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Chapter 5 Aestivation in Mammals and Birds

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Abstract Aestivation, which in the context of this paper refers to avian and mammalian torpor in summer/at high ambient temperatures (T_a), does not appear to differ functionally from other forms of torpor, and to a large extent reflects the higher body temperatures (T_b) caused by high T_a . However, from an ecological point of view, aestivation results in different challenges and requirements than does torpor use in winter, because heat can cause reduced food and water availability in many regions, but without the access to low T_a for a substantial reduction of T_b . Aestivation is used by a diversity of adult mammals and birds both in the field and laboratory, as well as by growing young to reduce thermoregulatory energy expenditure. Torpor occurs at high T_a including the thermo-neutral zone and even under these conditions the reduction in energy expenditure and water requirements or water loss is substantial. Although data from the laboratory and, especially, from the field are limited, they show that torpor at high T_a is an effective survival strategy and suggest that it is employed by many mammals and birds in a diversity of habitats.

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5.1 Introduction

Endothermic mammals and birds have the ability to maintain a constant high body temperature (T_b) over a wide range of ambient temperatures (T_a) primarily by producing heat internally by combustion of fuels. Because the surface area/volume ratio of animals increases with decreasing size, the amount of heat loss, and therefore the amount of endogenous heat required per gram tissue for maintenance of a stable T_b , increases with decreasing size. While heat loss is most pronounced at low T_a , energy expenditure in small endotherms even at mild T_a is still much higher than in ectotherms (Hulbert and Else 1989; Withers 1992). These high metabolic rates (MR) in small endotherms demand intake of large amounts of food, and, when food supply is low or fluctuating, energy requirements may exceed energy availability.

To cope with these challenges, not all mammals and birds are permanently homeothermic (i.e., maintain a constant high T_b), but during certain times of the day or the year enter a state of torpor (Lyman et al. 1982; Geiser and Ruf 1995; Boyer and Barnes 1999; Carey et al. 2003; Geiser 2004; Withers and Cooper 2009). Torpor in these "heterothermic endotherms" is characterized by a controlled reduction of T_b , MR, and other physiological functions, which importantly also include water loss. During torpor, T_b falls from high normothermic values of ~32–42°C to values between -3 and -30°C, but during steady-state torpor, T_b always remains above the T_a , even when the animals are thermo-conforming (Barnes 1989; Geiser and Ruf 1995). The minimum MR during torpor (torpor metabolic rate (TMR)) is, on average, reduced to 5 to 30% of the basal metabolic rate (BMR) and in some species TMR can be less than 1% of the resting MR (RMR) in normothermic animals at low T_a , emphasizing the effectiveness of torpor in reducing MR (Geiser and Ruf 1995; Boyer and Barnes 1999). Although torpid mammals and birds usually thermo-conform over a wide range of temperatures, thermoregulation is not abandoned (Florant and Heller 1977; Withers and Cooper 2009). The T_b during torpor is regulated by a proportional increase in heat production at a minimum that differs widely among species, apparently to avoid organ or tissue damage caused by low temperatures, or to prevent cooling to T_b s from which they cannot arouse.

Cold exposure in high latitudes/altitudes is widely seen as the main challenge to small mammals and birds because increased heat loss often is associated with low food availability. However, low food and water availability are not restricted to high latitudes or altitudes, but also are pronounced in desert regions to some extent due to extreme heat during summer, and even may be experienced in tropical and subtropical regions during the dry winter season. Recent evidence suggests that low food and water availability, not cold exposure, are the primary reasons for employment of torpor in mammals and birds. Torpor can be induced by withdrawal of food and water at relatively high T_a and even within the thermo-neutral zone (TNZ) at maintenance BMR, without thermoregulatory heat production, although cold exposure obviously will enhance torpor use because of increased energetic demands for thermoregulation (Geiser 2004).

