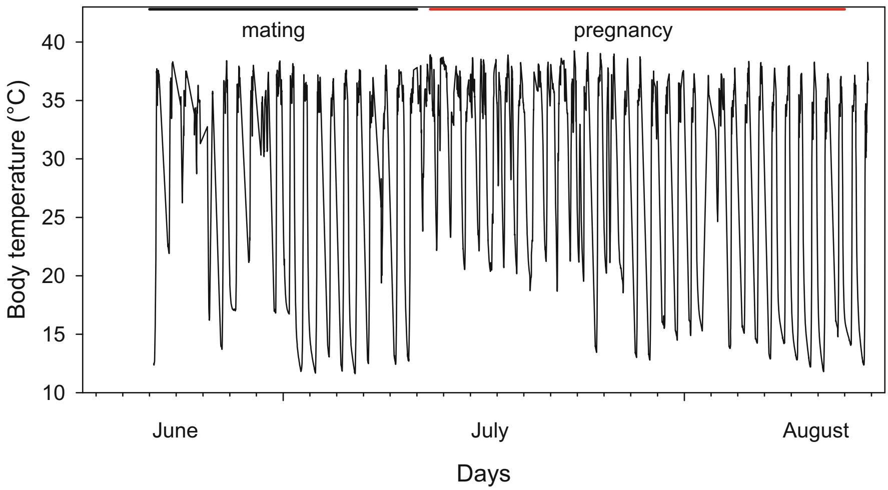

Fig. 8.1 Torpor expression in relation to reproductive activity in a free-ranging female mulgara (*D. blythi*). The back horizontal bar indices the mating period, the red horizontal bar the period of pregnancy. Data from Körtner et al. (2008)

carnivorous marsupials (Dasyuridae) and possums (Acrobatidae and Petauridae), also use it during the reproductive season.

Lactating *Dromiciops* with pouch young that were about 3 weeks old entered torpor and reduced T_b to near the T_a of 25 °C in captivity (Nespolo et al. 2021). A lactating fat-tailed dunnart (*Sminthopsis crassicaudata*) with six young about 45 days old were all found torpid in the field and the young were raised successfully because they were recaptured a month later (Morton 1978). In the closely related stripe-faced dunnart (*S. macroura*) torpor was used during the first half of their short ~10-day gestation period (Selwood and Woolley 1991; Geiser et al. 2005b). The TMR during torpor in the pregnant captive female was as low as in non-pregnant females, but the torpor bout lasted for only ~4 h in comparison to the ~6 h in the non-pregnant dunnarts (Geiser et al. 2005b). Male *S. macroura* used torpor when testes were large and also when reproductive hormones were present, however traits of torpor such as TBD, were somewhat shorter when testosterone was administered (McAllan et al. 2012). Female *S. macroura* also continued to display torpor when oestrogen and progesterone were administered. However, torpor frequency was reduced from 100% of days to about 60% of days when progesterone was administered and TBDs were significantly shorter than in controls (McAllan et al. 2012).

Reproductively active male and pregnant female mulgaras (*Dasycercus cristicauda, D. blythi*) use torpor during the winter reproductive season in the field (Fig. 8.1) and also when maintained with food *ad libitum* under mild laboratory conditions (Geiser and Masters 1994; Körtner et al. 2008). Captive females expressed spontaneous torpor on 32 of 46 days during pregnancy and increased their body mass by ~35% during that time presumably because they frequently used

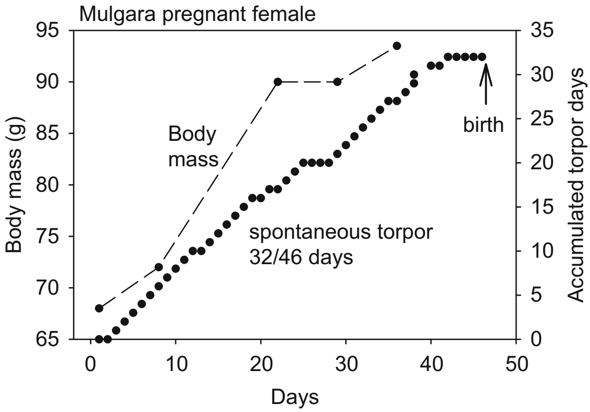

Fig. 8.2 Spontaneous expression of torpor in a captive mulgara (*Dasycercus* sp.) during pregnancy. Despite food availability, daily torpor occurred often until 5 days before birth and body mass increased by ~35%. Data from Geiser and Masters (1994)

torpor to conserve energy (Fig. 8.2). However, individuals remained normothermic in the last 5 days of pregnancy before giving birth. Because marsupial neonates weigh less than 1% of the mother's body mass this increase in body mass is not due to the growing young. It seems that females try to facilitate fat storage for the more energetically demanding period of lactation, which is the main period of energy and nutrient transfer to young marsupials (Nicoll and Thompson 1987; McAllan and Geiser 2014). In contrast to most other mammals, which tend to reduce torpor use during reproduction, free-ranging female mulgaras appeared to increase torpor expression during pregnancy compared to non-reproductive individuals. However, as for captive individuals, one free-ranging female did not enter torpor in the few days before giving birth and during early lactation. Males displayed only shallow and brief periods of torpor during the mating season in early winter, but after mating daily torpor was also pronounced (Körtner et al. 2008, 2016).

Torpor during the reproductive season also occurs in kowaris (*Dasyuroides byrnei*). Similar to mulgaras, reproductive state influenced thermoregulation in free-ranging females. Pregnant females did express daily torpor, but throughout lactation they maintained high normothermic T_bs (Körtner and Geiser 2011). Captive pregnant antechinus (*A. flavipes*) held outdoors also entered daily torpor for ~2.5 h with a minimum T_b of ~26 °C and these values did not differ from non-reproductive females (Stawski and Rojas 2016).

Torpor during reproduction also occurs in possums (diprotodont marsupials). In contrast to the dasyurids, which predominantly seem to express torpor during pregnancy, possums appear to use torpor mainly during lactation, perhaps because their neonates are substantially larger than those of dasyurids (Tyndale-Biscoe 1973). Torpor has been observed in lactating feathertail gliders (*Acrobates pygmaeus,* Fig. 3.21) with pouch young in the spring reproductive season, however it lasted for less than 1 day, unlike in non-reproductive individuals (Frey and Fleming 1984; Chap. 3). Similarly, free-ranging female sugar gliders (*Petaurus breviceps*), displayed daily torpor (T_b 20 to 27 °C) during lactation, when the pouch young were 19–34 days of age (Geiser et al. 2008). During pregnancy wild female sugar gliders maintained a high and rather constant T_b. Male sugar gliders only occasionally used torpor during the reproductive period (Geiser et al. 2008).

Placentals

Torpor during the reproductive period has been observed in many small placentals and is most prevalent in insectivorous bats (Chiroptera). However, tenrecs (Afrosoricida), hedgehogs (Lipotyphla), primates (Primates) and perhaps sloths (Xenarthra) also appear to use torpor while reproductively active.

Afrosoricida

Non-reproductive and reproductive tenrecs express torpor (Nowack et al. 2020). In comparison to non-reproductive females, the T_bs of torpid pregnant and lactating shrew-tenrecs (*Microgale dobsoni* 45 g and *M. talazaci*, 45 g) and large-eared tenrecs (*Geogale aurita* 7 g) were higher (Stephenson and Racey 1993; McKechnie and Mzilikazi 2011). Torpor was not observed during pregnancy in other tenrec species (*Hemicentetes semispinosus, H. nigriceps, Echinops telfairi, Setifer setosus*; see McKechnie and Mzilikazi 2011; McAllan and Geiser 2014). However, similar to marsupials and bats, the variability of recorded gestation periods in tenrecs is high, suggesting that this may be linked to the opportunistic use of torpor during the reproductive season (Stephenson 1993).

Xenarthra (Sloths)

A pregnant three-toed sloth, (*Bradypus* sp.) exposed to T_as ranging from 6 to 9 °C decreased its T_b from 35 to 29 °C within ~6 h and remained at that level for a further ~10 h; T_b then increased to ~33° after exposure to T_a 27 °C. Therefore, it is not certain whether the animal was torpid or hypothermic (Morrison 1945).

Lipotyphla, Insectivores

Female European hedgehogs (*E. europaeus*), displayed torpor during the summer breeding season when exposed to cold, similar to males. However, one female that gave birth a few days after the cold exposure began, remained normothermic during the experiment (Fowler 1988). Therefore it is not resolved whether torpor can be used by hedgehogs during pregnancy. To my knowledge, there are no data on torpor during development in hedgehogs.

Bats

One may argue that a reason for the differences in the lack of use of torpor in, for example, pregnant sciurid rodents and use of torpor in pregnant marsupials are simply related to the big differences in size and developmental stage of the embryos. However, in small insectivorous bats, embryos near parturition are well developed and large, weighing around 20% of the maternal body mass (Hayssen and Kunz 1996). Nevertheless, many small bats not only exhibit torpor in winter, they also use torpor in spring and summer including during the reproductive season (Stawski et al. 2014b).

Data on torpor during reproduction in ‘fruit bats’ (Pteropodidae) are limited to a single species, the nectarivorous blossom-bat (*Syconycteris australis*). This species displays daily torpor in captivity throughout the year including the reproductive period. Torpor in captive non-reproductive *S. australis* was used by all individuals after food restriction and exposure to T_a 18 °C. Torpor also was observed in a pregnant bats under the same experimental conditions, but this was discovered only after the measurements when the bat gave birth (Geiser et al. 2001). The TBD of the pregnant bat was about half of that in non-pregnant female and male bats, but the minimum TMR was similar.

Vespertilionid bats typically mate in late summer and early autumn (Wimsatt 1969; Stawski et al. 2014b). After mating, sperm is stored in the oviduct and, following the hibernation season and after fertilization, pregnancy commences. The energetic costs of pregnancy and lactation continue to increase until weaning and therefore food consumption increases especially for lactating females (Speakman 2008). To reduce these energetic costs many small vespertilionids use torpor both during pregnancy and lactation (Stawski et al. 2014b), Vespertilionids express torpor although the low T_b can delay gestation and reduce milk production. These delays in reproduction could result in insufficient pre-winter fattening to fuel the energy requirements during the long hibernation season (Speakman and Rowland 1999; Ruf and Geiser 2015).

In temperate or cold-climate northern hemisphere vespertilionids, torpor in reproductive individuals has been observed in many species (Table 8.1). To my knowledge, the oldest detailed information on torpor expression during reproduction is available for mouse-eared bats (*Myotis myotis*) (Eisentraut 1937). Bat were captured in the second half of the hibernation season in late February, fed and held in a warm room to induce fertilization and the start of embryonic development. After that bats were held at different T_as with food restriction. Pregnant bats held in a room at a T_a of about 20 °C displayed short bouts of torpor in the morning, although they were normothermic for much of the rest of time. Pregnant bats held in a cellar at T_a 11–14 °C regularly entered torpor, but also rewarmed on a daily basis in the evening. In contrast, pregnant bats held at T_a 4–8 °C in a shed displayed deep torpor lasting for up to 3 days in some individuals. These data show that in *M. myotis* T_a was the major influence on torpor expression during pregnancy (Eisentraut 1937).

Table 8.1 Torpor in reproductive endotherms

Group/species	Body mass (g)	Diet	Observation	Source
Birds				
Phalaenoptilus nuttallii Poorwill	48	Insects	Infrequent torpor during brooding and incubation	Kissner and Brigham (1993), Csada and Brigham (1994)
Selasphorus platycercus Broad-tailed hummingbird	3.5	Nectar, Birds	Deep torpor in incubating bird	Calder and Booser (1973)
Geococcyx californicus Roadrunner	350	Insects Small vertebrates	Incubating female uses torpor	Vehrencamp (1982)
Mammals				
Monotremes				
Tachyglossus aculeatus Echidna	4500	Insects	Torpor in pregnant female and during mating	Geiser and Seymour (1989), Morrow and Nicol (2009)
Marsupials				
Dromiciops gliroides Monito del Monte	30	Insects	Torpor in lactating females	Nespolo et al. (2021)
Sminthopsis crassicaudata Fat-tailed dunnart	17	Insects	Torpor in free-living lactating females; male torpor while testes large	Morton (1978), Holloway and Geiser (1996)
Sminthopsis macroura Stripe-faced dunnart	25	Insects	Torpor in pregnant female	Geiser et al. (2005b)
Antechinus flavipes Yellow-footed antechinus	30	Insects	Daily torpor during pregnancy, not lactation	Stawski and Rojas (2016)
Dasycercus cristicauda/ blythi Mulgara	100	Insects, small vertebrates	Frequent torpor in pregnant females and reproductive males, but not during lactation	Geiser and Masters (1994), Körtner et al. (2008)
Dasyuroides byrnei Kowari	95	Insects, small vertebrates	Torpor during pregnancy	Körtner and Geiser (2011)
Acrobates pygmaeus Feathertail glider	12	Insects, nectar	Torpor in free-living lactating gliders	Frey and Fleming (1984)

(continued)

Table 8.1 (continued)

Group/species	Body mass (g)	Diet	Observation	Source
Petaurus breviceps Sugar glider	100	Insects, nectar, gum	Torpor in free-living lactating gliders	Geiser et al. (2008)
Placentals				
Afrotherians				
Microgale dobsoni Shrew-tenrec	45	Insects	Shallow torpor in reproductive tenrecs	Stephenson and Racey (1993)
Microgale talazaci Shrew-tenrec	45	Insects	Shallow torpor in reproductive animals	Stephenson and Racey (1993)
Geogale aurita Large-eared tenrec	6.7	Insects	$T_b = 22$ °C in pregnant and lactating tenrecs	Stephenson (1993)
Setifer setosus Greater hedge-hog tenrec	225	Insects	Gestation length variance likely due to torpor	Stephenson (1993)
Echinops telfairi Lesser hedge-hog tenrec	180	Insects	Gestation length variance likely due to torpor	Stephenson (1993)
Xenarthrans				
Bradypus griseus Three-toed sloth	4000	Leaves	Heterothermy in pregnant sloth, minimum T_b 29 °C, But passive rewarming	Morrison (1945)
Insectivores				
Erinaceus europaeus Hedgehog	700	Insects, worms, fruit	Torpor during reproductive period at low T_a	Fowler (1988)
Bats				
Syconycteris australis Common blos-som-bat	18	Nectar, pollen	80% reduction of MR in preg-nant, torpid bat	Geiser et al. (2001)
Myotis lucifugus Little brown bat	5	Insects	Torpor pregnancy 61%, lacta-tion 91%, post-lactation 97%	Dzal and Brigham (2013)
Myotis myotis Mouse-eared bat	25	Insects	Pregnant bats torpid for several days	Eisentraut (1937)

(continued)

Table 8.1 (continued)

Group/species	Body mass (g)	Diet	Observation	Source
Myotis bechsteinii Bechstein's bat	10	Insects	Torpor in pregnant and lactating bats	Pretzlaff et al. (2010)
Myotis nattereri Natterer's bat	8	Insects	Torpor frequent in pregnant bats	Otto et al. (2015)
Plecotus auritus Brown long-eared bat	8	Insects	Torpor frequent in pregnant bats	Otto et al. (2015)
Pipistrellus pipistrellus Pipistrelle	6	Insects	Torpor during pregnancy slows fetal development	Racey (1973)
Eptesicus fuscus Big brown bat	19	Insects	Torpor during pregnancy and lactation period in both sexes. Deep torpor rare during lactation	Audet and Fenton (1988), Grinevitch et al. (1995)
Lasiurus cinereus Hoary bat	33	Insects	Deep, multiday torpor in free-ranging pregnant bats	Willis et al. (2006)
Nyctophilus geoffroyi Lesser long-eared bat	9	Insects	Torpor in captive pregnant and lactating females similar to non-reproductive bats	Turbill and Geiser (2006)
Nyctophilus gouldi Gould's long-eared bat	12	Insects	Torpor in captive pregnant and lactating females similar to non-reproductive bats	Turbill and Geiser (2006)
Nyctophilus bifax Northern long-eared bat	14	Insects	Occasional torpor in free-ranging pregnant bats	Stawski (2010)
Otonycteris hemprichii Hemprich's long-eared bat	20	Insects	Torpor in pregnant bats deeper than during lactation	Daniel et al. (2010)
Miniopterus schreibersii Common bent-wing bat	15	Insects	Retarded embryo growth, during hibernation	Dwyer (1963), Wimsatt (1969)
Miniopterus australis Little bent-wing bat	7	Insects	Retarded embryo growth during hibernation	Dwyer (1963), Wimsatt (1969)

(continued)

Table 8.1 (continued)

Group/species	Body mass (g)	Diet	Observation	Source
Carnivores				
Ursus americanus Black bear	100,000	Berries, plants, fish	Torpor during pregnancy and lactation	Hellgren (1998)
Primates				
Microcebus murinus Mouse lemur	90	Insects, fruit	Induced torpor during gestation and lactation	Canale et al. (2012)
Rodents				
Muscardinus avellanarius Hazel dormouse	30	Insects, pollen berries, nuts	Shallow torpor in pregnant females	Juškaitis (2005)

Similar measurements were made on palpably pregnant captive pipistrelles (*Pipistrellus pipistrellus*) in spring (Racey 1973). Pregnant bats maintained at T_as of 11–14 °C without food entered torpor and, in comparison to controls, gestation was prolonged by about 2 weeks. The delay of parturition was similar to the time bats were torpid, suggesting that foetal development was arrested (Racey 1973). A variable duration of gestation in bats between roost sites and over several years, probably due to torpor use, also have been observed in the lump-nosed bat, (*Corynorhinus rafinesquii*) (Johnson and Lacki 2013).

Detailed observations are available on reproductive little brown bats (*Myotis lucifugus*) in the field. These bats expressed torpor during both pregnancy and lactation, but less than during post-lactation (Dzal and Brigham 2013). Pregnant bats entered torpor on 61% of days, lactating bats on 91% and post-lactating bats on 97% of days. TBD in pregnant bats was just over 2 h with a minimum T_{skin} of ~25 °C, reduced from a normothermic T_{skin} of ~36 °C (Fig. 8.3) whereas in lactating bats TBD was 5.5 h and 8.5 h during post-lactation. The minimum T_{skin} was ~21 °C in lactating and post-lactating females (Dzal and Brigham 2013). In another field study on *M. lucifugus*, torpor was shallow and brief in lactating females. Environmental factors, such as increases in wind speed and precipitation, were associated with an increase in torpor use by pregnant females (Besler and Broders 2018).

In free-ranging big brown bats (*Eptesicus fuscus*), torpor also has been observed during both pregnancy and lactation although lactating females were torpid significantly less than pregnant and non-pregnant bats (Audet and Fenton 1988). Similarly, in another field study on *E. fuscus*, T_{skin} fell to an average minimum of ~15 °C during pregnancy, but only to ~26 °C during lactation (Hamilton and Barclay 1994). Solitary Canadian western long-eared bats (*Myotis evotus*) roost in rock crevices with different thermal conditions. Pregnant females select horizontal roosts that

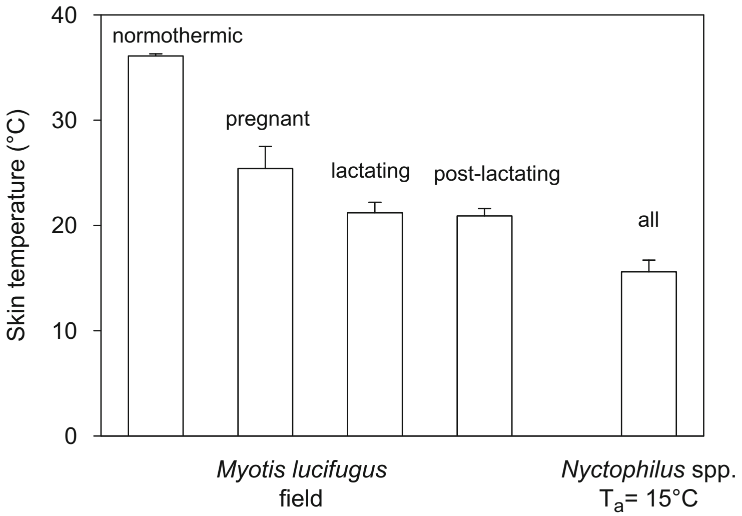

Fig. 8.3 Torpor expression during reproduction in bats. Free-ranging female *M. lucifugus* used torpor during lactation and post-lactation, but torpor was less deep during pregnancy. In *Nyctophilus* spp. torpor in captive females measured under the same conditions did not differ among reproductive states and males. Data from Dzal and Brigham (2013), Turbill and Geiser (2006)

cooled at night and warmed during the day to permit deep torpor and passive rewarming on the next day (Chruszcz and Barclay 2002). In contrast lactating females selected vertical roost that remained warm and used torpor less frequently.

Torpor during pregnancy and lactation also has been observed in free-ranging European vespertilionids (*Myotis bechsteinii* and *M. daubentonii*) although reproductive bats often remained normothermic (Pretzlaff et al. 2010; Dietz and Hörig 2011). Male Daubenton's bats (*M. daubentonii*) and male Bechstein's bats (*M. bechsteinii*) also use torpor during the reproductive periods in summer, although to a lesser extent than other times of year (Dietz and Hörig 2011).

In the desert-dwelling Hemprich's long-eared bats (*Otonycteris hemprichii)* shallow torpor occurred in pregnant females mainly during the first two trimester of pregnancy, but torpor was shallower than in non-reproductive bats (Daniel et al. 2010). Shallow torpor was also expressed in lactating females, although the incidence of torpor use was reduced. Similarly, subtropical long-eared bats (*Nyctophilus bifax*) also use torpor occasionally during pregnancy in the field (Stawski 2010).

All told many studies have reported torpor during reproduction in bats, but torpor use in the wild was typically less frequent and less pronounced than in non-reproductive bats. To some extent this may be due to the warm weather in summer or social thermoregulation in maternity roosts. When captive long-eared bats, *Nyctophilus geoffroyi*, were measured overnight under constant thermal conditions at T_a 15 °C during the reproductive period in spring, they regularly used torpor (Turbill and Geiser 2006). All males, pregnant females and lactating females entered

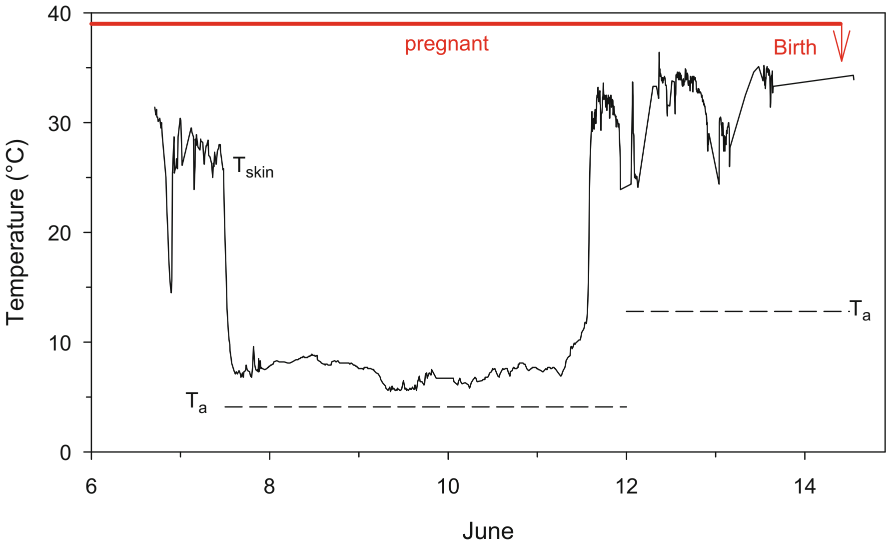

Fig. 8.4 Torpor in a pregnant (red horizontal bar) hoary bat (*L. cinereus*) during a cold snap in late spring. The bat entered deep torpor when T_a was 4.1 °C on average, remained torpid for about 4 days, rewarmed from torpor when T_a was 12.8 °C on average, and gave birth (red arrow) about 3 days after the arousal. Data from Willis et al. (2006)

torpor under these rather mild thermal conditions, and during torpor, their minimum T_{skin} was essentially the same for all groups with a value of 15.6 ± 1.1 °C (Fig. 8.3) which was only ~0.5 °C above T_a. The minimum TMR was only ~4% of BMR as predicted for small hibernators. Reproductive *N. gouldi* behaved similarly (Turbill and Geiser 2006). This strongly suggests that the less pronounced torpor in some pregnant and lactating female bats reflects largely ecological differences rather than physiological constraints.

The extended pregnancy, or delay of birth, due to torpor use observed in many reproductive species is often seen as the major drawback of expressing torpor during reproduction. However, prolonged torpor during pregnancy does not necessarily reduce fitness. Migrating pregnant hoary bats (*Lasiurus cinereus*) exposed to a late spring snow storm in southern Canada displayed deep multiday torpor while roosting in foliage (Fig. 8.4). Three individuals used prolonged torpor for up to 5.6 days when the mean T_a was 4.1 °C, and bats reduced T_{skin} to a minimum of 5.5 °C (Fig. 8.4). Bats were thermoconforming as they maintained a small T_b-T_a differential throughout almost all of their torpor bouts, as long as T_a was >4 °C, which suggests that they were not attempting to regulate T_b to increase offspring growth rate (Willis et al. 2006). Bats gave birth within 3.1 days after arousal from multiday torpor when the T_a had increased to 12.8 °C on average (Fig. 8.4). By reducing the immediate risk of death by starvation for mother and pups, the benefits of multiday torpor during pregnancy for these bats clearly outweighed any long-term fitness costs of reduced offspring growth and therefore the extension of gestation via the use of torpor actually increased fitness. Thus the physiological advantage for hoary bats seems to be that any transient energy shortfalls are managed in a way that ensures both mother and offspring remain viable, although reproductive activities are somewhat delayed (Willis et al. 2006).

Bent-wing bats (Miniopteridae) also mate in autumn or winter, but the egg is fertilised and females enter hibernation in a 'pregnant' condition. However, embryonic development is delayed, and births do not occur until the following spring (Dwyer 1963; Wimsatt 1969). One could argue these bat hibernate in a pregnant state, but, as the development is arrested, physiologically these bats are to a large extent, non-reproductive (Wimsatt 1969). Male *Miniopterus* also exhibit seasonal changes in reproduction, with spermatogenesis arrested until spring (Wimsatt 1969).

Carnivora (Bears and Badgers)

Bears (*Ursus americanus*) mate in summer and the fertilized egg is arrested at the blastocyst stage until implantation in late November or early December. Parturition occurs in January or February (Wimsatt 1969; Hellgren 1998). As *U. americanus* hibernate for much of this time (Tøien et al. 2011) they express torpor during pregnancy and suckle their young during the second part of the hibernation season, however, these reproductive activities occur when female T_b is around 30 °C.

Badger hibernation appears independent of the reproductive season for males, and delayed embryonic implantation occurs in females, with post-implantation gestation occurring during the middle of winter (Fowler and Racey 1988). In a female European badger (*Meles meles*) T_b fell to a minimum of 28 °C immediately before ovo-implantation. During post-implantation, T_b was raised to between 32.1 and 34.7 °C for the remainder of the gestation period (Fowler and Racey 1988).

Primates (Lemurs)

In the wild, Malagasy mouse-lemurs (*Microcebus murinus*) may remain torpid for up to 4 consecutive days (Schmid and Ganzhorn 2009). In captive *M. murinus*, held at a high T_a of 24–25 °C, food restriction by 80% induced torpor in one female towards the end of gestation with a minimum T_{skin} of 25.2 °C, whereas most females only expressed torpor during early lactation (Canale et al. 2012).

Rodents

Knowledge on torpor use by reproductive adult rodents is scarce. Wild hazel dormice (*Muscardinus avellanarius*) hibernate for prolonged periods from autumn to spring, but they also frequently express short bouts of torpor during summer (Pretzlaff and Dausmann 2012; Pretzlaff et al. 2014). As quantified via observations, adult male *M. avellanarius* used torpor more frequently than females during the active season in summer (Juškaitis 2005). Pregnant females used only shallow torpor and females with litters were observed in torpor occasionally (Juškaitis 2005).

Why is Torpor used during Reproduction?

Thus unlike for many sciurid and cricetid rodents and other mammals, who avoid using torpor during reproduction, several, mainly small, birds and mammals, but also large bears, use torpor extensively during pregnancy and/or lactation. In small species it is clearly related to food availability as most feed on insects, nectar, and other food items that fluctuate (Table 8.1). In these species, including the marsupials, pregnancy and lactation are relatively short and a small extension beyond the usual reproductive phase will not enormously change the yearly timing, but it permits reproduction on limited resources or to overcome adverse weather events during the warm season. Without question it is more appropriate to use torpor and avoid losing offspring than begin reproduction all over again. In bears, because their reproductive phase is so long it cannot occur in spring and summer. Neonate bears are small and undeveloped and it makes sense to suckle the young while denning in winter so they can increase size sufficiently and develop enough to be able to walk by the time of spring emergence. Thus, counter to prevailing dogma that torpor and reproduction are incompatible, its use appears crucial to successful reproduction of many species (McAllan and Geiser 2014; Stawski et al. 2014b).

Development

The energetically expensive period of reproduction is followed by the likewise energetically expensive period of young development. After hatching or birth, the offspring have to develop and grow which requires a significant supply of nutrients and energy, usually provided by the parents (Thompson and Nicoll 1986; Speakman and Thomas 2003). Development is especially expensive in endothermic mammals and birds because developing young require energy expenditure for thermoregulation as well as the costs for development (Koteja 2000; Farmer 2003).

However, the pattern of development in endotherms is not always the same. Most small endothermic species are ‘altricial’ and are hatched or born in an undeveloped, naked state, requiring care and feeding by the parents. In fewer, mainly for large species, the hatchlings or neonates are ‘precocious’, well developed, insulated and mostly independent as, for example, megapode birds (mound builders) or ungulate mammals.

Essentially all mammals and birds are competent endotherms as adults. However, the vast majority are altricial and hatch or are born at an early developmental stage when endothermy is not fully established. Altricial neonates or hatchlings are small, naked and uncoordinated and, when removed from the nest or away from their

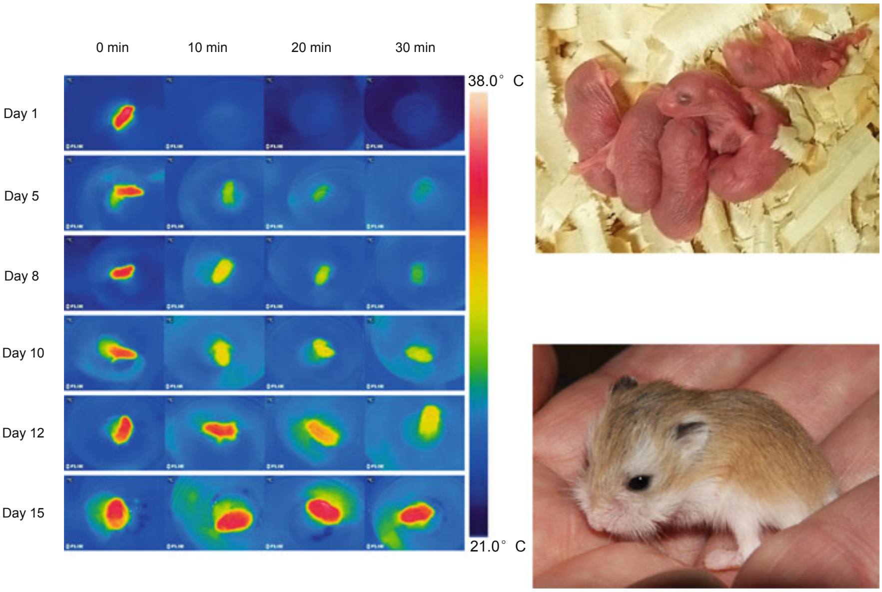

Fig. 8.5 The development of endothermic thermoregulation in desert hamsters (*P. roborovskii*), as measured with a thermal camera (left). On day 1 when pups weighed about 1 g and were naked (top right), they cooled rapidly over 30 min, from red (T_s ~33 °C) to blue (T_s ~22 °C) similar to that of T_a at 21 °C. At 15 days and ~ 5.5 g (bottom right), they could regulate a high $T_b > 34$ °C at T_a 21 °C. Data from Geiser et al. (2019a), photos F. Geiser

parents, they cool rapidly, for example in desert hamsters (*Phodopus roborovskii*, Figs. 8.5, 8.6). Neonate hamsters 1 day after birth, show a change in surface temperature (T_s) based on a thermal camera image (Fig. 8.5) from red (T_s ~33 °C) to blue (T_s ~22 °C), approaching T_a within 30 minutes. The corresponding cooling curves of T_s measured with an infrared thermometer, also show a fast reduction of T_s on day 1 (Fig. 8.6). Small neonates cannot avoid this because they are naked (Fig. 8.5) and unable to produce sufficient endogenous heat to maintain a high and constant T_b (Dawson and Evans 1960; Morrison and Petajan 1962; Hill 1976; Holloway and Geiser 2000; Wacker et al. 2017). At that stage, developing altricial endotherms are often referred to as poikilothermic, but even some small precocial species go through this developmental stage (Price and Dzialowski 2018; Aharon-Rotman et al. 2020). Importantly, these developing endotherms are not ectothermic as is often implied or stated, because their MR is well above that of similar-sized ectotherms (Fig. 8.7).

As young animals grow to larger size, fur or feathers develop for better heat retention. Growth is associated with a maturation of the nervous and other organ systems, the MR increases and the ability for endogenous heat production via shivering and/or non-shivering thermogenesis improves (Dawson and Evans 1960; Hill 1976; Oelkrug et al. 2015; Nowack et al. 2017b). Eventually, as in desert

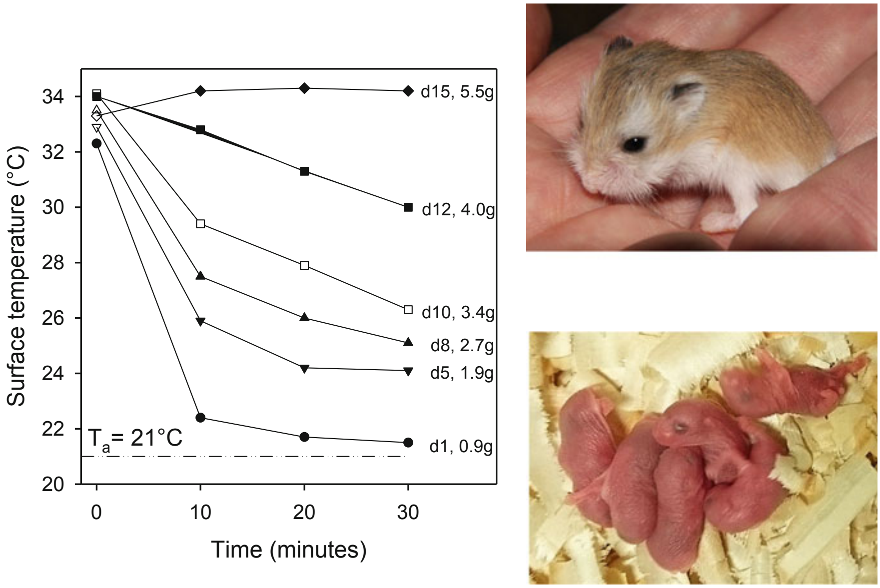

Fig. 8.6 The change of surface temperature (T_s) during the development of endothermic thermoregulation in desert hamsters (*P. roborovskii*), as measured with an infrared thermometer (left). On day 1 when pups weighed about 1 g and were naked (bottom right), they cooled rapidly over 30 min, from T_s ~33 °C to T_s ~22 °C similar to that of T_a at 21 °C. At 15 days and ~5.5 g (top right), they could regulate a high T_b >34 °C at T_a 21 °C. Data from Geiser et al. (2019a) photos F. Geiser

hamsters at around day 15 and ~5.5 g body mass, they are able to maintain a constant high T_b, at least during exposure to moderate T_as (Figs. 8.5 and 8.6).

There is also a change in RMR associated with growth at T_a 30 °C, a temperature that is within the TNZ of adults. The transition to competent endothermy is exemplified by marsupial kowaris (*Dasyuroides byrnei*, Fig. 8.7). Marsupials are well suited for examining developmental details because their rate of development is about half of that for placental mammals (Lee and Cockburn 1985). Initially, below 20 g and at an age of <80 days, the RMR of young *D. byrnei* was almost half of the BMR predicted for adult marsupials of that mass, but ~five-fold the SMR of reptiles (Fig. 8.7). When young kowaris were growing fast (from about 30 to 80 g; ~100 to 180 days) and had reached competent endothermy most RMRs were above or near that predicted for marsupial BMR (Geiser et al. 1986). When kowari body mass had reached the adult body mass of ~100 g at >200 days, the RMR was the same as predicted for marsupial BMR. This approximation in RMR of the young to BMR is because the young at that stage were no longer growing and therefore their RMR is BMR.

Newly endothermic young, typically at about 20–50% of adult body mass (for desert hamsters this is at ~15 days and 5.5 g body mass, Fig. 8.5) are highly vulnerable to heat and energy loss. They also are prone to suffer death by starvation especially if they maintain a high constant T_b at low T_a when heat loss is high

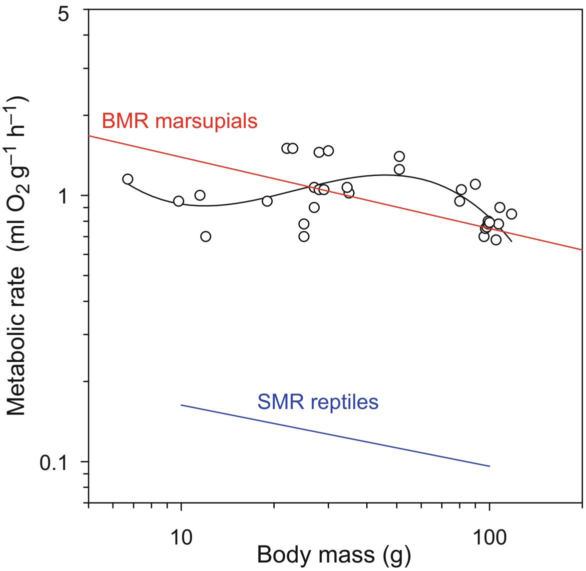

Fig. 8.7 The resting metabolic rate (RMR, circles, polynomial fit with black solid line) of developing kowaris, *Dasyuroides byrnei* (Dasyuridae) as a function of body mass plotted on logarithmic scales. Animals were measured at T_a 30 °C, which is within the TNZ of adults, in comparison to the predicted BMR of dasyurid marsupials (red solid line, MacMillen and Nelson 1969). Initially at body mass <20 g (<90 days), when animals were poikilothermic, the RMR was well below the predicted BMR. From about 30–80 g when animals were growing rapidly and had reached endothermy MR was near or above the predicted BMR, and around 100 g when they had reached adult body mass, RMR fell close to the prediction (kowari data from Geiser et al. 1986). The standard MR (SMR) of ectothermic reptiles, also measured at T_a 30 °C (blue solid line, Bennett and Dawson 1976), is shown for comparison and is well below those of poikilothermic kowaris >20 g, showing that developing mammals, even early during development, are partially endothermic, not ectothermic

(Prinzinger and Siedle 1988; Bize et al. 2007; Geiser et al. 2008). Juveniles at that developmental stage also lack the experience, or are physically unable to obtain food on their own. While mammalian parents are able to store fat that can be transferred to the growing young as milk, this is not possible in birds (apart from 'crop milk' in pigeons). Birds therefore cannot bridge adverse periods by using stored energy to feed the young, which in turn may require adaptive responses to enhance the chance of survival.

