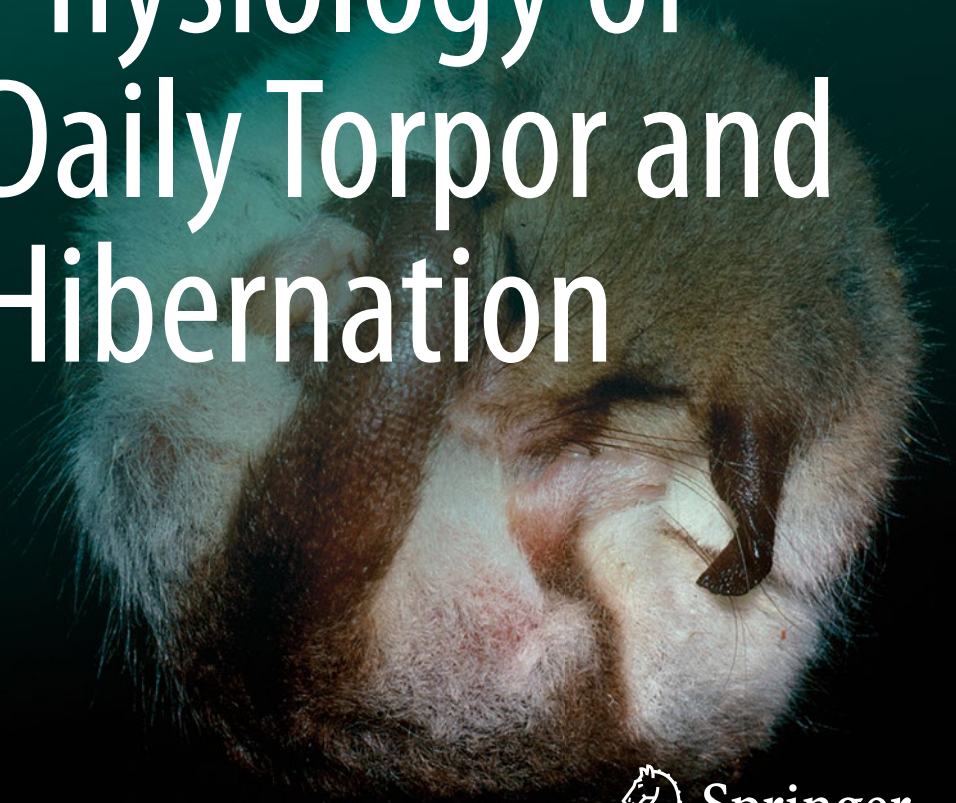


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Fritz Geiser

Ecological Physiology of Daily Torpor and Hibernation



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Ecological Physiology of Daily Torpor and Hibernation

 Springer

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*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 Bondarenko, 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 Bondarenko, 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.

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Armidale, NSW, Australia
March 2021

Fritz Geiser

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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

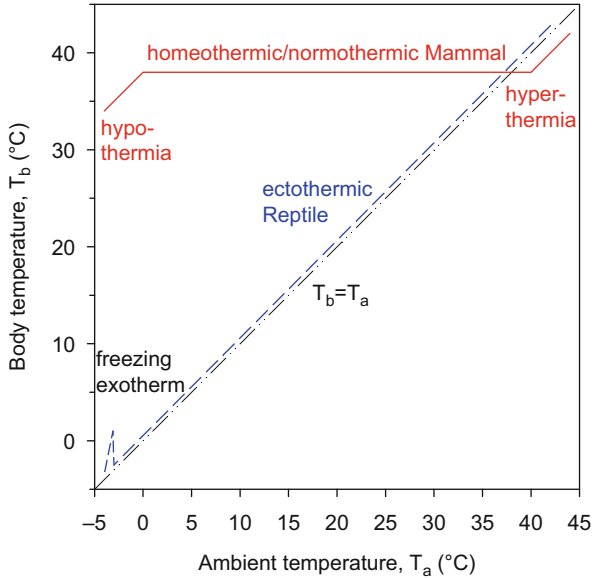


Fig. 1.1 Body temperature (T_b) as a function of ambient temperature (T_a) in a 25-g endothermic mammal (red solid line) and an ectothermic reptile (blue broken line). This size was selected because most endotherms and especially heterothermic endotherms are small. The normothermic T_b of mammals of 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_a s 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).