The purpose of this review is to provide a brief summary of torpor in mammals and birds in general, and then to synthesize what is known about "aestivation" specifically. Aestivation (from Latin *aestas*, summer) is often defined as "torpor during heat and drought during summer in some animals" (Lawrence 2008) i.e., with a seasonal connotation, or a "form of torpor usually in response to high temperatures or scarcity of water" (Pough et al. 2009), i.e., simply with reference to thermal and hygric conditions. Therefore, in this review, aestivation in endotherms will be viewed as shallow torpor at relative mild T_a at all times of the year; nevertheless, torpor in summer specifically will also be discussed. Suitable examples to illustrate both have been selected from the literature, but this paper does not aim to be exhaustive.

5.2 Prolonged, Multiday Torpor or Hibernation

Most heterothermic mammals and birds appear to use one of two common patterns of torpor: (a) hibernation or prolonged, multiday torpor is employed by the "hibernators," and (b) daily torpor is employed by the "daily heterotherms." Hibernation, often, is seasonal and usually lasts from late summer/autumn to late winter/spring. However, hibernators do not remain torpid throughout the hibernation season. Bouts of torpor, during which T_b are low and bodily functions are reduced to a minimum, last for several days or weeks, but are interrupted by periodic rewarming and brief (usually less than 1 day) normothermic resting periods with high T_b and high energy turnover (French 1985; Geiser and Kenagy 1988; Körtner and Geiser 2000; Carey et al. 2003; Geiser 2004). Torpor bouts of hibernators at low T_b usually last for several days to several weeks, but importantly bout duration is strongly temperature-dependent. Torpor bout duration decreases with increasing T_a over the T_a range that torpid hibernators are thermo-conforming and, of special interest to the present review, a high T_a around 20 to 30°C torpor bouts even in hibernators often last for less than a day (French 1985; Geiser and Kenagy 1988; Song et al. 1997; Geiser and Brigham 2000). Hibernation is currently known to occur in many mammalian orders (Lyman et al. 1982; Geiser 1998), but only in a single bird species, the poorwill, *Phalaenoptilus nuttallii* (Withers 1977; Brigham 1992; Geiser and Ruf 1995; Geiser 1998; McKechnie and Lovegrove 2002; Woods and Brigham 2004). Hibernators that reduce their T_b by >10°C during torpor are generally small (median mass 85 g), most weigh between 10 and 1,000 g, and all weigh <10 kg (Geiser and Ruf 1995). Many hibernators fatten extensively before the hibernation season, refuse to hibernate when lean, and rely to a large extent on stored fat (or in some species stored food) for an energy source in winter.

Hibernating species usually reduce their T_b to below 10°C, with a minimum of -3°C in arctic ground squirrels, *Spermophilus parryii* (Barnes 1989), and most, with the exception of large carnivores (which express shallow torpor with <10°C T_b reduction) and perhaps tropical hibernators, have T_b minima of around 5°C (Geiser and Ruf 1995; Fietz et al. 2003; Grigg et al. 2004; Dausmann et al. 2005). The

TMR in hibernators is on average reduced to about 5% of the BMR, but can be as little as 1–2% of the BMR in small hibernating species that employ extensive metabolic inhibition to reduce MR in addition to temperature effects due to the low T_b (Storey and Storey 1990; Geiser and Ruf 1995; Guppy and Withers 1999; Geiser 2004; Willis et al. 2005). Even when the high cost of periodic arousals is considered, energy expenditure during the mammalian hibernation season is still reduced to 4–15% of that of an animal that would have remained normothermic throughout winter (Wang 1978; Geiser 2007). This enormous reduction in energy expenditure is, perhaps, best illustrated by the fact that many hibernating mammals can survive for 6–8 months or more entirely on body fat that has been stored prior to the hibernation season (French 1985; Geiser 2007; Bieber and Ruf 2009).