Using torpor would potentially provide an avenue to overcome energetic bottlenecks for small, newly endothermic young. The likeliness of torpor use during development is supported by the inverse relationship between torpor expression and size in adult birds and mammals (Chap. 5), which seems to be related to their rate of heat loss at low T_a. Further, because the T_{lc} of the TNZ of small species or individuals is often around 30 °C or even above (Fig. 1.5) and T_as experienced in the wild are generally below that, they typically have to produce endogenous heat more or less constantly to maintain the large T_b-T_a differential (Bartholomew 1982; Tattersall et al. 2012; Kronfeld-Schor and Dayan 2013; Riek and Geiser 2013; Withers et al. 2016; Mitchell et al. 2018).

When developing young become endothermic they are a fraction the size of adults, meaning energetic challenges will be exaggerated. For the majority of small avian and mammalian species, energetic bottlenecks are likely faced by developing young occasionally or even frequently as, for example, during bad weather (Bize et al. 2007). Nevertheless, current information on torpor during development (Table 8.2) is limited to only a few birds and mammals (Nagel 1977; Beard and Grigg 2000; Geiser 2008; Eichhorn et al. 2011; Giroud et al. 2014; Wacker et al. 2017; Geiser et al. 2019a; Renninger et al. 2020; Aharon-Rotman et al. 2020). For many of the studied species the rate of development is slow. This is especially the case in marsupials, for which detailed data are available. Following a prolonged poikilothermic phase, much of which occurs during pouch life in marsupials, first expression of torpor is observed some months after birth (Geiser et al. 2006; Wacker et al. 2017). However, torpor during development also has been observed in altricial species with rapid development such as swifts, hamsters and mice, as well as in small precocial quail (Aharon-Rotman et al. 2020).

Birds

While observation on torpor during reproduction in birds are rare, some data are available for several orders during development. Because of the inability of birds to store fat that can transferred to the young in the form of milk, birds must forage to supply food to growing young under all environmental conditions. If foraging is not possible or unsuccessful, adaptive responses such as torpor by the developing young provide a possible avenue for survival.

Avian torpor expression during development has been observed post-hatching in the Galliformes (land fowl), Caprimulgiformes (nightjar relatives), Apodiformes (swifts), Trochiliformes (hummingbirds), Sphenisciformes (penguins), Procellariformes (petrels), Coliiformes (mousebirds), and Passeriformes (songbirds). Detailed measurements are available for some of the species (Table 8.2), whereas for others data are limited to field observations. Two of the birds expressing torpor during development (the storm-petrel and king penguin) are not known to be heterothermic as adults.

During a brief developmental window, shallow nocturnal torpor was observed in captive king quail (*Coturnix chinensis*, Galliformes) (Aharon-Rotman et al. 2020). King quail became fully endothermic at about 12 days of age, having achieved a body mass of 13 g, and soon thereafter (day 14 and 17) they entered shallow torpor for several hours around midnight with a reduction of MR by >40% of RMR, lower than that observed in adults (Hohtola et al. 1991). Quail chicks were able to endogenously rewarm from this torpor bout, however towards the morning they became hypothermic reducing T_b and MR again and were apparently unable to

Table 8.2 Torpor during development of young

Birds	
King quail, *Coturnix chinensis*	Torpor in developing chicks (Aharon-Rotman et al. 2020)
Poorwill, *Phalaenoptilus nuttalii*	Torpor in chick brooded by torpid male (Kissner and Brigham 1993)
Swift, *Apus apus*	Daily torpor in 4–5 week old chicks after fasting, minimum T_b 21 °C (Koskimies 1948)
Alpine swift (*Apus melba*)	Torpor in chicks, during bad weather and reduced muscle (Bize et al. 2007)
Hummingbird, *Selasphorus platycercus*	Torpor in hummingbird chicks (Calder and Booser 1973)
King penguin, *Aptenodytes patagonicus*	Chicks enter torpor during prolonged fasts at ~3–4 months, ~8 kg (Eichhorn et al. 2011)
Storm-petrel, *Oceanodroma furcata*	Torpor in starving chicks from ~5 to 28 days, ~10 to 50 g, minimum T_b 10.6 °C (Boersma 1986)
Mousebird, *Urocolius macrourus*	Torpor in chicks at ~10 days, ~30 g, minimum T_b 22 °C (Finke et al. 1995)
Crimson chat, *Ephthianura tricolor*	Nocturnal torpor in free-ranging chicks, passive rewarming (Ives 1973)
Banded whiteface, *Aphelocephala nigricincta*	Nocturnal torpor in chicks, passive rewarming (Ives 1973)
House martin, *Delichon urbica*	Torpor in chicks after starvation at 13 days, minimum T_{skin} 22 °C, TMR ~30% of RMR (Prinzinger and Siedle 1986, 1988)
Mammals	
Monotremes	
Echidna, *Tachyglossus aculeatus*	Torpor in young after 50 days and ~ 200 g (Beard and Grigg 2000)
Marsupials	
Dunnart, *Sminthopsis crassicaudata*	Daily torpor from ~80 days, ~9 g, minimum T_b 16 °C (Wacker et al. 2017)
Dunnart, *Sminthopsis macroura*	Daily torpor from ~80 days, ~10 g (Geiser et al. 2006b)
Antechinus, *Antechinus stuartii*	Daily torpor from ~3 months, 18 g (Geiser 1988a)
Antechinus, *Antechinus flavipes*	Daily torpor from ~3 months, 23 g (Geiser 1988a)
Kowari, *Dasyuroides byrnei*	Daily torpor from ~3 months, 50 g (Geiser et al. 1986)
Placentals	
White-toothed shrew, *Crocidura russula*	Juvenile daily torpor from ~7 days, ~5 g (Nagel 1977)
Hazel dormouse, *Muscardinus avellanarius*	Torpor in juveniles, occasionally with mother (Juškaitis 2005). In autumn torpid young of year heavier than active ones
Garden dormouse, *Eliomys quercinus*	Torpor in juveniles enhances growth when food restricted (Giroud et al. 2012, 2014)
Siberian hamster, *Phodopus sungorus*	Juvenile daily torpor from 13 days (Bae et al. 2003)
Desert hamster, *Phodopus roborovskii*	Juvenile daily torpor from 13 days, min T_s 22 °C (Geiser et al. 2019a)
House mouse, *Mus musculus*	Juvenile daily torpor from ~14 days, 6 g, minimum T_s 24.6 °C (Renninger et al. 2020)

rewarm endogenously. The chicks were rewarmed passively and survived. Perhaps this observation in captivity is really ‘nocturnal hypothermia’ as observed in passerines in the wild (see Chap. 3 and below).

Torpor was also observed during development in poorwills (*Phalaenoptilus nuttallii*, Caprimulgiformes) in mid-summer in the wild (Kissner and Brigham 1993). A brooding male together with a 17–20 day old chick were found in torpor, both with a T_b of 18.9 °C and both had rewarmed 1.5 h after the disturbance. Five days later the chick had left the nest and likely fledged (Kissner and Brigham 1993).

Juvenile insectivorous common swifts (*Apus apus*, Apodiformes) displayed torpor after 6 days of fasting (Koskimies 1948). The T_b fell to lower values on consecutive fast days and the minimum was 20.1 °C on the seventh fast day. T_b began to decline at about 19:00, nocturnal T_b minima were observed between 01:00 and 03:00, and T_b then increased to normothermic levels (~37 °C) by 05:00, with the exception of day 12 when it remained lower. Swift chicks were able to survive fasting for up to 12 days, despite frequent disturbance to undertake T_b measurements. Apparently survival for up to 21 days has been observed, probably because of their large storage of fat (juveniles body mass was 49 g vs 42 g in adults) and use of nocturnal torpor (Koskimies 1948). Adult swifts also entered torpor with a T_b of 29 °C apparently after a short period of starvation.

The importance of torpor for survival of chicks in the wild is emphasized by the observation that free-ranging Alpine swift chicks (*A. melba*, ~65 g) living under a roof of a clock tower on the Swiss plateau in summer. Alpine swift chicks become feathered at 10 days of age and adults stop brooding, suggesting chicks are endothermic from that time. A weeklong period of bad weather commenced when chicks were 22 days old (Bize et al. 2007). During this week adults temporarily abandoned nests and did not feed the young for at least two consecutive days which led to starvation and death in some. Surviving chicks had significantly reduced pectoral muscle size, a slight reduction in body mass and reduced T_b from a mean of ~36.5 °C to a minimum of 19.7 °C (Bize et al. 2007). Growth recommenced after the bad weather and T_b was regulated at a mean of about 37 °C (Bize et al. 2007).

Torpor also has been observed in hummingbird chicks (*Selasphorus platycercus*, Apodiformes). When nectar supply was reduced towards the end of the reproductive season in the Rocky Mountains, torpor in hummingbird chicks was observed twice (Calder and Booser 1973).

Adult king penguins (*Aptenodytes patagonicus*, Sphenisciformes) are well known for their ability to withstand extreme cold exposure for prolonged periods aided by huddling and an impressive fasting capability (Gilbert et al. 2010; Eichhorn et al. 2011). Free-ranging chicks from 3 to 4 months and at a body mass of ~8 to 10 kg experience intermittent feeding during 5 winter months and can express pronounced heterothermy with core T_b falling from ~40 °C to below 30 °C for several hours after prolonged rain. However, after feeding events, when they can consume large cold meals, abdominal T_b also falls, which is not likely a controlled event. Use of shallow torpor may aid survival, but it reduces growth rate in king penguin chicks (Eichhorn et al. 2011).

Storm petrels (*Oceanodroma furcata*, Procellariformes) are plankton and crustacean eating pelagic birds. Free-ranging chicks became endothermic at ~5 days post-hatching in their natural burrows on the artic Barren Islands, Alaska. When adults did not provide sufficient food, the young entered torpor from about 5 to 28 days during the growth phase (Boersma 1986). Although there was some mortality, most chicks survived from T_bs as low as 10.6 °C and were able to rewarm at least after partial passive rewarming. Body mass during the time of torpor expression increased from ~10 to the adult mass of 60 g.

In herbivorous/frugivorous African mousebird chicks (*Urocolius macrourus*, Coliiformes), torpor was first observed 10–12 days after hatching, essentially at the same time when they were capable of endothermic thermoregulation (Finke et al. 1995). During torpor, quantified at a T_a of 15 °C, the minimum TMR measured was 10% of RMR and the minimum T_b was 22 °C. Birds at that stage and at ~55% of adult body mass were able to rewarm endogenously. Torpor was quantified by respirometry and active arousal was induced by T_b measurements to insure that individuals were torpid and not simply hypothermic without the ability of endothermic arousal. Therefore TBD was not determined (Finke et al. 1995).

Torpor has also been observed during the post-hatching development of songbirds (Passeriformes). House martin chicks (*Delichon urbica*) were capable of entering and arousing from torpor 11 days post-hatching, one day after endothermic thermoregulation was fully established (Prinzinger and Siedle 1986, 1988). Torpor in birds at a body mass of about 12 g (~60% of adult mass) could be induced by starvation, with T_s falling from ~32 to 22 °C when TMR was ~30% of RMR. However, the time required for torpor induction increased with increasing body mass (Prinzinger and Siedle 1986, 1988). Torpor during development has also been observed in several Australian arid zone passerine (Ives 1973; Chap. 3).

Mammals

Monotremes

After hatching and a pouch life of 45 to 50 days and a body mass of ~200 g, young echidnas (*T. aculeatus*) are maintained in nursery burrows for 3–4 months. The mothers visit to feed only at 3 to 16 day intervals (Beard and Grigg 2000). A burrow young at an age of about 83 days and a body mass of 474 g reduced its T_b to a minimum of 12.8 °C after not having been fed for 16 days (Griffiths et al. 1988). This young was removed from the burrow, rewarmed and fed. However another burrow young reduced T_b from a normothermic T_b of ~32.5 °C to ~27.5 °C (Griffiths et al. 1988; Beard and Grigg 2000), suggesting they can express torpor during development. Echidnas become independent only at 5 to 5.5 months (Griffiths et al. 1988; Beard and Grigg 2000).

Marsupials

Marsupials are born in an extremely underdeveloped altricial state at <1% of the mother's body mass and they develop slowly (Lee and Cockburn 1985). Endothermy develops months after birth, rather than the days or weeks seen in many small birds or placentals and therefore marsupials permit a detailed examination of functional changes during development and growth.

Torpor during development has been investigated in insectivorous/carnivorous marsupials (Dasyuridae) and feathertail gliders (Acrobatidae). Adult body masses of the species known to express torpor during development range from 12 to 110 g and all species investigated for expression of torpor during development also use torpor as adults (Chap. 3).

In dunnarts (*Sminthopsis macroura* and *S. crassicaudata*) the development of endothermy was slow and required about 60–80 days in comparison to the ~14 days for the small placental desert hamsters (see Fig. 8.5). Both dunnarts were able to enter torpor essentially from the day they had reached endothermy. In fat-tailed dunnarts, *S. crassicaudata*, the development of torpor was especially interesting (Wacker et al. 2017). Dunnarts were able to regulate T_b from around 60 days and at a body mass of ~8.5 g and at this point they also were able to enter an apparent state of torpor. Dunnarts at this age maintained a high T_b and MR at a T_a of 15 °C for most of the night (Fig. 8.8). However, at around 03:00, MR rapidly fell during torpor entry, ahead of T_b (unlike during hypothermia, Fig. 5.18). Cooling was fast when MR was low and the high thermal conductance because of their small size contributed to this fast cooling rate. However, despite the fast apparent torpor entry the young were

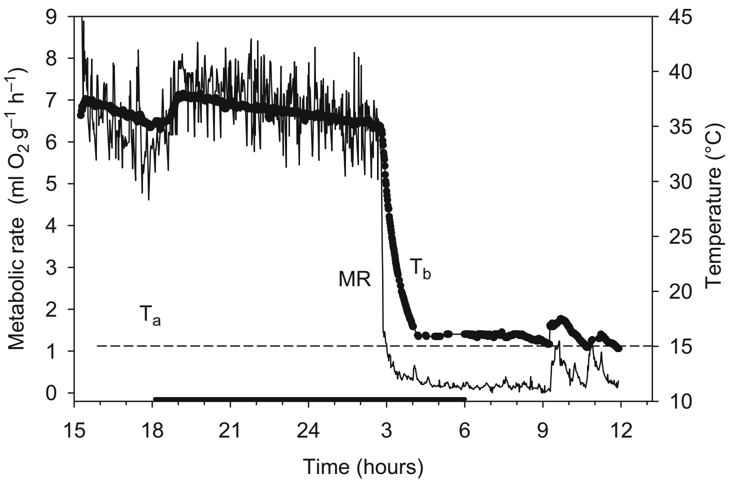

Fig. 8.8 Metabolic rate (MR, solid line) and body temperature (T_b, filled circles) measured overnight at T_a 15 °C (broken line, average) in a juvenile endothermic *S. crassicaudata* at age 62 days, and a body mass of 8.6 g. The black horizontal bar indicates night. Data from Wacker et al. (2017)

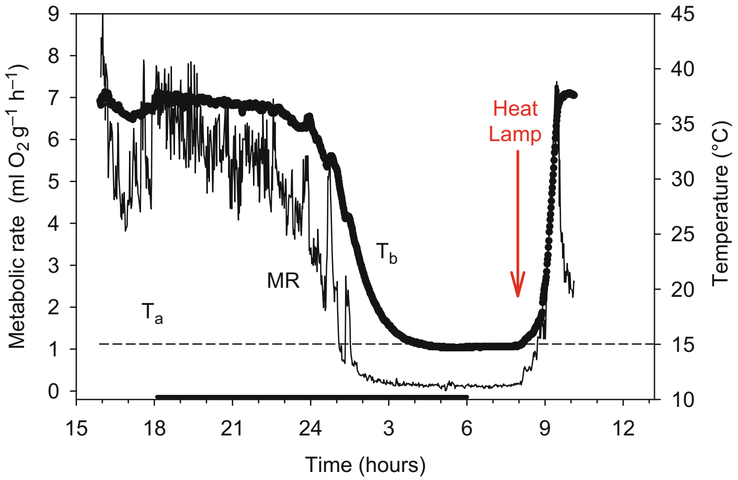

Fig. 8.9 Metabolic rate (MR, solid line) and body temperature (T_b, filled circles) measured overnight at T_a 15 °C (broken line, average) in a juvenile endothermic *S. crassicaudata* at age 64 days, and a body mass of 8.9 g. The red arrow indicates when the heat lamp was switched on. The black horizontal bar indicates night. Data from Wacker et al. (2017)

unable to produce enough heat to rewarm endogenously from low T_b during torpor at a T_a of 15 °C. Although they attempted to raise T_b by increasing MR between ~09:30 and 11:30 (Fig. 8.8), which resulted in a slight rise in T_b, the heat production was not enough to complete the arousal process. Therefore, by definition, these young could be classified as being hypothermic. However, the decline of T_b and MR (Fig. 8.8) exhibited the pattern expressed during entry into daily torpor and hibernation, with a fast initial reduction of MR, followed by a reduction in T_b that further reduces MR. This differs from the opposite pattern observed during entry into cold-induced hypothermia during which animals try to maintain a high T_b via a high MR, but fail to do so because heat loss exceeds heat production (Figs. 5.17, 5.18). The early torpor entry of juvenile dunnarts during the second half of the night rather than in the morning (Fig. 8.8), and the fast decline of MR and T_b during the entry phase strongly suggests that the T_b reduction was not caused by energy depletion. It also was not likely due to low capacity for endogenous heat production as during hypothermia, but instead appears an 'intended' and regulated torpor entry. While these dunnarts at <9 g were unable to rewarm endogenously, when offered a basking lamp, they moved and positioned themselves under the lamp and used the radiant heat to rewarm (Fig. 8.9). However, only a few days later at ~10 g, young *S. crassicaudata* were able to raise T_b endogenously. The same was the case for *S. macroura* at 80 days and ~10 g body mass (Table 8.2). As basking during rewarming from torpor is common in adult desert dasyurids (Chap. 7), it is likely that juvenile dasyurids in the wild, similar to passerines, use torpor and basking perhaps even before being fully endothermic.

In small dasyurid marsupials, torpor expression appears to develop concurrently with the ability for endothermic thermoregulation. In juvenile dunnarts (*Sminthopsis* spp.) and kowaris (*D. byrnei*) from the arid zone, the ability to enter torpor occurs essentially immediately after endothermic thermoregulation had developed. Whereas in *Antechinus* spp. from coastal, mesic or subtropical areas torpor was observed soon after the time endothermic thermoregulation was established (Table 8.2). However, in all species that have been examined in detail, torpor was more pronounced (i.e. deeper and longer) at an early stage of juvenile development than later (Table 8.2). Average maximum torpor bout duration in the juveniles, decreased with growth and was about twice as long on average in the same individuals once they had reached adult size, and the same was the case for developing rodents (see below).

A prolongation of torpor bouts increases the potential for energy conservation. It has been suggested that a change in the duration of torpor bouts by adult mammals is limited somewhat, because it is achieved only by adjusting the time of torpor entry (Tucker 1966; Brown and Bartholomew 1969). In response to low food rationing or T_a, only the time of torpor entry was affected and occurred earlier, whereas the time of arousal appeared to be largely fixed by a circadian rhythm (Tucker 1966; Brown and Bartholomew 1969). In developing *S. macroura* both torpor entry as well as arousal times were related to body mass with earlier entry times and later arousal times in small individuals and vice versa (Geiser et al. 2006b). Thus, the prolongation of torpor duration in juvenile dunnarts was achieved both by entering torpor earlier and arousing late. Perhaps a prolongation of torpor bouts at both ends is especially crucial during development when foraging experience is limited and nutrients and energy are not only needed for maintenance, but also for growth.

Pouch young of feathertail gliders (*Acrobates pygmaeus*, Diprotodontia), and also of *Dromiciops* (see above), experienced a reduction of T_b when their mothers expressed torpor during lactation. Although rewarming of pouch young almost certainly was passive with the rise of T_b of the mother, the low T_b did not appear to adversely affect the development of feathertail gliders because the juveniles were later recaptured with their mothers (Frey and Fleming 1984).

Placentals

Torpor during development also occurs in placental mammals. It is known to be used in insectivores (Lipotyphla), bats (Chiroptera) and rodents (Rodentia).

To my knowledge, data on torpor during pregnancy and lactation of adult shrews are not available, however torpor has been observed during their fast development (Nagel 1977). European white-toothed shrews (*Crocidura russula*), were able to enter daily torpor as early as day 7 post-partum at a body mass of ~5 g (~40% of adult mass). At T_a 20 °C, juvenile shrews at that age reduced T_b from ~33 to 24 °C, remained torpid for several hours and were able to rewarm endogenously (Nagel 1977, 1985).

Detailed information on torpor during development in bats is scarce. However, juvenile *E. fuscus* do enter torpor (Audet and Fenton 1988). Early pre-volant juvenile *E. fuscus* appeared to be poikilothermic, whereas post-lactating pre-volant juveniles displayed torpor patterns similar to those of post-lactating adult females (Hollis and Barclay 2008).

Data on torpor during the development of rodents are more common than data during reproduction. Hamsters, *Phodopus sungorus* and *P. roborovskii*, use daily torpor during development. Desert hamsters, *P. roborovskii*, became endothermic at ~15 days and a body mass of around 5.5 g (Fig. 8.6). On the next day they were able to enter torpor with a reduction in MR by >90%, followed by endothermic arousal (Geiser et al. 2019a). In the congener *P. sungorus*, torpor after food restriction was observed only ~13 days after endothermic thermoregulation had developed (Bae et al. 2003), suggesting this species has an about 2-week homeothermic phase. However, a torpor-like state could be induced in *P. sungorus* soon after endothermy was established by administration of the metabolic inhibitor 2-deoxy-D-glucose (2-DG), suggesting that they may be physiologically capable of entering torpor soon after they become endothermic (Bae et al. 2003).

White mice (*Mus musculus*) are ubiquitous laboratory animals and one could surmise that all basic functional traits have been examined or revealed. However, although they use daily torpor as adults (Chap. 3), it was not known until recently that during development, when heat loss in pups is high, they can use daily torpor for energy conservation (Renninger et al. 2020). At 5 or 6 days and a body mass of ~3 g, the still naked mice cooled rapidly, similar to similar-sized desert hamsters (Fig. 8.6). At ~14 days of age and a body mass of ~6 g, mice could maintain a high, constant T_b. These pups, at ~20% of adult body mass, were able to enter into and arouse from torpor based on the rate of oxygen consumption (Fig. 8.10). During torpor, metabolism fell by up to >90%, or to ~1/3 of BMR, and torpor lasted for up to 12 h. As mice grew, torpor was still used, but was less pronounced, with TMR increasing with growth and a decrease of RMR (Fig. 8.11).

Wild hazel dormice (*Muscardinus avellanarius*) also express torpor during development (Juškaitis 2005). Although torpor expression in young-of-the-year was lower in spring/summer than in adults, three cases of torpid mothers sharing a nest box with their torpid young and torpid (or cold) juveniles without their mothers were observed. In autumn the average body mass of torpid young-of-the-year was ~25% higher than that of normothermic individuals suggesting they may have used torpor for fattening similar to marsupials and bats (Geiser and Masters 1994; Speakman and Rowland 1999).

In garden dormice (*Eliomys quercinus*) torpor use in juveniles also appears to be used to spare nutrients and energy for growth (Giroud et al. 2012, 2014). Body mass gain of fasted juvenile dormice (food removed for 1 day twice/week) was correlated with torpor frequency (bouts/week). Juveniles that showed 3 bouts/week increased body mass by more that two-fold in comparison to individuals that remained normothermic (Fig. 8.12).

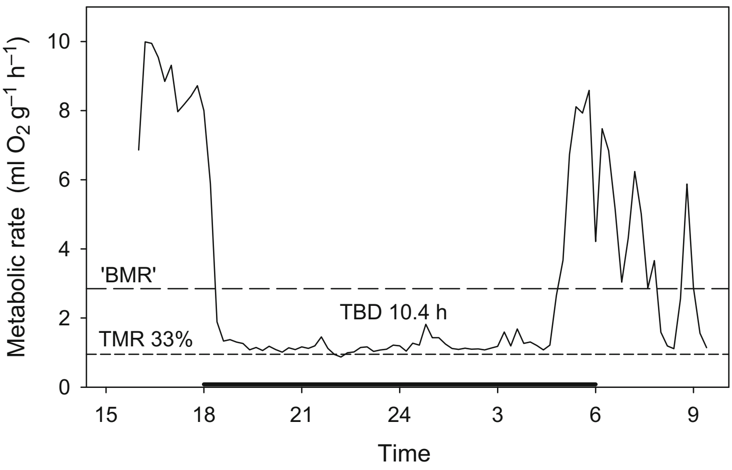

Fig. 8.10 Metabolic rate (ml O_2 g^{-1} h^{-1}) measured overnight at T_a 20 °C in a mouse pup, *Mus musculus*, shortly after endothermy was established at a body mass of 5.4 g. Data from Renninger et al. (2020). 'BMR' was calculated from Hayssen and Lacy (1985), the minimum TMR was 33% of BMR and the duration of the torpor bout (TBD) was 10.4 h. The black horizontal bar indicates night. Note that, after the first endothermic arousal at around 05:00 h, the mouse re-entered torpor again in the morning.

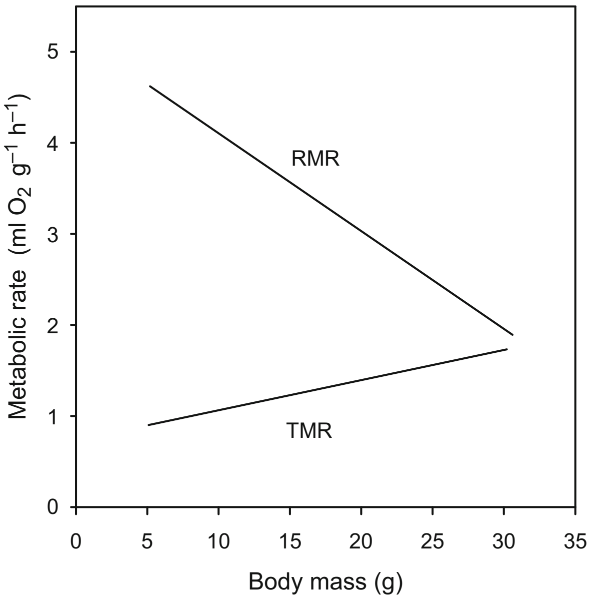

Fig. 8.11 The regression lines for change of resting MR (RMR) and torpor MR (TMR) measured at a T_a of 20 °C during the growth phase of mice, *Mus musculus*, after endothermy was established. Data from Renninger et al. (2020)

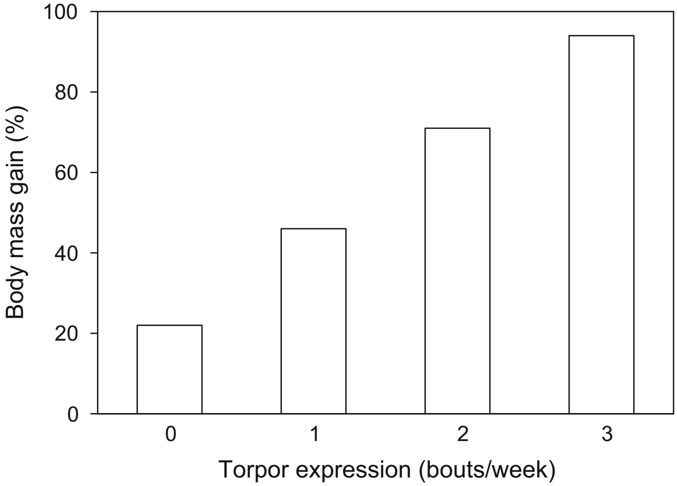

Fig. 8.12 Growth in juvenile garden dormice (*E. quercinus*) in autumn when food was removed for 1 day twice/week was a function of the number of torpor bouts expressed during that time. Data derived from regression line from Giroud et al. (2012)

The Limited Data on Torpor During Reproduction and Development

In this chapter, I have shown that torpor can be used during the energetically expensive periods of reproduction and development in both birds and mammals. While observations of torpor expression during incubation of eggs in birds is rare, more birds are known to use torpor during the period of development. Perhaps young birds use torpor because of the inability of adults to store fat and deliver it to growing young as milk. Therefore periods of adverse weather and food storage may be more challenging for young birds.

In mammals there is more information on torpor during reproduction than during development, or specifically pregnancy and lactation, whereas data on torpor use in developing young are scarce. As for torpor in general, torpor during reproduction and development occurs in predominantly small species and those species that have to cope with adverse condition and food shortages.

The data for mammals suggest that in the small (<100 g) placentals, endothermy is reached and torpor can be expressed at a smaller size (body mass ~5 to 6 g) and in a shorter time (~2 weeks) than in marsupials. In small birds development rate is similar to placentals, but chicks at the time they reach endothermy and begin to use torpor tend to be larger than placental mammals, although this may reflect to some extent the limited data set. In small marsupials endothermy and use torpor occur from a body mass of ~10 g and only after 2–3 months. In large heterothermic mammals, torpor during development has not been examined but in penguins it has been observed late in development and at a large size.

Investigations of torpor during both reproduction and development are often hindered by the understandable reluctance of researchers to expose reproductive or developing individuals to energetically or thermally challenging conditions. Animals in the wild must of course be able to deal with them. The limited number of studies, often the result of unplanned observations, seems to be the major reason why many of the data are not extensive. Torpor during reproduction and development in birds and mammals is clearly understudied in general. However, it is important to know which species are capable of using it and whether more species that are homeotherms as adults can express torpor during development.

Chapter 9
Dietary Lipids, Thermoregulation and Torpor Expression

Organismal function at low T_b requires biochemical adjustments. These modifications often involve synthesis of new proteins, such as enzymes, that have evolved to function optimally under different thermal conditions (Hochachka and Somero 2002). However, it is also the composition of lipids in tissues and cellular membranes that play a central role for maintaining physiological processes at different temperatures (Hazel 1995; Arnold et al. 2015; Else 2021). To a large extent this alteration is related to the physical properties of fatty acids.

Fatty acids are long-chain hydrocarbons, in animals they are typically about 12 to 22 carbons long, and are mainly used to store energy in the form of fat or oil, or form part of building blocks for cellular membranes (Gurr et al. 2002). Fatty acids can be saturated (SFA), unsaturated (UFA) or polyunsaturated (PUFA). Take for example, a common saturated fatty acid in animals called stearic acid, a chain of 18 carbons with hydrogen molecules without a double bond (C18:0; 18 carbons, 0 double bonds). In triglyceride molecules (3 fatty acids attached to 1 glycerol) the C18:0 chains pack straight and tightly because the carbons along the fatty acid chain can rotate freely. Therefore the triglycerides made from a large proportions of C18:0 are highly ordered and their melting point is also high (~70 °C). At room temperature they form a fat such as many animal fats or butter (Gurr et al. 2002).

If a single double bond is introduced into the 18-carbon fatty acid it is called oleic acid (C18:1; 18 carbons, one double bond), a mono-unsaturated fatty acid (MUFA). The double bond causes a kink in the fatty acid, which increases the disorder of the fatty acid chains and therefore decreases its melting point to ~10 °C (Gurr et al. 2002). The fluidity of triglycerides rich in C18:1 is high and at room temperature form an oil; olive oil contains high proportions of C18:1. If a second double bond is introduced into the fatty acid a second kink is created and the molecule it is now called a polyunsaturated fatty acid (PUFA) with a further decrease in the ordered nature of the fatty acid tails and a lowering of the melting point. The 18-carbon PUFA with two double bonds is called linoleic acid (C18:2) and its melting point is about −5 °C; this fatty acid is abundant in sunflower oil. PUFAs are essential fatty acids because they cannot be synthesized by animals and must be ingested (Gurr

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6_9

et al. 2002; Hulbert and Abbott 2012; Arnold et al. 2015), can be long-chained and can have many double bonds. To characterise UFAs further the position on the first double bond with reference to the end (terminal methyl group) of the fatty acid is identified by ‘n’ or ‘omega’. Common PUFAs are n-6 fatty acids (e.g. linoleic acid C18:2 n-6) which are found in oily seeds, whereas n-3 fatty acids (e.g. linolenic acid, C18:3 n-3) are found in green leaves and in fish oil, but the latter have been originally synthesized by algae, which are then eaten by fish and incorporated into the tissue (Gurr et al. 2002; Hulbert and Abbott 2012).

Since fatty acids are hydrocarbons they are energy-rich because they are made almost entirely from carbon and hydrogen molecules that can be oxidised to obtain chemical or thermal energy. They are often used for energy storage usually in the form of triglycerides in depot fat that in animals, can be stored without water in contrast to sugars and therefore are light. Depot fat used to store triglycerides is also called white adipose tissue (WAT). In contrast, brown adipose tissue (BAT) or brown fat, is rich in mitochondria and is an important organ for non-shivering thermogenesis via oxidation of fatty acids in placental mammals (Cannon and Nedergaard 2004; Oelkrug et al. 2015; Rice et al. 2021). However, when fat molecules are used as building blocks of cell membranes as phospholipids, one of the triglyceride fatty acid tails is substituted by a polar phosphate group (i.e. 2 fatty acids tails plus one phosphate group attached to one glycerol), making the molecule polar. In a lipophobic aqueous environment, phospholipids form a membrane bilayer. Large proportions of cellular membranes are composed of these phospholipid bilayers (Gurr et al. 2002).

The composition of fatty acids is crucial for organismal function at different temperatures and therefore these molecules are key components of thermal biology. A change in the composition of fatty acids is used by organisms to maintain a stable fluidity of lipids in tissues and cell membranes over a range in temperatures and this is often referred to a ‘homeoviscous adaptation’ (White and Somero 1982; Cossins and Bowler 1987; Hochachka and Somero 2002). Homeoviscous adaptation describes the differences in lipid composition and thus fuidity of ectothermic organisms living at different T_a or organisms with a different T_b, as for example cold water fish relative to warm water fish or homeotherms (Hochachka and Somero 2002). Cold water fish with low T_bs contain relatively large amounts of UFA, whereas warm water fish and many homeotherms with high T_bs contain large amounts of SFA affecting the fluidity of their tissues and cell membranes; i.e. homeoviscous due to long-term selection at a certain temperature. However, in the context of this chapter the often-observed seasonal or temperature-induced changes in the physical properties of tissues or cell membrane lipids, are to a large extent due to acclimation (exposure to the change of typically a single environmental factor in the laboratory, such as T_a), acclimatisation (exposure to the change of multiple environmental factors in nature such as during winter vs summer), or phenotypic plasticity, because they occur within the lifetime of the organism, rather than due to selection over generations.

Ectotherms

In ectothermic organisms acclimated to low T_b, the concentration of UFAs and PUFAs increases and the concentration of SFAs decreases within weeks of acclimation in tissues and cell membranes (Hazel 1995; Hochachka and Somero 2002). This enrichment of UFA and PUFA results in maintenance of a suitable fluidity for physiological processes at low T_b (Cossins et al. 1977; Hazel 1995; Simandle et al. 2001; Hulbert and Abbott 2012). Strong correlations have been observed between the behaviour of fish acclimated to different thermal conditions and the fluidity of brain synaptosomes, cell membranes composed largely of phospholipids (Cossins et al. 1977). When exposed to short-term temperature changes, warm-acclimated fish performed better at high T_a than cold-acclimated fish and vice versa and fish behaviour was paralleled by the change in brain synaptosome fluidity (reduced fluidity in warm-acclimated, increased fluidity in cold-acclimated fish), reflecting the change in phospholipid fatty acid saturation (Cossins et al. 1977). During cold-acclimation in ectothermic vertebrates the increase in the proportion of UFA can be achieved by the synthesis of MUFAs, and often the enzyme Δ9 desaturase is used to convert stearic acid (C18:0) into oleic acid (C18:1) resulting in a reduction of the melting point of the fatty acid by ~60 °C (Gurr et al. 2002).

However, changes in lipid composition of animal tissues can also be achieved via ingestion of dietary lipids (McMurchie 1988; Hulbert and Abbott 2012). Dietary supplementation with fatty acids can significantly change the composition of tissues albeit usually to a lesser extent in membrane phospholipids. Such diet-induced compositional changes can in turn affect the thermal biology of organisms. For example, dietary PUFA enhances recovery from cold chill coma induced by exposure to ice water in ectothermic *Drosophila* (Holmbeck and Rand 2015). PUFA ingestion improves cardiac function at low temperatures in endothermic rats (Huttunen and Johansson 1963). Further, the composition of dietary fatty acids affects behavioural thermoregulation in ectothermic terrestrial reptiles (Simandle et al. 2001).

As is evident from previous Chapters, ectothermic organisms have low metabolic rates and usually lack insulation. Therefore they cannot use physiological thermoregulation via an increase of heat production effectively for regulating T_b, but rather must rely on behavioural thermoregulation and adjust T_b by moving to an appropriate thermal environment. In reptiles this often, although not always, involves shuttling movements into and out of the sun, to select a preferred T_b that may, however, change with season (Hammel 1968; Rismiller and Heldmaier 1988; Angilletta 2009; Tan and Knight 2018). The selection of T_b (preferred T_b or selected T_b), which requires a suitable thermal environment, assures optimal bodily functions such as effective locomotion, feeding, digestion and reproduction. However, usually the selected T_b differs between night time and daytime in terrestrial organisms due to the change of T_a in nature, but also because a circadian rhythm (Heatwole and Taylor 1987; Rismiller and Heldmaier 1988).

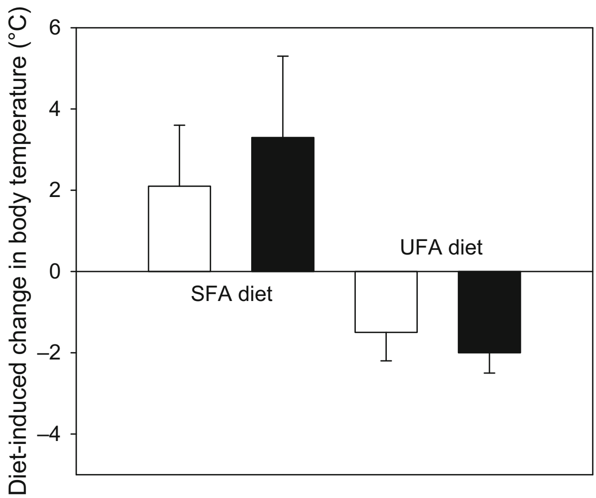

Fig. 9.1 Change in selected T_b (mean with SD) of the agamid lizard (*Ctenophorus nuchalis*) over 3 weeks by individuals fed a diet enriched with saturated (SFA) versus unsaturated (UFA) fatty acids. White bars daytime, black bars night-time. Data from Geiser and Learmonth (1994)

The preferred T_b of reptiles can be altered by feeding animals dietary fatty acids of different saturation. This was shown for three captive lizard species from three families (Simandle et al. 2001). These lizards were allowed to move freely in a thermal gradient in which they could select a range of T_a from low to high to adjust their T_b, while their T_b was measured over a period of weeks to determine their preferred T_b.