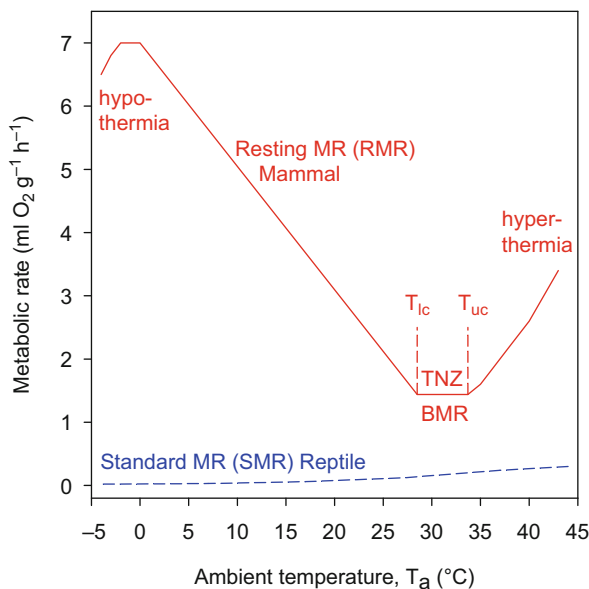


Fig. 1.2 Metabolic rate (MR) as a function of ambient temperature (T_a) in an endothermic mammal (red solid line) and an ectothermic reptile (blue broken line). The resting MR (RMR) of mammals is at or near basal (BMR) in the thermo-neutral zone (TNZ) as there is no thermoregulatory heat production. 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 asynchronous 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_a s 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-neutral conditions (no energy is used for thermo-regulatory 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 use BMR mainly to allow for comparison with other physiological states.

When experiencing $T_{a,s}$ 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 (Bondarenko 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_a s 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

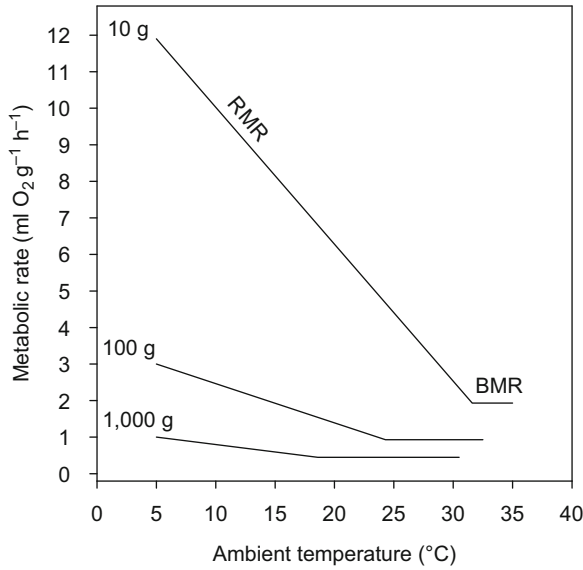


Fig. 1.3 The resting MR (RMR) and the basal MR (BMR) as a function of ambient temperature (T_a) in three mammals ranging from 10 g to 1000 g. Note that in the TNZ, which becomes wider with increasing size (Fig. 1.4), the BMR in the 10-g mammal is about four-fold that of the 1000-g mammal. The RMR at 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_a s 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_a s, which is analogous to the increase in RMR at T_a s 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

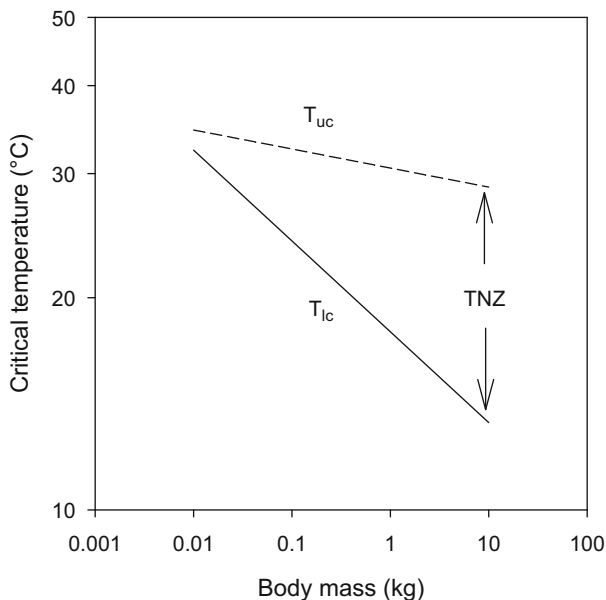
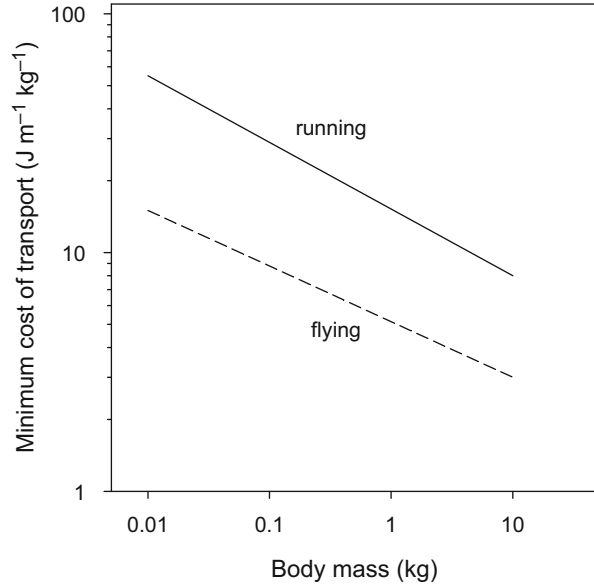