5.3 Daily Torpor

Daily torpor in the daily heterotherms is the other widely used pattern of torpor in mammals and, in contrast to hibernation, also is commonly found in birds (Geiser and Ruf 1995; McKechnie and Lovegrove 2002). Daily heterotherms, in contrast to the hibernators, are incapable of multiday torpor bouts. Daily torpor lasts only for hours rather than days and is usually, but not always (Körtner and Geiser 2009), interrupted by daily foraging and feeding. Nevertheless, daily torpor may occur continuously over several days and up to months (Körtner and Geiser 2009). On average, daily heterotherms are smaller (median mass 19 g) than hibernators, most weigh between 5 and 100 g and their overall mass range is ~2–9,000 g (Geiser and Ruf 1995). In diurnal species, such as many birds, daily torpor is usually restricted to the night, whereas in nocturnal mammals and birds it is common in the second part of the night and/or the early morning. Generally, daily torpor is less seasonal than hibernation and can occur throughout the year, although its use often increases in winter. Although daily torpor may be expressed as a response to acute energy shortage, in some species, it is employed regularly to balance energy budgets, even when food availability appears favorable. For example, several small arid zone marsupials regularly enter daily torpor in the laboratory when food is freely available (spontaneous torpor), which appears to reflect the generally low energy availability in their natural desert environment where they may enter torpor on every night in winter (Geiser and Baudinette 1987; Geiser 2003; Warnecke et al. 2008; Körtner and Geiser 2009). Moreover, both in the laboratory and field, some of these desert marsupials, as for example the mulgara (*Dasyurus cristicauda*), appear to use daily torpor during pregnancy to facilitate fat storage for the following energetically demanding period of lactation (Geiser and Masters 1994; Körtner et al. 2008).

Many daily heterotherms, unlike most hibernators, do not show extensive fattening before the season when torpor is most commonly employed, and mainly enter torpor at times when body mass is low (Heldmaier and Steinlechner 1981; Geiser 1988; Holloway and Geiser 1996). Administration of the hormone leptin, which simulates

the presence of high fat stores, inhibits daily torpor, further supporting the interpretation that daily torpor is employed predominantly when animals are lean (Geiser et al. 1998). When food is withheld from small daily heterotherms for several days in captivity they will perish (Kennedy and MacFarlane 1971), whereas small hibernators can survive for months and up to an entire year (Geiser 2007; Bieber and Ruf 2009). The main energy supply of daily heterotherms, even in the main torpor season, remains food rather than stored body fat, and they appear to attempt to balance energy expenditure and uptake on a daily or at least short-term basis (Körtner and Geiser 2000). In most of the daily heterotherms, such as small insectivorous/carnivorous marsupials (e.g., *Sminthopsis* spp.) and mice (e.g., *Peromyscus* spp.), T_b usually falls to between 10 and 20°C (mean 17°C), whereas in some hummingbirds values below 10°C have been reported (Carpenter 1974; Geiser and Ruf 1995; McKechnie and Lovegrove 2002). In others, mainly large species, such as tawny frogmouths (*Podargus strigoides*) or American badgers (*Taxidea taxus*), T_b is maintained just below 30°C (Harlow 1981; Geiser and Ruf 1995; Körtner et al. 2000). The TMRs of daily heterotherms are, on average, reduced to about 30% of BMR although this percentage is strongly affected by body mass and other factors. When RMR at low T_b is used as a point of reference, reductions of MR during daily torpor to about 10 to 20% of that in normothermic individuals at the same T_b are common. Overall, daily energy expenditure is usually reduced to 10–80% on days when daily torpor is employed in comparison to days when no torpor is used, primarily depending on the duration and intensity of activity, the duration of the torpor bout and torpor depth, and whether or not they employ basking during rewarming from torpor and during normothermia (Ruf et al. 1991; Holloway and Geiser 1995; Geiser et al. 2002; Warnecke et al. 2008; Körtner and Geiser 2009).

5.4 Aestivation

While hibernation and daily torpor differ functionally with regard to fat storage, metabolic rate reduction, and, perhaps most importantly, the ability to express or not express multiday torpor bouts, aestivation or torpor at high T_b or in summer does not appear to differ functionally from other forms of torpor and to a large extent reflects the higher T_b caused by high T_a (Song et al. 1997; Geiser and Brigham 2000; Wilz and Heldmaier 2000). Moreover, hibernation and aestivation are often difficult to distinguish temporally because some hibernators begin to aestivate in late summer, often around the hottest part of the year, but then continue to hibernate throughout the autumn and the winter and some species even into the spring. Clearly, it is of no significance to the hibernator whether they “aestivate” before 22 September (first day of northern hemisphere autumn) or “hibernate” thereafter; rather, what is of significance to the hibernator is that soil temperatures in late summer/autumn will be substantially higher than in winter (e.g., Nicol and Andersen 2007).