Shingle-back lizards (*Tiliqua rugosa*) are largely herbivorous Australian skinks of the family Scincidae. For individuals captured in late spring and measured in early summer, a 2-week period of feeding a UFA diet (enriched with 10% sunflower oil, 30% C18:2) led lizards to reduce the selected T_b by about 5.5 °C at night and about 3.5 °C during the day. A SFA diet (enriched with 10% sheep fat, 5% C18:2) did not significantly affect the selected T_b (Geiser et al. 1992b), suggesting that the selected T_b of these skinks captured in summer was already near the yearly maximum for the species.

Australian central netted dragons (*Ctenophorus nuchalis*), an insectivorous species of the family Agamidae with a preference for a high T_b of around 40 °C in the wild (Heatwole and Taylor 1987), showed similar responses in principle, but differed in detail. In these lizards captured in summer and measured in autumn over a 3-week period while on a UFA diet (sunflower oil: 23% SFA, 77% UFA, 32% PUFA), showed a fall in selected T_b by 1.5 °C during the daytime and by 2.0 °C during the night (Fig. 9.1). In contrast, the T_b of individuals maintained on a SFA diet (sheep fat: 59% SFA, 39% UFA, 9% PUFA) rose by 2.1 °C (daytime) and by 3.3 °C (night-time). These changes in thermoregulation were accompanied by significant changes in tissue fatty acid composition with a large number of fatty acids especially in depot fat differing between the two diets. The ratio of SFA/UFA was significantly lower in animals on the UFA diet for depot fat (by 45%), liver (by 33%) and muscle (by 11%) total lipids than in animals on the SFA diet, demonstrating that tissue composition reflected diet to a large extent (Geiser and Learmonth 1994).

Californian desert iguanas (*Dipsosaurus dorsalis*), a herbivorous lizard from the family Iguanidae, also selected higher night-time T_bs on a SFA diet than those on a UFA diet and the preferred T_b fell by >4 °C at night in comparison to daytime on the UFA diet but not on the SFA diet (Simandle et al. 2001). However, the critical minimum T_b, at which animals lose coordination, did not differ between treatments perhaps because of the compositional conservatism of the brain (Simandle et al. 2001). The metabolism of iguanas on the SFA diet nearly doubled when T_b was raised from 30 to 40 °C, as predicted by Q_{10}-effects, whereas those on UFA did not change significantly, suggesting that body function at high T_b can be better maintained when the proportion of SFA in tissues is increased as seen for fish. Diet-induced compositional changes were observed in most tissues examined both for triglycerides and phospholipids (Simandle et al. 2001).

These data support the view that dietary fats modulate the thermal biology of reptiles and thus likely other ectothermic vertebrates, probably via a change in the lipid composition of tissues and cell membranes, either directly via their physical properties or indirectly via other mechanisms, or perhaps to some extent the digestibility of food.

Endotherms

Winter survival in heterothermic endotherms not only requires energy, but, similar to ectotherms, also the ability to function at low T_b during torpor. Although heterotherms also show seasonal changes in the composition of somatic lipids, these shifts in tissue and membrane fatty acid composition and fluidity from summer to winter, the time of year when torpor typically is expressed is generally less clear-cut than in ectotherms (Goldman 1975; Geiser et al. 1984; Montaudon et al. 1986; Aloia 1988; Raison et al. 1988; Cochet et al. 1999; Dark 2005; Arnold et al. 2015; Klug and Brigham 2015). As the melting point of SFAs is well above that the T_b of 0 to 5 °C, values often experienced during hibernation (Chap. 5), high levels of UFA at least in the body fat used to fuel energy metabolism, might be expected and this is generally the case (Geiser 1990; Dark 2005). Moreover, some compositional changes have been observed in torpid sciurid hibernators, which burn predominantly SFA and conserve PUFA in the triglycerides of depot fat during winter (Florant et al. 1990; Cochet et al. 1999; Price et al. 2013). Hibernating mammals also show increases in UFA/SFA ratios of phospholipids of liver mitochondria, heart mitochondria, brain synaptosomes and heart microsomes during the hibernation season when they experience low T_bs (Aloia 1988; Dark 2005). Furthermore, rather than increasing total UFA or PUFA, the ratio of n-6 to n-3 PUFA seems to increase during torpor in some species, perhaps to maintain the activity of the membrane-bound pumps of the heart when tissue are at low temperatures (Ruf and Arnold 2008; Rice et al. 2021).

In daily heterotherms acclimation to short winter photoperiod results in a significant increase in torpor expression in several small mammals, including deer mice (*Peromyscus maniculatus*) and Djungarian hamsters (*Phodopus sungorus*) (Tannenbaum and Pivorun 1988; Heldmaier and Klingenspor 2003). In both these species, physiological changes were accompanied by, or perhaps to some extent caused by, changes in tissue fatty acid composition of brown adipose tissue, white adipose tissue, heart muscle and leg muscle (Geiser et al. 2007b, 2013). The proportions of fatty acids detected in tissues were correlated with the minimum measured T_s of individual *P. sungorus* acclimated to different photoperiods. Further, *P. sungorus* acclimated to long photoperiod increased their preference for SFA diet when exposed to high T_a and reversed this choice to prefer high levels of dietary UFA when exposed low T_a (Hiebert et al. 2003a). In house mice (*Mus musculus*) a UFA diet increased cold resistance substantially in comparison to mice given a SFA diet (Gordon and Ferguson 1980).

Changes in the lipid composition of tissues and cell membranes have been observed during seasonal acclimatization or photoperiod acclimation in heterothermic endotherms. However, the seasonal changes are typically less obvious or pronounced than those in ectotherms. Perhaps this is necessary for mammalian heterotherms to rewarm periodically from low T_b during torpor and for their cellular processes to continue to function appropriately despite short-term temperature fluctuations. During torpor in hibernating thirteen-lined ground squirrels (*Ictidomys tridemlineatus*) the organelle membrane lipids of the nervous system sequester into protein-free domains that laterally displace membrane proteins. When the animals rewarm from torpor, these lipid components return to their normal configurations (Azzam et al. 2000). It appears that such transient lateral changes in the membrane domain are important for functional reasons at low T_b and these can be achieved without major changes in lipid composition. Nevertheless, heterothermic mammals and birds tend to contain relatively large proportions of UFA in some tissues and membranes throughout the year (White 1973; Aloia 1979, 1988; Aloia and Raison 1989; Geiser 1990; Frank 1991; Dark 2005; Arnold et al. 2015). Therefore, heterotherms require relatively small compositional changes on a seasonal basis. It is, however, likely that these compositional changes are physiologically important, because rather small changes in membrane fatty acid composition result in significant changes in the activity of membrane-associated enzymes, perhaps due to their arrangement as annular lipids around the proteins (McMurchie 1988; Else and Hulbert 2003; Lee 2011).

The compositional changes of fatty acids provide a convenient modulator of cellular physiology over a range of T_bs. Typically, MUFAs are synthesized from SFA during cold acclimation. However, for function to occur at low T_bs, essential PUFAs are required, and these cannot be synthesised by vertebrates but must be ingested (Cossins and Bowler 1987; Hazel 1995; Rice et al. 2021). The essential fatty acids linoleic acid (C18:2 n-6) and linolenic acid (C18:3 n-3) (Hulbert and Abbott 2012; Arnold et al. 2015) are required as precursors for the production of most long chain PUFAs, which appear to be import particularly in those organisms that are active at low T_b (Hazel 1995). Torpid hibernators do show significant increases of PUFAs in depot fat and some membrane fractions (Aloia 1988; Florant et al. 1990). As there is strong evidence suggesting links between animal function, the composition of tissues and cell membrane lipid composition and the thermal biology of ectotherms all in the context of dietary lipids, it is likely that patterns of daily torpor and hibernation in mammals are also affected.

Dietary Lipids and Hibernation in Captive Mammals

Dietary preferences of heterothermic rodents suggest that they alter their uptake of seed types and prefer oily seeds that are rich in PUFA in autumn. This may be of functional significance. The increase in intake of seeds rich in UFA and PUFA coincides with late summer fattening in sciurid hibernators (Florant and Healy 2012). Early studies on the effect of dietary fatty acids on hamsters (*Mesocricetus auratus*) fed diets rich in SFA or UFA recorded significant changes in the melting point and iodine value (a measure of unsaturation) of depot fat (Fawcett and Lyman 1954). However, no differences in the onset of hibernation between experimental groups were observed. In a preliminary study on ground squirrels (likely *Callospermophilus lateralis*), animals maintained on a diet supplemented with soy oil (rich in oleic and linoleic acid) hibernated more often and displayed more prolonged torpor bouts than those maintained on a diet supplemented with beef tallow (rich in SFA and oleic acid; Aloia 1979). Linoleic acid concentration was found to be three times higher in erythrocytes from the soy oil-fed animals than those from the tallow-fed animals, showing a diet-induced change in cell membrane composition (Aloia 1979).

More detailed information on the effects of dietary fatty acids on thermal energetics is available for hibernating yellow-pine chipmunks (*Tamias amoenus*). Individuals caught in autumn, about 8 weeks before they would naturally begin hibernating, were maintained in the laboratory at a T_a of 22 °C on three diets (Geiser and Kenagy 1987). The first was a control diet of rodent chow, the second contained 10% sunflower seed oil (UFA rich diet; containing ~60% C18:2), and the third contained 10% sheep fat (SFA rich diet; >50% SFA, ~7% C18:2).

Once chipmunks had reached their peak body mass (an increase of ~38% from capture mass) after 8 weeks on these diets, they were exposed to low T_as, initially T_a 10 °C, to promote hibernation. As soon as chipmunks were in deep hibernation, the T_a was further decreased to 5 °C. On day 2 or 3 of a torpor bout (when they are in deep steady-state torpor and show little sensitivity to disturbance), chipmunks torpid at T_a 5 °C were carefully transferred to a respirometry chamber at the same T_a and then further cooled slowly while MR was measured until TMR increased to defend minimum T_b. These measurements revealed that thermal energetics differed among the three diet groups. All chipmunks increased MR during the cooling trials to regulate their T_b, but the minimum T_bs differed among animals as a function of diet. Torpid chipmunks fed the SFA diet regulated their T_b at a minimum of 2.2 °C, with a corresponding minimum T_a of 1.0 °C measured at the time TMR increased. In

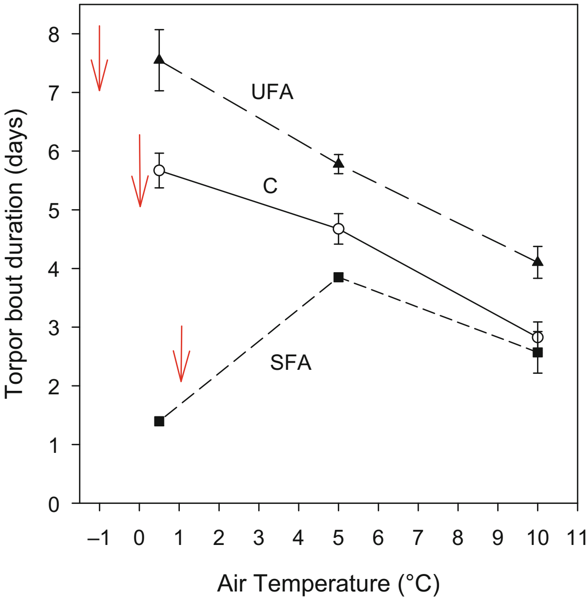

Fig. 9.2 Duration of torpor bouts (TBD) of chipmunks (*Tamias amoenus*) on different diets (UFA unsaturated, C control, SFA saturated) as a function of T_a. The red arrows show the minimum T_a at which torpid animals of each dietary group began to defend their T_b. Animals on UFA and C diets at T_a 0.5 °C hibernated at a T_a above the arrow i.e. they were thermoconforming, whereas animals on the SFA diet were at a T_a below the arrow i.e. they were thermoregulating and unlike the UFA and C animals, which continued to increase TBD at T_a 0.5 °C, SFA animals reduced TBD. Data from Geiser and Kenagy (1987)

contrast, chipmunks fed the UFA diet allowed T_b to fall to a minimum of 0.6 °C, with a corresponding minimum T_a of −1.0 °C, controls were intermediate. Similar differences were observed for TMR with the lowest values occurring in chipmunks fed the UFA diet, which was almost half that of those on SFA diets, and controls were intermediate.

Thermoregulatory differences of torpid chipmunks were reflected in the thermal response of TBD (Fig. 9.2). All animals on all diets hibernated at T_a 10 °C and TBD increased when T_a was lowered to 5 °C, as expected (Chap. 5). At T_as of 10 and 5 °C individuals fed UFA expressed somewhat longer TBDs than individuals on SFA and control diets (Fig. 9.2). However, when T_a was further reduced to 0.5 °C, permitting continued thermoconformation for UFA and control animals because they were hibernating above their minimum T_b and T_a (~T_a −1 and 0 °C respectively, Fig. 9.2), their TBD continued to increase, again as expected (Twente and Twente 1965; French 1985, Chap. 5). In contrast, chipmunks fed the SFA diet, which were forced to physiologically thermoregulate at T_a 0.5 °C because their minimum T_a was ~1 °C, requiring an increase in TMR for maintenance of T_b at ~2 °C, TBD decreased substantially (Fig. 9.2). Therefore, torpid chipmunks on the SFA diet had to increase energy expenditure for thermoregulation as well as for more frequent expensive arousals.

At a T_a of 0.5 °C, which is commonly experienced by hibernators in the wild (Wang 1978; Young 1990; Arnold 1993; Webb et al. 1996; Boyer and Barnes 1999), the difference in TBD between chipmunks on the UFA (thermoconforming) and SFA (thermoregulating) diets was greater than five-fold. The lower TMR and less frequent arousals in chipmunks fed UFAs has substantial implications for energy use and survival during hibernation because animals on a SFA diet hibernating at T_a 0.5 °C only have stored fat supplies that would last for only about 1 month, whereas in animals on UFA and control diet stores would last for >6 months, as required in the wild. The extra fat reserves after hibernation in spring especially for UFA animals will likely increase reproductive success (Williams et al. 2017).

Diet-induced changes in torpor patterns in chipmunks were accompanied by significant changes in the composition of depot fat and mitochondrial membranes. The PUFA content of depot fat total lipids and heart mitochondrial phospholipids was highest in animals on the UFA diet, intermediate in animals on the control diet and lowest in animals fed the SFA diet (Geiser 1990). The SFA/UFA ratio showed the opposite response with high values for depot fat for animals on SFA diet and low values in animals on a UFA diet. The SFA/UFA ratio from heart mitochondrial phospholipids was similar between animals on UFA diet and chow, but significantly higher in animals on the SFA diet. Likely important for function at low T_b, the diet-induced differences in fatty acid composition for liver and heart mitochondrial phospholipids of heterothermic chipmunks were around 20%. This diet-induced change in cellular phospholipids is much higher than the difference often observed in homeotherms, which is typically around 1-8% (Geiser 1990; Hulbert and Abbott 2012).

The results on chipmunks on SFA, UFA and control diets were confirmed using isocaloric diets. These contained a 5% addition of dietary fatty acids with the same number of carbons (C18) but containing 0 (stearic acid), 1 (oleic acid), or 2 (linoleic acid) double bonds (Geiser et al. 1994). As for the SFA-UFA comparison, chipmunks fed the unsaturated diets (C18:1 and C18:2) showed lower minimum T_bs with several individuals regulating T_b during torpor <0 °C (Fig. 9.3). Chipmunks on C18:1 and C18:2 diets also expressed longer TBDs than chipmunks on the saturated diet (C18:0) especially at low T_as. Importantly, there were significant correlations between variables of torpor of individual chipmunks and the fatty acid saturation (SFA/UFA ratio) of triglycerides from their depot fats (Fig. 9.3), as well as phospholipid PUFA concentration from heart mitochondria (Fig. 9.4). These correlations are consistent with a functional link between lipid composition and thermal physiology of hibernating chipmunks.

Captive golden-mantled ground squirrels (*Callospermophilus lateralis*) used torpor more often when fed a PUFA diet. They exhibited about two-fold longer TBDs and were less likely to die during hibernation when maintained on a diet rich in linoleic acid (C18:2) than when maintained on a diet low in linoleic acid (Frank 1991, 1992; Frank and Storey 1996). Similarly, prairie dogs (*Cynomys leucurus* and *C. ludovicianus*) entered torpor earlier, had lower T_bs and about doubled TBD when

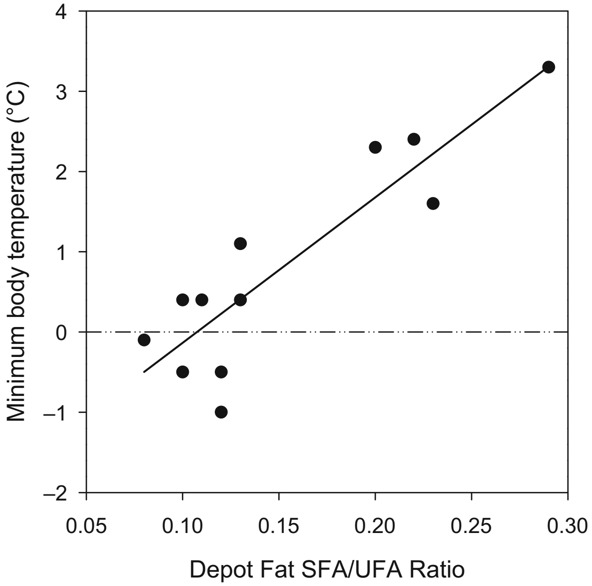

Fig. 9.3 Minimum regulated core T_b as a function of the depot fat total lipid SFA/UFA ratio of torpid chipmunks (*Tamias amoenus*, $r^2 = 0.79$). Note that four of the twelve individuals with low SFA/UFA ratios defended $T_b < 0$ °C. Data from Geiser et al. (1994)

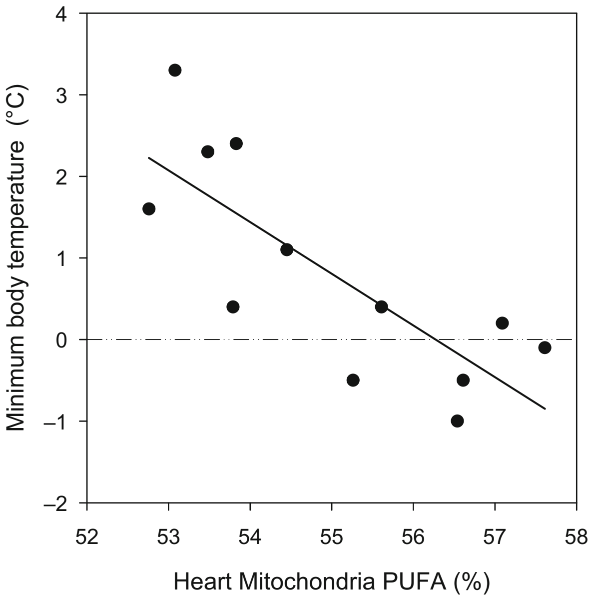

Fig. 9.4 Minimum regulated core T_b as a function of heart mitochondrial phospholipid PUFA of torpid chipmunks (*Tamias amoenus*, $r^2 = 0.62$). Note that four of the twelve individuals with high PUFA defended $T_b < 0$ °C. Data from Geiser et al. (1994)

maintained on a diet rich in C18:2 (Harlow and Frank 2001; Fig. 9.5). For Cascade golden-mantled ground squirrels (*C. saturatus*), patterns of torpor were also significantly affected after feeding of SFA and UFA diets of similar composition as for *T. amoenus*. Significant diet-induced changes were observed for the minimum regulated T_b and the minimum TMR of torpid individuals, with lower values

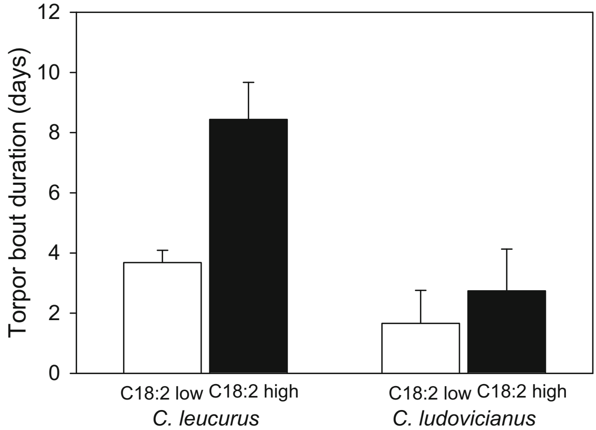

Fig. 9.5 Torpor bout duration (means with SE) of prairie dogs (*Cynomys leucurus* and *C. ludovicianus*) fed a diet low in C18:2 diet (9.7%) white bars, versus a diet high in C18:2 (62.4%) black bars. Data from Harlow and Frank (2001)

recorded in animals fed the UFA diet. For TBD, the main differences were again observed when torpid *C. saturatus* on SFA diet were forced to thermoregulate at low T_a, whereas animals on a UFA and control diet were still able to thermoconform because of their lower minimum T_b (Geiser and Kenagy 1993).

Yellow-bellied marmots (*Marmota flaviventris*), another sciurid rodent, displayed shorter TBDs when fed a diet low in essential fatty acids and rewarmed about twice as often as marmots on a control diet (Florant et al. 1993). Moreover, marmots retained C18:2 in depot fat during hibernation suggesting it is selectively spared from use (Florant et al. 1993). Similarly, *M. flaviventris* showed lower TMRs and longer TBDs on a diet rich in C18:2 (Thorp et al. 1994).

In contrast, when the diet of *C. lateralis* was enriched with linolenic acid C18:3 n-3, an omega 3 fatty acid, the opposite was observed with fewer individuals hibernating (Frank and Storey 1995). It was later suggested that the reduced torpor use may be due to autoxidation of fatty acids (Hill and Florant 1999). However, effects on the activity of cardiac sarcoplasmic activity Ca^{2+} ATPase (SERCA) provide an alternative explanation (Ruf and Arnold 2008; Giroud et al. 2018). In garden dormice (*Eliomys quercinus*) fed a diet rich in n-3 fatty acid including docosahexaenoic acid (C22:6 n-3) the onset of hibernation was delayed in comparison to a diet rich in linoleic acid (C18:2 n-6) (Giroud et al. 2018). Hibernation onset for *E. quercinus* was positively correlated with C22:6 n-3 levels and negatively correlated with C18:2 n-6 levels (earlier entry when C18:2 high) in depot fat prior to hibernation (Giroud et al. 2018). The activity of SERCA in dormice was positively correlated with C18:2 n-6 and negatively correlated with C22:6 n-3 (Giroud et al. 2018). In hamsters (*M. auratus*) subjected to a similar treatment, those with increased SERCA activity reached lower T_b during torpor (Giroud et al. 2013).

The effect of dietary fatty acids on torpor patterns of hibernators does not appear to be restricted to rodents. One of the smallest possums, the marsupial feathertail glider (*Acrobates pygmaeus*, ~12 g), which displays deep and prolonged torpor at low T_a (Chap. 3), doubles TBD, for up to about 1 week, and lowers its minimum regulated T_b when maintained on a UFA (46% C18:2; mean T_b 2.4 °C, mean TBD 5 days) diet, compared to a SFA diet (16% C18:2; mean T_b 3.9 °C, mean TBD 2.1 days) (Geiser et al. 1992a). Given that marsupial and placental mammals diverged ~140 Mya (Chap. 10), it is likely that dietary fats also affect the nature of torpor in other mammalian orders.

Cholesterol is another important component of cell membranes (McMurchie 1988; Gurr et al. 2002). Cholesterol reduces the flexibility of fatty acids chains above the phase transition from a fluid to a more solid state that occurs in membranes during cooling and enhances the flexibility below the phase transition or, in other words, it creates an intermediate state of membrane fluidity (Aloia 1979; Gurr et al. 2002). As cholesterol in the diet strongly affects membrane composition (McMurchie 1988), it also may affect torpor patterns, but the effect could either be positive or negative because cholesterol is also used for the synthesis of steroid hormones, specifically testosterone, which inhibits torpor expression in rodents (Goldman et al. 1986).

In chipmunks (*T. amoenus*), a diet rich in cholesterol lowered the minimum regulated T_b defended during torpor to below 0 °C (mean T_b −0.2 °C) in comparison to a control diet (mean T_b +0.6 °C). Moreover, the minimum TMR was lower and TBD, especially in thermoregulating torpid individuals, was longer on the cholesterol diet than the control (Geiser et al. 1997). These physiological changes were accompanied by significant changes in the cholesterol content of blood plasma and liver, whereas plasma testosterone was low in both groups. It is probable that chipmunks, while largely herbivorous, also eat substantial amounts of fungi (Tevis 1953; Cork and Kenagy 1989) and therefore take up mycosterol, a molecule similar to cholesterol. Moreover, sciurids and wood mice (*Apodemus*, sp.), despite being considered to be herbivorous, if they manage to capture or find small mammals, preferentially consume the brains, which also are rich in cholesterol (Tevis 1953; Boonstra et al. 1990; Haarsma and Kaal 2016).

Whereas most of the studies cited above showed positive effects of UFA or PUFA diets enriched by C18:1 or C18:2 on the expression and patterns of torpor or survival in hibernators, the responses were not always the same. Some of these differences are likely due to differences among species, whereas others are probably due to differences in experimental protocol. Hibernating Turkish hamsters (*M. brandti*) showed little or no response to dietary fatty acid composition (Bartness et al. 1991), perhaps because the content of PUFA between experimental diets was rather small ~4% different in comparison to the 30 to 50% differences between experimental diets in other studies (Munro and Thomas 2004). Moreover, only observations rather than physiological measurements were made to quantify torpor expression (Bartness et al. 1991), similar to an earlier study on golden hamsters (*M. auratus*) (Fawcett and Lyman 1954). In normothermic *M. auratus*, a PUFA diet enhances non-shivering thermogenesis and reduces the RMR during cold exposure (Jefimov and Wojciechowski 2013). In thirteen-lined ground squirrels (*I. tridemlineatus*), although different amounts of linoleic acid in the diet did affect mitochondrial metabolism, it did not affect hibernation patterns (Gerson et al. 2008). These thirteen-lined ground squirrels were hibernating at T_a 5 °C and therefore were thermoconforming (minimum T_b ~1.5 °C, Kisser and Goodwin 2012). Under such thermal conditions diet-induced differences observed in torpor patterns in chipmunks (*T. amoenus*) and ground squirrels (*C. saturatus*) were less pronounced than when animals were exposed to low T_a and torpid individuals on SFA diets had to thermoregulate, in contrast to thermoconforming individuals on UFA diets (e.g. Fig. 9.2).

Mouse lemurs (*Microcebus murinus*), which are generally classified as daily heterotherms, are capable of expressing deep multiday torpor bouts in the wild (Schmid and Ganzhorn 2009). When mouse lemurs were fed two diets, one a control diet and the other a diet enriched in PUFA C18:2, both diet groups expressed torpor, but variables of torpor did not differ significantly (Faherty et al. 2017). These mouse lemurs were maintained at a rather high T_a of 20 °C, well above the minimum T_b of 7.8 °C reported for the species (Schmid 2000). Moreover, the 'control' diet contained 5-times the amount of cholesterol than the PUFA diet which, as pointed out by the authors, may have masked the effect of dietary fatty acids (Faherty et al. 2017). In another study of *M. murinus*, torpor depth increased with time in individuals containing higher contents of UFAs in tissues (Vuarin et al. 2014).

Field Studies

Given that UFA diets can have such profound effect on torpor expression and especially TBD in captive animals they are likely import during hibernation in nature. It would be predicted that animals should select diets of appropriate lipid composition in preparation for hibernation. The clearest observations are the consumption of oily seeds by hibernating sciurid rodents in autumn (Tevis 1953; Healy et al. 2012). The seeds were generally rich in C18:2, in addition to fungi. In free-ranging golden-mantled ground squirrels (*C. lateralis*) during pre-hibernation fattening, the stomach content had high PUFA levels, and similarly captive individuals selected diets rich in PUFA (Frank 1994). In free-ranging European marmots (*M. marmota*), the T_b-T_a differential during hibernation significantly decreased with an increased in C18:2 in depot fat, the minimum T_b measured during hibernation decreased with PUFA content of depot fat, and mass loss was reduced in marmots with PUFA content in depot fat during the hibernation season, suggesting a high PUFA diet might increase winter survival (Bruns et al. 2000). In free-ranging eastern chipmunks (*T. striatus*), a food storing hibernator, hibernation was mainly affected by the size and energy content of the cashed food (non-supplemented 'controls' vs supplemented experimental groups), but it was not tested how much of the various diets of different composition was actually consumed (Munro et al. 2005). Free-ranging bats (*Myotis lucifugus*), which express torpor in summer (Dzal and Brigham 2013) and also *M. yumanensis* selected insects that were higher in PUFA content than the average insects captured in summer, suggesting that selection of a PUFA diet may linked to their thermal biology (Schalk and Brigham 1995). However, in *M. californicus* no difference was observed (Schalk and Brigham 1995).

Most investigations on the influence of dietary lipids on torpor use have involved essential PUFAs because these cannot be synthesized by mammals. However, based on the results for ectotherms, MUFAs, specifically oleic acids (C18:1), form an important part of the preparation for winter (Hochachka and Somero 2002). MUFAs appear to be crucial for those hibernators that do not have access to ample supply of PUFA. Free-ranging short-beaked echidnas (*Tachyglossus aculeatus*) feed to a large extent on ants, which are rich in C18:1 and the content of C18:1 in these ants was almost identical to that in echidna depot fat (both ~60%; Falkenstein et al. 2001). During about 5 months of hibernation, when body mass declined by about 18%, the main fatty acid that declined in depot fat was C18:1. In contrast, the relative proportion of C18:2 increased in depot fat suggesting that MUFAs served as the main energy source during hibernation in echidnas (Falkenstein et al. 2001). Similar observations have been reported for tropical fat-tailed lemurs (*Cheirogaleus medius*), which feed predominately on the pulp of fruits, containing mainly carbohydrates (Fietz et al. 2003). The depot fat of these lemurs contained little PUFA, but large amounts of MUFA (about 60%). The proportion of these fats changed little with season and it appears that the lemurs synthesize C18:1 from ingested carbohydrates. Thus, at least in hibernators that do not experience extremely low T_bs during torpor, MUFAs seem sufficient as energy source and for physiological function. The composition of cell membranes in relation to torpor and diet has not been investigated in these species.

Effects of Dietary Lipids on the Physiology of Daily Heterotherms

Daily heterotherms have also been investigated with regard to dietary fats in relation to torpor patterns. Although the T_b during daily torpor typically does not fall by the same extent as that during hibernation, it still regularly is reduced to about 15 °C, well below that of homeotherms, and animals must maintain physiological processes under these thermal conditions.

In insectivorous marsupial dunnarts (*Sminthopsis macroura*), expressing daily torpor (Chap. 3), a diet rich in PUFA increased the proportion of individuals expressing torpor and TBD was approximately doubled. The minimum TMR of the species was not affected by the diet (Withers et al. 1996).

When compared to deer mice (*Peromyscus maniculatus*) maintained on a SFA diet (~7% C18:2), deer mice fed a UFA diet (~60% C18:2) expressed more frequent torpor (100 vs 43% of days), deeper (minimum TMR 47 vs 76% of RMR) (Fig. 9.6) and TBD was about twice as long (4.5 vs 2.3 h). Moreover, daily loss of body mass was lower in deer mice on the UFA than those on the SFA diet (2.4 g vs 3.9 g), when food and water was restricted for both. Control animals on rodent chow responded similarly to individuals on the UFA diet for most variables, but were intermediate between animals on the UFA diet and animals on the SFA diet in their use of torpor

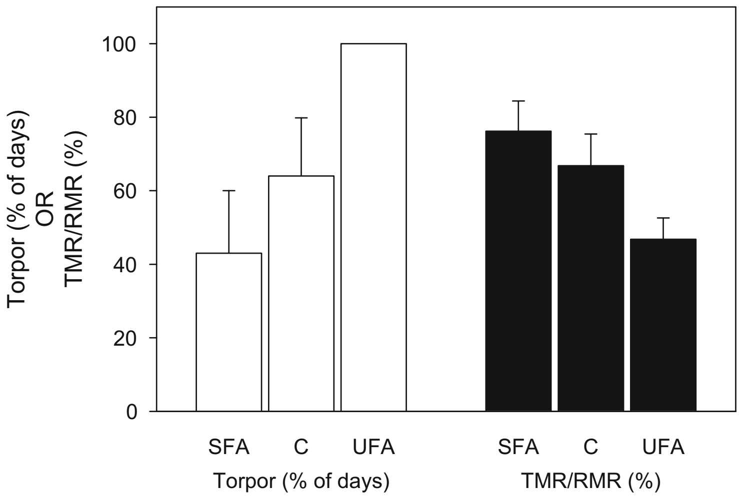

Fig. 9.6 Torpor expression (Torpor % of days with SE, white bars) during metabolic trials at T_a 17 °C and mean metabolic rate with SE during the entire torpor bout in comparison to rest (TMR/RMR %, black bars) in deer mice (*Peromyscus maniculatus*). Animals were fed three diets: a diet enriched with saturated fatty acids (SFA), a control diet (C, chow) and a diet enriched with unsaturated fatty acids (UFA). Data from Geiser (1991)

(Fig. 9.6). Changes in patterns of torpor were accompanied by significant changes in fatty acid composition of depot fat and muscle and to a lesser extent in brain and mitochondrial membranes. The content of PUFA in depot fat muscle total lipids was highest in *P. maniculatus* on the UFA diet, lowest in those on the SFA diet and intermediate in those on chow. As expected, the SFA/UFA ratio of depot fat and muscle total lipids was higher in animals on the SFA diet and lower in animals on the UFA diet (Geiser 1991). Somewhat surprisingly, the change in leg muscle total lipid 22:6 n3, was less pronounced (~2%) between experimental diets than that induced by photoperiod acclimation in the same species (~16%). This likely reflects the low level of that fatty acid in the diet (Geiser et al. 2007b). However, under both treatments, torpor expression and fatty acid composition of tissues appeared related.

The effects of dietary UFA on torpor patterns have been investigated in Djungarian hamsters (*P. sungorus*). Short-term (16 days) feeding of sunflower seeds in addition to rodent chow did not have obvious effects on the occurrence of torpor (Ruf et al. 1991). However, in animals held under short photoperiod and a T_a of 18 °C, prolonged feeding (September to January) of a UFA diet (10% safflower oil, rich in C18:2) resulted in more frequent spontaneous torpor use (torpor occurrence 42%; November to January) compared to hamsters on SFA diet (10% coconut fat, rich in SFA; torpor occurrence 23%). The minimum T_s of *P. sungorus* on the SFA diet was >21 °C, whereas in those on the UFA diet it fell as low as 19 °C (Geiser and Heldmaier 1995). Moreover, the seasonal change in body mass in hamsters on diets rich in C18:1 and C18:2 was more pronounced than in hamsters on SFA and control diets. Similar to studies on other mammals, at a high T_a of 23 °C only small differences in torpor expression were observed in *P. sungorus*. In a related study, *P. sungorus* a diet rich in n-6 fatty acids increased torpor occurrence in comparison to one low in n-6 fatty acids (Diedrich et al. 2014).

Dietary Lipids, Thermal Physiology and their Implications

The changes in thermal physiology of ectothermic lizards and heterothermic mammals and the accompanying changes in fatty acid composition of tissues and mitochondrial membranes suggest that compositional and physiological differences are linked. Compositional differences in depot fat may influence thermal physiology in a number of ways. It is likely that body fat stores can only be effectively metabolised when the fat is in a fluid state. Therefore, animals may have to regulate their T_b above the melting point of fats to ensure access to fat reserves. Large amounts of PUFAs or MUFAs, as commonly observed in depot fat of heterothermic mammals and cold acclimated ectotherms, may permit regulation of a lower T_b than when levels of SFA in fat are high. The low T_bs and especially the low TMRs of torpid animals on PUFA diets, may appear to contradict the membrane pacemaker theory (Hulbert and Else 2005), which proposes that high BMRs in small endotherms are caused by high levels of membrane PUFAs. However, it is possible, considering the effects of temperature on lipid fluidity, that MR and T_b during torpor can be reduced further when membrane PUFAs are in high proportions, whereas at high T_b, MR is increased. It is also possible that the compositional differences of fat stores affect thermal physiology directly via the fatty acid substrate. Depot fat rich in UFA may, for example, result in a different MR than depot fat rich in SFA via a greater inhibition of nuclear T3 binding, as has been observed for rat livers (Wiersinga and Platvoet-ter Schiphorst 1990). Different fatty acid substrates may also explain some of the differences in MR observed for torpid hibernators on diets of different fatty acid composition.

Compositional differences in mitochondrial and other cell membranes could affect thermal physiology via other mechanisms. It is well documented that membrane-bound enzymes are affected by the membrane fatty acid composition (McMurchie 1988; Lee 2011). Therefore it is likely that thermal energetics are influenced by the composition of the enzyme lipid environment. It also is possible that cellular metabolism is influenced by the content of PUFA and membrane permeability (Hulbert and Else 1989). High proportions of UFA in cellular membranes may improve function of neural of other membrane-associated enzymes at low temperatures and therefore allow regulation or selection of low T_bs. This view is supported by data on cardiac function in hypothermic rats, in which hearts continued to beat at lower T_bs when maintained on UFA diet (7.2 °C) than those on SFA diet (12.9 °C) (Huttunen and Johansson 1963). This effect is possibly due to the activity of cardiac sarcoplasmic activity Ca^{2+} ATPase (SERCA) which is affected by the n3/n6 ratio of fatty acids and was increased by and increased proportion of C18:2 n-6 in comparison to C22:6 n-3 (Ruf and Arnold 2008; Arnold et al. 2015). This also may explain why heterotherms on a diet enriched with C18:2 function at lower T_b than those that are not. Furthermore, it is likely that the lipid environment surrounding neural receptors affects receptor binding activity (Loh and Law 1980). Therefore, diet-induced changes in fatty acid composition of neural membranes may explain changes in thermoregulation via a number of mechanisms.

Lower T_b during torpor in mammals and lower selected T_b by lizards on UFA diet may result from similar or different diet-induced mechanisms. It appears that in mammals the influence of dietary fatty acids are only apparent after a long time (weeks) on a treatment diet. This suggests that in mammals the dietary lipids affect torpor patterns via changes in body lipid composition and therefore require some time. While this also appears to be of importance in the lizards, because body lipid composition was changed by lipid diet, dietary effects on selection of T_b were observed within a relatively short time period (days). It is therefore possible that the selection of T_b in lizards is directly affected by digestion of dietary fatty acids. Digestion and absorption of solid fats at low T_b is likely slow because digestive efficiency of lipids in lizards is slowed at low temperatures (Pafilis et al. 2007). Therefore, selection of a high T_b may be required for successful or fast uptake of SFA. In contrast, digestion of UFA may be possible at low T_b as these fatty acids remain fluid at low temperatures.