Fig. 1.4 The upper critical temperature (T_{uc} , broken line), the lower critical temperature (T_{lc} , solid line) and the width of the thermo-neutral zone (TNZ, indicated by arrows) as a function of body mass in mammals. Note that TNZ widens with increasing size. The TNZ is the temperature range, 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)

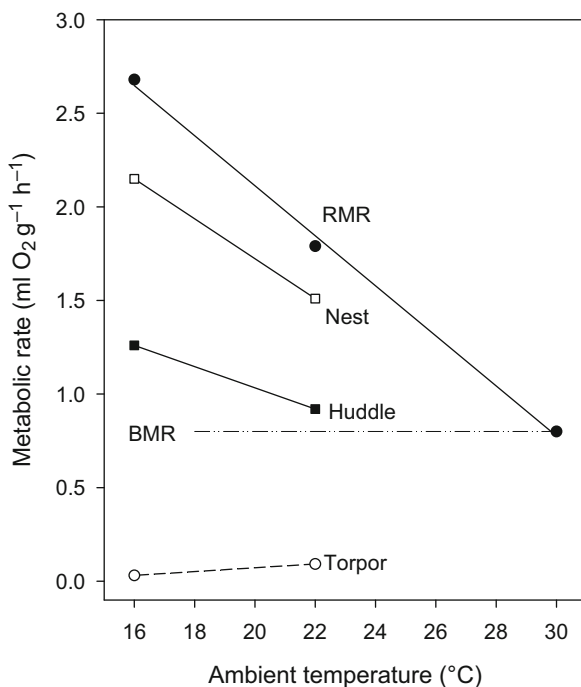


species, such as mice and other small mammals cannot move over long distances because running in small species is slow (Garland et al. 1988) and energetically almost 10-times more expensive than flying over the same distance and at the same body mass (Tucker 1975). Therefore sedentary species have to 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_b s 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