Thus, from an ecological point of view, aestivation in summer has different challenges and requirements than torpor in winter. Summer, often, is hot, which can

reduce food and water availability in many regions, but without access to low T_a for a substantial reduction of T_b . However, in comparison to studies on torpor at low T_a , quantitative information on torpor at high T_a or during summer is limited and in the past was to a large extent, based on laboratory investigations as reviewed by Hudson and Bartholomew (1964). New data from the laboratory and also from the field are now available and these suggest that use of torpor during mild thermal conditions is far more common than is widely believed at present (Song et al. 1995, 1997; Turbill et al. 2003a, 2003b; Stawski et al. 2008).

5.4.1 Torpor in Summer

Animals often enter torpor in secluded places, including burrows and caves where T_b is buffered from thermal extremes and therefore well below that of the maximum daily T_a of the surrounding air. Thus, torpor does not appear to be induced by heat stress *per se*, but rather a reduction of food and water caused by heat, and the animals often make use of cool underground conditions to lower T_b . If animals do not shelter in thermally stable and relatively cool refugia in summer, as for example, bats roosting under leaves or in tree hollows, then they enter torpor during the coolest, not hottest, part of the day (Turbill et al. 2003a; Stawski et al. 2008).

Torpor in summer occurs in diverse mammals including monotremes (echidna), marsupials (small dasyurids and possums), placentals (bats, rodents), and birds (nightjars and hummingbirds), as is described below.

Monotremes: Free-ranging echidnas (*Tachyglossus aculeatus*) in Tasmania commence hibernation during the warmest part of the year (in late summer) with initial minimum T_b of around 20°C and short torpor bouts and continue to hibernate for up to 7 months (Nicol et al. 2008). Even in warm areas such as southwestern Queensland, echidnas occasionally enter torpor for 1 day in summer (Brice et al. 2002).

Marsupials: Use of summer torpor in marsupial mammals is well documented. Captive arid zone insectivorous/carnivorous marsupials (*Sminthopsis* spp. and *Dasyuroides byrnei*) display torpor throughout the year, although use of spontaneous torpor (food ad libitum) is reduced in summer and torpor is generally deeper in winter than in summer (Geiser and Baudinette 1987; Geiser 2003). Pygmy-possums (*Cercartetus* spp.) also display torpor, including prolonged torpor, in summer (Geiser and Körtner 2004); however, a detailed seasonal investigation has not been conducted in this group to see whether there are functional changes during the year. In the wild, torpor in the eastern pygmy-possum *Cercartetus nanus* occurs in all seasons including in early summer, but not in late summer to midwinter, when banksia trees (*Banksia integrifolia*), a major source of nectar, are flowering and animals reproduce (Bladon et al. 2002). Torpor in spring and autumn also occurs in honey possums (*Tarsipes rostratus*) captured in pit traps (Collins et al. 1987).

Placentals: Summer torpor in placental mammals is best known for bats. It was already recognized over 170 years ago that small insectivorous bats (Microchiroptera or microbats) display prolonged torpor in winter and brief bouts of torpor in summer

(Hall 1832). Nevertheless, detailed information on torpor in free-ranging bats in summer has only recently become available with the development of small temperature-sensitive radio transmitters. Long-eared bats (*Nyctophilus* spp.), which hibernate and display bouts of torpor lasting up to 2 weeks in winter in a cool-temperate area of Australia (Turbill and Geiser 2008), enter torpor essentially every day in summer, even when daily maximum T_a reaches 30°C (Turbill et al. 2003b). On cool summer days, they may extend torpor bouts for up to 2 days (Turbill et al. 2003b). Similarly, a Canadian bat (*Myotis evotis*) uses torpor every day between May and August and even when reproductively active (Chruszcz and Barclay 2002). Female *Myotis daubentonii* in central Germany enter torpor mainly during postlactation in late summer, whereas males use torpor frequently even during their reproductive period in early summer (Dietz and Kalko 2006). Pregnant female hoary bats (*Lasiurus cinereus*) enter prolonged torpor in southern Canada during inclement weather in late spring/early summer; this is likely not just to conserve energy, but also to delay parturition until conditions are more favorable for neonatal survival (Willis et al. 2006). Even in subtropical areas of Australia and South Africa, small insectivorous bats display short bouts of torpor in summer in the wild (Turbill et al. 2003a; Vivier and van der Merwe 2007; Stawski et al. 2008). Although torpor is widely used by insectivorous microbats in summer, their torpor bouts are generally shorter and are not as deep as in winter, apparently reflecting ambient thermal conditions, rather a seasonal change in physiology (Geiser and Brigham 2000).