While the importance of seasonal changes in body lipid composition of ectotherms are generally recognized, the involvement of membrane composition and specifically fluidity at low T_b in hibernation is controversial (Aloia and Raison 1989; Cossins and Wilkinson 1982). However, significant correlations between cell membrane and tissue composition and the thermal physiology of individual animals make it hard to argue that there are no functional links, especially since the SFA/UFA ratio is a reliable indicator of lipid or membrane fluidity (Cossins and Lee 1985). Significant relationships exist between the minimum TMR, the minimum T_b (Figs. 9.3 and 9.4) and the TBD at low T_a of individual chipmunks (*T. amoenus*) and the SFA/UFA ratio of depot fat total lipid fatty acids and heart mitochondrial phospholipid PUFAs (Geiser et al. 1994). Significant correlations between variables of torpor and the composition of somatic fatty acids after photoperiod acclimation in hamsters (*P. sungorus*, Geiser et al. 2013) provide further support that membrane composition, structure and function are important for function at low T_a and T_b during daily torpor and hibernation.

From an ecological perspective, the effects of dietary UFA resulting in longer and deeper daily torpor and hibernation may reduce winter mortality and thus increase longevity. Moreover, deeper and longer torpor may also have implications for reproductive fitness. Lower metabolic rates during torpor, lower T_b and longer torpor bouts will reduce the use of stored fat during the hibernation season. This should help males to allocate more energy towards reproductive efforts rather than feeding at the time of emergence (Kenagy and Barnes 1988; Williams et al. 2017). Females may be able to reproduce earlier in the year and allocate surplus fat stores towards growing young. Thus, UFA diet-induced energy savings during the torpor season season may be an important determinant of reproductive success as well as long-term survival.

Chapter 10
Evolution of Endothermy and Torpor

Superficially, torpor may appear to be a partial reversion to an ectothermic state, and it is widely assumed that this is the case. However, as we have seen, torpid animals are not ectothermic because they are able to defend T_b during torpor using endogenous heat production and also have the ability to rewarm from torpor. Nevertheless, as the T_b of heterotherms fluctuates and torpid animals are able to thermoconform over a range of T_as, their TMR often approaches those of ectotherms (Chap. 5). As a consequence, the evolution of torpor and its function relative to the evolution of endothermy in general, have attracted much scientific attention (Grigg et al. 2004; Lovegrove 2019).

The traditional view was that torpor, as it occurs in 'primitive' mammals, such as the monotremes and marsupials, is a physiologically primitive trait. Heterothermic species, were viewed as 'poor thermoregulators', because the normothermic T_b of many species was somewhat below that of homeothermic placental species (Martin 1902; Kayser 1961; Schmidt-Nielsen et al. 1966; Dawson 1972; Dawson 1983). For some time, torpor was believed to be both evolutionarily and functionally primitive (Eisentraut 1956; Kayser 1961). However, improved technology resulted in more reliable comparative data, demonstrating that thermoregulatory capabilities of many heterothermic animals are similar to those of many homeotherms. Therefore, the interpretation of torpor as a primitive thermoregulatory state, was no longer supported.

Since the 1960s, torpor has been widely viewed as a physiological adaptation that is precisely regulated (Hainsworth and Wolf 1970; Heller and Hammel 1972). It was also proposed that torpor is not a hangover of reptilian physiology, but is a polyphyletic trait that has evolved from homeothermic ancestors living during in the warm Cretaceous period (Bartholomew and Hudson 1962; Twente and Twente 1964). The possibility was raised that perhaps torpor evolved convergently in mammalian and avian taxa from different lineages, when the earth underwent a cooling process after the Cretaceous-Palaeogene (K-Pg) boundary and adverse environmental conditions required a reduction of the high homeothermic MR to

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ensure survival (Bartholomew and Hudson 1962; Twente and Twente 1964; Mrosovsky 1971).

More recently, the interpretation of a polyphyletic derivation of torpor has been challenged because convergent evolution of a complex phenomenon, such as hibernation, with many astonishing similarities among diverse taxa seems unlikely (Augee and Gooden 1992). These authors proposed that the parsimonious explanation for the evolution of torpor at least in mammals is that it is a plesiomorphic (ancestral) trait, but not functionally primitive (Augee and Gooden 1992; Grigg et al. 2004). In this scenario, torpor in mammals is interpreted to have evolved only once, is monophyletic and must have been modified in species displaying daily torpor and hibernation, whereas in strictly homeothermic species the ability to use torpor was entirely lost. In this interpretation, homeothermy is an apparent abandonment of heterothermy (Lovegrove 2019). This hypothesis is further supported by the argument that the genes underlying torpor must be ancestral because it is unlikely that the many mutations required for organ and tissue function at low T_b and MR can occur simultaneously (Malan 1996). It was proposed that the genes required for hibernation and daily torpor were common to all ancestors of mammals and perhaps also birds, but were lost or inactivated in some now homeothermic orders (Carey et al. 2003). Some physiological traits, such as hypometabolism and metabolic inhibition, are also found in ectothermic vertebrates (Chaps. 1 and 3) and invertebrates, suggesting that some of the genes required for heterothermy in endotherms predate chordate evolution.

The evolutionary tree of birds and mammals shows that both were derived from likely ectothermic cotylosaur reptiles around 360 Mya (Pough and Janis 2019). One group, the synapsids (Fig. 10.1), gave rise to the pelycosaurs, then the therapsids, and finally the mammals at approximately 220 Mya (Lovegrove 2019). The mammals initially appear to have split into two lineages, one leading to the Monotremata (Prototheria) and the other to the Marsupialia (Metatheria) and Placentalia (Eutheria) approximately 190 Mya. The marsupials and placentals were then separated into two groups approximately 140 Mya (Archer 1984; O'Leary et al. 2013). The resulting mammalian lineages were likely endothermic and they diversified in the Cretaceous, but all remained small, ranging in size from mice to rabbits (McNab 2002; Lovegrove 2019; Pough and Janis 2019). These mammals were decimated during the K-Pg extinction event around 65 Mya. Only a few species survived, but these again radiated from around 60 Mya (Bininda-Edmonds et al. 2007; O'Leary et al. 2013; Lovegrove 2019).

The other reptilian group, the diapsids, gave rise to the birds, via bipedal dinosaurs at approximately 150 Mya (Feduccia 2003; Lovegrove 2019). Birds also showed an extensive radiation in the Cretaceous (Feduccia 2003). However, like the mammals, birds suffered mass-extinctions at the K-Pg boundary, and then diversified again. Extant groups of birds can be divided into the Paleognathae, the ratites and tinamous, and the Neognathae, the rest of the extant birds (Feduccia 2003).

With the exception of the avian paleognaths, torpor is known to be used by members of all major avian and mammalian evolutionary lineages (Fig. 10.1). The paleognaths contain mainly large ratites such as ostriches and emus, but also the

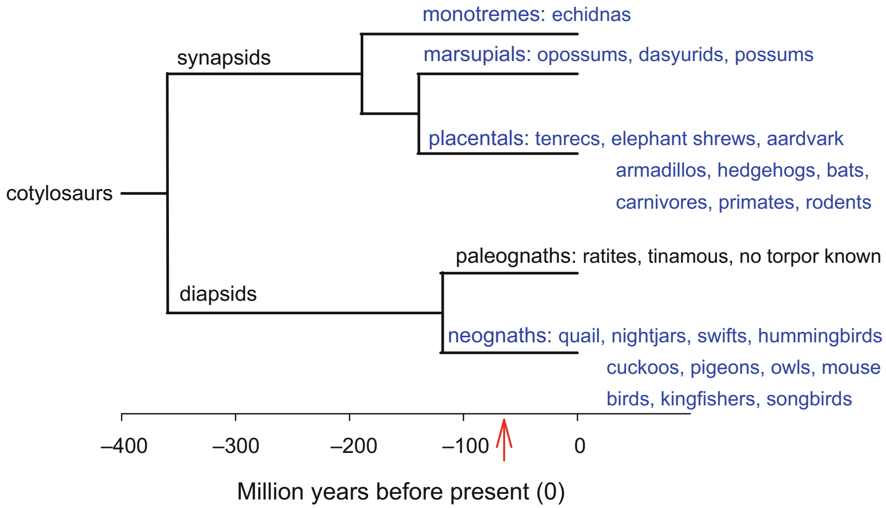

Fig. 10.1 Evolutionary tree of endothermic lineages. Major extant groups that express torpor as adults are shown in blue, black indicates extinct taxa and extant taxa that are considered to be homeothermic. The red arrow indicates the K-Pg boundary

kiwis of New Zealand, the smallest species of which weighs just over 1 kg (Winkler et al. 2020). The tinamous from South America, weigh up to 2 kg, but the smallest species, the dwarf tinamou (*Taoniscus nanus*) has a body mass of about 43 g and eats seeds and invertebrates (Cabot et al. 2020). To my knowledge, neither the kiwis nor the dwarf tinamou have been investigated with regard to torpor expression.

A possible evolutionary history of torpor may be revealed by comparing the age of avian and mammalian orders and their relationships. Current data suggest that heterothermy is more widely used in mammals than in birds. Within the mammals many of the phylogenetically old mammalian groups, such as the monotremes, marsupials and afrotherians contain heterothermic species. With regard to the evolution of heterothermy and homeothermy and the sequence of their appearance, is seems important that an ancestral group of the marsupials, the South American Microbiotheria (Fig. 10.2), is now represented by a single hibernator, *Dromiciops gliroides*. The small Microbiotheria gave rise to all Australian marsupials (Australidelphia) comprised of both heterothermic (e.g. carnivorous marsupials Dasyuridae, pygmy-possums Burramyidae, feathertail gliders Acrobatidae, small possums Petauridae) as well as homeothermic (e.g. koalas Phascolarctidae, kangaroos Macropodidae) families (Fig. 10.2). Thus it appears that both homeothermic and heterothermic Australian marsupials were derived from a lineage of small South American hibernators. The other old marsupial group are the opossums belonging to the American marsupials (Ameridelphia). Extant opossums also contain both heterothermic and homeothermic species (Riek and Geiser 2014; Fig. 10.2). Thus in marsupials, both in South America and Australia, it seems that the phylogenetically old groups were heterothermic.

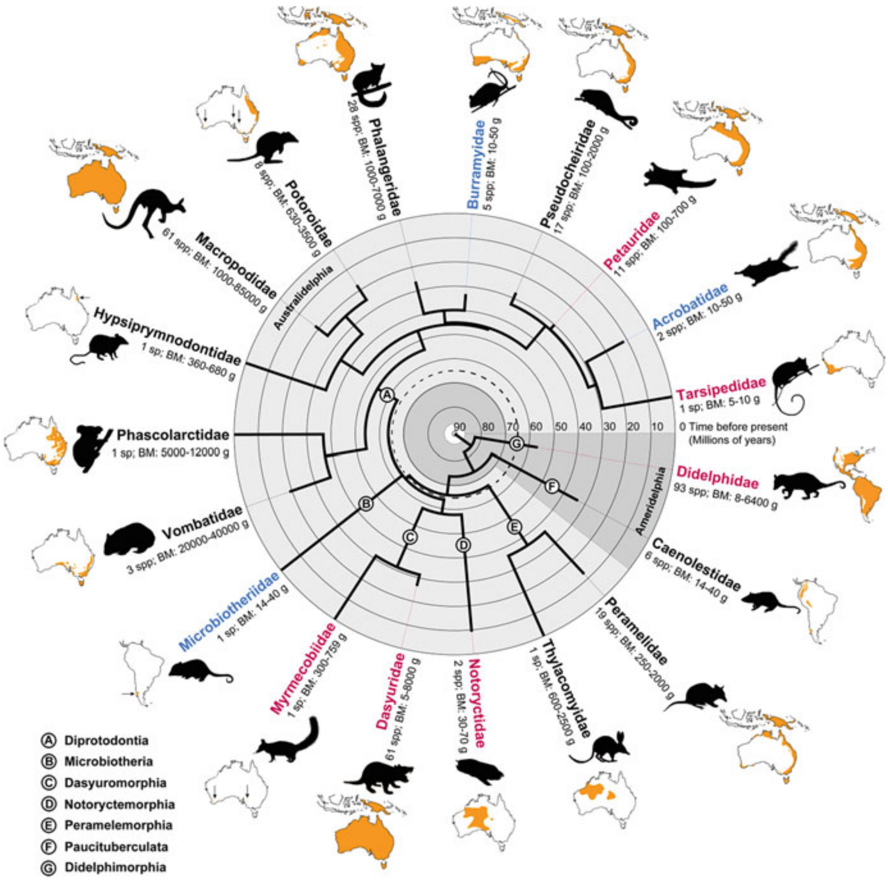

Fig. 10.2 Phylogeny and divergence times of marsupial families (derived from the mammalian Supertree, Bininda-Emonds et al. 2007) with information on approximate present day numbers of species per family and body mass (BM) range (the dashed black circle marks the Cretaceous-Paleogene extinction event 65 million years ago = K-Pg boundary). Representative animal icons and the present day distribution ranges of each marsupial family are depicted. Light gray highlighted branches belong to the superorder Australidelphia and dark grey highlighted branches to the superorder Ameridelphia while capital letters on branches refer to marsupial orders. The ends of the lines for orders indicate the times when they diversified. Black family names represent homeothermic families, blue family names contain hibernators, red family names contain daily heterotherms. From Riek and Geiser 2014, with permission

However, the mammalian groups that contain most species and also most heterotherms are rodents and bats, which consist of predominately small species. Both groups may have old roots, but diverged more recently after the K-Pg boundary (Cade 1964; O'Leary et al. 2013). In birds the orders containing most known heterothermic species are the small caprimulgiforms (nightjars), apodiforms (swifts) and trochiliforms (hummingbirds) (Chap. 3). These groups are now considered to be phylogenetically old and closely related (Prum et al. 2015). In contrast, the most diverse order, the passerines, which also contains some heterothermic species, is considered to be a phylogenetically new group (Feduccia 2003; Prum et al. 2015).

These relationships show that firstly, both phylogenetically old and phylogenetically newer orders contain heterothermic species. Secondly, both extant heterothermic and homeothermic endotherms have been derived from likely heterothermic ancestors. Thirdly, all heterotherms of all taxonomic groups, apart from the carnivores, expressing deep torpor are small.

These observations imply that pronounced heterothermy occurs in both ancestral (e.g. nightjars, monotremes and marsupials) and derived groups (e.g. bats and passerines). Therefore torpor in some species is likely ancestral and these lineages probably have used heterothermy throughout their evolutionary history. In others, in which torpor is derived, its expression was perhaps selected for, after a homeothermic phase, at times when thermal end energetic pressures demanded the evolution of a strategy for energy conservation, which is more likely to occur in small than in large species. Although this may seem a plausible interpretation considering the available data, a weakness of these arguments is the similarity of torpor patterns among taxa, and that some of the physiological variables often can be simply described by body mass (Chap. 5). Thus the question that remains unanswered is whether such similar expressions of torpor at the organismal level are due to convergent evolution. Perhaps the explanation is that physiological "toolbox" available to mammals and birds expressing torpor limit the variety of approaches and therefore result in a common solution. If the major mechanisms that are available to birds and mammals for energy conservation during torpor are de-activation of normothermic thermoregulation, reduction of T_b and metabolic inhibition and these are selected according to size, nutritional and thermal requirements the observed patterns may be explained.

The Link Between the Evolution of Endothermy and Heterothermy

We have seen that endothermy is characterised by high endogenous heat production via combustion of metabolic fuels. This is in contrast to ectothermy in most living organisms, which generally do not produce substantial amounts of internal heat for physiological thermoregulation (Tattersall et al. 2012; Withers et al. 2016). In comparison to the SMR in ectothermic terrestrial vertebrates, namely the amphibians and reptiles, the BMR of normothermic or homeothermic animals at rest in the TNZ is four to eight-fold higher in endotherms (Chap. 1). However, at low T_as these differences are much larger because during normothermia the MR of small mammals and birds must increase substantially and can be 100-fold or more of that in ectotherms (Fig. 1.2). This increase in MR is energetically costly and can be risky.

What were the reasons for this large increase in MR from ectotherms to endotherms, what are the advantages of doing it, and how could it have been functionally achieved? Although endothermy is energetically costly, it brings about many advantages. The most obvious advantage is that endotherms can be active under a wide range of thermal conditions throughout the day and night including in winter or at high latitudes or elevations. Endothermy requires a high MR and high stamina and muscle performance, all made possible by a better oxygen and fuel delivery system (Bennett and Ruben 1979; Nespolo et al. 2017; Lovegrove 2019). It therefore also permits fast assimilation and high growth rates due to better processing of food and improved metabolic machinery.

The above listed endothermic characteristics may apply to many homeothermic birds and mammals, but not necessarily heterothermic species. Many heterothermic birds and mammals use torpor during reproduction and development and show pronounced reductions of MR and T_b, which slows the rate of growth (Chap. 8). In these endothermic species, the period of pregnancy is usually extended by the time the animal spends in torpor, which can be by days or even weeks (Racey 1973; Willis et al. 2006). However, positive aspects include that torpor expression either enables reproduction on limited resources, delays parturition until thermal conditions are more benign, or permits survival during periods of adverse conditions while reproducing (Geiser and Masters 1994; Willis et al. 2006; Stawski 2010; Morrow and Nicol 2009). Torpor during development also can slow growth rate, but it ensures survival. Therefore a rapid production of young is not a generic trait of small endotherms because many heterothermic birds and mammals opt for a slow reproductive rate that permits survival which improves reproductive success.

The mechanism for how endothermy could have been achieved is a key evolutionary question. The assumption often seems to be that reptilian ectothermy evolved into mammalian and avian endothermy via a gradual increase in metabolism that, together with insulation via fur or feathers, permitted an intermediate homeothermic T_b of around 20–30 °C (Crompton et al. 1978; Ruben 1995). However, the drawbacks of this interpretation are that homeothermy with a low MR even at low T_b is difficult to achieve. This is especially the case for small endotherms like the ancestral mammals, even during the slightly warmer conditions in the Cretaceous. The reasons why this scenario is unlikely are: (1) a minor increase in MR is insufficient for maintenance of a constant high or even slightly elevated T_b when the $T_b - T_a$ differential is large as for example at night (see Figs. 1.1 and 1.2), (2) an intermediate T_b would have interfered with maximum heat production (Fig. 5.17) and hindered the contribution of metabolism to thermoregulation, (3) extant terrestrial ectotherms show large daily fluctuations in T_b and it is highly probable that partially endothermic ancestors did exactly the same. Therefore it seems more plausible that endothermy evolved via heterothermy (Geiser et al. 2002; Grigg et al. 2004; Lovegrove 2019) and developmental data support that contention.

As detailed in Chap. 8, marsupial dunnarts (*Sminthopsis* spp.), small insectivorous mammals, are born naked at a minute size and with a low endogenous heat production. At the time of pouch exit young dunnarts are partially furred, but like other small mammals and birds during development are still only partially endothermic as they cool rapidly when exposed to low T_a. However, almost competent endothermic thermoregulation develops at around 30–50% of adult body mass.

These young can maintain a high T_b under mild cold exposure for some of the night, but in the second part of the night they enter an apparent bout of torpor (Figs. 8.8 and 8.9). They enter torpor although they lack high enough endogenous heat production to rewarm from a low T_b, but instead they seem to 'know' that they can rely on behavioural thermoregulation via sun basking in the wild and in captivity bask under a radiant heat source to raise T_b back to a high level. However, soon thereafter their heat production is high enough for endothermic rewarming (Chaps. 7 and 8). This developmental pattern is not restricted to marsupials, as a poikilothermic phase followed by torpor use during development has been observed in birds and placental mammals. It seems likely that partially endothermic ancestors could have used behavioural thermoregulation because not only modern reptiles bask, but also extant small adult mammals and birds.

The transition from poikilothermy to endothermy in developing young provides a highly plausible and functionally possible model as to how endothermy could have evolved via a transient partially endothermic heterothermic phase. This would have required behavioural thermoregulation, but permitted some crepuscular and nocturnal activity and foraging to avoid diurnal dinosaur predators in the Cretaceous (McNab 2002). The ability of using a combination of behavioural and physiological thermoregulation to reach high T_b would have maximised biological functions during a somewhat prolonged activity phase after dusk. Over time an increased MR and stamina would have been selected for, and if nutrition was sufficient, would have allowed for the production and fast growth of many young.

The proposal that homeothermy in mammals must have evolved via heterothermy seems to make functional sense, because this avenue provides a plausible explanation as to how metabolism could have increased gradually over time (Grigg et al. 2004; Lovegrove 2019). Heterothermy would have permitted a low T_b and energy conservation during cold exposure and inactivity, and passive rewarming from low T_b before the activity phase would have been possible with a relatively low MR (Schmid 1996; Lovegrove et al. 1999; Geiser and Drury 2003; Grigg et al. 2004; Currie et al. 2015a, b; Wacker et al. 2017). Consequently, prolonged activity and foraging during the first part of the night to avoid predation appears to be the initial selective advantage of an increased MR in ancestral mammals. In birds, flight would have aided in predator avoidance. With time, activity would have been extended and probably some species evolved homeothermy during the warm Cretaceous. However, others continued to be heterothermic, which is consequential for the survival of mammals, and perhaps birds, of the calamity that occurred about 65 Mya and caused the extinction of many terrestrial animals.

The Role of Heterothermy at the K-Pg Boundary

The asteroid impact at the K-Pg boundary about 65 Mya, ended the era of dinosaurs and resulted in mass-extinctions of these famous reptile and many other organisms. However, it was the beginning of the diversification of extant birds and mammals.

Geological evidence suggests that the asteroid caused global wildfires that killed all terrestrial life unable to seek safe refuge which would have been mainly underground (Morgan et al. 2013). The disappearance of the dinosaurs opened new niches and permitted a rapid radiation of avian and mammalian lineages (Feduccia 2003; O'Leary et al. 2013). However, before animals could diversify they first had to survive the fires caused by the asteroid impact and second the post-impact winter that lasted for many months. As for the evolution of endothermy *per se*, heterothermy and torpor expression were likely crucial for both events (Lovegrove et al. 2014; Nowack et al. 2016a).

A homeothermic small mammal may have had the ability to survive the immediate effect of the fires if hidden underground, however, it would not have been able to survive without food for months (Fig. 7.13) during the post-impact winter (Morgan et al. 2013). The only avenue for small sedentary endotherms to achieve this without enormous food caches would have been to use torpor, which would have permitted these mammals to stay inactive and hidden for long periods without the need to forage (Turbill et al. 2011a). During multiday torpor in hibernators, the metabolic rate can be reduced to a fraction of that of normothermic animals and substantial energy savings can also be achieved at relative high T_b (Tøien et al. 2011; Ruf and Geiser 2015). Huddling in groups could have further enhanced energy savings (Arnold 1993; Gilbert et al. 2010; Nowack and Geiser 2016). Many hibernating mammals can survive without food for about 6 months, but several are known last up to a year (Fig. 7.13). This period of time was likely sufficient for survival of the post-impact winter for at least some individuals.

New evidence also suggests that torpor expression is used specifically to deal with fires or the scorched post-fire environment in extant mammals (Chapter 7). Echidnas, *T. aculeatus*, egg-laying mammals, representatives of the most ancient mammalian group with many ancestral functional and morphological traits (Nicol 2017), hide and enter torpor during forest fires (Nowack et al. 2016a). Before a fire, echidnas expressed brief and shallow bouts of torpor whereas after the fire animals entered prolonged periods of torpor although T_a was rather mild (Fig. 7.9). Important with regard to the K-Pg boundary asteroid strike, echidnas also reduce activity, but with reduced energy demands were able to remain within their now burned original home range. Similarly, antechinus (*Antechinus stuartii* and *A. flavipes*), small insectivorous marsupials, increased torpor expression and duration after forest fires (Fig. 7.10), and at the same time decreased daily activity (Stawski et al. 2015a; Matthews et al. 2017). The reduction in activity was mainly achieved by reducing diurnal activity, likely avoiding exposure to hungry predators prowling the burned area with little vegetation cover, as would have been the case during the post-impact winter caused by the asteroid strike. Initially, the observed post-fire increase in torpor use in extant mammals was assumed to be mainly related to a decrease in food availability that typically follows a fire, but the presence of charcoal-ash substrate and smoke enhances mammalian torpor use beyond that simply induced by food restriction (Stawski et al. 2015a, 2017b). This suggests that these post-fire cues signal a period of imminent food shortage and perhaps danger to the animals (Fig. 7.11). This evidence supports the view that during the post-impact winter, when mammals would have been confronted with food shortage, cold, a habitat with limited cover, ash/charcoal substrate and perhaps smoke, torpor expression would have increased to minimise energy expenditure and foraging requirements, allowing the mammals to survive.

Birds also suffered extinctions during the K-Pg calamity, but the survivors likely relied on mobility rather than prolonged torpor because only one extant avian species is known to hibernate (Brigham 1992) in contrast to the many mammalian hibernators. However, it cannot be excluded that birds also employed torpor to some extent, especially since caprimulgiforms (nightjars), apodiforms (swifts) and trochiliforms (hummingbirds) have phylogenetic roots that reach back beyond the K-Pg extinctions (Prum et al. 2015) and extant species of these groups continue to use torpor extensively (McKechnie and Lovegrove 2002).

More evidence is accumulating that during severe environmental challenges heterotherms have an on the adaptive edge over homeothermic species (Nowack et al. 2017a). As I have documented in this book, heterothermic species do not only use torpor to survive seasonal energetic and thermal challenges, but can also endure the consequences of unpredictable bottlenecks or natural disasters and consequently have a lower risk of becoming extinct. Ancestral mammals were small and nocturnal and presumably had a relaxed thermoregulation, expressing some form of torpor during the colder periods of the day and possibly were able to use multiday bouts of hibernation for highly effective energy conservation in winter (Grigg et al. 2004). Many of today's heterotherms enter torpor or hibernate in underground burrows and sheltered places that allow survival largely independent of the conditions on the Earth's surface, as would have been a requirement at the K-Pg boundary. Thus both during the initial evolution of endothermy in birds and mammals as well as the survival of mammals during the K-Pg boundary, heterothermy likely played a key role because it permitted an intermediate metabolism during the evolution of endothermy and prolonged survival without food during the post-impact winter.

Chapter 11
Concluding Remarks

The information I present in this book demonstrates that daily torpor and hibernation are used for energy and water conservation by a large diversity of birds and mammals from all climate zones. Torpor is used extensively under cold conditions, but also during heat waves or other unpredictable weather conditions. However, torpor is not only used to deal with acute energetic challenges, but also to permits endothermic organisms to live in regions with low food supply and allows reproduction and growth on limited or fluctuating food supply, such as experienced in desert environments. It appears torpor is used to deal with droughts, floods, storms, fire and predator avoidance, and may permit island colonization and help resolve inter-and intra-specific competition. Thus, torpor is an adaptation of birds and mammals that affects many aspects of both their physiology and ecology.

Although recent advances in our understanding of torpor use are substantial, many important questions with regard to its diversity, function and ecology remain unanswered.

Diversity

Much of the improved recent understanding about the diversity and functions of torpor was gained from work on free-ranging animals. Due to logistics these studies were typically undertaken using an opportunistic approach, on available, easily accessible and often single species. While this approach is entirely appropriate, one problem arising from it is that conclusions and interpretations are mainly based on data from that group or species, although they may not be representative of heterotherms in general. Thus, a targeted comparative approach investigating species specifically from groups for which no data are available or reliable data are lacking seems an obvious approach for future work.

Considering that heterotherms are more resistant to extinction that homeotherms, expanding knowledge on the diversity of torpor seems to be crucial for animal

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conservation. Diverse groups that have not been extensively studied with regard to torpor are especially suitable for new investigations. These include passerines, which seem to require some research effort, to verify the many anecdotal reports of torpor expression and identify unknown heterothermic species. The distribution of body masses in mammals (Fig. 4.2), with most heterothermic species appearing in the size group that is most diverse, suggest that there are many more heterothermic species than are currently known. Since many of the now known heterothermic species were considered to be homeotherms in the past, chances of discovering more heterotherms seem to be excellent. However, it is likely that mainly daily heterotherms, both avian and mammalian, will contribute to an expanded species list, because their use of torpor is more cryptic than that of hibernators. The microtine voles (Arvicolinae, including lemmings), which are a species-rich group are a possible new heterothermic group. Until recently they were believed to be entirely homeothermic, but seem to use at least shallow torpor (Monarca et al. 2019) and have not been systematically investigated. It was suggested earlier in the book that swifts may enter torpor while on the wing for months at high altitudes and low T_as. The concept may appear fantastical, but considering that swifts can sleep on the wing and birds can fly at T_bs < 30 °C, this no longer sounds that improbable. If it can be confirmed, it will open up an entire new area for research.

Function

With regard to thermal physiology, it is paramount that we better understand the physiological mechanisms of thermal tolerance. Why can hibernators reduce T_b to near 0 °C, continue physiological functions and survive, whereas homeotherms often die when T_b falls by only a few degrees? This is not only an important research topic in the context of torpor, but also for medical applications. The reasons for the much higher thermal and also ischemic tolerance of the tissues of hibernators and daily heterotherms than those of homeotherms are still not understood, even though revealing these mechanisms may have spin-offs for organ storage and other aspects of human medicine. Some potential applications include improved cardiac surgery or other organ transplants that have to be conducted at relatively high temperatures to avoid tissue damage, but could be better performed at low temperatures. Further, an understanding of the reasons behind the low muscle disuse atrophy in hibernators, despite extremely long inactive phases, has obvious implications for long-term hospital care, but also for space flight.

A better understanding of the mechanisms of metabolic inhibition may also have practical applications. For example prolonged droughts or natural disasters typically result in the decimation of food stock for farm animals and eventually the farm animals themselves, which are homeothermic birds and mammals. These farm animals cannot be maintained because of their high energetic demands. If the metabolism of these animals could be reduced only by a few percent, using knowledge gained on metabolic inhibition from hibernators, survival could be prolonged on low resources and at least breeding stock could be maintained. Although space travel, addressed above with regard to muscle atrophy, may not appear to fit into this category, metabolic inhibition applied to astronauts on long flights through space could reduce energy use and requirements for food and oxygen, and reduction of faeces and carbon dioxide production.

Another unresolved problem in our understanding is periodic arousals from hibernation. Despite considerable effort in this area over many years, we are still discussing theories on topics that may have led in part to the evolution of periodic arousals, but not all identified and correlated changes are necessarily the cues responsible for the timing of arousals. Clearly this is an area that deserves further scrutiny.

Ecology

Although recent advances have been made in our understanding about the multiple functions of torpor, we are only beginning to understand its role in the life of animals in the wild (Nowack et al. 2017a). The concept that ice and snow are the major reason, or the only reason, for torpor use has long been abandoned. However, for some of the new functions of torpor that have been identified (Chapters 7 and 8), much more work is required to verify their ecological importance.

For example, knowledge on torpor expression during floods is based on accidental observations on a few captive individuals. Vast areas of different continents are subject to flooding, and animals stranded on islands have the option of dying or using torpor to ensure survival of at least a few individuals. As flooding often lasts for a few days, torpor use seems a perfect approach for bridging the event. It appears the function of torpor during floods requires more attention.

Data on torpor during reproduction and especially for development of the young are also often not compelling because they are based on single observations or rely on small sample sizes. However, this vastly understudied area can easily be expanded and is perfectly suited for student projects. It seems vital to know whether animals have the options to deal with energetic problems during these periods of high energy demand and can adjust energy needs via torpor use. As data on torpor during development in species that are considered to be homeothermic as adults, is known from only two birds, it also would be important to know whether torpor expression during development is widely used by homeothermic mammals and birds.

Overall, great advances have been made over past decades in the understanding of the physiology and ecology of daily torpor and hibernation. With new equipment and a consolidated background in the biology of torpor it should be possible to further advance this field and help it gain the standing it deserves in the domains of animal physiology and ecology.

Appendix 1 Glossary

Acclimation

Exposure to the change of typically a single environmental factor in the laboratory, such as T_a or photoperiod.

Acclimatisation

Exposure to the change of multiple environnmental factors in nature or in outdoor enclosures, such as during winter vs summer.

Aestivation

A state of torpor or dormancy in summer or under warm conditions. Typically T_b and MR during aestivation is higher than at low T_a or in winter and this may be due to temperature effects, but it also may involve seasonal phenotypic plasticity.

Daily Heterotherms

Mammal and bird species that exclusively use daily torpor (Latin: 'torpere' numb or sluggish), lasting for several hours under a variety of thermal and nutritional conditions.

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6

Daily Torpor

A period of controlled reduction of MR and T_b and other physiological functions in daily heterotherms lasting for less than one day, typically 4 to 12 hours, often during the rest phase. In some species more than one torpor bout per day may be expressed and in diurnal birds daily torpor usually occurs at night.

Ectotherm

Ectothermic (Greek: 'ectos' outside, 'therme' heat) organisms have a low MR and heat production and most plants and animals are ectothermic. Ectotherms obtain body heat from the environment, usually lack insulation, and therefore T_b usually tracks that of the environment. However, if the thermal environment permits, ectotherms often use behavioural thermoregulation to maintain T_b at a preferred level.

Endotherm

Endothermic (Greek: 'endon' within, 'therme' heat) organisms have a high basal metabolic rate and the capacity for metabolic heat production by shivering and/or non-shivering thermogenesis resulting in the ability of maintaining a high and constant T_b over a wide range of T_a. Endothermy is common in birds and mammals, but also is found in some flowers, insects and reproducing reptiles.

Eutherm or Normotherm

The physiological state during which a heterothermic endotherm displays high (typically >30 °C) T_bs, often during periodic arousal from torpor or during activity. (Greek: 'eu-' good, well; normotherm, a condition of 'normal' T_b).

Heterothermic Endotherm

Heterothermic (Greek: 'heteros' other, different, 'therme' heat) organisms are capable of homeothermic or normothermic thermoregulation, but at certain times of the day or the year enter a state of torpor. Heterothermic organisms also can be considered as those that show large daily fluctuations of T_b, such as some large birds and mammals that do not enter torpor, but that exceed the range defined for homeothermy.

Hibernation or Multiday Torpor

Hibernation (Latin: 'hibernatio' passing the winter) is a sequence of multiday torpor bouts often, but not exclusively, expressed during winter, during which MR decreases significantly below BMR, and T_b is often lowered. In endotherms, hibernation is typically interrupted by periodic arousal episodes. As the duration of torpor bouts is strongly temperature-dependent, torpor bouts at high T_a may last for <24 h, but functionally this does not appear to be daily torpor. Hibernation also occurs in ectotherms.

Homeotherm

Homeothermic (Greek: 'homeo' similar or equal, 'therme' heat) organisms can maintain a more or less constant T_b at a mean $\pm$ 2 °C (Hetem et al. 2016) either *via* a balance between heat production and heat loss, or by living in a thermally stable environment. Homeothermy is common in birds and mammals.

Hypometabolism

A reduction of metabolic rate below basal metabolic rate typically associated with decreased core T_b. However, it may be also associated with regional heterothermy or metabolic inhibition at high T_as.

Hypothermia

A substantial reduction of T_b below euthermia or normothermia (Greek: hypo' below, therme, heat). Commonly viewed as an uncontrolled or pathological reduction of T_b often due to drugs or extreme cold exposure. Although 'nocturnal hypothermia' is often used to describe shallow torpor in birds, hypothermia is used in this book only for describing uncontrolled reductions of T_b, rather than the controlled reductions of T_b and MR during torpor (see Lyman et al. 1982).

Metabolic Rate

A measure of the total metabolic energy use. Can be quantified indirectly by measuring oxygen consumption or carbon dioxide production or heart rate, or directly by measuring heat production. Metabolic rate is often expressed as the total MR of an organism, or as mass-specific MR per unit body mass.

Poikilotherm

On organism with an unstable body temperature usually due to insufficient heat production (Greek 'poikilo' = variable, 'therme' = heat). The term describes the change in body temperature with time rather than the heat source used for thermoregulation as in 'ectotherm'.

Torpor

A period of controlled and reversible reduction of MR, typically core T_b, and other physiological processes. Torpor is a general term and can be daily torpor in daily heterotherms or multiday torpor in the hibernators, and also occurs in ectotherms. A torpor bout is the time during which the animal is in a state of torpor.

Appendix 2. International Hibernation Symposia

Lyman CP, Dawe AR (eds) (1960) Mammalian Hibernation, Proceedings of the first International Symposium on Natural Mammalian Hibernation, Dedham Massachusetts, May 1959. Bull Mus Comp Zool Harvard College, Vol 24.

Suomalinen P (ed) (1964) Mammalian Hibernation II, Proceedings of the second International Symposium on Natural Mammalian Hibernation, Helsinki, August 1962. Annales Academiae Scientiarum Fennicae Series A IV Biologica 71.

Fisher KC, Dawe AR, Lyman CP, Schönbaum E, South FE (eds) (1967) Mammalian Hibernation III, Proceedings of the third International Symposium on Natural Mammalian Hibernation, Toronto, September 1965. Oliver and Boyd, Edinburgh and London.

South FE, Hannon JP, Wills JS, Pengelley ET, Alpert NR (eds) (1972) Hibernation and Hypothermia, Perspectives and Challenges. Colorado, January 1971. Elsevier, Amsterdam, London, New York.

Wang LCH, Hudson JW (eds) (1978) Strategies in Cold: Natural Torpidity and Thermogenesis. Jasper, October 1977. Academic Press New York, San Francisco, London.

Musacchia XJ, Jansky L (eds) (1981) Survival in the Cold, Hibernation and other Adaptations. Prague, July 1980. Elsevier/North Holland, New York, Amsterdam, Oxford.

Heller HC, Musacchia XJ, Wang LCH (eds) (1986) Living in the Cold, Physiological and Biochemical Adaptations. California, October 1985. Elsevier, New York, Amsterdam, London.

Malan A, Canguilhem B (1989) Living in the Cold, second International Symposium. Alsace, April 1989, John Libbey Eurotext, London, Paris.

Carey C, Florant GL, Wunder BA, Horwitz B (eds) (1993) Life in the Cold, Ecological, Physiological and Molecular Mechanisms. Colorado, October 1993. Westview Press, Boulder, San Francisco, Oxford.

Geiser F, Hulbert AJ, Nicol SC (eds) (1996) Adaptation to the Cold, Tenth International Hibernation Symposium. Tasmania, July 1996. University of New England Press, Armidale.

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6

Heldmaier G, Klingenspor M (eds) (2000) Life in the Cold, Eleventh International Hibernation Symposium, Austria, August 2000. Springer Verlag, Berlin, Heidelberg, New York.

Barnes GM, Carey HV (eds) Life in the Cold: Evolution, Mechanisms, Adaptation, and Application. 12th International Hibernation Symposium. Inside Passage Cruise, British Columbia to Alaska, July/August 2004. Biological Papers, University of Alaska #27. Inst. Arctic Biology, University of Alaska, Fairbanks.

Lovegrove BG, McKechnie AE (eds) (2008) Hypometabolism in Animals, Hibernation, Torpor and Cryobiology. 13th International Hibernation Symposium. Namibia, August 2008. University of KwaZulu-Natal, Pietermaritzburg.

Ruf T, Bieber C, Arnold W, Millesi E (eds) (2012) Living in a Seasonal World, Thermoregulatory and Metabolic Adaptations. Austria, August 2012. Springer Heidelberg, New York, Dordrecht, London.

