

# Hibernation: Endotherms

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Advanced article

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**The main function of hibernation and daily torpor in heterothermic mammals and birds (i.e. species capable of expressing torpor) is to conserve energy and water and thus to survive during adverse environmental conditions or periods of food shortage no matter if they live in the arctic or the tropics. However, the reduced energy requirements also permit survival of bad weather during reproduction to prolong gestation into more favourable periods, conservation of nutrients for growth during development, and overall result in reduced foraging needs and thus exposure to predators, which appear major contributing reasons why heterotherms are often long lived and have lower extinction rates than strictly homeothermic species that cannot use torpor. Known heterothermic mammals and birds are diverse with about 2/3 of mammalian orders and 1/3 of avian orders containing heterothermic species, and their number continues to grow.**

## Introduction

Endothermic mammals and birds differ from ectothermic organisms primarily in their ability to regulate body temperature by high internal heat production that is achieved through combustion of fuels. Because the surface area/volume ratio of animals increases with decreasing size, many small endotherms must produce enormous amounts of heat to compensate for heat loss via their surface during cold exposure. Obviously, prolonged periods of such high metabolic heat production can only be sustained by high food intake, and during adverse environmental conditions and/or food shortages, costs for thermoregulation may be prohibitively high. Therefore, many mammals and birds are

permanently homeothermic (i.e. maintain a constant high body temperature), but during certain times of the day or the year enter a state of torpor (Lyman *et al.*, 1982). Torpor in these 'heterothermic endotherms' is characterised by a controlled reduction of body temperature, metabolic rate and other physiological functions. **See also:** [Hibernation: Poikilotherms; Thermoregulation in Vertebrates](#)

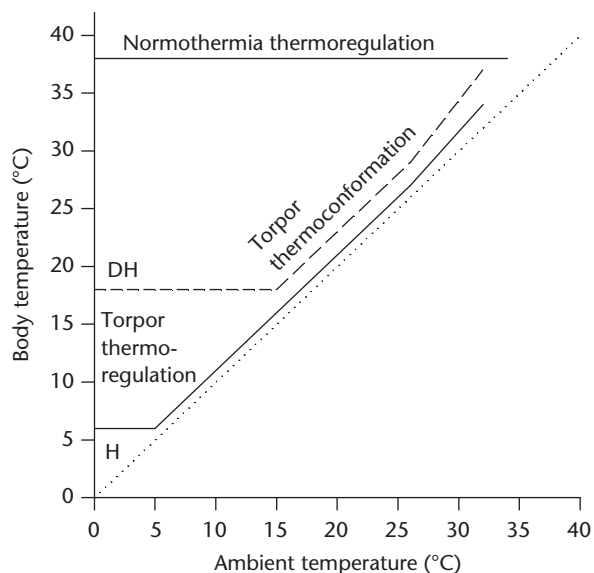
Thus the main function of torpor is to substantially reduce energy expenditure by substantially lowering metabolic rates. Other physiological changes during torpor include a substantial reduction of heart rate (in bats from about 500–1000 to about 20–40 beats per minute; in ground squirrels from about 300 to a minimum of 3 beats per minute), but although the cardiac output can fall as much as 98% during deep torpor, the blood pressure usually falls only by about 20–40% because blood viscosity increases with decreasing temperature. Breathing in many species, such as pygmy-possums, bats, hedgehogs and ground squirrels, is not continuous, but periods of poly-pnoea (a number of breaths in sequence – about 50 in hedgehogs) are interrupted by periods of apnoea (no breathing) that can last over an hour.

Although the reduction of metabolism and body temperature during torpor in heterothermic endotherms may be reminiscent of that in ectotherms, there are two features that clearly distinguish them from the latter. The first difference is that at the end of a torpor bout heterothermic endotherms can rewarm themselves from the low body temperatures during torpor using internal heat production, whereas ectotherms must rely on uptake of external heat. The second difference is that body temperature during torpor is regulated at or above a species-specific or population-specific minimum by a proportional increase in heat production that compensates for heat loss (Heller *et al.*, 1977). During entry into torpor the setting for body temperature is downregulated ahead of body temperature to a new lower set point. When body temperature reaches the new set point, metabolic heat production is used to maintain body temperature at or above the minimum during torpor (**Figure 1** and **Figure 2**), to prevent tissue damage and to maintain the ability of active rewarming from torpor. The control centres for this regulation are situated in the hypothalamus of the brain.