Interestingly, seasonal changes in the use of torpor by the nectarivorous blossom-bat *Syconycteris australis* (Megachiroptera) from the subtropical east coast of New South Wales were the opposite of those observed for insectivorous microbats and many other heterothermic mammals. For *S. australis* captured in winter, average torpor bout duration was short (5.5 h) and shallow, whereas in summer torpor was deep and bouts lasted for 7.3 h on average (Coburn and Geiser 1998). While these findings may seem counterproductive at first glance, different day length and food availability in summer and winter appear to explain the unusual seasonal response. In winter, T_a on the New South Wales north coast is relatively mild and bats can forage for prolonged periods during long nights and have access to an abundance of flowering plants (Coburn and Geiser 1998). 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 by *S. australis* appears to be an appropriate physiological adaptation to ecological constraints of their subtropical habitat.

Rodents are another group of placental mammals known to aestivate. During a severe drought in Pennsylvania, free-ranging woodchucks (*Marmota monax*) entered short bouts of torpor in August with T_b fluctuating between ~25 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). For five ground squirrel species (*Spermophilus* spp.) from a wide range of North-American habitats, the period of heterothermy begins in late summer/early autumn (Barnes 1996) and often this coincides with the reduction of green vegetation.

For the small South-American cricetid rodent *Calomys musculus*, torpor was employed in summer at T_a 25°C when MR fell by 75% in comparison to resting values at the same T_a (Bozinovic and Rosenmann 1988). European dormice (*Glis glis*) hibernate for 7–8 months from autumn to spring, but after their final arousal in spring, nonreproductive individuals may reenter a period of dormancy from early or midsummer (Bieber and Ruf 2009). Summer-acclimated African dormice (*Graphiurus murinus*) exhibit torpor at T_a 25°C (Webb and Skinner 1996), and other dormice (*Muscardinus avellanarius*, *Glirulus japonicus*, *Dryomys nitedula*, and *Eliomys quercinus*), as well as birchmice, *Sicista betulina*, also are known to display torpor in summer (French 2008).

Birds: Although it is widely believed that birds migrate to avoid adverse conditions and employ torpor less frequently than mammals, several birds are known to display torpor use even in summer. Free-ranging American poorwills (*P. nuttallii*) occasionally enter torpor in June (Woods and Brigham 2004). They also used torpor when incubating, but only rarely and during inclement weather (Kissner and Brigham 1993). Summer torpor also has been observed for a captive spotted nightjar (*Eurostopodus argus*) in Australia in response to a 13% loss of body mass (Dawson and Fisher 1969). Andean humming birds (*Oreotrochilus estella*) roosting in caves at about 4,000 m elevation will enter torpor in both winter and summer, although summer torpor is less frequent and shorter than winter torpor (Carpenter 1974). Migrant North American hummingbirds (*Selasphorus rufus*) use nocturnal torpor extensively in summer, not in response to energy shortage, but rather to reduce thermoregulatory energy expenditure and enhance fat storage for migration (Carpenter and Hixon 1988; Hiebert 1993). Captive passerine sunbirds (*Nectarina famosa*) from South Africa also enter nocturnal torpor in summer at low T_a (Downs and Brown 2002).

5.4.2 Torpor during Development and Growth

A substantial part of the development of birds and mammals occurs during summer when the young ones are small and often not well insulated, and require substantial amounts of energy for thermoregulation. Although high energy costs are likely to provide a strong selection pressure for heterothermy in these young ones during this time, only limited data are available on torpor during development in summer.