Van Breukelen F, Utz JC (eds) (2016) Living in a Seasonal World: 15th International Hibernation Symposium. Nevada, August 2016. J Comp Physiol B 187:689–897.

References

Abu Baker MA, Reeve N, Mohedano I, Conkey AAT, MacDonald DW, Yamaguchi N (2016) Caught basking in the winter sun: preliminary data on winter thermoregulation in the Ethiopian hedgehog, *Paraechinus aethiopicus*. J Arid Environ 125:52–55

Aharon-Rotman Y, Körtner G, Wacker CB, Geiser F (2020) Do small precocial birds enter torpor to conserve energy during development? J Exp Biol 223:jeb231761. https://doi.org/10.1242/jeb.231761

Aldridge HDJN, Brigham RM (1988) Load carrying and manoeuvrability in insectivorous bats: a test of the 5% "rule" of radio telemetry. J Mammal 69:379–382

Aloia RC (1979) Membrane structure and function during hibernation. Chem Zool 11:1–48

Aloia RC (1988) Lipid, fluidity and functional studies of membranes of hibernating mammals. In: Aloia RC, Curtain CC, Gordon LM (eds) Physiological regulation of membrane fluidity. Liss, New York, pp 1–39

Aloia RC, Raison JK (1989) Membrane function in mammalian hibernation. Biochim Biophys Acta 988:123–146

Ancilletto L, Santini L, Ranc N, Russo D (2016) Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation. Sci Nat 10:15

Anderson MD (2004) Aardwolf adaptations: a review. Trans Royal Soc South Africa 59:99–104

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Angilletta MJ, Sears MW (2000) The metabolic cost of reproduction in an oviparous lizard. Funct Ecol 14:39–45

Archer M (1984) The Australian marsupial radiation. In: Archer M, Clayton G (eds) Vertebrate zoogeography and evolution in Australasia. Hesperian Press, Perth, pp 633–808

Archer M, Bates H, Hand SJ, Evans T, Broome L, McAllan BM, Geiser F, Jackson S, Myers T, Gillespie A, Palmer C, Hawke T, Horn AM (2019) The Burramys project: a conservationist's reach should exceed history's grasp, or what's the fossil record for? Philos Trans B 374:20190221

Arendt T, Bullmann T (2013) Neuronal plasticity in hibernation and the proposed role of the microtubule-associated protein tau as a 'master switch' regulating synaptic gain in neural networks. Am J Physiol 305:R478–R489

Arlettaz R, Ruchet C, Aeschimann J, Brun E, Genoud M, Vogel P (2000) Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. Ecology 81 (4):1004–1014

Armitage KB (2004) Badger predation on yellow-bellied marmots. Am Midl Nat 151:378–387

F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6

Armstrong DP (1991) Nectar depletion and it implications for honeyeaters in heathland near Sydney. Aust J Ecol 16:100–109

Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). Oecologia 158:151–156

Arnold W (1993) Energetics of social hibernation. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 65–80

Arnold W, Heldmaier G, Ortmann S, Pohl H, Ruf T, Steinlechner S (1991) Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). J Therm Biol 16:223–226

Arnold W, Ruf T, Kuntz R (2006) Season adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equuus ferus przewalski*) II energy expenditure. J Exp Biol 209:4566–4573

Arnold W, Ruf T, Frey-Roos F, Bruns U (2011) Diet-independent remodelling of cellular membranes precedes seasonally changing body temperature in a hibernator. PLoS One 6(4):e18641. https://doi.org/10.1371/journal.pone.0018641

Arnold W, Giroud S, Valencak TG, Ruf T (2015) Ecophysiology of omega fatty acids: a lid for every jar. Physiology 30:232–240

Audet D, Fenton MB (1988) Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. Physiol Zool 61:197–204

Audet D, Thomas DW (1997) Facultative hypothermia as a thermoregulatory strategy in the phyllostomid bats, *Carollia perspicillata* and *Sturnia lilium*. J Comp Physiol B 167:146–152

Augee ML, Gooden BA (1992) Monotreme hibernation - some afterthoughts. In: Augee ML (ed) Platypus and echidnas. Royal Zoological Society, New South Wales, pp 174–176

Austin GT, Bradley WG (1969) Additional responses of the poor-will to low temperatures. Auk 86:717–725

Azzam NA, Hallenbeck JM, Kachar B (2000) Membrane changes during hibernation. Nature 407:317

Backus SB, Sustaita D, Odhner LU, Dollar AM (2015) Mechanical analysis of avian feet: multiarticular muscles in grasping and perching. R Soc Open Sci 2:140350

Bae HH, Larkin JE, Zucker I (2003) Juvenile Siberian hamsters display torpor and modified locomotor activity and body temperature rhythms in response to reduced food availability. Physiol Biochem Zool 76:858–867

Baerwald EF, Barclay RMR (2011) Patterns of activity and fatality of migratory bats at wind facilities in Alberta, Canada. J Wildl Res 75:1103–1114

Bahat O, Chosniak I, Houston DC (1998) Nocturnal variation in body temperature of griffon vultures. Condor 100:1680171

Barak O, Geiser F, Kronfeld-Schor N (2018) Flood-induced multiday torpor in golden spiny mice, *Acomys russatus*. Aust J Zool. https://doi.org/10.1071/ZO19061

Barclay RMR, Kalcounis MC, Crampton LH, Stefan C, Vonhof MJ, Wilkinson L, Brigham RM (1996) Can external radiotransmitters be used to asses body temperature and torpor in bats? J Mammal 77(4):1102–1106

Barclay RMR, Lausen CL, Hollis L (2001) What's hot and what's not: defining torpor in free-ranging birds and mammals. Can J Zool 79:1885–1890

Barnes BM (1989) Freeze avoidance in a mammal: body temperatures below 0°C in an Arctic hibernator. Science 244:1593–1595

Barnes BM (1996) Relationship between hibernation and reproduction in male ground squirrels. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: tenth international hibernation symposium. University of New England Press, Armidale, pp 71–80

Barnes BM, Kretzmann M, Licht P, Zucker I (1986) The influence of hibernation on testes growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. Biol Reprod 35:1289–1297

Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). J Comp Physiol B 168:233–239

Bartholomew GA (1982) Energy metabolism. In: Gordon MS (ed) Animal physiology. Macmillan, New York, pp 46–93

Bartholomew GA, Cade TJ (1957) Temperature regulation, hibernation and aestivation in the little pocket mouse, *Perognathus longimembris*. J Mammal 38:60–72

Bartholomew GA, Hudson JW (1962) Hibernation, estivation, temperature regulation, evaporative water loss, and heart rate of the pygmy possum *Cercaertus nanus*. Physiol Zool 35:94–107

Bartholomew GA, Lighton JRB (1986) Oxygen consumption during hover-feeding in free-ranging Anna hummingbirds. J Exp Biol 123:191–199

Bartholomew GA, Howell TR, Cade TJ (1957) Torpidity in the white-throated swift, anna hummingbird and poor-will. Condor 59:145–155

Bartholomew GA, Leitner P, Nelson JE (1964) Body temperature, oxygen consumption, and heart rate in three species of Australian flying foxes. Physiol Zool 37:179–198

Bartholomew GA, Vleck CM, Bucher TL (1983) Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. Physiol Zool 56:370–379

Bartness TJ, Milner R, Geloen A, Trayhurn P (1991) Effects of high fat diets on hibernation and adipose tissue in Turkish hamsters. J Comp Physiol B 161:451–459

Bartonička T, Bandouchova H, Berková H, Blažek J, Lučan R, Horáček I, Martínková N, Pikula J, Řehák Z, Jan Zukal J (2017) Deeply torpid bats can change position without elevation of body temperature. J Therm Biol 63:119–123

Bartsiokas A, Arsuaga JL (2020) Hibernation in hominins from Atapuerca, Spain half a million years ago. L'anthopologie 124:102797

Batavia M, Nguyen G, Harman K, Zucker I (2013) Hibernation patterns of Turkish hamsters: influence of sex and ambient temperature. J Comp Physiol 183:269–277

Beard LA, Grigg GC (2000) Reproduction in the short-beaked echidna, *Tachyglossus aculeatus*: field observations at an elevated site in south-East Queensland. Proc Linn Soc NSW 122:89–99

Bech C, Nicol S (1999) Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*, a low-metabolic avian species. Aust J Zool 47:143–153

Bech C, Nicol S, Andersen NA (1992) Ventilation in the echidna, *Tachyglossus aculeatus*. In: Augee ML (ed) Platypus and echidnas. The Royal Zoological Society of NSW, Sydney, pp 134–139

Bech C, Abe AS, Steffensen JF, Berger M, Bicudo JEPW (1997) Torpor in three species of Brazilian hummingbirds under semi-natural conditions. Condor 99:780–788

Bech C, Steffensen JF, Berger M, Abe AS, Bicudo JEPW (2006) Metabolic aspects of torpor in hummingbirds. Acta Zool Sinica 52(supplement):397–400

Becker NI, Tschapka M, Kalko EKV, Encarnação JA (2013) Balancing the energy budget in free-ranging male *Myotis daubentonii* bats. Physiol Biochem Zool 86:361–369

Ben-Hamo M, Munoz-Garcia A, Williams JB, Korine C, Pinshow B (2013) Waking to drink: rates of evaporative water loss determine arousal frequency in hibernating bats. J Exp Biol 216:573–577

Bennett AF, Dawson WR (1976) Metabolism. In: Gans C, Dawson WR (eds) Biology of the Reptilia. Vol. 5 physiology. Academic, New York

Bennett AF, Ruben JA (1979) Endothermy and activity in vertebrates. Science 206:649–654

Bennett NB, Jarvis JUM, Davis KC (1988) Daily and seasonal temperatures in the burrows of African rodent moles. S Afr J Zool 3:189–195

Besler NK, Broders HG (2018) Combinations of reproductive, individual, and weather effects best explain torpor patterns among female little brown bats (*Myotis lucifugus*). Ecol and Evol 9 (9):5029–5031

Bicego KC, Barros RCH, Branco LGS (2007) Physiology of temperature regulation: comparative aspects. Comp Biochem Physiol A 147:616–639

Biebach H (1978) Regulationsmechanismen zur Reduktion der Wärmeverluste bei Amseln (*Turdus merula*). Verh Dtsch Zool Ges 1978:203

Bieber C, Ruf T (2009) Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. Naturwissenschaften 96:165–171

Bieber C, Lebl K, Stalder G, Geiser F, Ruf T (2014) Body mass dependent use of hibernation: why not prolong the active season, if they can? Funct Ecol 28:167–177

Bininda-Edmonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A (2007) The delayed rise of present-day mammals. Nature 446:507–512

Bize P, Klopfenstein A, Jeanneret C, Roulin A (2007) Intra-individual variation in body temperature and pectoral muscle size in nestling alpine swifts *Apus melba* in response to an episode of inclement weather. J Ornithol 148:387–393

Blackburn TM, Gaston KJ (1994) The distribution of body sizes of the world's bird species. Oikos 70:127–130

Blackstone E, Morrison M, Roth MB (2005) H_2S induces a suspended animation-like state in mice. Science 308:518

Bladon RV, Dickman CR, Hume ID (2002) Effect of habitat fragmentation on the demography, movements and social organization of the eastern pygmy-possums (*Cercartetus nanus*) in northern New South Wales. Wildl Res 29:105–116

Blanco MB, Dausmann KH, Ranaivoarisoa JF, Yoder AD (2013) Underground hibernation in a primate. Sci Rep 3:1768

Blanco MB, Green LK, Schopler R, Williams CV, Lynch D, Browning J, Welser K, Simmons M, Klopfer PH, Ehmke EE (2021) On the modulation and maintenance of hibernation in captive dwarf lemurs. Sci Rep 11:5740

Blomberg AS, Vasko V, Meierhofer MB, Johnson JS, Eeva T, Lilley TM (2021) Winter activity of boreal bats. Mamm Biol. https://doi.org/10.1007/s42991-021-00111-8

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationship between body size and some life history parameters. Oecologia 37:257–272

Boersma PD (1986) Body temperature, torpor, and growth in chicks of fork-tailed storm-petrels (*Oceanodroma furcata*). Physiol Zool 59:10–19

Bondarenco A (2014) Torpor and thermal energetics in Australian arid zone bats. Zoology. University of New England, Armidale, PhD dissertation

Bondarenco A, Körtner G, Geiser F (2013) Some like it cold: summer torpor by freetail bats in the Australian arid zone. J Comp Physiol B 183:1113–1122

Bondarenco A, Körtner G, Geiser F (2014) Hot bats: extreme thermal tolerance in a desert heat wave. Naturwissenschaften 101:679–685

Bondarenco A, Körtner G, Geiser F (2016) How to keep cool in a hot desert: torpor in two species of free-ranging bats in summer. Temperature 3:476–483

Boonstra R, Krebs CJ, Kanter M (1990) Arctic ground squirrel predation on collard lemmings. Can J Zool 68:757–760

Boratyński JS, Iwińska K, Bogdanowicz W (2018) Body temperature variation in free-living and food-deprived yellow-necked mice sustains an adaptive framework for endothermic thermoregulation. Mamm Res 63:493–500

Bouma HR, Koese FGM, Kok JW, Talaei F, Boerema AS, Herwig A, Draghiciu O, van Buiten A, Epema AH, van Dam A, Strijkstra AM, Henning RH (2011) Low body temperature governs the decline of circulating lymphocytes during hibernation through sphingosine-1-phosphate. PNAS 108:2052–2057

Bouma HR, Verhaag EM, Otis JP, Heldmaier G, Swoap SJ, Strijkstra AM, Henning RH, Carey HV (2012) Induction of torpor: mimicking natural metabolic suppression for biomedical applications. J Cell Physiol 227:1285–1290

Boyer BB, Barnes BM (1999) Molecular and metabolic aspects of mammalian hibernation. Bioscience 49:713–724

Boyles JG, Smit B, McKechnie AE (2011) A new comparative metric for estimating heterothermy in endotherms. Physiol Biochem Zool 84:115–123

Boyles JG, Thompson AB, McKechnie AE, Malan AE, Humphries MM, Careau V (2013) A global heterothermic continuum in mammals. Glob Ecol Biogeogr 22:1029–1039

Boyles JG, Johnson JS, Blomberg A, Lilley TM (2020) Optimal hibernation theory. Mammal Rev 50:91–100

Bozinovic F, Marquet PA (1991) Energetics and torpor in the Atacama desert-dwelling rodent *Phyllotis darwini rupestris*. J Mammal 72:734–738

Bozinovic F, Ruiz G, Rosenmann M (2004) Energetics and torpor of a South American "living fossil", the microbiotheriid *Dromiciops gliroides*. J Comp Physiol B 174:293–297

Brack V (2007) Temperatures and locations used by hibernating bats, including *Myotis sodalis* (Indiana bat), in a limestone mine: implications for conservation and management. Environ Manag 40:739–746

Bradley SR, Deavers DR (1980) A re-examination of the relationship between thermal conductance and body weight in mammals. Comp Biochem Physiol 65A:465–476

Bradshaw D, Bradshaw F (2012) The physiology of the honey possum, *Tarsipes rostratus*, a small marsupial with a suite of highly specialize characters: a review. J Comp Physiol B 182:469–489

Bradshaw D, Phillips R, Tomlinson S, Holley R, Jennings S, Bradshaw F (2007) Ecology of the honey possum, *Tarsipes rostratus*, in Scott National Park, Western Australia. Aust Mammal 29:25–38

Brice PH, Grigg GC, Beard LA, Donovan JA (2002) Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. Aust J Zool 50:461–475

Brigham RM (1987) The significance of winter activity by the big brown bats (*Eptesicus fuscus*): the influence of energy reserves. Can J Zool 65:1240–1242

Brigham RM (1992) Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Physiol Zool 65:457–472

Brigham RM, Geiser F (2012) Do red squirrels (*Tamiasciurus hudsonicus*) use daily torpor in winter? Ecoscience 19:127–132

Brigham RM, Körtner G, Maddocks TA, Geiser F (2000) Seasonal use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Physiol Biochem Zool 73:613–620

Brigham RM, Woods CP, Lane JE, Fletcher QE, Geiser F (2006) Ecological correlates of torpor use among five caprimulgiform birds. Proceedings, 23rd international ornithological congress. Acta Zool Sin 52S:401–404

Brigham RM, Willis CKR, Geiser F, Mzilikazi N (2011) Baby in the bathwater: should we abandon the use of body temperature thresholds to quantify expression of torpor? J Therm Biol 36:376–379

Brigham RM, McKechnie AE, Doucette LI, Geiser F (2012) Heterothermy in caprimulgid birds: a review of inter- and intraspecific variation in free-ranging populations. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 175–187. https://doi.org/10.1007/978-3-642-28678-0_16

Broome L, Archer M, Bates H, Shi H, Geiser F, McAllan BM, Heinze D, Hand S, Evans T, Jackson S (2012) A brief review of the life history of, and threats to, *Burramys parvus* with a prehistory-based proposal for ensuring it has a future. In: Lunney D, Hutchings P (eds) Wildlife and climate change. Royal Zoological Society of NSW, Mosman, pp 114–126

Brown JH, Bartholomew GA (1969) Periodicity and energetics of torpor in the kangaroo mouse, *Microdipodops pallidus*. Ecology 70:705–709

Brown CR, Bernard RTF (1994) Thermal preference of Schreiber's long-fingered (*Miniopterus schreibersii*) and cape horseshoe (*Rhinolophus capensis*) bats. Comp Biochem Physiol A 107 (3):439–499

Bruns U, Frey-Roos F, Pudritz S, Tataruch F, Ruf T, Arnold W (2000) Essential fatty acids: their impact on free-living marmots (*Marmota marmota*). In: Heldmaier G, Klingenspor M (eds) Life in the cold: eleventh international hibernation symposium. Springer, Berlin, pp 215–222

Bucher TL, Chappell MA (1992) Ventilatory and metabolic dynamics during entry into and arousal from torpor in *Selasphorus* hummingbirds. Physiol Zool 65(5):978–993

Buck CL, Barnes BM (2000) Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. Am J Physiol Regulatory Integrative Comp Physiol 279: R255–R262

Buffenstein R (1985) The effect of starvation, food restriction, and water deprivation on thermoreguation and average daily metabolic rates in *Gerbillus pusillus*. Physiol Zool 58:320–328

Buffenstein R, Yahav S (1991) Is the naked mole-rat *Heterocephalus glaber* an endothermic yet poikilothermic mammal? J Therm Biol 16:227–232

Burton RS, Reichman OJ (1999) Does immune challenge affect torpor duration? Funct Ecol 13:232–237

Butler PJ, Woakes AJ (2001) Seasonal hypothermia in a large migrating bird: saving energy for fat deposition? J Exp Biol 204:1361–1367

Buttemer WA, Nicol SC, Sharman A (2003) Thermoenergetics of pre-moulting and moulting kookaburras (*Dacelo novaeguineae*): they're laughing. J Comp Physiol B 173:223–230

Cabot J, Christie DA, Jutglar F, Sharpe CJ (2020) Dwarf Tinamou (*Taoniscus nanus*), version 1.0. In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.dwatin1.01

Caccamise DF, Hedin RS (1985) An aerodynamic basis for selecting transmitter loads in birds. Wilson Bull 97:306–318

Cade TJ (1964) The evolution of torpidity in rodents. Ann Acad Scientiarum Fennicae A IV Biol 71:77–111

Calder WA (1996) Size, function and life history. Dover Publications, New York

Calder WA, Booser J (1973) Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. Science 180:751–753

Canale CI, Perret M, Henry PY (2012) Torpor use during gestation and lactation in a primate. Naturwissenschaften 99:159–163

Canguilhem B, Pevet MM, Koehl C, Pevet P, Bentz I (1988) Non-gonadal mediated effect of photoperiod on hibernation and body weight cycles of the European hamster. Comp Biochem Physiol A 89:575–578

Cannon B, Nedergaard J (2004) Brown adipose tissue: function and physiological significance. Physiol Rev 84:277–359

Careau V (2013) Basal metabolic rate, maximum thermogenic capacity and aerobic scope in rodents: interaction between environmental temperature and torpor use. Biol Lett 9:20121104

Carey HV, Andrews MT, Martin SL (2003) Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. Physiol Rev 83:1153–1181

Carpenter FL (1974) Torpor in an Andean hummingbird: its ecological significance. Science 183:545–547

Carpenter FL, Hixon MA (1988) A new function of torpor: fat conservation in a wild migrant hummingbird. Condor 90:373–378

Caviedes-Vidal E, Codelia EC, Roig V, Doña R (1990) Facultative torpor in the south American rodent *Calomys venustus* (Rodentia: Cricetidae). J Mammal 71:72–75

Chi QS, Wan XR, Geiser F, Wang DH (2016) Fasting-induced daily torpor in desert hamsters (*Phodopus roborovskii*). Comp Biochem Physiol A 199:71–77

Choi I-H, Cho Y, Oh YK, Jung N-P, Shin H-C (1998) Behaviour and muscle performance in heterothermic bats. Physiol Zool 17:257–266

Christian KA, Bedford GS (1995) Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. Ecology 76:124–132

Christian N, Geiser F (2007) To use or not to use torpor? Activity and body temperature as predictors. Naturwissenschaften 94:483–487

Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. Funct Ecol 16:18–26

Clawson RL, LaVal RK, LaVal ML, Caire W (1980) Clustering behavior of hibernating *Myotis sodalis* in Missouri. J Mammal 61:245–253

Cliffe RN, Scantlebury DM, Kennedy SJ, Avey-Arroyo J, Mindich D, Wilson RP (2018) The metabolic response of the *Bradypus* sloth to temperature. Peer J 6:e5600

Coburn DK, Geiser F (1998) Seasonal changes in energetics and torpor patterns in the sub-tropical blossom-bat *Syconycteris australis* (Megachiroptera). Oecologia 113:467–473

Cochet N, Georges B, Meister R, Florant GL, Barre H (1999) White adipose tissue fatty acids of alpine marmots during their yearly cycle. Lipids 34:275–281

Colak E, Yigit N (1998) Ecology and biology of *Allactaga elater*, *Allactaga euphratica* and *Allactaga williamsi* (Rodentia: Dipodidae) in Turkey. Turkish J Zool 22:105–117

Collins BC, Briffa P (1984) Nocturnal energy expenditure by honeyeaters experiencing food shortage and low environmental temperatures. Comp Biochem Physiol A 78:77–81

Congreve P (1972) Torpidity in the white-backed swallow. Emu 72:32–33

Cooper SJ, Swanson DL (1994) Seasonal acclimatization of thermoregulation in the black-capped chickadee. Condor 96:638–646

Cooper CE, Withers PC (2004) Patterns of body temperature variation and torpor in the numbat, *Myrmecobius fasciatus* (Marsupialia: Myrmecobiidae). J Therm Biol 29:277–284

Cooper CE, Withers PC (2009) Effects of measurement duration on the determination of basal metabolic rate and evaporative water loss of small marsupials: how long is long enough? Physiol Biochem Zool 82:438–446

Cooper CE, Withers PC (2010) Comparative physiology of Australian quolls (*Dasyurus*; Marsupialia). J Comp Physiol B 180:857–868

Cooper CE, McAllan BM, Geiser F (2005) Effect of torpor on the water economy of an arid-zone marsupial, the striped-faced dunnart (*Sminthopsis macroura*). J Comp Physiol B 175:323–328

Cooper CE, Körtner G, Brigham RM, Geiser F (2008) Body temperature and activity patterns of free-living laughing kookaburras: the largest kingfisher is heterothermic. Condor 110:110–115

Cooper CE, Withers PC, Cruz-Neto V (2009) Metabolic, ventilator, and hygric physiology of the gracile mouse opossum (*Gracilinanus agilis*). Physiol Biochem Zool 82:153–162

Cork SJ, Kenagy GJ (1989) Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. Ecology 70:577–586

Cory Toussaint D, McKechnie AE (2012) Interspecific variation in thermoregulation among three sympatric bats inhabiting a hot, semi-arid environment. J Comp Physiol B 182:1129–1140

Cossins AR, Bowler K (1987) Temperature biology of animals. Chapman and Hall, London

Cossins AR, Lee JAC (1985) The adaptation of membrane structure and lipid composition to cold. In: Gilles R (ed) Circulation, respiration and metabolism. Springer, Berlin, pp 543–552

Cossins AR, Wilkinson HL (1982) The role of homeoviscous adaptation in mammalian hibernation. J Therm Biol 7:107–110

Cossins AR, Friedlander MJ, Prosser CL (1977) Correlations between behavioral temperature adaptations of goldfish and the viscosity and fatty acid composition of their synaptic membranes. J Comp Physiol 120:109–121

Cowles RB (1958) Possible origin of dermal temperature regulation. Evolution 12:347–357

Cramp RL, Franklin CE (2005) Arousal and re-feeding rapidly restores digestive tract morphology following aestivation in green-striped burrowing frogs. Comp Biochem Physiol A 142:451–460

Cranford JA (1978) Hibernation in the western jumping mouse (*Zapus princeps*). J Mammal 59:496–509

Crompton AW, Taylor CR, Jagger JA (1978) Evolution of homeothermy in mammals. Nature 272:333–336

Csada RD, Brigham RM (1994) Reproduction constrains the use of daily torpor by free ranging common poorwills (*Phalaenoptilus nuttallii*). J Zool 234:209–216

Cubuk C, Bank JHH, Herwig A (2016) The chemistry of cold: mechanisms of torpor regulation in the Siberian hamster. Physiology 31:51–59

Currie SE (2015) Cardiorespiratory function and metabolism of heterothermic bats. PhD dissertation. University of New England, Armidale

Currie SE (2018) No effect of season on the electrocardiogram of long eared bats (*Nyctophilus gouldi*) during torpor. J Comp Physiol B 188:695–705

Currie SE, Körtner G, Geiser F (2014) Heart rate as a predictor of metabolic rate in heterothermic bats. J Exp Biol 217:1519–1524
Currie SE, Körtner G, Geiser F (2015a) Measuring subcutaneous temperature and differential rates of rewarming from hibernation and daily torpor in two species of bats. Comp Biochem Physiol A 190:26–31
Currie SE, Noy K, Geiser F (2015b) Passive rewarming from torpor in hibernating bats: minimizing metabolic costs and cardiac demands. Am J Physiol 308:R34–R41
Currie SE, Stawski C, Geiser F (2018) Cold-hearted bats: uncoupling of heart rate and metabolism at subzero temperatures. J Exp Biol. https://doi.org/10.1242/jeb.170894
Czenze ZJ, Willis CKR (2015) Warming up and shipping out: arousal and emergence timing in hibernating little brown bats (*Myotis lucifugus*). J Comp Physiol B 185:575–586
Czenze ZJ, Jonasson KA, Willis CKR (2017a) Thrifty females, frisky males: winter energetics of hibernating bats from a cold climate. Physiol Biochem Zool 90:502–511
Czenze ZJ, Brigham RM, Hickey AJR, Parsons S (2017b) Cold and alone? Roost choice and season affect torpor patterns in lesser long-eared bats. Oecologia 183:1–8
Czenze ZJ, Brigham RM, Hickey AJR, Parsons S (2017c) Winter climate affects torpor patterns and roost choice in New Zealand lesser short-tailed bats. J Zool 303:236–343
Czenze ZJ, Brigham RM, Hickey AJR, Parsons S (2017d) Stressful summers? Torpor expression differs between high- and low-latitude populations of bats. J Mammal 98:1249–1255
Daan S (1973) Periodicity of heterothermy in the garden dormouse, *Eliomys quercinus* (L). Netherlands J Zool 23:237–265
Daan S, Barnes BM, Strijkstra AM (1991) Warming up for sleep? – ground squirrels sleep during arousal from hibernation. Neurosci Lett 128:265–268
Daniel S, Korine C, Pinshow B (2010) The use of torpor in reproductive female Hemprich's long-eared bats (*Otonycteris hemprichii*). Physiol Biochem Zool 83:142–148
Dark J (2005) Annual lipid cycles in hibernators: integration of physiology and behaviour. Annu Rev Nutr 25:469–497
Dark J, Miller DR, Zucker I (1994) Reduced glucose availabilty induces torpor in the Siberian hamster. Am J Physiol 267:R496–R501
Dausmann KH (2005) Measuring body temperature in the field – evaluation of external vs internal transmitters in a small mammal. J Thermal Biol 30:195–202
Dausmann KH (2014) Flexible patterns in energy savings: heterothermy in primates. J Zool 292:101–111
Dausmann KH, Warnecke L (2016) Primate torpor: ghost of the climatic past. Physiology 31:398–408
Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826
Dausmann KH, Wein J, Turner JM, Glos J (2013) Absence of heterothermy in the European red squirrel (*Sciurus vulgaris*). Mamm Biol 78:332–335
Dawson TJ (1972) Primitive mammals and patterns in the evolution of thermoregulation. In: Bligh J, Moore RE (eds) Essays on temperature regulation. North Holland Publishing Company, Amsterdam
Dawson TJ (1983) Monotremes and marsupials: the other mammals. Edward Arnold, London
Dawson TJ, Fanning D (1981) Thermal and energetic problems of semiaquatic mammals: a study of the Australian water rat, including comparisons with the platypus. Physiol Zool 54:285–296
Dawson WR, Evans FC (1960) Relation of growth and development to temperature regulation in nestling vesper sparrows. Condor 62:329–340
Dawson WR, Fisher CD (1969) Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). Condor 71:49–53
Dawson WR, Hudson JW (1970) Birds. In: Whittow GC (ed) Comparative physiology of thermoregulation, vol 1. Academic, New York, pp 223–310
Deboer T, Tobler I (1994) Sleep EEG after daily torpor in the Djungarian hamster: similarity to the effects of sleep deprivation. Neurosci Lett 166:35–38

Dechmann DKN, Wikelski M, Ellis-Soto D, Safi K, O'Mara MT (2017) Determinants of spring migration departure decision in bats. Biol Lett 13:20170395
Degen AA, Kam M (1995) Scaling of field metabolic rate to basal metabolic rate in homeotherms. Ecoscience 2:48–54
Dehnel A (1949) Studies on the genus *Sorex* L. Ann Univ Marie Curie-Sklodowska, Sect C 4:17–102
Dickman CR (2003) Distributional ecology of dasyurid marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishers, Melbourne, pp 318–331
Diedrich V, Kumstel S, Steinlechner S (2012) Spontaneous daily torpor and fasting-induced torpor in Djungarian hamsters are characterized by distinct patterns of metabolic rate. J Comp Physiol B 185:355–366
Diedrich V, Steinlechner S, Scherbarth F (2014) Effects of unsaturated fatty acids on torpor frequency and diet selection in Djungarian hamsters (*Phodopus sungorus*). J Exp Biol 217:4313–4319
Dietz M, Hörig A (2011) Thermoregulation of tree-dwelling temperate bats – a behavioural adaptation to force live history strategy. Folia Zool 60:5–16
Dietz M, Kalko EKV (2006) Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). J Comp Physiol B 176:223–231
Diffenbaugh NS, Field CB (2013) Changes in ecologically critical terrestrial climate conditions. Science 341:486–492
Diffendorfer J, Fleming GM, Tremor S, Spencer W, Beyers JL (2012) The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral. Int J Wildland Fire 21:436–448
Doty AC, Stawski C, Law BS, Geiser F (2016a) Post-wildfire physiological ecology of an Australian microbat. J Comp Physiol B 186:937–946
Doty AC, Stawski C, Currie SE, Geiser F (2016b) Black or white? Physiological implications of roost colour and choice in a microbat. J Therm Biol 60:162–170
Doty AC, Currie SE, Stawski C, Geiser F (2018) Can bats sense smoke during deep torpor? Physiol Behav 185:31–38
Doucette LI, Geiser F (2008) Seasonal variation in thermal energetics of the Australian owlet-nightjar (*Aegotheles cristatus*). Comp Biochem Physiol A 151:615–620
Doucette LI, Brigham RM, Pavey CR, Geiser F (2011) Roost type influences torpor use by Australian owlet-nightjars. Naturwissenschaften 98:845–854
Doucette LI, Brigham RM, Pavey CR, Geiser F (2012) Prey availability affects daily torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Oecologia 169:361–372
Dove HS (1923) Semi-hibernation of swallows. Emu 23:149
Downs CT, Brown M (2002) Nocturnal heterothermy and torpor in the malachite sunbird (*Nectarinia famosa*). Auk 119:251–260
Drew KL, Buck CL, Barnes BM, Christian SL, Rasley BT, Harris MB (2007) Central nervous system regulation of mammalian hibernation: implications for metabolic suppression and ischemia tolerance. J Neurochem 102:1713–1726
Dunbar MB, Brigham RM (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. J Comp Physiol B 180:885–893
Dunbar MB, Tomasi TE (2006) Arousal patterns, metabolic rate, and an energy budget of eastern red bats (*Lasiurus borealis*) in winter. J Mammal 87:1096–1102
Dwyer PD (1963) Reproduction and distribution in *Miniopterus* (Chiroptera). Aust J Sci 25:435–436
Dwyer PD (1964) Seasonal changes in activity and weight of *Miniopterus schreibersii blepotis* (Chiroptera) in northeastern New South Wales. Aust J Zool 12:52–69
Dzal YA, Brigham RM (2013) The tradeoff between torpor use and reproduction in little brown bats (*Myotis lucifugus*). J Comp Physiol B 183:279–288
Edwards SV, Boles WE (2002) Out of Gondwana: the origin of passerine birds. TREE 17:347–349

Eichhorn G, Groscolas R, Le Glaunec G, Parisel C, Arnold L, Medina P, Handrich Y (2011) Heterothermy in growing king penguins. Nat Comm 2:435. https://doi.org/10.1038/ncomms1436

Eisenberg JF (1981) The mammalian radiations. University of Chicago Press, Chicago

Eisentraut M (1937) Die Wirkung niedriger Temperatur auf die Embryonalentwicklung bei Fledermäusen. Biol Zbl 57:59–74

Eisentraut M (1956) Der Winterschlaf mit seinen ökologischen und physiologischen Begleiterscheinungen. G Fischer, Jena

El Ouezzani S, Janati IA, Magoul R, Pevet P, Saboureau M (2011) Overwinter body temperature patterns in captive jerboas (*Jaculus orientalis*): influence of sex and group. J Comp Physiol B 181:299–309

Ellison GTH (1995) Thermoregulatory responses of cold-acclimated fat mice (*Steatomys pratensis*). J Mammal 76:240–247

Else PL (2021) Mammals to membranes: a reductionist story. Comp Biochem Physiol B 253:110552

Else PL, Hulbert AJ (2003) Membranes as metabolic pacemakers. Clin Exp Pharm Physiol 30:559–564

Eppley TM, Watzek J, Dausmann KH, Ganzhorn JU, Donati G (2017) Huddling is more important than rest site selection for thermoregulation in southern bamboo lemurs. Anim Behav 127:153–161

Estok O, Zsebok S, Siemers BM (2009) Great tits search for, capture, kill and eat hibernating bats. Biol Lett 6:59–62

Eto T, Sakamoto SH, Okubo Y, Koshimoto C, Kashimura A, Morita T (2014) Huddling facilitates expression of daily torpor in the large Japanese field mouse *Apodemus speciosus*. Physiol Behav 133:22–29

Eto T, Hayashi R, Okubo Y, Kashimura A, Koshimoto C, Sakamoto SH, Morita T (2015) Magnitude of food overabundance affects expression of daily torpor. Physiol Behav 139:519–523

Evans AL, Singh NJ, Friebe A, Arnemo JM, Laske TG, Fröbert O, Swenson JE, Blanc C (2016) Drivers of hibernation in the brown bear. Front Zool 13:7

Faherty SL, Campbell CR, Hilbig SA, Yoder AD (2017) The effect of body mass and diet composition of torpor patterns in a Malagasy primate (*Microcebus murinus*). J Comp Physiol B 187:677–688

Falkenstein F, Körtner G, Watson K, Geiser F (2001) Dietary fats and body lipid composition in relation to hibernation in free-ranging echidnas. J Comp Physiol B 171:189–194

Falvo CA, Koons DN, Aubry LM (2019) Seasonal climate effects on the survival of a hibernating mammal. Ecol Evol 9:3756–3769

Farmer CG (2003) Reproduction: the adaptive significance of endothermy. Am Nat 162:826–840

Fawcett DW, Lyman CP (1954) The effect of low environmental temperature on the composition of depot fat in relation to hibernation. J Physiol 126:235–247

Feduccia A (2003) 'Big bang' for tertiary birds? TREE 18:172–176

Feng NY, Junkins MS, Merriman DK, Bagriantsev SN, Gracheva EO (2019) Osmolyte depletion and thirst suppression allow hibernators to survive months without water. Curr Biol 29:1–6

Fernandez TN, Young RJ (2008) Fluctuations in the tympanic membrane temperatures of non-restrained captive giant anteaters and southern tamanduas. J Zool 274:94–98

Fielden LJ, Waggoner JP, Perrin MR, Hickman GC (1990) Thermoregulation in the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). J Arid Env 18:221–237

Fietz J, Tataruch F, Dausmann KH, Ganzhorn JU (2003) White adipose tissue composition in the free-ranging fat-tailed dwarf lemur (*Cheirogaleus medius*; primates), a tropical hibernator. J Comp Physiol B 173:1–10

Fietz J, Pflug M, Schlund W, Tataruch F (2005) Influences of the feeing ecology on body mass and possible implications for reproduction in the edible dormouse (*Glis glis*). J Comp Physiol B 175:45–55

Fietz J, Schmid J, Speakman JR (2012) Seasonal variation in energy turnover and body temperature in free-living edible dormice, *Glis glis*. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 85–97

Finke C, Misovic A, Prinzinger R (1995) Growth, the development of endothermy, and torpidity in blue-naped mousebirds *Urocolius macrourus*. Ostrich 66:1–9

Fisher KC, Mrosovsky N (1970) Effectiveness of KCl and NaCl injections in arousing 13-lined ground squirrels from hibernation. Can J Zool 48:595–596

Flannigan M, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob Change Biol 15:549–560

Fleming MR (1980) Thermoregulation and torpor in the sugar glider, *Petaurus breviceps* (Marsupialia: Petauridae). Aust J Zool 28:521–534

Fleming MR, Frey H (1984) Aspects of the natural history of feathertail gliders (*Acrobates pygmaeus*) in Victoria. In: Smith AP, Hume ID (eds) Possums and gliders. Australian Mammal Society, Sydney, pp 403–408

Fletcher QE, Fisher RJ, Willis CKR, Brigham RM (2004) Free-ranging common nighthawks use torpor. J Thermal Biol 29:9–14

Flint WE (1966) Die Zwerghamster der Paläarktischen Fauna. Ziemsen Verlag, Wittenberg

Florant GL (1998) Lipid metabolism in hibernators: the importance of essential fatty acids. Amer Zool 38:331–340

Florant GL, Healy JE (2012) The regulation of food intake in mammalian hibernators. J Comp Physiol B 182:451–467

Florant GL, Heller HC (1977) CNS regulation of body temperature in euthermic and hibernating marmots (*Marmota flaviventris*). Am J Physiol 232:R203–R208

Florant GL, Nuttle LC, Mulinex DE, Rintoul DA (1990) Plasma and white adipose tissue lipid composition in marmots. Am J Physiol 258:R1123–R1131

Florant GL, Hester L, Ameenuddin S, Rintoul DA (1993) The effect of a low essential fatty acid diet on hibernation in marmots. Am J Physiol 264:R747–R753