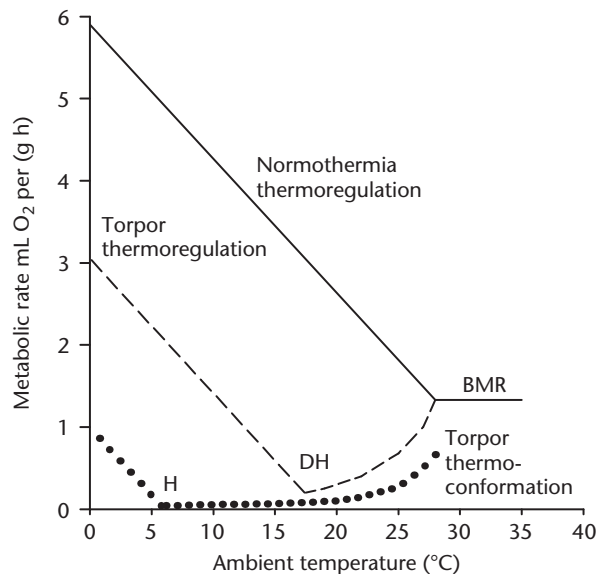
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**Figure 1** Body temperatures as a function of ambient temperature during normothermia (solid horizontal line, about 38°C) and torpor in a hibernator (H, solid line) and a daily heterotherm (DH, broken line) of similar size. The diagonal dotted line represents body temperature = ambient temperature. Averages from Geiser and Ruf (1995).



**Figure 2** Schematic diagram of metabolism, measured indirectly as oxygen consumption and expressed as per gram body tissue, during normothermia (solid line) and torpor (dashed or dotted line) of a 25 g hibernator (H) and a 25 g daily heterotherm (DH). In the temperature range in which torpid animals are thermoconforming (not using thermoregulatory heat production), the metabolic rate decreases curvilinearly with ambient temperature and thus body temperature. In the temperature range in which animals are thermoregulating during normothermia and torpor, the metabolic rate increases with decreasing ambient temperature to compensate for heat loss (see Figure 1). Values from Geiser and Ruf (1995) and Geiser (2004). BMR, basal metabolic rate.

Torpor is often confused with 'hypothermia', which also is characterised by reduced body temperatures and metabolism. However, whereas torpor is a physiological state that is under precise control, hypothermia, especially in a medical context, is nothing but a failure of thermoregulation often due to depletion of energy reserves, excessive cold exposure, or influence of drugs. Thus, the two terms should not be exchanged or confused. **See also:** [Cold-related and Heat-related Medical Problems](#)

## Hibernation and Daily Torpor

The two most common patterns of torpor appear to be hibernation (sequence of multiday torpor bouts) in the 'hibernators' and daily torpor in the 'daily heterotherms'. Both groups use bouts of torpor, which semantically makes them confusing.

Hibernation is often seasonal and usually lasts from autumn to spring. However, hibernators do not remain torpid throughout the 'hibernation season' (i.e. the time during which a sequence of multiday torpor bouts is expressed). Bouts of torpor, during which body temperatures are low and bodily functions are reduced to a minimum, last for several days or weeks, but are interrupted by periodic rewarming often by the use of internal heat production, followed by brief (usually less than one day) resting periods with high body temperatures and high energy turnover (= normothermic periods). Hibernating mammals are generally small (<10 000 g), most weigh between 10 and 1000 g, and their median mass is 85 g (Geiser and Ruf, 1995). Many hibernators fatten extensively before the hibernation season, rely to a large extent on stored fat for an energy source in winter, and during hibernation many adopt a ball-shape to minimise heat loss (Figure 3). **See also:** [Ecology of Storage and Allocation of Resources: Animals](#)

Hibernating species usually reduce their body temperature to below 10°C, with a minimum of -3°C in arctic ground squirrels (Barnes, 1998), although most have minimum body temperatures around 5°C (Figure 2) (Geiser and Ruf, 1995). The metabolic rate in torpid hibernators is on average reduced to about 5% of the basal metabolic rate (BMR) (the minimum maintenance metabolic rate of normothermic animals at rest and without thermoregulatory heat production) and can be less than 1% of that in active individuals. Even if the high cost of periodic arousals is considered, energy expenditure during the mammalian hibernation season is still reduced to about 2–15% of that of an animal that would have remained normothermic throughout winter. 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 before the hibernation season. In the most extreme case, hibernating eastern pygmy-possums (approximately 50 g pre-hibernation body mass) can survive for up to 12 months on approximately 30 g of stored fat (Geiser, 2007). However,