Torpor during development and growth has been observed for small (adult body mass 25–110 g) insectivorous/carnivorous marsupials (family Dasyuridae) (Geiser et al. 2006; Geiser 2008). For the four species examined (*Sminthopsis macroura*, *Antechinus* spp., and *D. byrnei*), torpor was deeper and longer at some stage of juvenile development, usually in summer, compared with adults in other parts of the year (Geiser 2008), suggesting that it may be an important measure for energy conservation during growth.

In placental mammals, torpor has been described during development in the insectivores, bats, and rodents. Juveniles of the insectivorous shrew (*Crocidura russula*) entered daily torpor at a body mass of ~5 g (~40% adult mass) from day 7

postpartum (Nagel 1977). Free-ranging early volant juvenile bats (*Eptesicus fuscus*), which hibernate for prolonged periods in winter, entered shallow bouts of torpor in summer (Hollis and Barclay 2008). Captive juveniles of the herbivorous hamster *Phodopus sungorus* displayed daily torpor in response to food restriction by 2 weeks after they became endothermic (Bae et al. 2003).

Avian species known to be heterothermic during development include the orders Charadriiformes (shorebirds), Coliiformes (mousebirds), Apodiformes (swifts) and Passeriformes (songbirds). Juvenile storm-petrels (*Oceanodroma furcata*), in their natural burrows in Alaska, employed torpor soon after becoming endothermic over a period of ~2 weeks during the growth phase when body mass increased from ~10 to the adult mass of 60 g (Boersma 1986). In mousebirds (*Urocolius macrourus*) from the Afrotropics, torpor was first observed at 55% of adult mass, 10 days after hatching, essentially at the same time as they were capable of endothermic thermoregulation (Finke et al. 1995). Juvenile swifts (*Apus apus*) from Finland (Koskimies 1948) displayed torpor after 6 days of fasting. They were able to survive fasting for up to 12 days, likely because of their large storage of fat and use of nocturnal torpor. Juvenile martins (*Delichon urbica*) from cool-temperate Europe were able to enter and arouse from torpor by 11 days posthatching, 1 day after endothermic thermoregulation was established (Prinzinger and Siedle 1988). Torpor could be induced by starvation at a body mass of about 12 g (~60% of adult mass).

Thus, although not widely investigated, it appears that torpor is an important adaptation during the development of mammals and birds in summer to minimize energy loss and, perhaps, to spare valuable nutrients for the growth of young ones.

5.4.3 Torpor in or Near the TNZ

Within the T_a range in which torpor is usually expressed, use of torpor is generally less frequent at high T_a than at low T_a . For example, dunnarts (*S. macroura*), under a range of food and water regimes, have a higher torpor frequency at T_a 18°C than at T_a 28°C, which is near their lower critical T_a of the TNZ (Song and Geiser 1997). Nevertheless, the species still used torpor at T_a 28°C, especially when food and water were withheld, but to a lesser extent than when they were available (Song and Geiser 1997). *S. macroura* even enter daily torpor at and slightly above T_a 30°C within the TNZ, with a reduction of T_b by about 5°C and MR by about 33% in comparison to the BMR (Song et al. 1995). Pygmy-possums *C. nanus* also enter torpor in the TNZ at T_a 29°C; in this species, a reduction of T_b by only 2.9°C results in a reduction of MR in comparison to BMR by ~50% (Song et al. 1997), emphasizing the effective metabolic savings possible even at high T_b in hibernating species.

Bats also use torpor at T_a slightly below or within the TNZ. For example, small tropical megabats, the blossom bats (*Macroglossus minimus*), enter daily torpor at T_a of 25°C only slightly below the TNZ (Bartels et al. 1998). It has been known for some time that small micobats, such as *Myotis lucifugus*, which are capable of hibernation, may successfully employ small reductions of T_b for energy conservation

at high T_a (Hock 1951; Studier 1981). Torpid long-eared bats (*Nyctophilus geoffroyi*), like pygmy-possums, can reduce MR by $>2/3$ at high T_a near the lower critical T_a of the TNZ, with only a small reduction of T_b by about 6°C (Geiser and Brigham 2000; Turbill et al. 2008). If these micobats relied on temperature (Q_{10}) effects alone, then MR would be reduced by only one-third and this would limit the potential for energy and water conservation.