Foley WJ, Engelhardt WV, Charles-Dominique P (1995) The passage of digesta, particle size, and in vitro fermentation in the three-toed sloth *Bradypus tridactylus* (Edentata: Bradypodidae). J Zool 236:681–696

Ford HA (1989) Ecology of birds. Surrey Beatty and Sons, Chipping Norton

Fowler PA (1988) Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season. J Reprod Fertil 82:285–292

Fowler PA, Racey PA (1988) Overwintering strategies of the badger, *Meles meles*, at 57 °N. J Zool 214:635–651

Frank CL (1991) Adaptations for hibernation in the depot fats of a ground squirrel (*Spermophilus beldingi*). Can J Zool 69:2707–2711

Frank CL (1992) The influence of dietary fatty acids on hibernation by golden-mantled ground squirrels (*Spermophilus lateralis*). Physiol Zool 65:906–920

Frank CL (1994) Polyunsaturate content and diet selection by ground squirrels (*Spermophilus lateralis*). Ecology 75:458–463

Frank CL, Storey KB (1995) The optimal depot fat composition for hibernation by golden-mantled ground squirrels (*Spermophilus lateralis*). J Comp Physiol B 164:536–542

Frank CL, Storey KB (1996) The effect of total unsaturated content on hibernation. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold. Tenth international hibernation symposium. University of New England Press, Armidale, pp 211–216

Frank CL, Dierenfeld ES, Storey KB (1998) The relationship between lipid peroxidation, hibernation, and food selection in mammals. Amer Zool 38:341–350

Frank CL, Davis AD, Herzog C (2019) The evolution of a bat population with white-nose syndrome (WNS) reveals a shift from epizootic to enzootic phase. Front Zool 16:40

Freeman DA, Lewis DA, Kaufman AS, Blum RM, Dark J (2004) Reduced leptin concentrations are permissive for display of torpor in Siberian hamsters. Am J Physiol 287:R97–R103

Freeman MT, Czenze ZJ, Schoeman K, McKechnie AE (2020) Extreme hyperthermia tolerance in the world's most abundant wild bird. Sci Rep 10:13098
French AR (1977) Periodicity of recurrent hypothermia during hibernation in the pocket mouse, *Perognathus longimembris*. J Comp Physiol A 115:87–100
French AR (1982) Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. J Comp Physiol B 148:83–91
French AR (1985) Allometries of the duration of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. J Comp Physiol B 156:13–19
French AR (1986) Patterns of thermoregulation during hibernation. In: Heller HC, Musacchia XJ, Wang LCH (eds) Living in the cold. Elsevier, New York, pp 393–402
French AR (1993) Hibernation in birds: comparisons with mammals. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 43–53
French AR (2008) Patterns of heterothermy in rodents. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: torpor, hibernation and cryobiology. 13th international hibernation symposium. University of KwaZulu-Natal, Pietermaritzburg, pp 337–352
Frerichs KU, Smith CB, Brenner M, DeGarcia DJ, Krause GS, Marrone L, Dever TE, Hallenbeck JM (1998) Suppression of protein synthesis in brain during hibernation involves inhibition of protein initiation and prolongation. PNAS 95:14511–14516
Frey H (1979) La température corporelle de *Suncus etrucus* (Sorcidae, Insectivora) au cours de l'activité, du respos normothermique et du la torpeur. Revue Suisse Zool 86:653–662
Frey H (1980) Le métabolisme énergétique de *Suncus etrucus* (Sorcidae, Insectivora) en torpeur. Revue Suisse Zool 87:739–748
Frey H, Fleming MR (1984) Torpor and thermoregulatory behaviour in free-ranging feathertail gliders (*Acrobates pygmaeus*) (Marsupialia: Burramyidae) in Victoria. In: Smith AP, Hume ID (eds) Possums and gliders. Surrey Beatty. Australian Mammal Society, Sydney, pp 393–401
Frick WF, Cheng TL, Langwig KE, Hoyt JR, Janicki AF, Parise KL, Foster JT, Kilpatrick AM (2017) Pathogen dynamics during invasion and establishment of white-nose syndrome explain mechanisms of host persistence. Ecology 98:624–631
Gaertner RA, Hart JS, Roy OZ (1973) Seasonal spontaneous torpor in the white-footed mouse *Peromyscus leucopus*. Comp Biochem Physiol A 45:169–181
Gagnon MF, Lafleur C, Landry-Cuerrier M, Humphries MM, Kimmins S (2020) Torpor expression is associated with differential spermatogenesis in hibernating eastern chipmunks. Am J Physiol 319:R455–R465
Galster WA, Morrison P (1972) Cyclic changes in carbohydrate concentrations during hibernation in the arctic ground squirrel. Am J Physiol 218:1228–1232
Garland T, Geiser F, Baudinette RV (1988) Comparative locomotor performance of marsupial and placental mammals. J Zool 215:505–522
Gattermann R, Fritzsche P, Neumann K, Al-Hussein I, Kayer A, Abiad M, Yakti R (2001) Notes on the current distribution and ecology of wild golden hamsters (*Mesocricetus auratus*). J Zool 254:359–365
Geiser F (1986) Thermoregulation and torpor in the kultarr, *Antechinomys laniger* (Marsupialia: Dasyuridae). J Comp Physiol B 156:751–757
Geiser F (1988a) Daily torpor and thermoregulation in *Antechinus* (Marsupialia): influence of body mass, season, development, reproduction, and sex. Oecologia 77:395–399
Geiser F (1988b) Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? J Comp Physiol B 158:25–37
Geiser F (1990) Influence of polyunsaturated and saturated dietary lipids on adipose tissue, brain, and mitochondrial membrane fatty acid composition of a mammalian hibernator. Biochim Biophys Acta 1046:159–166

Geiser F (1991) The effect of unsaturated and saturated dietary lipids on the pattern of daily torpor and the fatty acid composition of tissues and membranes of the deer mouse *Peromyscus maniculatus*. J Comp Physiol B 161:590–597

Geiser F (2003) Thermal biology and energetics of carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishers, Melbourne, pp 234–249

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Geiser F (2007) Yearlong hibernation in a marsupial mammal. Naturwissenschaften 94:941–944

Geiser F (2008) Ontogeny and phylogeny of endothermy and torpor in mammals and birds. Comp Biochem Physiol A 150:176–180

Geiser F (2011) Hibernation: endotherms. In: Encyclopedia of life sciences. John Wiley & Sons, Ltd, Chichester. Advanced article. https://doi.org/10.1002/9780470015902.a0003215.pub2

Geiser F (2019) Frequent nocturnal torpor in a free-ranging Australian honeyeater, the noisy miner. Sci Nat 106:28

Geiser F (2020) Seasonal expression of avian and mammalian daily torpor and hibernation: not a simple summer-winter affair. Front Physiol 11:436

Geiser F, Baudinette RV (1985) The influence of temperature and photophase on torpor on *Sminthopsis macroura* (Dasyuridae: Marsupialia). J Comp Physiol B 156:129–134

Geiser F, Baudinette RV (1987) Seasonality of torpor and thermoregulation in three dasyurid marsupials. J Comp Physiol B 157:335–344

Geiser F, Baudinette RV (1988) Daily torpor and thermoregulation in the small dasyurid marsupials *Planigale gilesi* and *Ningaui yvonneae*. Aust J Zool 36:473–481

Geiser F, Baudinette RV (1990) The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. J Exp Biol 151:349–359

Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). J Comp Physiol B 170:153–162

Geiser F, Brigham RM (2012) The other functions of torpor. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 109–121. https://doi.org/10.1007/978-3-642-28678-0_10

Geiser F, Broome LS (1991) Hibernation in the mountain pygmy possum *Burramys parvus* (Marsupialia). J Zool 223:593–602

Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. J Comp Physiol B 163:133–137

Geiser F, Coburn DK (1999) Field metabolic rates and water uptake in the blossom-bat *Syconycteris australis* (Megachiroptera). J Comp Physiol B 169:133–138

Geiser F, Drury RL (2003) Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. J Comp Physiol B 173:55–60

Geiser F, Ferguson C (2001) Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feathertail gliders. J Comp Physiol B 171:569–576

Geiser F, Heldmaier G (1995) The impact of dietary fats, photoperiod, temperature and season on morphological variables, torpor patterns, and brown adipose tissue fatty acid composition of hamsters, *Phodopus sungorus*. J Comp Physiol B 165:406–415

Geiser F, Kenagy GJ (1987) Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. Am J Physiol 252:R897–R901

Geiser F, Kenagy GJ (1988) Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. Physiol Zool 61:442–449

Geiser F, Kenagy GJ (1990) Development of thermoregulation and torpor in the golden-mantled ground squirrel *Spermophilus saturatus*. J Mammal 71:286–290

Geiser F, Kenagy GJ (1993) Dietary fats and torpor patterns in hibernating ground squirrels. Can J Zool 71:1182–1186

Geiser F, Körtner G (2004) Thermal biology, energetics, and torpor in the possums and gliders. In: Goldingay RL, Jackson SM (eds) The biology of Australian possums and gliders. Beatty, Surrey, pp 186–198

Geiser F, Körtner G (2010) Hibernation and daily torpor in Australian mammals. Aust Zool 35:204–215

Geiser F, Learmonth RP (1994) Dietary fats, selected body temperature and tissue fatty acid composition of agamid lizards (*Amphibolurus nuchalis*). J Comp Physiol B 164:55–61

Geiser F, Martin GM (2013) Torpor in the Patagonian opossum (*Lestodelphys halli*): implications for the evolution of daily torpor and hibernation. Naturwissenschaften 100:975–981

Geiser F, Masters P (1994) Torpor in relation to reproduction in the Mulgara, *Dasycercus cristicauda*, (Dasyuridae: Marsupialia). J Therm Biol 19(1):33–40

Geiser F, Mzilikazi N (2011) Does torpor in elephant shrews differ from that of other heterothermic mammals? J Mammal 92:452–459

Geiser F, Pavey CR (2007) Basking and torpor in a rock-dwelling desert marsupial: survival strategies in a resource-poor environment. J Comp Physiol B 177:885–892

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68(6):935–966

Geiser F, Seymour RS (1989) Torpor in a pregnant echidna, *Tachyglossus aculeatus* (Monotremata: Tachyglossidae). Aust Mammal 12:81–82

Geiser F, Stapp P (2000) Energetics and thermal biology of gliding mammals. In: Goldingay R, Scheibe JS (eds) Biology of gliding mammals. Filander Verlag, Erlangen, pp 149–166

Geiser F, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions and the evolution of endothermy. Int Comp Biol 51:337–348

Geiser F, Turbill C (2009) Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften 96:1235–1240

Geiser F, Augee ML, Raison JK (1984) Thermal response of liver mitochondrial membranes of the heterothermic bat (*Miniopterus schreibersii*) in summer and winter. J Thermal Biol 9:183–188

Geiser F, Matwiejczyk L, Baudinette RV (1986) From ectothermy to heterothermy: the energetics of the kowari, *Dasyuroides byrnei* (Marsupialia: Dasyuridae). Physiol Zool 59:220–229

Geiser F, Baudinette RV, McMurchie EJ (1989) The effect of temperature on isolated perfused hearts of heterothermic marsupials. Comp Biochem Physiol A 93:331–335

Geiser F, Hiebert S, Kenagy GJ (1990) Torpor bout duration during the hibernation season of two sciurid rodents: interrelations with temperature and metabolism. Physiol Zool 63:489–503

Geiser F, Stahl B, Learmonth RP (1992a) The effect of dietary fatty acids on the pattern of torpor in a marsupial. Physiol Zool 65:1236–1345

Geiser F, Firth BT, Seymour RS (1992b) Polyunsaturated dietary lipids lower the selected body temperature of a lizard. J Comp Physiol B 162:1–4

Geiser F, McAllan BM, Kenagy GJ (1994) The degree of dietary fatty acid unsaturation affects torpor patterns and lipid composition of a hibernator. J Comp Physiol B 164:299–305

Geiser F, Song X, Körtner G (1996) The effect of He–O_2 exposure on metabolic rate, thermoregulation and thermal conductance during normothermia and daily torpor. J Comp Physiol B 166:190–196

Geiser F, Kenagy GJ, Wingfield JC (1997) Dietary cholesterol enhances torpor in a rodent hibernator. J Comp Physiol B 167:416–422

Geiser F, Körtner G, Schmidt I (1998) Leptin increases energy expenditure of a marsupial by inhibition of daily torpor. Am J Physiol 275:R1627–R1632

Geiser F, Holloway J, Körtner G, Maddocks TA, Turbill C, Brigham RM (2000) Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier G, Klingenspor M (eds) Life in the cold. 11th international hibernation symposium. Springer, Berlin, pp 95–102

Geiser F, Körtner G, Law BS (2001) Daily torpor in a pregnant common blossom-bat (*Syconycteris australis*: Megachiroptera). Aust Mammal 23:53–56

Geiser F, Goodship N, Pavey CR (2002) Was basking important in the evolution of mammalian endothermy? Naturwissenschaften 89:412–414
Geiser F, Drury RL, McAllan BM, Wang D-H (2003) Effects of temperature acclimation on maximum heat production, thermal tolerance, and torpor in a marsupial. J Comp Physiol B 173:437–442
Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanisms, adaptation, and application. 12th international hibernation symposium. Biological papers. University of Alaska #27. Inst. Arctic Biology, University of Alaska, Fairbanks, pp 51–62
Geiser F, Law BS, Körtner G (2005a) Daily torpor in relation to photoperiod in a subtropical blossom-bat, *Syconycteris australis* (Megachiroptera). J Thermal Biol 30:574–579
Geiser F, McAllan BM, Brigham RM (2005b) Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia). Mammal Biol 70:117–121
Geiser F, Körtner G, Maddocks TA, Brigham RM (2006a) Torpor in Australian birds. Proceedings, 23rd international ornithological congress. Acta Zool Sin 52S:405–408
Geiser F, Westman W, McAllan BM, Brigham RM (2006b) Development of thermoregulation and torpor in a marsupial: energetic and evolutionary implications. J Comp Physiol B 176:107–116
Geiser F, Holloway JC, Körtner G (2007a) Thermal biology, torpor and behaviour in sugar gliders: a laboratory-field comparison. J Comp Physiol B 177:495–501
Geiser F, McAllan BM, Kenagy GJ, Hiebert SM (2007b) Photoperiod affects daily torpor and tissue fatty acid composition in deer mice. Naturwissenschaften 94:319–325
Geiser F, Christian N, Cooper CE, Körtner G, McAllan BM, Pavey CR, Turner J, Warnecke L, Willis CKR, Brigham RM (2008) Torpor in marsupials: recent advances. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: torpor, hibernation and cryobiology. 13th international hibernation symposium. University of KwaZulu-Natal, Pietermaritzburg, pp 297–306
Geiser F, Stawski C, Bondarenco A, Pavey CR (2011) Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals? Naturwissenschaften 98:447–452
Geiser F, Klingenspor M, McAllan BM (2013) A functional nexus between photoperiod acclimation, torpor expression and somatic fatty acid composition in a heterothermic mammal. PLoS One 8(5):e63803
Geiser F, Currie SE, O'Shea KA, Hiebert SM (2014) Torpor and hypothermia: reversed hysteresis of metabolic rate and body temperature. Am J Physiol 307:R1324–R1329
Geiser F, Gasch K, Bieber C, Stalder GL, Gerritsmann H, Ruf T (2016) Basking hamsters reduce resting metabolism, body temperature and energy costs during rewarming from torpor. J Exp Biol 219:2166–2172
Geiser F, Stawski C, Wacker CB, Nowack J (2017) Phoenix from the ashes: fire, torpor and the evolution of endothermy. Front Physiol 8:842
Geiser F, Stawski C, Doty AC, Cooper CE, Nowack J (2018) A burning question: what are the risks and benefits of mammalian torpor during and after fires? Conserv Physiol 6(1):Coy057. https://doi.org/10.1093/conphys/coy057
Geiser F, Wen J, Sukhchuluun G, Chi QS, Wang DH (2019a) Precocious torpor in an altricial mammal and the functional implications of heterothermy during development. Front Physiol 10:469
Geiser F, Bondarenco A, Currie SE, Doty AC, Körtner G, Law BS, Pavey CR, Riek A, Stawski C, Turbill C, Willis CKR, Brigham RM (2019b) Hibernation and daily torpor in Australian and New Zealand bats: does the climate zone matter? Aust J Zool 67:316–330
Geiser F, Willis CKR, Brigham RM (2020) No evidence for hibernation in rockwrens. J Exp Biol 223. https://doi.org/10.1242/jeb.230524
Genoud M (1993) Temperature regulation in subtropical tree bats. Comp Biochem Physiol A 104:321–331

Gerson AR, Brown JCL, Thomas R, Bernards MA, Staples JF (2008) Effects of dietary polyunsaturated fatty acids on mitochondrial metabolism in mammalian hibernation. J Exp Biol 211:2689–2699

Gessaman JA, Folk CE (1969) Body temperature and thermal conductance of the snowy owl. Physiologist 12:234

Gilbert C, McCafferty D, LeMaho Y, Martrette JM, Giroud S, Blanc S, Ancel A (2010) One for all and all for one: the energetics benefits of huddling in endotherms. Biol Rev 85:545–569

Giroud S, Turbill C, Ruf T (2012) Torpor use and body mass gain during pre-hibernation in late-born juvenile garden dormice exposed to food shortage. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 481–491

Giroud S, Frare C, Strijkstra A, Boerema A, Arnold W, Ruf T (2013) Membrane phospholipid fatty acid composition regulates cardiac SERCA activity in a hibernator, the Syrian hamster (*Mesocricetus auratus*). PLoS One 8(5):e63111

Giroud S, Zahn S, Criscuolo F, Chery I, Blanc S, Turbill C, Ruf T (2014) Late-born intermittently fasted juvenile garden dormice use torpor to grow and fatten prior to hibernation: consequences for ageing processes. P Roy Soc B 281(1797). https://doi.org/10.1098/rspb.2014.1131

Giroud S, Stalder G, Gerritsmann H, Kűbber-Heiss A, Kwak J, Arnold W, Ruf T (2018) Dietary lipids affect the onset of hibernation in the garden dormouse (*Eliomys quercinus*): implications for cardiac function. Front Physiol 9:1235

Giroud S, Habold C, Nespolo RF, Mejias C, Terrien J, Logan SM, Henning RH, Storey KB (2021) The torpid state: recent advances in metabolic adaptations and protective mechanisms. Front Physiol 11:623665

Glanville EJ, Seebacher F (2010) Advantage to lower body temperatures for a small mammal (*Rattus fuscipes*) experiencing chronic cold. J Mammal 91:1197–1204

Glazier DS (2005) Beyond the '3/4-power law': variation in the intra-and interspecific scaling of metabolic rate in animals. Biol Rev 80:611–662

Gluck EF, Stephens N, Swoap SJ (2006) Peripheral ghrelin deepens torpor bouts in mice through the arcuate nucleus neuropeptide Y signalling pathway. Am J Physiol 291:R1303–R1309

Goldman SS (1975) Cold resistance of the brain during hibernation. III evidence for a lipid adaptation. Am J Physiol 228:834–839

Goldman BD (1989) Effect of photoperiod on the hibernation cycle of the Turkish hamster. In: Malan A, Canguilhem B (eds) Living in the cold. Colloque INSERM/John Libbey Eurotext, London, pp 5–15

Goldman BD, Darrow JM, Duncan MJ, Yogev L (1986) Photoperiod, reproductive hormones, and winter torpor in three hamster species. In: Heller HC, Musacchia XJ, Wang LCH (eds) Living in the cold. Elsevier, New York, pp 341–350

Goldzieher A (2004) Fattening and torpor in the eastern pygmy-possum, *Cercartetus nanus*. Honours thesis. University of New England, Armidale

Golzales B, Brook F, Martin GM (2020) Variability and variation in *Rhynchlestes raphanurus* Osgood (Paucituberculata, Caenolestidae). Rev Chilena History Nat 91:1

Gordon CJ, Ferguson JH (1980) Role of dietary lipids in cold survival and changes in body composition in white mice. J Thermal Biol 5:29–35

Grant TR, Temple-Smith PD (1987) Observations on torpor the small marsupial *Dromiciops australis* (Marsupialia: Microbiotheriidae) from southern Chile. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and The Royal Zoological Society of NSW, Sydney, pp 273–277

Greig EI, Wood EM, Bonter DN (2017) Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. Proc R Soc B 284:20170256

Griffiths M, Kristo F, Green B, Fogerty AC, Newgrain K (1988) Observations on free-living, lactating echidnas, *Tachyglossus aculeatus* (Monotremata: Tachyglossidae), and sucklings. Aust Mammal 11:135–144

Grigg GC, Beard LA, Augee ML (1989) Hibernation in a monotreme, the echidna (*Tachyglossus aculeatus*). Comp Biochem Physiol A 92:609–612

Grigg GC, Augee ML, Beard LA (1992a) Thermal relations of free-living echidnas during activity and in hibernation in a cold climate. In: Augee ML (ed) Platypus and echidnas. Royal Zool Soc NSW, Sydney, pp 160–173

Grigg GC, Beard LA, Grant TR, Augee ML (1992b) Body temperature and diurnal activity patterns in the platypus, *Ornithorhynchus anatinus*. Aust J Zool 40:135–142

Grigg GC, Beard LA, Barnes JA, Perry LI, Fry GJ, Hawkins M (2003) Body temperature in captive long-beaked echidnas (*Zaglossus bartoni*). Comp Biochem Physiol A 136:911–916

Grigg GC, Beard LA, Augee ML (2004) The evolution of endothermy and its diversity in mammals and birds. Physiol Biochem Zool 88:982–997

Grimpo K, Legler K, Heldmaier G, Exner C (2013) That's hot: golden spiny mice display torpor even at high ambient temperatures. J Comp Physiol B 183:567–581

Grinevitch L, Holroyd SL, Barclay RMR (1995) Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. J Zool 235:301–309

Gummer DL (2005) Geographic variation in torpor patterns: the northernmost prairie dogs and kangaroo rats. PhD dissertation. University of Saskatchewan, Saskatoon

Guppy M, Withers PC (1999) Metabolic depression in animals: physiological perspectives and biochemical generalizations. Biol Rev 74:1–40

Gurr MI, Harwood JL, Frayn KN (2002) Lipid biochemistry: an introduction. Wiley, London

Gustafson T, Lindkvist B, Gotborn L, Gyllin R (1977) Altitudes and flight times for swifts *Apus apus* L. Ornis Scand 8:87–95

Gutman R, Choshniak I, Kronfeld-Schor N (2006) Defending body mass during food restriction in *Acomys russatus*: a desert rodent that does not store food. Am J Physiol 290:R881–R891

Haarsma A-J, Kaal R (2016) Predation of wood mice (*Apodemus sylvaticus*) on hibernating bats. Pop Ecol 58:567–576

Haase CG, Fuller NW, Hranac CR, Hayman DTS, Olson SH, Plowright RK, McGuire LP (2019) Bats are not squirrels: revisiting the cost of cooling in hibernating mammals. J Thermal Biol 81:185–193

Hainsworth FR, Wolf LL (1970) Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. Science 168:368–369

Hall M (1832) On hybernation. Trans Royal Soc London B 122:335–360

Hallam SL, Mzilikazi N (2011) Heterothermy in the southern African hedgehog, *Atelerix frontalis*. J Comp Physiol B 181:437–445

Hallsall AL, Boyles JG, Whitaker JO (2012) Body temperature patterns of big brown bats during winter in a building hibernaculum. J Mammal 93:497–503

Hamilton IM, Barclay RMR (1994) Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). Can J Zool 72:744–749

Hammel HT (1968) Regulation of internal body temperature. Annu Rev Physiol 30:641–710

Hammel HT, Dawson TJ, Adams RM, Anderson HT (1968) Total calorimetric measurements on *Citellus lateralis* in hibernation. Physiol Zool 41:341–357

Hand SJ, Beck RMD, Archer M, Simmons AB, Gunnell GF, Scofield RP, Tennyson AJD, DePietri VL, Salisbury SW, Worthy TH (2017) A new large-bodied omnivorous bat (Nocilionidea: Mystacinidae) reveals lost morphological and ecological diversity since the Miocene in New Zealand. Sci Rep 8:235

Hanna E, Cardillo M (2014) Clarifying the relationship between torpor and anthropogenic extinction risk in mammals. J Zool 293:211–217. https://doi.org/10.1111/jzo.12136

Harlow HJ (1981) Torpor and other physiological adaptations of the badger (*Taxidea taxus*) to cold environment. Physiol Zool 54:267–275

Harlow HJ, Frank CL (2001) The role of dietary fatty acids in the evolution of spontaneous and facultative hibernation patterns in prairie dogs. J Comp Physiol B 171:77–84

Harlow HJ, Menkens GE (1986) A comparison of hibernation in the black-tailed prairie dog, white-tailed prairie dog, and Wyoming ground squirrel. Can J Zool 64:793–796

Harmata W (1987) The frequency of winter sleep interruptions in two species of bats hibernating in limestone tunnels. Acta Theriol 32(21):331–332

Hayssen V, Kunz TH (1996) Allometry of litter mass in bats: maternal size, wing morphology, and phylogeny. J Mammal 77:476–490

Hayssen V, Lacy RC (1985) Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comp Biochem Physiol 81A:741–754

Hazel JR (1995) Thermal adaptation in biological membranes: is homeoviscous adaptation the explanation? Annu Rev Physiol 57:19–42

Healy JE, Ostrom CE, Wilkerson GK, Florant GL (2010) Plasma ghrelin concentrations change with physiological state in a sciurid hibernator (*Spermophilus lateralis*). Gen Comp Endocrinol 166:372–378

Healy JE, Burdett KA, Buck CL, Florant GL (2012) Sex differences in torpor patterns during natural hibernation in golden-mantled ground squirrels (*Callospermophilus lateralis*). J Mammal 93:751–758

Heath JE (1962) Temperature fluctuations in the Turkey vulture. Condor 64:234–235

Heath ME, Hammel HT (1986) Body temperature and rate of O_2 consumption in Chinese pangolins. Am J Physiol Regulatory Integr Comp Physiol 19:R377–R382

Heatwole HF, Taylor J (1987) Ecology of reptiles. Surrey Beatty & Sons, Chipping Norton

Hedenström A, Norevik G, Boano G, Andersson A, Bäckman J, Akesson S (2019) Flight activity in pallid swifts *Apus pallidus* during the non-breeding period. J Avian Biol 2019:e01972

Heinrich B, Bartholomew GA (1971) An analysis of pre-flight warm-up in the sphinx moth, *Manduca sexta*. J Exp Biol 55:223–239

Heldmaier G, Klingenspor M (2003) Role of photoperiod during seasonal acclimation in winter-active small mammals. In: Heldmaier G, Werner D (eds) Environmental signal processing and adaptation. Springer, Berlin, pp 251–279

Heldmaier G, Ruf T (1992) Body temperature and metabolic rate during natural hypothermia in endotherms. J Comp Physiol B 162:696–706

Heldmaier G, Steinlechner S (1981a) Seasonal control of energy requirements for thermoregulation in the Djungarian hamster (*Phodopus sungorus*) living in natural photoperiod. J Comp Physiol B 142:429–437

Heldmaier G, Steinlechner S (1981b) Seasonal pattern and energetics of short daily torpor in the Djungarian hamster, *Phodopus sungorus*. Oecologia 48:265–270

Heldmaier G, Böckler H, Buchberger A, Lynch GR, Puchalski W, Steinlechner S, Wiesinger H (1985) Seasonal acclimation and thermogenesis. In: Gilles R (ed) Circulation, respiration, and metabolism. Springer, Berlin, pp 490–501

Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and daily torpor in mammals. Resp Physiol and Neurobiol 141:317–329

Heller HC, Hammel HT (1972) CNS control of body temperature during hibernation. Comp Biochem Physiol A 41:349–359

Heller HC, Colliver GW, Beard J (1977) Thermoregulation during entrance into hibernation. Pflügers Arch 369:55–59

Heller HC, Elsner R, Rao N (1987) Voluntary hypometabolism in an Indian yogi. J Therm Biol 12:171–173

Hellgren EC (1998) Physiology of hibernation in bears. Ursos 10:467–477

Hennekam JJ, Benson RB, Herridge VL, Jeffery N, Torres-Roig E, Alcover JA, Cox PG (2020) Morphological divergence in giant fossil dormice. Proc R Soc B 287:20202085

Henshaw RE, Folk GE (1966) Relation of thermoregulation to seasonally changing microclimate in two species of bats (*Myotis lucifugus* and *M. sodalis*). Physiol Zool 39:223–236

Herter K (1956) Der Winterschlaf. In: Helmcke JG, Lengerken HV (eds) Handbuch der Zoologie Vol 8. Walter de Gruyter, Berlin, pp 1–60

Hetem RS, Maloney SK, Fuller A, Mitchell D (2016) Heterothermy in large mammals: inevitable or implemented? Biol Rev 91:187–205

Hiebert SM (1990) Energy costs and temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). Physiol Zool 63:1082–1097

Hiebert SM (1992) Time-dependent thresholds for torpor initiation in the rufous hummingbird (*Selasphorus rufus*). J Comp Physiol B 162:249–255

Hiebert SM (1993a) Seasonal changes in body mass and use of torpor in a migratory hummingbird. Auk 110:787–797

Hiebert SM (1993b) Seasonality of daily torpor in a migratory hummingbird. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 25–32

Hiebert SM, Fulkerson E, Lindermayer K, McClure S (2000) The effect of temperature on preference for dietary unsaturated fatty acids in the Djungarian hamster (*Phodopus sungorus*). Can J Zool 78:1361–1368

Hiebert SM, Hauser K, Ebrahim AJ (2003a) Long day Djungarian hamsters exhibit temperature-dependent dietary fat choice. Physiol Biochem Zool 76:850–857

Hiebert SM, Leininger E, Huneryager R, Le L, Pannorfi R, Pike E (2003b) Dietary lipids, temperature, and melatonin: behavioural preference adjustments consistent with the membrane homeoviscosity model. Int Comp Biol 43:1018

Hill RW (1975) Daily torpor in *Peromyscus leucopus* on an adequate diet. Comp Biochem Physiol A 51:413–423

Hill RW (1976) The ontogeny of homeothermy in neonatal *Peromyscus leucopus*. Physiol Zool 49:292–306

Hill RW, Wyse GA, Anderson M (2016) Animal physiology. Sinauer Associates, Massachusetts

Hill VL, Florant GL (1999) Patterns of fatty acid composition in free-ranging yellow-bellied marmots (*Marmota flaviventris*) and their diet. Can J Zool 77:1494–1503

Hinds DS, Baudinette RV, MacMillen RE, Halpern EA (1993) Maximum metabolism and the aerobic factorial scope of endotherms. J Exp Biol 182:41–56

Hissa R (1997) Physiology of the European brown bear (*Ursus arctos arctos*). Ann Zool Fenn 34:267–287

Hochachka PW, Somero GN (2002) Biochemical adaptation: mechanism and process in physiological evolution. Oxford University press, New York

Hock RJ (1951) The metabolic rates and body temperatures of hibernating bats. Biol Bull 101:289–299

Hoelzl F, Bieber C, Cornils JS, Gerritsmann H, Stalder GL, Walzer C, Ruf T (2015) How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-reproductive years. J Comp Physiol B 185:931–939

Hoffmann RA, Prinzinger R (1984) Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). J Ornithol 125:225–237

Hohtola E (2004) Shivering thermogenesis in birds and mammals. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanisms, adaptation, and application. Twelfth international hibernation symposium. Biological papers of the University of Alaska #27. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 241–252

Hohtola E, Hissa R, Pyörnilä A, Rintamäki H, Saarela S (1991) Nocturnal hypothermia in fasting Japanese quail: the effect of ambient temperature. Physiol Behav 49:563–567

Hohtola E, Pyörnilä A, Rintamäki H (1994) Fasting endurance and cold resistance without hypothermia in a small predatory bird: the metabolic strategy of Tengmalm's owl, *Aegolius funereus*. J Comp Physiol B 164:430–437

Hollis L, Barclay RMR (2008) Developmental changes in body temperature and use of torpor by the big brown bat (*Eptesicus fuscus*). In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: torpor, hibernation and cryobiology, 13th International Hibernation Symposium. University of KwaZulu-Natal, Pietermaritzburg, pp 361–372

Holloway JC, Geiser F (1995) Influence of torpor on daily energy expenditure of the dasyurid marsupial *Sminthopsis crassicaudata*. Comp Biochem Physiol A 112(1):59–66

Holloway JC, Geiser F (1996) Reproductive status and torpor of the marsupial *Sminthopsis crassicaudata*: effect of photoperiod. J Therm Biol 21:373–380
Holloway JC, Geiser F (2000) Development of thermoregulation in the sugar glider *Petaurus breviceps* (Marsupialia: Petauridae). J Zool 252:389–397
Holloway JC, Geiser F (2001) Effects of helium/oxygen and temperature on aerobic metabolism in the marsupial sugar glider, *Petaurus breviceps*. Physiol Biochem Zool 74:219–225
Holmbeck MA, Rand DM (2015) Dietary fatty acids and temperature modulate mitochondrial function and longevity in *Drosophila*. J Gerontol A 70:1343–1354
Holyoak DT (2001) Nightjars and their allies. Oxford University Press, Oxford
Homberger B, Jenni L, Duplian J, Lanz M, Schaub M (2021) Strong effects of radio-tags, social group and release date on survival of reintroduced grey partridges. Anim Conserv. https://doi.org/10.1111/acv.12673
Hope PR, Jones G (2012) Warming up for dinner: torpor and arousal in hibernating Natterer's bat, (*Myotis natteri*) studied by radio telemetry. J Comp Physiol B 182:569–578
Hosken DJ, Withers PC (1997) Temperature regulation and metabolism of an Australian bat, *Chalinolobus gouldii* (Chiroptera: Vespertilionidae) when euthermic and torpid. J Comp Physiol B 167:71–80
Hrvatin S et al. (2020) Neurons that regulate mouse torpor. Nature:583. https://doi.org/10.1038/s41586-020-2387-5
Hudson JW (1965) Temperature regulation and torpidity in the pygmy mouse, *Baiomys taylori*. Physiol Zool 38:243–254
Hudson JW (1978) Shallow, daily torpor: a thermoregulatory adaptation. In: Wang LCH, Hudson JW (eds) Strategies in cold: natural torpidity and thermogenesis. Academic, New York, pp 67–108
Hudson JW, Scott IM (1979) Daily torpor in the laboratory mouse *Mus musculus* var albino. Physiol Zool 52:205–218
Hulbert AJ (2014) A sceptics view: "Kleiber's Law" or the "3/4 rule" is neither a law nor a rule but rather an empirical approximation. Systems 2014(2):186–202
Hulbert AJ, Abbott SK (2012) Nutritional ecology of essential fatty acids: an evolutionary perspective. Aust J Zool 59:369–379
Hulbert AJ, Else PL (1989) Evolution of mammalian endothermic metabolism: mitochondrial activity and cell composition. Am J Physiol 256:R63–R69
Hulbert AJ, Else PL (2005) Membranes and the setting of energy demand. J Exp Biol 208:1593–1599
Hume ID (1999) Marsupial Nutrition. Cambridge University Press, Cambridge
Hume T, Geiser F, Currie SE, Körtner G, Stawski C (2020) Responding to the weather: energy budgeting by a small mammal in the wild. Curr Zool 66:15–20. https://doi.org/10.1093/cz/zoz023
Humphries MM, Thomas DW, Speakman RJ (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418:313–316
Humphries MM, Thomas DW, Kramer DL (2003) The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiol Biochem Zool 76:165–179
Hut RA, Barnes BM, Daan S (2002) Body temperature patterns before, during, and after semi-natural hibernation in European ground squirrels. J Comp Physiol B 172:47–58
Huttunen M, Johansson BW (1963) The influence of dietary fat on the lethal temperature in the hypothermic rat. Acta Physiol Scand 59:7–11
Hwang TY, Lariviere S, Messier F (2007) Energetic consequences and ecological significance of heterothermy and social thermoregulation in striped skunks (*Mephitis mephitis*). Physiol Biochem Zool 80(1):138–145
Ibuka N, Fukumura K (1997) Unpredictable deprivation of water increases the probability of torpor in the Syrian hamsters. Physiol Behav 62:551–556
Inouye SW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. PNAS:1630–1633

IPCC (2014) In: Pachauri RK, Meyer LA (eds) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change Core writing team. IPCC, Geneva

Irving L, Andersen KL, Bolstad A, Elsner R, Hildes JA, Løyning Y, Nelms JD, Peyton LJ, Whaley RD (1960) Metabolism and temperature of Arctic Indian men during a cold night. J Appl Physiol 15:635–644

IUPS Thermal Commission (2003) Glossary and terms in thermal physiology. J Therm Biol 28:75–106

Ives N (1973) Overnight torpidity in Australian arid-zone birds. Emu 73:140

Iwabuchi M, Minato S, Aiba H, Morita T (2017) Body temperature and microhabitat use in the hibernating Japanese dormouse (*Glirulus japonicus*). Mammalia 81:23–32. https://doi.org/10.1515/mammalia-2015-0139

Jastroch M, Giroud S, Barrett P, Geiser F, Heldmaier G, Herwig A (2016) Seasonal control of mammalian energy balance: recent advances in the understanding of daily torpor and hibernation. J Neuroendocrinol 28. https://doi.org/10.1111/jne.12437

Jefimov M, Wojciechowski MS (2013) Effects of dietary fatty acids on metabolic rate and nonshivering thermogenesis in golden hamsters. J Exp Zool A 321(2):98–107

Jinka TR, Rasley BT, Drew KL (2012) Inhibition of NMDA-type glutamate receptors induces arousal from torpor in hibernating arctic ground squirrels (*Urocitellus parryii*). J Neurochem 122:934–940

Johansson BW (1996) The hibernator heart – nature's model of resistance to ventricular fibrillation. Cardiovasc Res 31:826–832

Johnson JS, Lacki MJ (2013) Summer heterothermy in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) roosting in tree cavities in bottomland hardwood forests. J Comp Physiol B 183:709–721

Johnson JS, Treanor JJ, Slusher AC, Lacki MJ (2019) Buildings provide vital habitat for little myotis (*Myotis lucifugus*) in a high-elevation landscape. Ecosphere 10(11):e02925

Jonasson KA, Willis CKR (2012) Hibernation energetics of free-ranging little brown bats. J Exp Biol 215:2141–2149

Jones C (1973) Body temperatures of *Manis gigantea* and *Manis tricuspis*. J Mammal 54:263–266

Juškaitis R (2005) Daily torpor in free-ranging common dormice (*Muscardinus avellanarius*) in Lithuania. Mammalian Biol 70:242–249

Kalabukhov NI (1960) Comparative ecology of hibernating mammals. Bull Mus Comp Zool Harvard 124:45–74

Kart Gür M, Refinetti R, Gür H (2009) Daily rhythmicity and hibernation in the Anatolian ground squirrel under natural and laboratory conditions. J Comp Physiol B 179:155–164

Kart Gür M, Bulut S, Gür H, Refinetti R (2014) Body temperature patterns and use of torpor in an alpine glirid species, woolly dormouse. Acta Theriol 59:299–309

Kawamichi M, Kawamichi T (1993) Factors affecting hibernation commencement and spring emergence in Siberian chipmunks (*Eutamias sibiricus*). In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 81–89