**Figure 3** A hibernating pygmy-possum (*Cercartetus concinnus*) curled into a tight ball to minimise the body surface area. Note: the animal has been turned over to show the position of appendages. Photo Geiser F.

some species such as chipmunks use stored food in addition to fat to get them through the winter. Whereas hibernation is mainly used by adult animals to survive the winter, recent evidence has shown that bats may use it to prolong the gestation period during adverse conditions in spring to delay parturition until weather and the chances for neonate survival improve (Willis *et al.*, 2006).

Entry into torpor in hibernators appears to be caused by the initial cessation of heat production for normothermic thermoregulation because the set point for body temperature falls below the body temperature (Heller *et al.*, 1977). As metabolic heat production at that point is no longer high enough to maintain a high thermal gradient between the body and the surroundings, body temperature declines. This fall in body temperature and the resulting temperature effects on the metabolic processes and an additional physiological inhibition of metabolism appear to be the reasons for the substantial fall in the metabolic rate below the BMR during hibernation (Geiser, 2004).

In some species, such as ground squirrels, entry into hibernation may involve a number of short torpor bouts with relatively high body temperature. However, such 'test drops' are not a prerequisite for hibernation since some species, such as arctic ground squirrels and pygmy-possums, can express long and deep bouts from the beginning of the hibernation season. Nevertheless, body temperature and metabolic rate generally are lowest in the middle of the hibernation season when torpor bouts are longest.

Daily torpor is the other widely used pattern of torpor in mammals and also in birds. This form of torpor is used by the 'daily heterotherms' and is usually not as deep as hibernation, lasts only for hours rather than days or weeks, and is usually interrupted by daily foraging and feeding.

Importantly, unlike hibernators, daily heterotherms cannot express multiday torpor. In many species, such as small carnivorous marsupials, blossom-bats and deermice, daily torpor is less seasonal than hibernation, and can occur throughout the year, although its use often increases in winter and in some species from high latitudes, such as Djungarian hamsters, appears to be restricted to winter (Körtner and Geiser, 2000). In contrast, in some warm climate species, such as in subtropical nectarivorous blossom-bats, daily torpor is deeper and longer in summer than in winter and this unusual seasonal pattern appears to be explained by the reduced nectar availability in summer (Coburn and Geiser, 1998). Daily torpor in some species appears to be used regularly to balance energy budgets even when environmental conditions appear favourable. In some hummingbirds, daily torpor is used not only to lower energy expenditure during adverse conditions, but apparently also to conserve energy during migration when birds are fat (Carpenter and Hixon, 1988). The marsupial mulgara appears to use torpor during pregnancy to store fat for the energetically demanding period of lactation (Körtner and Geiser, 2000). Daily torpor is also used during the development of several shrews, small marsupials and birds to spare energy and nutrients for growth (Nagel, 1977; Geiser, 2008). On average, daily heterotherms are even smaller than hibernators and most weigh between 5 and 50 g with a median of 19 g (Geiser and Ruf, 1995).

In contrast to hibernators, many daily heterotherms do not show extensive fattening before the season torpor is most commonly used, and often only enter torpor when their body mass is low. The main energy supply of daily heterotherms even in the main torpor season remains food rather than stored body fat. Body temperatures in daily heterotherms, such as small carnivorous marsupials and deermice, usually fall to around 18°C (Figure 2), although in some hummingbirds values below 10°C have been reported, whereas in other, mainly large species, such as tawny frogmouths, body temperatures just below 30°C are maintained (Geiser and Ruf, 1995; Körtner *et al.*, 2000). The metabolic rates during daily torpor are on average reduced to about 30% of the BMR although this percentage is strongly affected by body mass and other factors. When the energy expenditure at low ambient temperature is used as point of reference, reductions of metabolic rate during daily torpor to about 10–20% of that in normothermic individuals at the same ambient temperature are common (Figure 2). Overall daily energy expenditure is usually reduced by 10–80% on days when daily torpor is used in comparison to days when no torpor is used, primarily depending on the species, the duration of the torpor bout and torpor depth.