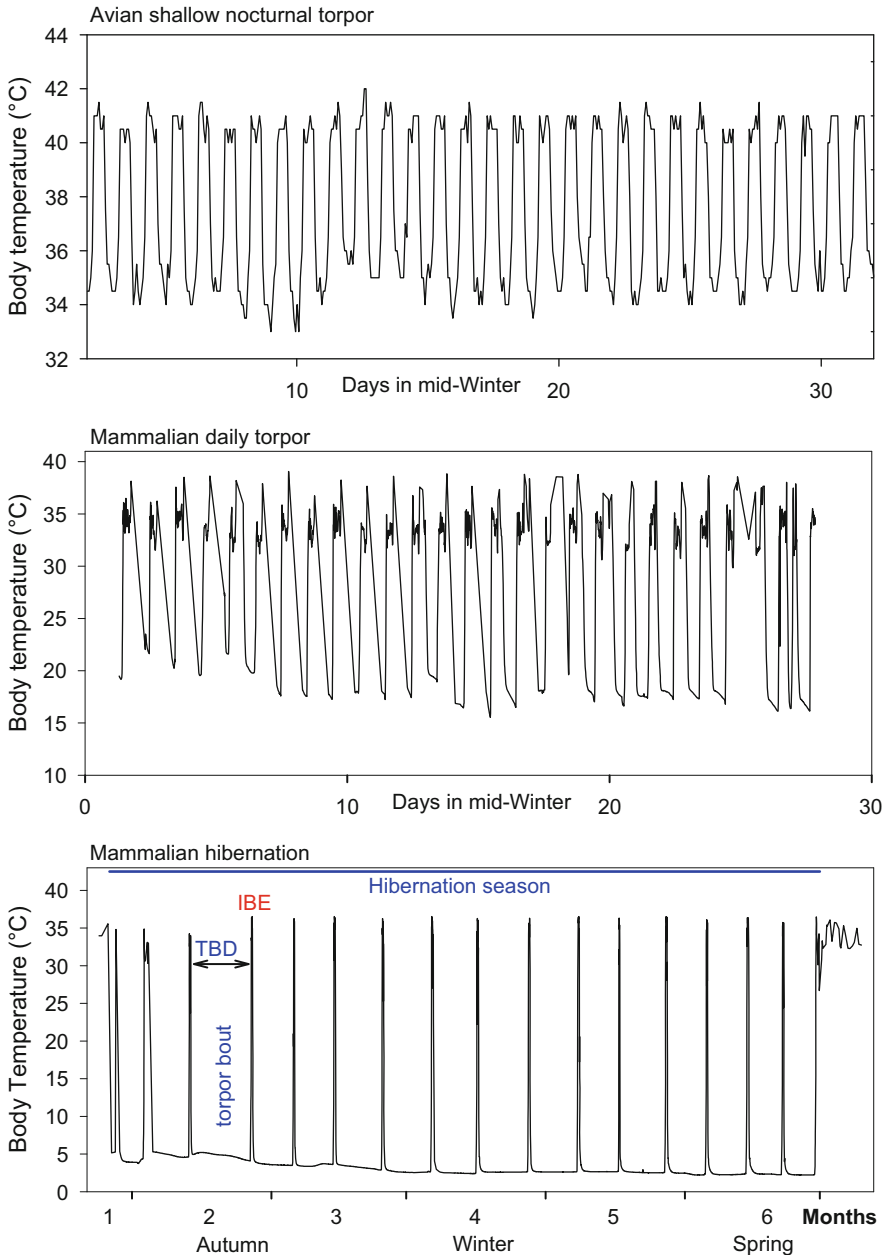


Fig. 1.7 Torpor in a free-ranging heterothermic bird expressing shallow nocturnal torpor (top graph), a free-ranging heterothermic mammal expressing daily torpor (middle graph) and a free-ranging mammal expressing multiday torpor during the hibernation season (blue horizontal bar, top of bottom graph). Note the daily return to high normothermic body temperatures (T_b) and the rather high T_b s during torpor in the two daily heterotherms (top and middle) in contrast to the low T_b s 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

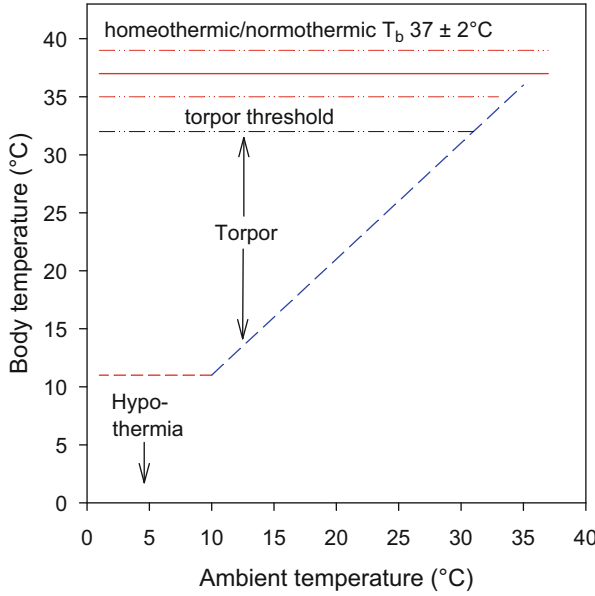


Fig. 1.8 The body temperature ($T_b = 37 \pm 2^\circ\text{C}$) of a homeothermic or normothermic or euthermic mammal (solid red horizontal line) as a function of ambient temperature (T_a). A mean T_b with a variance of $\pm 2^\circ\text{C}$ (red dash-dotted horizontal lines) is defined as being ‘homeothermic’ (Hetem et al. 2016). The ‘torpor threshold’ ($T_b 37 - 5^\circ\text{C} = T_b 32^\circ\text{C}$) 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_b s 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