Kayser C (1961) The physiology of natural hibernation. Pergamon, Oxford

Kelm DH, von Helversen O (2007) How to budget metabolic energy: torpor in a small Neotropical mammal. J Comp Physiol B 177:667–677

Kelt DA, Van Vuren DH (2001) The ecology and macroecology of mammalian home range area. Am Nat 157:637–645

Kenagy GJ (1989) Daily and seasonal uses of energy stores in torpor and hibernation. In: Malan A, Canguilhem B (eds) Living in the cold II. John Libbey Eurotext, London, pp 17–24

Kenagy GJ, Barnes BM (1988) Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. J Mammal 69:274–292

Kenagy GJ, Bartholomew GA (1985) Seasonal reproductive patterns in five coexisting California desert rodent species. Ecol Monogr 55:371–397

Kenagy GJ, Sharbaugh SM, Nagy KA (1989) Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269–282

Kennedy PM, MacFarlane WV (1971) Oxygen consumption and water turnover of the fat-tailed marsupials *Dasycercus cristicauda* and *Sminthopsis crassicaudata*. Comp Biochem Physiol A 40:723–732

Kilduff TS, Sharp FR, Heller HC (1982) 14C 2 deoxyglucose uptake in ground squirrel brain during hibernation. J Neurosci 2:143–157

Kim SS, Choi YS, Yoo JC (2013) Thermal preference and hibernation period of Hodgson's bats (*Myotis formosus*) in the temperate zone: how does the phylogenetic origin of a species affect its hibernation strategy? Can J Zool 91:47–55

Kimura H (2015) Hydrogen sulphide and polysulfides as signaling molecules. Proc Jpn Acad Ser B Phys Biol Sci 91:131–159

Kisser B, Goodwin HT (2012) Hibernation and overwinter body temperatures in free-ranging thirteen-lined ground squirrels, *Ictidomys tridecemlineatus*. Am Midl Nat 167:396–409

Kissner KJ, Brigham RM (1993) Evidence for the use of torpor by incubating and brooding common poorwills *Phalaenoptilus nuttallii*. Ornis Scand 24:333–334

Kleiber M (1961) The fire of life. Wiley, New York

Klingenspor M, Dickopp A, Heldmaier G, Klaus S (1996) Short photoperiod reduces leptin gene expression in white and brown adipose tissue of Djungarian hamsters. FEBS Lett 399:290–294

Klug BJ, Brigham RM (2015) Changes in metabolism and cell physiology that enable mammalian hibernation. Springer Science Reviews 3:39–56. https://doi.org/10.1007/s40362-015-0030-x

Klug-Baerwald BJ, Brigham RM (2017) Hung out dry? Intraspecific variation in water loss in a hibernating bat. J Comp Physiol B 183:977–985

Körtner G, Geiser F (1995) Effect of photoperiod and ambient temperature on activity patterns and body weight cycles of mountain pygmy-possums, *Burramys parvus* (Marsupialia). J Zool 235:311–322

Körtner G, Geiser F (1998) Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). Oecologia 113:170–178

Körtner G, Geiser F (2000a) The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. Chronobiol Int 17(2):103–128

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

Körtner G, Geiser F (2009) The key to winter survival: daily torpor in a small arid zone marsupial. Naturwissenschaften 96:525–530

Körtner G, Geiser F (2011) Activity and torpor in two sympatric Australian desert marsupials. J Zool 283:249–256

Körtner G, Brigham RM, Geiser F (2000) Winter torpor in a large bird. Nature 407:318

Körtner G, Brigham RM, Geiser F (2001) Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). Physiol Biochem Zool 74(6):789–797

Körtner G, Pavey CR, Geiser F (2008) Thermal biology, torpor and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. Physiol Biochem Zool 81:442–451

Körtner G, Rojas AD, Geiser F (2010) Thermal biology, torpor use and activity patterns of a small marsupial from a tropical desert: sexual differences. J Comp Physiol B 180:869–876

Körtner G, Riek A, Pavey C, Geiser F (2016) Activity patterns and torpor in two free-ranging carnivorous marsupials in arid Australia in relation to precipitation, reproduction and ground cover. J Mammal 97:1555–1564

Körtner G, Trachtenberg A, Geiser F (2019) Does aridity affect spatial ecology? Scaling of home range size in small carnivorous marsupials. Sci Nat 106:42

Koskimies J (1948) On temperature regulation and metabolism in the swift, *Micropus a apus* L during fasting. Experientia 4:274–276

Koteja P (2000) Energy assimilation, parental care and the evolution of endothermy. Proc R Soc B 267:479–484

Kristoffersson R, Soivio A (1964) Hibernation of the hedgehog (*Erinaceus europaeus* L.). The periodicity of hibernation of undisturbed animals during the winter in a constant ambient temperature. Ann Acad Sci Fennicae A IV Biol 80:1–22

Kronfeld-Schor N, Dayan T (2013) Thermal ecology, environments, communities, and global change: energy intake and expenditure in endotherms. Annu Rev Ecol Evol Syst 44:461–480

Kronfeld-Schor N, Richardson C, Silva BA, Kunz TH, Widmaier EP (2000) Dissociation of leptin secretion and adiposity during prehibernation fattening in little brown bats. Am J Physiol 279: R1277–R1281

Krüger K, Prinzinger R, Schuchmann K-L (1982) Torpor and metabolism in hummingbirds. Comp Biochem Physiol A 73:679–689

Kumar V, Shearer JC, Kumar A, Darmstadt GL (2009) Neonatal hypothermia in low resource settings: a review. J Perinatol 29:401–412

Kurta A (1990) Torpor patterns in food-deprived *Myotis lucifugus* (Chiroptera: Vespertilionidae) under simulated roost conditions. Can J Zool 69:255–257

Landau BR, Dawe AR (1960) Observations on a colony of captive ground squirrels throughout the year. Bull Mus Comp Zool Harv 124:173–189

Landry-Cuerrier M, Munro D, Thomas DW, Humphries MM (2008) Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. Ecology 89:3306–3316

Lane JE, Brigham RM, Swanson DL (2004) Daily torpor in free-ranging whip-poor-wills (*Caprimulgus vociferus*). Physiol Biochem Zool 77:297–304

Lasiewski RC (1963) Oxygen consumption of torpid, resting, active and flying hummingbirds. Physiol Zool 36:122–140

Lasiewski RC, Lasiewski RJ (1967) Physiological responses of the blue-throated and Rivoli's hummingbirds. Auk 84:34–48

Lasiewski RC, Acosta AL, Bernstein MH (1966) Evaporative water loss in birds. 1. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. Comp Biochem Physiol 19:445–457

Lausen CL, Barclay RMR (2003) Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. J Zool 260:235–244

Lausen CL, Barclay RMR (2006) Winter bat activity in the Canadian prairies. Can J Zool 84:1079–1086

Law BS (1993) Roosting and foraging ecology of the Queensland blossom-bat (*Syconycteris australis*) in North-Eastern New South Wales: flexibility in response to seasonal variation. Wildl Res 20:419–431

Lazaro J, Hertel M, Muturi M, Dechmann DKN (2019) Seasonal reversible size changes in the braincase and mass of common shrews are flexibly modified by environmental conditions. Sci Rep 9:2489

Lebl K, Bieber C, Adamik P, Fietz J, Morris P, Pilastro A, Ruf T (2011a) Survival rates in a small hibernator, the edible dormouse: a comparison across Europe. Ecography 34:683–692

Lebl K, Rotter B, Kürbisch K, Bieber C, Ruf T (2011b) Local environmental factors affect reproductive investment in female edible dormice. J Mammal 92:926–933

Lee AG (2011) Lipid-protein interactions. Biochem Soc Trans 39:761–766

Lee AK, Cockburn A (1985) Evolutionary ecology of marsupials. Cambridge Press, London

Lee TN, Barnes BM, Buck CL (2009) Body temperature patterns during hibernation in a free-ranging Alaska marmot (*Marmota broweri*). Ethol Ecol Evol 21:403–413

Lehmer EM, Biggins DE (2005) Variation in torpor patterns of free-ranging black-tailed and Utah prairie dogs across gradients of elevation. J Mammal 86:15–21

Leon B, Shkolnik A, Shkolnik T (1983) Temperature regulation and water metabolism in the elephant shrew *Elephantulus edwardii*. Comp Biochem Physiol A 74:399–407

Levesque DL, Lovasoa OMA, Rakotoharimalala SN, Lovegrove BG (2013) High mortality and annual fecundity in a free-ranging basal placental mammal, *Setifer setosus* (Tenrecidae: Afrosoricida). J Zool 291:205–212

Levesque DL, Nowack J, Stawski C (2016) Modelling mammalian energetics: the heterothermy problem. Climate Change Resp 3:7

Levin E, Plotnik B, Amichai E, Braulke LJ, Landau S, Yom-Tov Y, Kronfeld-Schor N (2015) Subtropical mouse-tailed bats use geothermally heated caves for winter hibernation. Proc R Soc B 282:20142781

Levy O, Dayan T, Kronfeld-Schor N (2011a) Adaptive thermoregulation in golden spiny mice: the influence of season and food availability on body temperature. Physiol Biochem Zool 84:175–184

Levy O, Dayan T, Kronfeld-Schor N (2011b) Interspecific competition and torpor in golden spiny mice: two sites of the energy acquisition coin. Int Comp Biol 51:441–448

Levy O, Dayan T, Rotics S, Kronfeld-Schor N (2012) Foraging sequence, energy intake and torpor: an individual-based field study of energy balancing in desert golden spiny mice. Ecol Lett 15:1240–1248

Lighton JRB (2008) Measuring metabolic rates: a manual for scientists. Oxford University Press, New York

Lincoln FC, Peterson SR (1979) Migration of birds. Fish & wildlife service. US Department of the Interior, Washington, D.C.

Lindstedt SL, Boyce MS (1985) Seasonality, fasting endurance, and body size in mammals. Am Nat 125:873–878

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC (2009) Lower extinction in sleep-or-hide mammals. Am Nat 173:264–272

Liu J-N, Karasov WH (2011) Hibernation in warm hibernacula by free-ranging Formosan leaf-nosed bats, *Hipposideros terasensis*, in subtropical Taiwan. J Comp Physiol B 181:125–135

Loh HH, Law PY (1980) The role of membrane lipids in receptor mechanisms. Ann Rev Pharmacol Toxicol 20:201–234

Lovegrove BG (2000) Daily heterothermy in mammals: coping with unpredictable environments. In: Heldmaier G, Klingenspor M (eds) Life in the cold: 11th international hibernation symposium. Springer, Berlin, pp 29–40

Lovegrove BG (2017) A phenology of the evolution of endothermy in birds and mammals. Biol Rev 92:1213–1240

Lovegrove BG (2019) Fires of life, endothermy in birds and mammals. Yale University Press, New Haven

Lovegrove BG, Genin F (2008) Torpor and hibernation in a basal placental mammal, the lesser hedgehog tenrec *Echinops telfairi*. J Comp Physiol B 178:691–698

Lovegrove BG, Körtner G, Geiser F (1999) The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. J Comp Physiol B 169:11–18

Lovegrove BG, Raman J, Perrin MR (2001) Heterothermy in elephant shrews, *Elephantulus* spp. (Macroscelidea): daily torpor or hibernation? J Comp Physiol B 171:1–10

Lovegrove BG, Lobban KD, Levesque DL (2014) Mammal survival at the cretaceous-Paleogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs. Proc R Soc B 281:20141303

Lunney D, Cullis B, Eby P (1987) Effect of logging and fire on small mammals in Mumbulla state forest near Bega, New South Wales. Aust Wild Res 14:163–181

Lyman CP (1948) The oxygen consumption and temperature regulation in hibernating hamsters. J Exp Zool 109:55–78

Lyman CP (1970) Thermoregulation and metabolism in bats. In: Wimsatt WA (ed) Biology of bats. Academic, New York, pp 301–330

Lyman CP (1982) Entering hibernation. In: Lyman CP, Willis JS, Malan A, Wang LCH (eds) Hibernation and torpor in mammals and birds. Academic, New York, pp 37–53

Lyman CP, Blinks DC (1959) The effect of temperature on the isolated hearts of closely related hibernators and non-hibernators. J Cell Comp Physiol 54:53–63

Lyman CP, Willis JS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Academic, New York

Lynch GR, White SE, Grundel R, Berger MS (1978) Effects of photoperiod, melatonin administration and thyroid block on spontaneous daily torpor and temperature regulation in the white-footed mouse, *Peromyscus leucopus*. J Comp Physiol B 125:157–163

MacCannell ADV, Staples JF (2021) Elevated ambient temperature accelerates aspects of torpor phenology in an obligate hibernator. J Thermal Biol 96:102839

MacMillen RE (1965) Aestivation in the cactus mouse *Peromyscus eremicus*. Comp Biochem Physiol 16:227–247

MacMillen RE (1972) Water economy of nocturnal desert rodents. Symp Zool Soc Lond 31:147–174

MacMillen RE (1983) Adaptive physiology of heteromyid rodents. Great Basin Nat Memoirs Number 7:65–76

MacMillen RE, Nelson JE (1969) Bioenergetics and body size in dasyurid marsupials. Am J Physiol 217:1246–1251

MacMillen RE, Trost CH (1967) Nocturnal hypothermia in the Inca dove *Scardafella inca*. Comp Biochem Physiol 23:243–252

Maddocks TA, Geiser F (1999) The thermoregulatory limits of an Australian passerine the silvereye *Zosterops lateralis*. J Therm Biol 24:43–50

Maddocks TA, Geiser F (2007) Heterothermy in an Australian passerine, the dusky Woodswallow (*Artamus cyanopterus*). J Ornithol 148:571–577

Malan A (1982) Respiration and acid-base state in hibernation. In: Lyman CP, Willis JS, Malan A, Wang LCH (eds) Hibernation and torpor in mammals and birds. Academic, New York, pp 237–282

Malan A (1986) pH as a control factor in hibernation. In: Heller HC, Musacchia XJ, Wang LCH (eds) Living in the cold. Elsevier, New York, pp 61–70

Malan A (1993) Temperature regulation, enzyme kinetics, and metabolic depression in mammalian hibernation. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 241–252

Malan A (1996) The origins of hibernation: a reappraisal. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: tenth international hibernation symposium. University of New England Press, Armidale, pp 1–6

Maloney SK, Bronner GN, Buffenstein R (1999) Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: a small mammal that uses hot roosts. Physiol Biochem Zool 72(4):385–396

Mansergh I, Broome LS (1994) The mountain pygmy-possum of the Australian Alps. New South Wales University Press, Kensington

Marin G, Ramos-H D, Cafaggi D, Sierra-Duran C, Gallegos A, Romero-Ruiz A, Medellin RA (2020) Challenging hibernation limits of hoary bats: the southernmost record of *Lasiurus cinereus* hibernating in North America. Mamm Biol. https://doi.org/10.1007/s42991-020-00080-4

Marom S, Korine C, Wojciechowski MS, Tracy CR, Pinshow B (2006) Energy metabolism and evaporative water loss in the European free-tailed bat and Hemprich's long-eared bat (Microchiroptera): species sympatric in the Negev Desert. Physiol Biochem Zool 79:944–956

Martin CJ (1902) Thermal adjustments and respiratory exchange in monotremes and marsupials. A study in the development of homoeothermism. Philos Trans Royal Soc Ser B 195:1–37

Matthews JK, Stawski C, Körtner G, Geiser F (2017) Torpor and basking after a severe wildfire: mammalian survival strategies in a scorched landscape. J Comp Physiol B 187:385–393

McAllan BM, Geiser F (2014) Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. Int Comp Biol 54:516–532

McAllan BM, Dickman CR, Crowther MS (2006) Photoperiod as reproductive cue in the marsupial genus *Antechinus*: ecological and evolutionary consequences. Biol J Linn Soc 87:365–379

McAllan BM, Feay N, Bradley AJ, Geiser F (2012) The influence of reproductive hormones on the torpor patterns of the marsupial *Sminthopsis macroura*: bet-hedging in an unpredictable environment. Gen Comp Endocrinol 179:265–276

McGregor HW, Legge S, Jones ME, Johnson CN (2016) Extraterritorial hunting expeditions to intense fire scars by feral cats. Sci Rep 6:22559

McGuire LP, Jonasson KA, Guglielmo CG (2014) Bats on a budget: torpor-assisted migration saves time and energy. PLoS One 9(12):e115724

McKechnie AE, Lovegrove BG (2001) Heterothermic responses in the speckled mousebird (*Colius striatus*). J Comp Physiol B 171:507–518

McKechnie AE, Lovegrove BG (2002) Avian facultative hypothermic responses: a review. Condor 104:705–724

McKechnie AE, Mzilikazi N (2011) Heterothermy in Afrotropical mammals and birds: a review. Int Comp Biol 51:349–363

McKechnie AE, Wolf BO (2004) The energetics of the rewarming phase of avian torpor. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanisms, adaptation, and application. Twelfth international hibernation symposium. Biological papers of the University of Alaska #27. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 265–273

McKechnie AE, Körtner G, Lovegrove BG (2004) Rest-phase thermoregulation in free-ranging white-backed mousebirds. Condor 106:143–149

McKechnie AE, Gerson AR, McWorther TJ, Krabbe Smith E, Talbot WA, Wolf BO (2017) Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation. J Exp Biol 220:2436–2444

McMurchie EJ (1988) Dietary lipids and the regulation of membrane fluidity and function. In: Aloia RC, Curtain CC, Gordon LM (eds) Physiological regulation of membrane fluidity. Liss, New York, pp 189–237

McNab BK (2002) The physiological ecology of vertebrates. Comstock. Cornell University Press, Ithaca

McNab BK, Bonaccorso FJ (1995) The energetics of Australasian swifts, frogmouths, and nightjars. Physiol Zool 68:245–261

McNab BK, Weston KA (2018) The energetics of torpor in a temperate passerine endemic to New Zealand, the rifleman (*Acanthisitta chloris*). J Comp Physiol B 188:855–862

Meierhofer MB, Johnson JS, Leivers SJ, Pierce BL, Evans JE, Morrison ML (2019) Winter habitats of bats in Texas. PLoS One 14(8):e0220839

Menzies A, Webber QMR, Baloun DE, McGuire LP, Muise KA, Cote D, Tinkler S, Willis CKR (2016) Metabolic rate, latitude and thermal stability of roosts, but not phylogeny, affect rewarming rates of bats. Physiol Behav 164:361–368

Merola-Zwatjes M, Ligon JD (2000) Ecological energetics of the Puerto Rican Tody: heterothermy, torpor, and intra-island variation. Ecology 81:990–1003

Merritt JF (2010) The biology of small mammals. Johns Hopkins University Press, Baltimore

Mertens A, Stiedl O, Steinlechner S, Mayer M (2008) Cardiac dynamics during daily torpor in the hamster (*Phodopus sungorus*). Am J Physiol 294:R639–R650

Michener GR (1992) Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. Oecologia 89:397–406

Millesi E, Prossinger H, Dittami JP, Fieder M (2001) Hibernation effects on the memory in European ground squirrels (*Spermophilus citellus*). J Biol Rhythm 16:264–271

Milsom WK (1993) Metabolic depression during hibernation: the role of respiratory acidosis. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 541–544

Milsom WK, Zimmer MB, Harris MB (1999) Regulation of cardiac rhythm in hibernating mammals. Comp Biochm Physiol A 124:383–391

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A (2018) Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. J Animal Ecol 87:956–973

Monaghan P, Nager RG (1997) Why don't birds lay more eggs? Trees 12:270–274

Monarca RI, Speakman JR, da Luz MM (2019) Energetic and thermal adaptation in semi-fossorial pine-voles *Microtus lusitanicus* and *Micropus duodecimcostatus*. J Comp Physiol B 189:309–318

Monarchino MN, Johnson JS (2020) Roost elevation and ambient temperature best predict use of summer heterothermy in eastern red bats. J Zool. https://doi.org/10.1111/jzo.12848

Montaudon D, Robert J, Canguilhem B (1986) Fluorescence anisotropy of kidney lipids and membranes of a hibernating mammal. Cryobiology 23:177–183

Morgan J, Artemieva N, Goldin T (2013) Revisiting wildfires at the K–Pg boundary. J Geophys Res 118:1508–1520

Morhardt JE (1970) Body temperatures of white-footed mice (*Peromyscus* sp.) during daily torpor. Comp Biochem Physiol 33:423–439

Morhardt JE, Hudson JW (1966) Daily torpor induced in white-footed mice (*Peromyscus* spp.) by starvation. Nature 212:1046–1047

Morrison PR (1945) Acquired homiothermism in the pregnant sloth. J Mammal 26:272–275

Morrison PR (1964) Adaptation of small mammals to the arctic. Fed Proc 23:1202–1206

Morrison PR (1965) Body temperature in some Australian mammals. V. Aboriginals. J Appl Physiol 20:1278–1282

Morrison PR, McNab BK (1962) Daily torpor in a Brazilian murine opossum (*Marmosa*). Comp Biochem Physiol 6:57–68

Morrison PR, Petajan JH (1962) The development of temperature regulation in the opossum, *Didelphis marsupialis virginiana*. Physiol Zool 35:52–65

Morrow G, Nicol SC (2009) Cool sex? Hibernation and reproduction overlap in the echidna. PLoS One 4(96):e6070

Morton SR (1978) Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). J Mammal 59:569–575

Morton SR (1980) Ecological correlates of caudal fat-storage in small mammals. Aust Mammal 3:81–86

Morton SR, Lee AK (1978) Thermoregulation and metabolism in *Planigale maculata* (Marsupialia: Dasyuridae). J Therm Biol 3:117–120

Mouhoub-Sayah C, Robin JP, Malan A, Pevet P, Saboureau M (2008) Patterns of body temperature change in the Algerian hedgehog (*Atelerix algericus*). In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: hibernation, torpor and cryobiology. University of KwaZulu-Natal, Pietermaritzburg, pp 307–316

Mrosovsky N (1971) Hibernation and the hypothalamus. Appleton Century Crofts, New York

Mrosovsky N (1977) Hibernation and body weight in dormice: a new type of endogenous cycle. Science 196:902–903

Mrosovsky N (1990) Rheostasis: the physiology of change. Oxford University Press, New York

Muchlinski AE, Ryback EN (1978) Energy consumption of resting and hibernating meadow jumping mice. J Mammal 59:435–437

Munks SA, Green B (1995) Energy allocation for reproduction in a marsupial arboreal folivore, the common ringtail possum (*Pseudocheirus peregrinus*). Oecologia 101:94–104

Munn AJ, Kern P, McAllan BM (2010) Coping with chaos: unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*). Naturwissenschaften 97:601–605

Munro D, Thomas DW (2004) The role of polyunsaturated fatty acids in the expression of torpor by mammals: a review. Zoology 107:29–48

Munro D, Thomas DW, Humphries MM (2005) Torpor patterns of hibernating eastern chipmunks *Tamias striatus* in response to the size and fatty acid composition of food hoards. J Anim Ecol 74:692–700

Muul I (1968) Behavioural and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. University of Michigan, Ann Arbor, Museum of Zoology, Miscellaneous Publication 134, pp 1–65

Mzilikazi N, Lovegrove BG (2002) Reproductive activity influences thermoregulation and torpor in pouched mice, *Saccostomus campestris*. J Comp Physiol B 172:7–16
Mzilikazi N, Lovegrove BG (2004) Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. Physiol Biochem Zool 77:285–296
Mzilikazi N, Lovegrove BG, Ribble DO (2002) Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. Oecologia 133:307–314
Mzilikazi N, Madikiza Z, Oelkrug R, Baxter RM (2012) Hibernation in free-ranging African woodland dormice, *Graphiurus murinus*. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 41–50
Nagel A (1977) Torpor in the European white-toothed shrews. Experientia 33:1455–1456
Nagel A (1985) Sauerstoffverbrauch, Temperaturregulation und Herzfrequenz bei europäischen Spitzmäusen (Soricidae). Z Säugetierkunde 50:249–266
Nagel A, Nagel R (1991) How do bats choose optimal temperatures for hibernation? Comp Biochem Physiol A 99:323–326
Nagorsen DW, Brigham RM (1993) The bats of British Columbia. UBC Press, Vancouver
Nagy KA, Suckling GC (1985) Field energetics and water balance of sugar gliders, *Petaurus breviceps* (Marsupialia: Petauridae). Aust J Zool 33:683–691
Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles and birds. Annu Rev Nutr 19:247–277
Namekata S, Geiser F (2009) Effects of nest use, huddling, and torpor on thermal energetics of eastern pygmy-possums. Aust Mammal 31:31–34
Nespolo RF, Verdugo C, Cortes PA, Bacigalupe LD (2010) Bioenergetics of torpor in the microbiotherid marsupial, monito del Monte (*Dromiciops gliroides*): the role of temperature and food availability. J Comp Physiol B 180:767–773
Nespolo RF, Solano-Iguaran JJ, Bozinovic F (2017) Phylogenetic analysis supports the aerobic-capacity model for the evolution of endothermy. Am Nat 189:13–27
Nespolo R, Mejias C, Espinoza A, Qunitero-Gavis J, Rezende EL, Fontubel FE, Bozinovic F (2021) Heterothermy as the norm, homeothermy as the exception: variable torpor patterns in the South American marsupial monito del monte (*Dromiciops gliroides*). Front Physiol 12:1026. https://doi.org/10.3389/fphys.2021.682394
Newman JR, Rudd RL (1978) Observations of torpor-like behaviour in the shrew, *Sorex sinuosus*. Acta Theriol 23:446–448
Nicol SC (2017) Energy homeostasis in monotremes. Front Neurosci 11:195
Nicol SC, Andersen NA (1996) Hibernation in the echidna: not an adaptation to the cold? In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold. 10th international hibernation symposium. University of New England Press, Armidale, pp 7–12
Nicol SC, Andersen NA (2002) The timing of hibernation in Tasmanian echidnas: why do they do it when they do? Comp Biochem Physiol B 131:603–611
Nicol SC, Andersen NA (2007) Cooling rates and body temperature regulation of hibernating echidnas (*Tachyglossus aculeatus*). J Exp Biol 210:586–592
Nicol SC, Andersen NA, Mesch U (1992) Metabolic rate and ventilatory pattern the echidna during hibernation and arousal. In: Augee ML (ed) Platypus and echidnas. Royal Zoological Society of NSW, Sydney, pp 150–159
Nicol SC, Pavlides D, Andersen NA (1997) Nonshivering thermogenesis in marsupials: absence of thermogenic response to ß3-adrenergic agonists. Comp Biochem Physiol A 117:399–405
Nicol SC, Andersen NA, Arnold W, Ruf T (2009) Rewarming rates of two large hibernators: comparison of a monotreme and a eutherian. J Therm Biol 34:155–159
Nicoll ME, Thompson SD (1987) Basal metabolic rates and energetics of reproduction in therian mammals: marsupials and placentals compared. Symp Zool Soc Lond 57:7–27
Nieminen P, Hohtola E, Pyykönen T, Paakkonen T, Aho J, Cittova-Kintu M, Asikaiene J, Mononen J, Mustonen AM (2005) Thermoregulatory adaptations of the overwintering captive racoon dog (*Nyctereutes procyonoides*). J Exp Zool A 303:776–784

Nilsson JF, Nilsson AA, Broggi J, Watson H (2020) Predictability of food supply modulates nocturnal hypothermia is a small passerine. Biol Lett 16:20200133

Nord A, Nilsson JF, Nilsson JA (2011) Nocturnal body temperature in wintering blue tits is affected by roost-site temperature and body reserves. Oecologia 167:21–25

Nordberg EJ, Cobb VA (2016) Midwinter emergence in hibernating timber rattlesnakes (*Crotalus horridus*). J Herpetol 50:203–208

Nowack J, Dausmann KH (2015) Can heterothermy facilitate the colonization of new habitats? Mammal Rev 45:117–127

Nowack J, Geiser F (2016) Friends with benefits: the role of huddling in mixed groups of torpid and normothermic animals. J Exp Biol 219:590–596

Nowack J, Mzilikazi N, Dausmann KH (2010) Torpor on demand: heterothermy in the non-lemur primate *Galago moholi*. PLoS One 5(5):e10797

Nowack J, Rojas AD, Körtner G, Geiser F (2015) Snoozing through the storm: torpor use during a natural disaster. Sci Rep 5:11243. https://doi.org/10.1038/srep11243

Nowack J, Cooper CE, Geiser F (2016a) Cool echidnas survive the fire. Proc R Soc B 283:20160382

Nowack J, Delesalle M, Stawski C, Geiser F (2016b) Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. Sci Nat 103:73

Nowack J, Stawski C, Geiser F (2017a) More functions of torpor and their roles in a changing world. J Comp Physiol B 187:889–897

Nowack J, Giroud S, Arnold W, Ruf T (2017b) Muscle non-shivering thermogenesis and its role in the evolution of endothermy. Front Physiol 8:889

Nowack J, Stawski C, Körtner G, Geiser F (2018) Physiological and behavioural responses of an arboreal mammal to smoke and charcoal-ash substrate. Physiol Behav 184:116–121

Nowack J, Tarmann I, Hoelzl F, Smith S, Giroud S, Ruf T (2019) Always a price to pay: hibernation at low temperatures comes with a trade-off between energy savings and telomere damage. Biol Lett 15:20190466

Nowack J, Levesque DL, Reher S, Dausmann KH (2020) Variable climates lead to varying phenotypes: "weird" mammalian torpor and lessons from lower latitudes. Front Ecol Evol. https://doi.org/10.3389/fevo.2020.00060

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo ZX, Meng J, Ni X (2013) The placental mammal ancestor and the post-K–Pg radiation of placentals. Science 339:662–667

O'Mara MT, Riker S, Wikelski M, Ter Maat A, Pollock HS, Dechmann DKN (2017) Heart rate reveals torpor at high body temperatures in lowland free-tailed bats. R Soc Open Sci 4:171359

Oberhammer R, Beikircher W, Hörmann C, Lorenz I, Pycha R, Adler-Kastner L, Brugger H (2008) Full recovery of an avalanche victim with profound hypothermia and prolonged cardiac arrest. Resuscitation 76:474–480

Oelkrug R, Polymeropoulos ET, Jastroch M (2015) Brown adipose tissue: physiological function and evolutionary significance. J Comp Physiol B 185:587–606

Ohmart RD, Lasiewski RC (1971) Roadrunners: energy consumption by hypothermia and absorption of sunlight. Science 172:67–69

Oklejewicz M, Daan S, Strijkstra AM (2001) Temporal organisation of hibernation in wild and tau mutant Syrian hamsters. J Comp Physiol B 171:431–439

Olsen MN, Bowman J, Burness G (2017) Seasonal energetics and torpor use in north American flying squirrels. J Thermal Biol 70:46–53

Otto MS, Becker NI, Encarnacao JA (2012) Cool gleaners: thermoregulation in sympatric bat species. Mamm Biol 78(3):212–215. https://doi.org/10.1016/j.mambio.2012.07.156

Otto MS, Becker NI, Encarnacao JA (2015) Stage of pregnancy dictates heterothermy in temperate forest-dwelling bats. J Thermal Biol 47:75–82

Pafilis P, Foufopoulos J, Poulakakis N, Lymberakis P, Valakos E (2007) Digestive performance in five Mediterranean lizard species: effects of temperature and insularity. J Comp Physiol B 177:49–60

Pajunen I (1970) Body temperature, heart rate, breathing pattern, weight loss and periodicity of hibernation in the Finnish garden dormouse, *Eliomys quercinus* L. Ann Zool Fenn 7:251–266

Pajunen I (1983) Ambient temperature dependence of the body temperature and of the duration of hibernation periods in the garden dormouse, *Eliomys quercinus* L. Cryobiology 20:690–697

Park KJ, Jones G, Ransome RD (2000) Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum)*. Funct Ecol 14:580–588

Parker CA, Geiser F, Stawski C (2019) Thermal physiology and activity in relation to reproductive status and sex in a free-ranging semelparous marsupial. Conserv Physiol 7(10):cos073

Pavey CR, Burwell CJ, Körtner G, Geiser F (2009) Vertebrate diet decrease winter torpor use in a desert marsupial. Naturwissenschaften 96:679–683

Pavey CR, Burwell CJ, Körtner G, Geiser F (2016) Why is the marsupial kaluta, *Dasykaluta rosamondae*, diurnally active in winter: foraging advantages or predator avoidance in arid norther Australia. J Arid Environ 133:25–28

Pavey CR, Nano CEM, Waltert M (2020) Population dynamics of dasyurid marsupials in dryland Australia: variations across habitat and time. Austral Ecol 45:283–290. https://doi.org/10.1111/aec.12854

Pearson OP, Koford MR, Pearson AK (1952) Reproduction of the lump-nosed bat *Corynorhinus rafinesquei* in California. J Mammal 33:273–320

Peiponen VA (1965) On hypothermia and torpidity in the nightjar (*Caprimulgus europaeus* L). Ann Acad Scientiarum Fennicae A IV Biol 87:1–15

Peiponen VA (1970) Body temperature fluctuation of the nightjar (*Caprimulgus e. europaeus* L.) in light conditions in southern Finland. Ann Zool Fennici 7:239–350

Pengelley ET, Asmundson SJ (1970) The effect of light on the free-running circannual rhythm of the golden-mantled ground squirrel, *Citellus lateralis*. Comp Biochem Physiol 32:155–160

Pengelley ET, Fisher KC (1961) Rhythmical arousal from hibernation in the golden-mantled ground squirrel, *Citellus lateralis tescorum*. Can J Zool 39:105–120

Pengelley ET, Kelly KH (1966) A "circannian" rhythm in hibernating species of the genus *Citellus* with observations on the physiological evolution. Comp Biochem Physiol 19:603–617

Pengelley ET, Asmundson SJ, Barnes BM, Aloia RC (1976) Relationship of light intensity and photoperiod to circannual rhythmicity in hibernating ground squirrels, *Citellus lateralis*. Comp Biochem Physiol A 53:273–277

Perrin MR, Ridgard BW (1999) Thermoregulation and patterns of torpor in the spectacled dormouse, *Graphiurus ocularis* (A. Smith 1829) (Gliridae). Tropical Zool 12:253–266

Pessato A, McKechnie AE, Buchanan KL, Mariette MM (2020) Vocal panting: a novel thermoregulatory mechanism for enhancing heat tolerance in a desert-adapted bird. Sci Rep 10:18914

Pettett CE, Johnson PJ, Moorhouse TP, Hambly C, Speakman JR, Macdonald DW (2016) Daily energy expenditure in the face of predation: hedgehog energetics in rural landscapes. J Exp Biol 220:460–468

Pettigrew JD, Wilson P (1985) Nocturnal hypothermia in the white-throated needletail, *Hirandapus caudacutus*. Emu 85:200–201

Phillips WR, Inwards SJ (1985) The annual activity and breeding cycles of Gould's long-eared bat, *Nyctophilus gouldi* (Microchiroptera: Vespertilionidae). Aust J Zool 33:111–128

Podlutsky AJ, Khritankov AM, Ovodov ND, Austad SN (2005) A new field record for bat longevity. J Gerontol 60:1266–1368

Pohl H (1961) Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern. Z Vergl Physiol 45:109–153

Pohl H (1987) Circadian pacemaker does not arrest in deep hibernation: evidence for desynchronisation from light cycle. Experientia 43:293–294

Popov VI, Bocharova LS, Bragin AG (1992) Repeated changes of dendritic morphology in the hippocampus of ground squirrels in the course of hibernation. Neuroscience 48:45–51

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692

Pough FH, Janis CM (2019) Vertebrate Life. Sinauer, Oxford

Powers DR (2004) The impact of social interaction on torpor use in hummingbirds. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanisms, adaptation, and application. Twelfth international hibernation symposium. Biological papers of the University of Alaska #27. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 253–263

Powers DR, Nagy KA (1988) Field metabolic rate and food consumption by free-ranging Anna's hummingbirds (*Calypte anna*). Physiol Zool 61:500–506

Prendergast BJ, Freeman DA, Zucker I, Nelson RJ (2002) Periodic arousal from hibernation is necessary for initiation of immune responses in ground squirrels. Am J Physiol 282:R1054–R1062

Pretorius M, Narkotter W, Kearney T, Seamark E, Broders H, Keith M (2021) No evidence of pre-hibernation or pre-migratory body mass gain in *Miniopterus natalensis* in North-Eastern South Africa. J Vert Biol 70:20088

Pretzlaff I, Dausmann KH (2012) Impact of climatic variation and the hibernation physiology of *Muscardinus avellanarius*. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 85–97

Pretzlaff I, Kerth G, Dausmann KH (2010) Communally breeding bats use physiological and behavioural adjustments to optimise daily energy expenditure. Naturwissenschaften 97:353–363

Pretzlaff I, Rau D, Dausmann KH (2014) Energy expenditure increases during the active season in the small, free-living hibernator *Muscardinus avellanarius*. Mammal Biol 79:208–212

Price ER, Dzialowski EM (2018) Development of endothermy in birds: patterns and mechanisms. J Comp Physiol B 188:373–391

Price ER, Armstrong C, Guglielmo CG, Staples JF (2013) Selective mobilization of saturated fatty acids in isolated adipocytes of hibernating 13-line ground squirrels *Ictidomys tridecemlineatus*. Physiol Biochem Zool 86:205–212

Prinzinger R, Siedle K (1986) Experimenteller Nachweis von Torpor bei jungen Mehlschwalben. J Ornithologie 127:95–96

Prinzinger R, Siedle K (1988) Ontogeny of metabolism, thermoregulation and torpor in the house martin *Delichon u. urbica* (L.) and its ecological significance. Oecologia 76:307–312

Prinzinger R, Göppel R, Lorenz A, Kulzer E (1981) Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. Comp Biochem Physiol A 69:689–692

Prinzinger R, Pressmar A, Schleucher E (1991) Body temperature in birds. Comp Biochem Physiol A 99:499–506

Prum RO, Berv JS, Dornburg A, Field DJ, Townsend JP, Lemmon EM, Lemmon AR (2015) A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526:569–577

Racey PA (1973) Environmental factors affecting the length of gestation in heterothermic bats. J Reprod Fertil 19:175–189

Rahn H, Paganelli C, Ar A (1975) Relation of avian egg weight to body weight. Auk 92:750–765

Raison JK, Augee ML, Aloia RC (1988) Mitochondrial membrane transitions in heart and other organs of a hibernator. Am J Physiol 254:E378–E383

Ramenofsky M, Wingfield JC (2006) Behavioural and physiological conflicts in migrants: the transition between migration and breeding. J Ornithol 147:135–145

Ransome RD (1990) The natural history of hibernating bats. Christopher Helm, London

Rasweiler JJ IV (1973) Care and management of the long-tongued bat, *Glossophaga soricina* (Chiroptera: Phyllostomatidae), in the laboratory, with observations on estivation induced by food deprivation. J Mammal 54:391–404

Rattenborg NC (2006) Do birds sleep in flight? Naturwissenschaften 93:413–424

Recher HF, Lunney D, Matthews A (2009) Small mammal populations in a eucalypt forest affected by fire and drought. I. Long-term patterns in an area of climate change. Wildl Res 36:143–158

Reher S, Dausmann KH (2021) Tropical bats counter heat by combining torpor with adaptive hyperthermia. Proc R Soc B 288:20202059. https://doi.org/10.1098/rspb.2020.2059