Other placental mammals that employ torpor at high T_a include spiny mice (*Acomys russatus*) held at T_a 30°C, that by employing torpor can maintain a more or less stable body mass with only 50% of ad libitum food (Gutman et al. 2006). Gerbils (*Gerbillus pusillus*) use daily torpor at about T_a 30°C to substantially reduce energy expenditure in comparison to normothermic resting individuals (Buffenstein 1985). Pouched mice (*Saccostomus campestris*) enter torpor near their TNZ at T_a 25°C when food is reduced to 70% of ad libitum rations (Lovegrove and Raman 1998). Moreover, gray mouse lemurs (*Microcebus murinus*) express short bouts of shallow torpor at T_a 30°C when acclimated to long summer photoperiod and food is reduced by 80% (Giroud et al. 2009). The most extreme cases in this regard are free-ranging fat-tailed lemurs (*Cheirogaleus medius*) from tropical Madagascar and long-eared bats (*Nyctophilus bifax*) from subtropical Australia (Dausmann et al. 2005; Stawski et al. 2009). Both species use multiday torpor bouts when hibernating in rather exposed conditions with T_b fluctuating daily by up to 15–20°C, but without obvious endothermic arousals even when T_a and T_b rise to about 30°C. Similarly, the Madagascar tenrec (*Echinops telfairi*) occasionally used multiday torpor bouts at high T_a with pronounced daily fluctuations of T_b , but mainly displayed short bouts of torpor with daily arousals (Lovegrove and Génin 2008).

In birds, limited information is available on torpor at high T_a . However, captive cloven-feathered doves (*Drepanoptila holosericea*) enter shallow torpor at T_a 27°C even when food is available (Schleucher 2001).

5.4.4 Torpor Induction via Water Restriction

As we have seen in the previous section, torpor can be induced even under thermo-neutral or near thermo-neutral conditions mainly by restriction of food. If aestivation, as often stated, is a response to water shortage, then we would assume that withdrawal of water has a similar effect as withdrawal of food. Surprisingly, information on this topic is limited and the results are equivocal.

Cactus mice (*Peromyscus eremicus*), when water deprived in midwinter, did not enter torpor, lost weight and died after 6–11 days, although they had free access to mixed bird seeds. In contrast, food restriction resulted in torpor use in other individuals (MacMillen 1965). In summer, similar results were obtained after water deprivation for eight out of ten individuals. However, the two individuals that regularly displayed torpor did survive, suggesting that torpor use due to water deprivation allows some individuals to survive water shortages (MacMillen 1965).

For gerbils (*G. pusillus*), 20% of individuals with access to dry food but without water entered torpor, although torpor use increased to 88% when both food and water were withheld (Buffenstein 1985). Similarly, shallow torpor was observed for Inca doves (*Scardafella inca*) with access to food but experiencing water deprivation, although simultaneous withdrawal of food and water resulted in deeper torpor (MacMillen and Trost 1967). For dunnarts (*S. macroura*), daily torpor was expressed at T_a 18 (63%) and 28°C (35%) when food and water were available; when food and water were withheld, torpor use increased substantially, 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 reduced consumption of dry food by the animals without access to water rather than the lack of water *per se* (Song and Geiser 1997).

5.4.5 Energy Conservation at High T_a

High T_a prevents T_b from falling to low levels and therefore should limit the energy-conserving potential of torpor. Nevertheless, even small reductions in T_b result in substantial reductions in energy expenditure (Fig. 5.1). In comparison to BMR, a reduction of TMR associated with an approximately 10°C fall of T_b (i.e., at T_a 25°C) amounts to a 79% saving in an 85-g (average mass) hibernator and 58% in a 19-g (average mass) daily heterotherm (calculated from Geiser and Ruf 1995; Geiser 2004).