Reinertsen RE (1983) Nocturnal hypothermia and its energetic significance for small birds living in arctic and subarctic regions. A review. Polar Res 1:269–284
Reinertsen RE, Haftorn S (1996) Different metabolic strategies of northern birds for nocturnal survival. J Comp Physiol B 156:655–664
Renfree MB (2010) Marsupials: placental mammals with a difference. Placenta 24:S21–S26
Renninger M, Sprau L, Geiser F (2020) White mouse pups can use torpor for energy conservation. J Comp Physiol B 190:253–259
Rice S, Mikes M, Bibus D, Berdyshev E, Reisz JA, Gehrke S, Bronova I, D'Allessandro A, Drew KL (2021) Omega 3 fatty acids stimulate thermogenesis during torpor in the Arctic ground squirrel. Sci Rep 11:1340. https://doi.org/10.1038/s41598-020-78763-8
Richter MM, Williams CT, Lee TN, Tøien Ø, Florant GL, Barnes BM, Buck CL (2015) Thermogenic capacity at subzero temperatures: how low can a hibernator go? Physiol Biochem Zool 88:81–89
Riedesel ML, Williams BA (1976) Continuous 24-hour oxygen consumption studies of *Myotis velifer*. Comp Biochem Physiol A 54:95–99
Riek A, Geiser F (2012) Developmental phenotypic plasticity in a marsupial mammal. J Exp Biol 215:1552–1558
Riek A, Geiser F (2013) Allometry of thermal variables in mammals: consequences of body size and phylogeny. Biol Rev 88:564–572
Riek A, Geiser F (2014) Heterothermy in pouched mammals – a review. J Zool 292:74–85
Riek A, Stölzl A, Bernedo RM, Ruf T, Arnold W, Hamby C, Speakman JR, Gerken M (2019) Energy expenditure and body temperature variations in llamas living in the high Andes of Peru. Sci Rep 9:4037
Rismiller PD, Heldmaier G (1988) How photoperiod influences temperature body selection in *Lacerta viridis*. Oecologia 75:125–131
Rismiller PD, McKelvey MW (2000) Spontaneous arousal in reptiles? Body temperature ecology of Rosenberg's goanna, *Varanus rosenbergi*. In: Heldmaier G, Klingenspor M (eds) Life in the cold: eleventh international hibernation symposium. Springer, Berlin, pp 57–64
Rödel HG, Valencak TG, Handrek A, Monclus R (2016) Paying the energetic costs of reproduction: reliance on postpartum foraging and stored reserves. Behav Ecol 27:748–756
Rojas AD, Körtner G, Geiser F (2010) Do implanted transmitters affect maximum running speed of two small marsupials? J Mammal 91:1360–1364
Rojas AD, Körtner G, Geiser F (2012) Cool running: locomotor performance at low body temperature in mammals. Biol Lett 8:868–870. https://doi.org/10.1098/rsbl.2012.0269
Romano AB, Hunt A, Welbergen JA, Turbill C (2019) Nocturnal torpor by superb fairy-wrens: a key mechanism for reducing winter daily energy expenditure. Biol Lett 15:20190211
Romanovsky AA (2007) Thermoregulation: some concepts have changed. Functional architecture of the thermoregulatory system. Am J Physiol 292:R37–R46
Ruben J (1995) The evolution of endothermy in mammals and birds: from physiology to fossils. Annu Rev Physiol 57:69–95
Ruby NF, Dark J, Heller HC, Zucker I (1998) Suprachiasmatic nucleus: role in circannual body mass and hibernation rhythms of ground squirrels. Brain Res 782:63–72
Ruczynski I, Siemers BM (2011) Hibernation does not affect memory retention in bats. Biol Lett 7:153–155
Ruediger J, van der Zee EA, Strijkstra AM, Aschoff A, Daan S, Hut RA (2007) Dynamics in the ultrastructure of asymmetric axospinous synapses in the frontal cortex of hibernating European ground squirrels (*Spermophilus citellus*). Synapse 61:343–352
Ruf T, Arnold W (2000) Mechanisms of social thermoregulation in hibernating alpine marmots (*Marmota marmota*). In: Heldmaier G, Klingenspor M (eds) Life in the cold: eleventh international hibernation symposium. Springer, Berlin, pp 81–94
Ruf T, Arnold W (2008) Effects of polyunsaturated fatty acids on hibernation and torpor: a review. Am J Physiol 294:R1044–R1052

Ruf T, Bieber C (2020) Physiological, behavioural, and life-history adaptations to environmental fluctuations in the edible dormouse. Front Physiol 11:423

Ruf T, Geiser F (2015) Daily torpor and hibernation in birds and mammals. Biol Rev 90:891–926

Ruf T, Heldmaier G (1992) The impact of daily torpor on energy requirements in the Djungarian hamster, *Phodopus sungorus*. Physiol Zool 65:994–1010

Ruf T, Klingenspor M, Preis H, Heldmaier G (1991) Daily torpor in the Djungarian hamster (*Phodopus sungorus*): interactions with food intake, activity and social behaviour. J Comp Physiol B 160:609–615

Ruf T, Stieglitz A, Steinlechner S, Blank JL, Heldmaier G (1993) Cold exposure and food restriction facilitate physiological responses to short photoperiod in Djungarian hamsters (*Phodopus sungorus*). J Exp Zool 267:104–112

Ruf T, Streicher U, Stalder GL, Nadler T, Walzer C (2015) Hibernation in the pygmy slow Loris (*Nycticebus pygmaeus*): multiday torpor in primates is not restricted to Madagascar. Sci Rep 5:17392

Rutovskaya MV, Diatroptov ME, Kuznetsova EV, Anufrief AI, Feoktistova NY, Surov AV (2019) The phenomenon of negative body temperature on hibernating hedgehogs of the genus *Erinaceus*. J Evol Biochem Physiol 55:515–516

Salinas-Ramos VB, Herrera MLG, Flores-Martinez JJ, Johnston DS (2014) Winter and summer torpor in a free-ranging subtropical desert bat: the fishing myotis (*Myotis vivesi*). Acta Chiropterol 16:327–336

Sato Y, Eto T, Kashimura A, Hatanaka M, Morita T (2016) Idle reduction by torpor: torpor expression without energy constraints in the musk shrew *Suncus murinus*. 15th International Hibernation Symposium, Las Vegas, USA, 31 July to 4 August, Abstracts, pp 59–60

Scantlebury M, Lovegrove BG, Jackson CR, Bennett NC, Lutermann H (2008) Hibernation and non-shivering thermogenesis in the Hottentot golden mole (*Amblysomus hottentottus longiceps*). J Comp Physiol 178:887–897

Scesny AA (2006) Detection of fire by eastern red bats (*Lasiurus borealis*): arousal from torpor. Master of science dissertation. Missouri State University, Springfield

Schalk G, Brigham RM (1995) Prey selection by insectivorous bats: are essential fatty acids important? Can J Zool 73:1855–1959

Schlegel R (1969) Der Ziegenmelker. A Ziemsen Verlag, Wittenberg

Schleucher E (2001) Heterothermia in pigeons and doves reduces energetic costs. J Therm Biol 26:287–293

Schleucher E (2004) Torpor in birds: taxonomy, energetics, and ecology. Physiol Biochem Zool 77:942–949

Schmid J (1996) Oxygen consumption and torpor in mouse lemurs (*Microcebus murinus* and *M. myoxinus*): preliminary results of a study in western Madagascar. In: Geiser F, Hulbert AJ, Nicol S (eds) Adaptations to the cold. 10th international hibernation symposium. University of New England Press, Armidale, pp 47–54

Schmid J (2000) Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: energetic consequences and biological significance. Oecologia 123:175–183

Schmid J, Ganzhorn J (2009) Optional strategies for reduced metabolism in gray mouse lemurs. Naturwissenschaften 96:737–741

Schmid J, Speakman JR (2009) Torpor and energetic consequences in free-ranging grey mouse lemurs (*Microcebus murinus*): a comparison of dry and wet forests. Naturwissenschaften 96:609–620

Schmidt-Nielsen K (1977) Problems of scaling: locomotion and physiological correlates. In: Pedley T (ed) Scale effects in animal locomotion. Academic, London, pp 1–21

Schmidt-Nielsen K (1997) Animal physiology. Cambridge University Press, Cambridge

Schmidt-Nielsen K, Schmidt-Nielsen S, Jarnum SA, Houpt TR (1957) Body temperature of the camel and its relation to water economy. Am J Physiol 188:103–112

Schmidt-Nielsen K, Dawson TJ, Cranford EC (1966) Temperature regulation in the echidna (*Tachyglossus aculeatus*). J Cell Physiol 67:63–72

Scholander PF, Hock RJ, Walters V, Johnson F, Irving L (1950) Heat regulation in some arctic and tropical mammals and birds. Biol Bull 99:237–258

Scott P et al. (1974) The world atlas of birds. Mitchell Beazley Publishers, London

Seebacher F, Franklin CE (2005) Physiological mechanisms of thermoregulation in reptiles: a review. J Comp Physiol B 175:533–541

Selwood L, Woolley PA (1991) A timetable of embryonic development, and ovarian and uterine changes during pregnancy, in the stripe-faced dunnart, *Sminthopsis macroura* (Marsupialia: Dasyuridae). J Reprod Fert 91:213–227

Serventy V (1970) Torpidity in the white-backed swallow. Emu 70:27–28

Serventy V, Raymond R (1973) Torpidity in desert mammals. Australia's Wildlife Heritage 14:2233–2240

Seymour RS (1973) Energy metabolism of dormant spadefoot toads (*Scaphiopus*). Copeia 1973:435–445

Seymour RS, Withers PC, Weathers WW (1998) Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). J Zool 244:107–117

Seymour RS, White CR, Gibernau M (2003) Heat reward for insect pollinators. Nature 426:243–344

Shankar A, Schroeder RJ, Wethington SM, Graham CH, Powers DR (2020) Hummingbird torpor in context: duration, more than temperature, is the key to nighttime energy savings. J Avian Biol 51:e02305. https://doi.org/10.1111/jav.02305

Sharbaugh SM (2001) Seasonal acclimatization to extreme climatic conditions by black-capped chickadees (*Poecile atricapilla*) in interior Alaska (64°N). Physiol Biochem Zool 74:568–575

Sheriff MJ, Williams CT, Kenagy GJ, Buck CL, Barnes BM (2012) Thermoregulatory changes anticipates hibernation onset by 45 days: data from free-living arctic ground squirrels. J Comp Physiol B 182:841–847

Sheriff MJ, Fridinger RW, Tøien Ø, Barnes BM, Buck CL (2013) Metabolic rate and prehibernation fattening in free-living arctic ground squirrels. Physiol Bochem Zool 86:515–427

Shipley JR, Gu DY, Salzman TC, Winkler DW (2015) Heterothermic flexibility allows energetics saving in a small tropical swift: the silver-rumped spinetail (*Rhaphidura leucopygalis*). Auk 132:697–703

Shipley AA, Sheriff MJ, Pauli NJ, Zuckerberg B (2019) Snow roosting reduces temperature-associated stress in a wintering bird. Oecologia 190:309–321

Signer C, Ruf T, Arnold W (2011) Hypometabolism and basking: the strategies of alpine ibex to endure harsh over-wintering conditions. Funct Ecol 25:537–547

Simandle ET, Espinoza RE, Nussear KE, Tracy CR (2001) Lizards, lipids, and dietary links to animal function. Physiol Biochem Zool 74:625–640

Simpson K, Day N (1993) Field guide to the birds of Australia. Lifetime Distributers, Girraween NSW, Australia

Singer FJ, Schreier W, Oppenheim J, Garton EO (1989) Drought, fires and large mammals. Bioscience 39:716–722

Siutz C, Ammann V, Millesi E (2012) Shallow torpor expression in free-ranging common hamsters with and without food supplements. Front Ecol Evol 6:190

Siutz C, Franceschini C, Millesi E (2016) Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. J Comp Physiol B 186:801–811

Siutz C, Ammann V, Millesi E (2018) Shallow torpor expression in free-ranging common hamsters with and without food supplementation. Front Ecol Evol 6:190

Smit B, McKechnie AE (2010) Do owls use torpor? Winter thermoregulation in free-ranging pearl-spotted owlets and African scops owls. Physiol Biochem Zool 83:149–156

Smit B, Boyles JG, Brigham RM, McKechnie AE (2011) Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. J Biol Rhythm 26:241–248

Smith AP, Wellham GS, Green SW (1989) Seasonal foraging activity and microhabitat selection by echidnas (*Tachyglossus aculeatus*) on the New England Tablelands. Aust J Ecol 14:457–466

Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP (2003) Body mass of quaternary mammals. Ecology 84:3403

Snapp BD, Heller HC (1981) Suppression of metabolism during hibernation in ground squirrels (*Citellus lateralis*). Physiol Zool 54:297–307

Snyder GK, Nestler JR (1990) Relationship between body temperature, thermal conductance, Q10 and energy metabolism during daily torpor and hibernation in rodents. J Comp Physiol B 159:667–675

Soivio AH, Tähti H, Kristoffersson R (1968) Studies on the periodicity of hibernation in the hedgehog (*Erinaceus europaeus* L.). Ann Zool Fenn 5:224–226

Song X, Geiser F (1997) Daily torpor and energy expenditure in *Sminthopsis macroura*: interactions between food and water availability and temperature. Physiol Zool 70:331–337

Song X, Körtner G, Geiser F (1995) Reduction of metabolic rate and thermoregulation during daily torpor. J Comp Physiol B 165:291–297

Song X, Körtner G, Geiser F (1996) Interrelations between metabolic rate and body temperature during entry into daily torpor in *Sminthopsis macroura*. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold. 10th international hibernation symposium. University of New England Press, Armidale, pp 63–69

Song X, Körtner G, Geiser F (1997) Thermal relations of metabolic rate reduction in a hibernating marsupial. Am J Physiol 273:R2097–R2104

Song X, Körtner G, Geiser F (2000) Temperature selection and energy expenditure in the marsupial hibernator *Cercartetus nanus*. In: Heldmaier G, Klingenspor M (eds) Life in the cold: eleventh international hibernation symposium. Springer Verlag, Berlin, pp 119–126

South FE, Hannon JP, Willis JR, Pengelley ET, Alperts NR (eds) (1972) Hibernation and hypothermia. Perspectives and challenges. Elsevier, Amsterdam

Speakman JR (2008) The physiological costs of reproduction in small mammals. Philos Trans R Soc B 363:375–398

Speakman JR, Rowland A (1999) Preparing for inactivity: how insectivorous bats deposit a fat store for hibernation. Proc Nutr Soc 58:123–131

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 430–490

Spence AR, Tingley MW (2021) Body size and environment influence both intraspecific and interspecific variation in daily torpor across hummingbirds. Funct Ecol doi. https://doi.org/10.1111/1365-2435.13782

Staples JF (2014) Metabolic suppression in mammalian hibernation: the role of mitochondria. J Exp Biol 217:2032–2036

Stawski C (2010) Torpor during the reproductive season in a free-ranging subtropical bat, *Nyctophilus bifax*. J Therm Biol 35:245–249

Stawski C, Currie SE (2016) Effect of roost choice on winter torpor patterns of a free-ranging insectivorous bat. Aust J Zool 64:132–137

Stawski C, Geiser F (2010a) Seasonality of torpor patterns and physiological variables of a free-ranging subtropical bat. J Exp Biol 213:393–399

Stawski C, Geiser F (2010b) Fat and fed: frequent use of summer torpor in a subtropical bat. Naturwissenschaften 97:29–35

Stawski C, Geiser F (2011) Do season and distribution affect thermal energetics of a hibernating bat endemic to the tropics and subtropics? Am J Physiol 301:R542–R547

Stawski C, Geiser F (2012) Will temperature effects or phenotypic plasticity determine the thermal response of a heterothermic tropical bat to climate change? PLoS One 7(7):e40278

Stawski C, Geiser F (2020) Growing up in a changing climate: how temperature affects the development of morphological, behavioural and physiological traits of a marsupials mammal. Front Physiol 11:49

Stawski C, Rojas AD (2016) Thermal physiology of a reproductive female marsupial, *Antechinus flavipes*. Mammal Res 61:417–421

Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). J Comp Physiol B 179:433–441

Stawski C, Körtner G, Geiser F (2014a) Warrumbungle National Park post-fire survey. For NSW NPWS Northern Plains Region, p 81

Stawski C, Willis CKR, Geiser F (2014b) The importance of temporal heterothermy in bats. J Zool 292:86–100

Stawski C, Körtner G, Nowack J, Geiser F (2015a) The importance of mammalian torpor for survival in a post-fire landscape. Biol Lett 11:20150134

Stawski C, Matthews JK, Körtner G, Geiser F (2015b) Physiological and behavioural responses of a small heterothermic mammal to fire stimuli. Physiol Behav 151:617–622

Stawski C, Hume T, Körtner G, Currie SE, Nowack J, Geiser F (2017a) Post-fire recovery of torpor and activity patterns of a small mammal. Biol Lett 13:20170036

Stawski C, Nowack J, Körtner G, Geiser F (2017b) A new cue for torpor induction: charcoal, ash and smoke. J Exp Biol 220:220–226

Steinlechner S, Heldmaier G, Weber C, Ruf T (1986) Role of photoperiod: pineal gland interaction in torpor control. In: Heller HC, Musacchia XJ, Wang LCH (eds) Living in the cold. Elsevier, New York, pp 301–307

Stephenson PJ (1993) Reproductive biology of the large-eared tenrec, *Geogale aurita* (Insectivora: Tenrecidae). Mammalia 57:553–563

Stephenson PJ, Racey PA (1993) Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). I. the large-eared tenrec, *Geogale aurita*. Physiol Zool 66(5):643–663

Storey KB (2010) Out cold: biochemical regulation of mammalian hibernation – a mini-review. Gerontology 56:220–230

Storey KB (2012) Biochemical regulation of carbohydrate metabolism in hibernating bats. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 411–421

Storey KB, Storey JM (1990) Metabolic rate depression and biochemical adaptation in anaerobiosis, hibernation and estivation. Q Rev Biol 65:145–174

Storey KB, Storey JM (2011) Hibernation: Poikilotherms. eLS John Wiley and Sons, Chichester. https://doi.org/10.1002/9780470015902.a0003214.pub2

Storey KB, Storey JM (2013) Molecular biology of freezing tolerance. Compr Physiol 3:1283–1308

Strijkstra AM, Daan S (1997) Sleep during arousal episodes as a function of prior torpor during in European ground squirrels. J Sleep Res 6:36–43

Strumwasser F (1959) Factors in the pattern, timing and predictability of hibernation in the squirrel, *Citellus beecheyi*. Am J Physiol 196:8–14

Studier EH, O'Farrell MJ (1972) Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) I. Thermoregulation. Comp Biochem Physiol A 41:567–595

Stulberg A, Myers M, Brigham RM (2018) Seasonal body mass fluctuations of captive tawny frogmouths (*Podargus strigoides*) are consistent with season heterothermy. J Ornithol 159:303–306

Superina M, Boily P (2007) Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). Comp Biochem Physiol A 148:893–898

Svihla A, Bowman HS (1954) Hibernation in the American black bear. Am Midl Nat 52:248–252

Swanson MT, Oliveros CH, Esselstyn JA (2019) A phylogenomic rodent tree reveals repeated evolution of masseter architectures. Proc R Soc B 286:20190672

Swoap SJ, Gutilla MJ (2009) Cardiovascular changes during daily torpor in the laboratory mouse. Am J Physiol 297:R769–R774

Swoap SJ, Gutilla MJ, Liles LC, Smith RO, Weinshenker D (2006) The full expression of fasting-induced torpor requires ß3-adrenergic receptor signalling. J Neurosci 26:241–245

Swoap SJ, Körtner G, Geiser F (2017) Heart rate dynamics in a marsupial hibernator. J Exp Biol 220:2929–2946

Szewczak JM, Jackson DC (1992) Acid-base state and intermittent breathing in the torpid bat, *Eptesicus fuscus*. Resp Physiol 88:205–215

Takahashi TM, Sunagawa GA, Soya S, Abe M, Sakurai K, Ishikawa K, Yanagisawa M, Hama H, Hasegawa E, Miyawaki A, Sakimura K, Sakurai T (2020) A discrete neural circuit induces a hibernation-like state in rodents. Nature 583:109–114

Talaei F, Hylkema MN, Bouma HR, Boerema AS, Strijkstra AM, Henning RH, Schmidt M (2011) Reversible remodeling of lung tissue during hibernation in the Syrian hamster. J Exp Biol 214:1276–1122

Tan CL, Knight ZA (2018) Regulation of body temperature by the nervous system. Neuron 98:31–48

Tannenbaum MG, Pivorun EB (1988) Seasonal study of daily torpor in southeastern *Peromyscus maniculatus* and *Peromyscus leucopus* from mountains and foothills. Physiol Zool 61:10–16

Tannenbaum MG, Pivorun EB (1989) Summer torpor in montane *Peromyscus maniculatus*. Am Midl Nat 121:194–197

Tattersall GJ (2016) Infrared thermography: a non-invasive window into thermal physiology. Comp Biochem Physiol A 202:78–98

Tattersall GJ, Sinclair BJ, Withers PC, Field PA, Seebacher F, Cooper CE, Maloney SK (2012) Coping with thermal challenges: physiological adaptations to environmental temperature. Compr Physiol 2:2151–2202

Tattersall GJ, Leite CAC, Sanders CE, Cadena V, Andrade DV, Abe AS, Milsom WK (2016) Seasonal reproductive endothermy in tegu lizards. Sci Adv 2:e1500951

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584

Tevis L (1953) Stomach contents of chipmunks and mantled squirrels in northeastern California. J Mammal 34:316–324

Thomas DW, Cloutier D (1992) Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. Physiol Zool 65:443–456

Thomas DW, Geiser F (1997) Periodic arousal in hibernating mammals: is evaporative water loss involved? Funct Ecol 11:585–591

Thomas DW, Dorais M, Bergeron J-M (1990) Winter energy budgets and cost of arousal for hibernating little brown bats, *Myotis lucifugus*. J Mammal 71:475–479

Thompson SD (1985) Subspecific differences in metabolism, thermoregulation, and torpor in the western harvest mouse *Reithrodontomys megalotis*. Physiol Zool 58:430–444

Thompson SD, Nicoll ME (1986) Basal metabolic rate and energetics of reproduction in therian mammals. Nature 321:690–692

Thorp CR, Ram PK, Florant GL (1994) Diet alters metabolic rate in the yellow-bellied marmot (*Marmota flaviventris*) during hibernation. Physiol Zool 67:1213–1229

Tidemann CR (1993) Reproduction in the bats *Vespadelus vulturnus*, *V. regulus* and *V. darlingtoni* (Microchiroptera: Vespertilionidae) in coastal South-eastern Australia. Aust J Zool 41:21–35

Tissier ML, Marchandeau S, Habold C, Handrich Y, Eidenschenk J, Kourkgy C (2019) Weeds as a predominant food source: a review of the diet of common hamsters *Cricetus cricetus* in farmlands and urban habitats. Mammal Rev 49:152–170

Tøien Ø, Blake J, Edgar DM, Grahn DA, Heller HC, Barnes BM (2011) Hibernation in black bears: independence of metabolic suppression from body temperature. Science 331:906–909

Tomlinson S, Withers PC, Cooper CE (2007) Hypothermia versus torpor in response to cold stress in the native Australian mouse *Pseudomys hermannsburgensis* and the introduced house mouse *Mus musculus*. Comp Biochem Physiol A 148:645–650

Trachsel L, Edgar DM, Heller HC (1991) Are ground squirrels sleep deprived during hibernation? Am J Physiol 260:R1123–R1129

Tucker VA (1966) Diurnal torpor and its relation to food consumption and weight changes in the California pocket mouse *Perognathus californicus*. Ecology 47:245–252

Tucker VA (1975) The energetic costs of moving about. Am Sci 63:413–419

Turbill C (2006) Roosting and thermoregulatory behaviour of male Gould's long-eared bats, *Nyctophilus gouldi*: energetic benefits of thermally unstable roosts. Aust J Zool 56:57–60

Turbill C, Geiser F (2006) Thermal biology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*. J Comp Physiol B 176:165–172
Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. J Comp Physiol B 178:597–605
Turbill C, Stojanovski L (2018) Torpor reduces predation risk by compensating for the energetic costs of antipredator foraging behaviours. Proc R Soc B 285:20182370
Turbill C, Law BS, Geiser F (2003a) Summer torpor in a free-ranging bat from sub-tropical Australia. J Therm Biol 28:223–226
Turbill C, Körtner G, Geiser F (2003b) Natural use of torpor by a small, tree-roosting bat during summer. Physiol Biochem Zool 76:868–876
Turbill C, Körtner G, Geiser F (2008) Timing of the daily temperature cycle affects the critical arousal temperature and energy expenditure of the lesser long-eared bat. J Exp Biol 211:3871–3878
Turbill C, Bieber C, Ruf T (2011a) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc R Soc B 278:3355–3363
Turbill C, Ruf T, Mang T, Arnold W (2011b) Regulation of heart rate and rumen temperature in red deer: effect of season and food intake. J Exp Biol 214:963–970
Turner JM, Geiser F (2017) The influence of natural photoperiod on seasonal torpor expression of two opportunistic marsupial hibernators. J Comp Physiol B 187:375–383
Turner JM, Körtner G, Warnecke L, Geiser F (2012a) Summer and winter torpor by a free-ranging marsupial. Comp Biochem Physiol A 162:274–280
Turner JM, Warnecke L, Körtner G, Geiser F (2012b) Opportunistic hibernation by a free-ranging marsupial. J Zool 286:277–284
Twente JW (1955) Some aspects of habitat selection on other behavior of cave-dwelling bats. Ecology 36:706–732
Twente JW, Twente JA (1964) A hypothesis concerning the evolution of heterothermy in bats. Ann Acad Scientiarum Fennicae Series A IV Biol 71:433–442
Twente JW, Twente JA (1965) Regulation of hibernating periods by temperature. PNAS 54:1058–1061
Twente JW, Twente JA (1968) Progressive irritability of hibernating *Citellus lateralis*. Comp Biochem Physiol 25:467–474
Tyndale-Biscoe H (1973) Life of marsupials. Edward Arnold, London
Tyndale-Biscoe H, Renfree M (1987) Reproductive physiology of marsupials. Cambridge University Press, Cambridge
Ultsch GR (1980) Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biol Rev 64:435–516
Utz JC, van Breukelen F (2013) Prematurely induced arousal from hibernation alters key aspects of warming in golden-mantled ground squirrels, *Callospermophilus lateralis*. J Thermal Biol 38:570–575
Van Breukelen F, Utz JC, Treat M, Pan P (2012) Putting on the brakes on protein synthesis in mammalian hibernation. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world. Springer, Berlin, pp 433–443
Vehrencamp SL (1982) Body temperatures of incubating versus non-incubating roadrunners. Condor 84:203–207
Vogel P (1974) Kälteresistenz und reversible Hypothermie der Etruskerspitzmaus (*Suncus etruscus*, Soricidae, Insectivora). Z Säugetierkd 39:78–88
Vuarin P, Henry PY, Guesnet P, Alessandri JM, Aujard F, Perret M, Pifferi F (2014) Shallow hypothermia depends on the level of fatty acid unsaturation in adipose and liver tissues in a tropical heterothermic primate. J Thermal Biol 43:81–88
Wacker CB, Rojas AD, Geiser F (2012) The use of small subcutaneous transponders for quantifying thermal biology and torpor in small mammals. J Thermal Biol 37:250–254
Wacker CB, McAllan BM, Körtner G, Geiser F (2016) The functional requirements of mammalian hair: a compromise between crypsis and thermoregulation? Sci Nat 103:53

Wacker CB, McAllan BM, Körtner G, Geiser F (2017) The role of basking in the development of endothermy and torpor in a marsupial. J Comp Physiol B 187:1029–1038

Walhovd H (1979) Partial arousal from hibernation in hedgehogs in outdoor hibernacula. Oecologia 40:141–153

Walker LE, Walker JM, Palca JW, Berger RJ (1983) A continuum of sleep and shallow torpor in fasting doves. Science 221:194–195

Wang LCH (1978) Energetics and field aspects of mammalian torpor: the Richardson's ground squirrel. In: Wang LCH, Hudson JW (eds) Strategies in cold, natural torpidity and thermogenesis. Academic, New York, pp 109–145

Wang LCH, Hudson JW (1970) Some physiological aspects of temperature regulation in normothermic and torpid hispid pocket mouse, *Perognathus hispidus*. Comp Biochem Physiol 32:275–293

Warnecke L (2012) Quantifying torpor in small mammals non-invasively using infrared thermocouples. J Therm Biol 37:380–383

Warnecke L (2017) Das Geheimnis der Winterschläfer. CH Beck, Munich

Warnecke L, Geiser F (2010) The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions. J Comp Physiol B 180:437–445

Warnecke L, Turner JM, Geiser F (2008) Torpor and basking in a small arid zone marsupial. Naturwissenschaften 95:73–78

Warnecke L, Turner JM, Bollinger TK, Lorch JM, Misra V, Cryan PM, Wibbelt G, Blehert DS, Willis CKR (2012) Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. PNAS 109:6999–7003

Warren JW (1960) Temperature fluctuation in the smooth-billed ani. Condor 62:293–294

Wassmer T (2004) Body temperature and above-ground patterns during hibernation in European hamsters (*Cricetus cricetus* L.). J Zool 262:281–288

Wassmer T, Wollnik F (1997) Timing of torpor bouts during hibernation in European hamsters (*Cricetus cricetus* L.). J Comp Physiol B 167:270–279

Wawrocka K, Bartonicka T, Reiter A (2012) *Pipistrellus kuhlii*, a bat species breeding and hibernating in the Czech Republic. Vespertilio 16:351–356

Webb CL, Milsom WK (2017) Effects of low temperature on breathing pattern and ventilator response during hibernation in the golden-mantled ground squirrel. J Comp Physiol B 187:793–802

Webb PI, Skinner JD (1996) Summer torpor in African woodland dormice *Graphiurus murinus* (Myoxidae: Graphiurinae). J Comp Physiol B 166:325–330

Webb PI, Speakman JR, Racey PA (1996) How hot is a hibernaculum? A review of the temperatures at which bats hibernate. Can J Zool 74:761–765

Weller TJ, Castle KT, Liechti F, Hein CD, Schirmacher MR, Cryan PM (2016) First direct evidence of long-distance seasonal movement and hibernation in a migratory bat. Sci Rep 6:34585

Wendt W (1989) Feldhamster *Cricetus cricetus* (L.). In: Stubbe H (ed) Buch der Hege, Band 1 Haarwild. Deutscher Landwirtschaftsverlag, Berlin, pp 667–684

Westman W, Geiser F (2004) The effect of metabolic fuel availability on thermoregulation and torpor in a marsupial hibernator. J Comp Physiol B 174:49–57

Weyer NM, Fuller A, Haw AJ, Meyer LCR, Mitchell D, Picker T, Rey B, Hetem RS (2020) Increased diurnal activity is indicative of energy deficit in a nocturnal mammal, the aardvark. Front Physiol 11:637

White DA (1973) The phospholipid composition of mammalian tissues. Biochim Biophs Acta Library 3:996–1002

White CR, Seymour RS (2005) Allometric scaling of mammalian metabolism. J Exp Biol 208:1611–1619

White CR, Cassey P, Schimpf NG, Halsey LG, Green JA, Portugal SJ (2013) Implantation reduces the negative effects of bio-logging devices on birds. J Exp Biol 216:537–542

White FN, Somero G (1982) Acid-base regulation and phospholipid adaptation to temperature: time courses and physiological significance of modifying the milieu for protein function. Physiol Rev 62:40–90

Wiersinga WM, Platvoet-ter Schiphorst M (1990) Inhibition of nuclear T3 binding by fatty acids: dependence on chain length, unsaturated bonds, cis-trans configuration and esterification. Int J Biochem 22:269–273

Wilkinson GS, South JM (2002) Life history, ecology and longevity of bats. Ageing Cell 1:124–131

Williams DR, Epperson LE, Li W, Hughes MA, Taylor R, Rogers J, Martin SL, Cossins AR, Gracey AY (2005) Seasonally hibernating phenotype assessed through transcript screening. Physiol Genomics 24:13–22

Williams CT, Sheriff MJ, Schmutz JA, Kohl F, Tøien Ø, Back CL, Barnes BM (2011) Data logging of body temperatures provides precise information on phenology of reproductive events in a free-ranging arctic hibernator. J Comp Physiol 181:1101–1109

Williams CT, Barnes BM, Buck CL (2016) Integrating physiology, behaviour, and energetics: biologging in a free-living hibernator. Comp Biochem Physiol A 202:53–62

Williams CT, Buck CL, Sheriff MJ, Richter MM, Krause JS, Barnes BM (2017) Sex-dependent phenological plasticity in an Arctic hibernator. Am Nat 190:854–859

Willig MR, Selcer KW (1989) Bat species density gradients in the New World: a statistical assessment. J Biogeogr 16:189–195

Willis JS (1982) The mystery of periodic arousal. In: Lyman CP, Willis JS, Malan A, Wang LCH (eds) Hibernation and torpor in mammals and birds. Academic, New York, pp 92–103

Willis JS, Goldman SS, Foster RF (1971) Tissue K concentration in relation to the role of the kidney in hibernation and the cause of periodic arousal. Comp Biochem Physiol A 39:437–445

Willis CKR (2007) An energy-based body temperature threshold between torpor and normothermia for small mammals. Physiol Biochem Zool 80:643–651

Willis CKR, Brigham RM (2003) Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. J Comp Physiol B 173:379–389

Willis CKR, Goldzieher A, Geiser F (2005a) A non-invasive method for quantifying patterns of torpor and activity under semi-natural conditions. J Thermal Biol 30:551–556

Willis CKR, Turbill C, Geiser F (2005b) Torpor and thermal energetics in a tiny Australian vespertilionid, the little forest bat (*Vespadelus vulturnus*). J Comp Physiol B 175:479–486

Willis CKR, Lane JE, Liknes ET, Swanson DL, Brigham RM (2005c) Thermal energetics of female big brown bats (*Eptesicus fuscus*). Can J Zool 83:871–879

Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. Naturwissenschaften 93:80–83

Wilson DE, Mittermeier RA (eds) (2019) Handbook of the mammals of the world – volume 9. Lynx Ediciones, Barcelona

Wilsterman K, Ballinger MA, Williams CM (2021) A unifying, eco-physiological framework for animal dormancy. Funct Ecol. https://doi.org/10.1111/1365-2435.13718

Wilz M, Heldmaier G (2000) Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*. J Comp Physiol 170:511–521

Wimsatt WA (1969) Some interrelations of reproduction and hibernation in mammals. In: Woolhouse HW (ed) Dormancy and survival. Symp Soc Exp Biol 23. Cambridge University Press, Cambridge, pp 511–549

Winkler DW, Billerman SM, Lovette IJ (2020) Kiwis (*Apterygidae*), version 1.0. In: Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.aptery1.01

Withers KW, Billingsley J, Hirning D, Young A, McConnell P, Carlin S (1996) Torpor in *Sminthopsis macroura*: effects of dietary fatty acids. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold. 10th international hibernation symposium. Armidale, Australia. University of New England Press, Armidale, pp 217–222

Withers PC (1977a) Respiration, metabolism, and heat exchange of euthermic and torpid poorwills and hummingbirds. Physiol Zool 50:43–53
Withers PC (1977b) Measurement of Vo_2, Vco_2, and evaporative water loss with a flow-through mask. J Appl Physiol 42:120–123
Withers PC (2001) Design, calibration and calculation for flow-through respirometry systems. Aust J Zool 49:445–461
Withers PC, Cooper CE (2010) Metabolic depression: a historical perspective. In: Navas CA, Carvalho JE (eds) Aestivation: molecular and physiological aspects. Springer, Berlin, pp 1–23
Withers PC, Thompson GG (2000) Cocoon formation and metabolic depression by the aestivating hylid frogs *Cyclorana australis* and *Cyclorana cultripes* (Amphibia: Hylidae). J Royal Soc Western Aust 83:39–40
Withers PC, Louw GN, Henschel J (1980) Energetics and water relations of Namib Desert rodents. S Afr J Zool 15:131–137
Withers PC, Richardson KC, Wooller RD (1990) Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. Aust J Zool 37:685–693
Withers PC, Thompson GG, Seymour RS (2000) Metabolic physiology of the north-western marsupial mole, *Notoryctes caurinus* (Marsupialia: Notoryctidae). Aust J Zool 48:241–258
Withers PC, Cooper CE, Nespolo RF (2012) Evaporative water loss, relative water economy and evaporative partitioning of a heterothermic marsupial, the monito del Monte (*Dromiciops gliroides*). J Exp Biol 215:2806–2813
Withers PC, Cooper CE, Maloney SK, Bozinovic F, Cruz-Neto AP (2016) Ecological and environmental physiology of mammals. Oxford University Press, Oxford
Wojciechowski MS, Pinshow B (2009) Heterothermy in small migrating passerine birds during stopovers: use of hypothermia at rest accelerates fuel accumulation. J Exp Biol 212:3068–3075
Wojciechowski MS, Jefimov M, Tegowska E (2007) Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). Comp Biochem Physiol A 147:828–840
Wolf BO, McKechnie AE, Schmitt JC, Czenze Z, Johnson AB, Witt CC (2020) Extreme and variable torpor among high-elevation Andean hummingbird species. Biol Lett 16:20200428
Woods CP (2002) Ecological aspects of torpor use and inactivity during winter by common poorwills. PhD dissertation. University of Regina, Regina
Woods CP, Czenze ZJ, Brigham RM (2019) The avian "hibernation" enigma: thermoregulatory patterns and roost choice of the common poorwill. Oecologia 189:47–53
Woolley P (1966) Reproduction in *Antechinus* spp. and others dasyurid marsupials. Symp Zool Soc Lond 15:281–294
Wyss OAM (1932) Winterschlaf und Wärmehaushalt, intersucht am Siebenschläfer (*Myoxis glis*). Pflügers Arch 229:599–635
Yang M, Xing X, Guan S, Zhao Y, Wang Z, Wang D-H (2011) Hibernation patterns and changes of body temperature in Daurian ground squirrels (*Spermophilus dauricus*) during hibernation. Acta Theriol Sinica 31:387–395
Young PJ (1990) Hibernation patterns of free-ranging Columbian ground squirrels. Oecologia 83:504–511
Yuan L, Geiser F, Lin B, Sun H, Chen J, Zhang S (2015) Down but not out: the role of microRNAs in hibernating bats. PLoS One 10(8):e0135064
Zervanos SM, Salsbury CM (2003) Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). J Mammal 84:299–310
Zervanos SM, Maher CR, Waldvogel JA, Florant GL (2010) Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). Physiol Biochem Zool 83:135–141
Zimmer MB, Milsom WK (2001) Effects of changing ambient temperature on metabolic, heart, and ventilation rates during steady state hibernation in golden-mantled ground squirrels (*Spermophilus lateralis*). Physiol Biochem Zool 74:714–723
Zimmerman ML (1982) Carbohydrate and torpor duration in hibernating golden-mantled ground squirrels (*Citellus lateralis*). J Comp Physiol B 147:129–135

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F. Geiser, *Ecological Physiology of Daily Torpor and Hibernation*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-75525-6

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