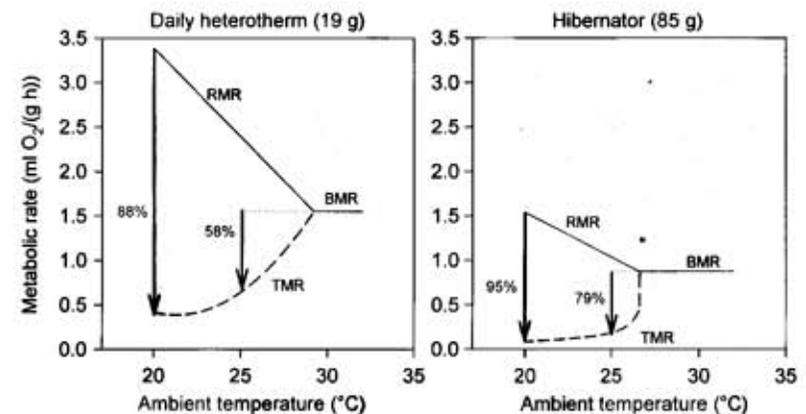


Fig. 5.1 Metabolic rates measured as the rate of oxygen consumption in an average daily heterotherm (body mass 19 g) and an average hibernator (85 g). Note the substantial reduction of metabolic rate from normothermic resting values at BMR (within TNZ) to torpid values (TMR) even at a high T_a of 25°C, which is associated by a fall of T_b by about 10°C. In comparison to RMR at T_a 20°C, which also entails a thermoregulatory component, and therefore is higher in the small daily heterotherm in comparison to the hibernator, the substantial fall of MR is associated by a fall of T_b by about 15°C

The greater reduction in the hibernator is due to the pronounced metabolic inhibition. In comparison to RMR of normothermic individuals at T_a 20°C, the reduction of TMR associated with a 15°C fall of T_b (i.e., at T_a 20°C) amounts to 95% in an average hibernator and 88% in an average daily heterotherm (calculated from Geiser and Ruf 1995; Geiser 2004; Geiser and Körtner 2004). The more pronounced MR reduction in the daily heterotherm in this case is largely due to its increased thermoregulatory cost (RMR) due to its small size (Withers 1992). These simple examples emphasize the enormous energy-conserving potential of both forms of torpor even at relatively mild T_a , even without considering the reduced costs of rewarming at high T_a and the possibility of passive rewarming (Lovegrove et al. 1999; Geiser et al. 2004).

5.4.6 Water Conservation

Although a reduction in energy expenditure is generally considered to be the major role of torpor, torpor also appears to be important for water conservation, especially, in species with limited access to free water. Free-ranging mouse-lemurs (*M. murinus*) using torpor have lower rates of water turnover than individuals remaining normothermic (Schmid and Speakman 2000). Evaporative water loss of torpid cactus mice (*P. eremicus*) is about 37% of that of normothermic individuals at the same T_a (MacMillen 1965). Similarly, for gerbils (*G. pusillus*) and marsupial dunnarts (*S. macroura*) daily torpor reduced evaporative water loss to about 20 to 40% of that in normothermic individuals (Buffenstein 1985; Cooper et al. 2005). More extreme reductions in evaporative water loss were observed for torpid bats (*Chalinolobus gouldii*) hibernating at T_a 10°C, which reduced evaporative water loss by almost 90% in comparison to normothermic individuals (Hosken and Withers 1997). Further, evaporative water loss of torpid honey possums (*T. rostratus*) during torpor was so low that it was not detectable with the available equipment (Withers et al. 1990).

Thus, torpor clearly reduces water loss and water turnover in mammals and is, therefore, of ecological importance. However, it would be worthwhile to unravel how much of the reduced water loss simply reflects a reduction in metabolism and T_b , rather than being a selective reduction in water requirements.

5.5 Conclusions

Torpor (i.e., aestivation) is widely used by mammals and birds in summer as well as at high T_a . Torpor during development in summer may be an important survival mechanism that not only helps in reduction of thermoregulatory energy expenditure but also may spare valuable nutrients for growth and therefore warrants further investigation. In adults, torpor even at relatively high T_a results in a substantial reduction of energy and water use and therefore plays a vital role in the survival of mammals and birds in a variety of habitats.

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