The reduction of metabolic rate in daily heterotherms appears to be largely caused by the initial decrease of heat production for normothermic thermoregulation during early torpor entry (Heller *et al.*, 1977) and, for reduction of metabolism below the BMR, temperature effects caused by the fall of body temperature (Geiser, 2004), which track ambient temperature above the body temperature set point

during torpor (Figure 1 and Figure 2). It appears that, in comparison to hibernators, daily heterotherms use less pronounced or no metabolic inhibition.

As stated above, torpor bouts in the daily heterotherms are shorter than one day, independent of food supply or prevailing ambient conditions. Hibernators can also show brief torpor bouts of less than one day early and late in the hibernation season or at high ambient temperatures. However, it appears that functionally these short torpor bouts are nothing but brief bouts of hibernation with metabolic rates well below those of the daily heterotherms even at the same body temperature (Song *et al.*, 1997). Thus, the term 'daily torpor' seems inappropriate to describe short torpor bouts of hibernators.

In contrast to hibernation and daily torpor, the term 'aestivation' is used to describe periods of torpor in summer or at high ambient temperatures, induced mainly by a reduced availability of food because of lack of water or heat. However, subtropical insectivorous bats enter torpor in summer even when insects appear abundant (Turbill *et al.*, 2003; Stawski and Geiser, 2010). In some ground squirrels, the hibernation season begins in the hottest part of the year and therefore qualifies as aestivation. The physiological differences between aestivation and hibernation or daily torpor, apart from the higher body temperature and thus metabolism during aestivation due to the relative high ambient temperatures, are generally small. However, some physiological differences have been observed between summer and winter torpor patterns suggesting that some seasonal changes do occur (Coburn and Geiser, 1998).

## Occurrence of Torpor in Mammals and Birds

In the past it was widely believed that hibernation and daily torpor were restricted to a few mammals and birds from cold climates. However, over recent years the number of

known heterothermic species has increased substantially and these are found in diverse avian and mammalian taxa and in a variety of climatic regions including arctic and alpine areas, deserts, as well as the subtropics and tropics (Table 1). See also: [Alpine Ecosystems](#); [Arctic Ecosystems](#); [Mammalia](#)

In birds, hibernation similar to that of mammals is presently known only for one North American nightjar relative, the common poorwill (*Phalaenoptilus nuttallii*; Brigham, 1992). Body temperatures of poorwills fall from about 38°C during normothermia to about 5°C during torpor and in southern California and Arizona they may remain torpid for several days in winter. See also: [Aves \(Birds\)](#)

In contrast to hibernation, daily torpor in birds is common. Many birds have normothermic body temperatures around 40°C whereas during daily torpor, body temperatures are usually in the range of 10–30°C, depending on the species. In diurnal birds daily torpor occurs at night. In nocturnal birds daily torpor often commences in the second part of the night or early in the morning, and two torpor bouts per day appear common (i.e. first torpor bout at night, second in the morning after arousal near sunrise; or first bout in the morning, second bout in the afternoon after arousal near midday). Daily torpor is known from many species in several avian orders including todies and kookaburras, mouse birds, swifts, hummingbirds, owls, nightjars, pigeons, and martins, woodswallows and sunbirds (McKechnie and Lovegrove, 2002; Schleucher, 2004; Smit and McKechnie, 2010). The largest bird presently known to enter daily torpor is the Australian tawny frogmouth (500 g), a nightjar relative (Körtner *et al.*, 2000). See also: [Hummingbirds \(Trochilidae\)](#)

In mammals, hibernation (multiday torpor) occurs in many species from all three mammalian subclasses (Geiser and Ruf, 1995). Hibernators include the egg-laying echidnas of Australia (Grigg *et al.*, 2004; Morrow and Nicol, 2009), the South American marsupial Monito del monte (Bozinovic *et al.*, 2004), and members of at least two Australian marsupial families, the pygmy-possums

**Table 1** Heterothermic birds and mammals

Birds	Mammals
Coraciiformes, kingfishers	Monotremata, egg-laying mammals
Coliiformes, mouse birds	Didelphiformes, opossums
Apodiformes, swifts	Microbiotheria, Monito del monte
Trochiliformes, hummingbirds	Dasyuromorphia, carnivorous marsupials
Strigiformes, owls	Notoryctemorphia, marsupial moles
Caprimulgiformes, nightjars	Diprotodontia, pygmy-possums and gliders
Columbiformes, pigeons	Edentata, armadillos
Passeriformes, songbirds	Rodentia, rodents
	Macroscelidea, elephant shrews
	Primates, primates
	Chiroptera, bats
	Insectivora, insectivores
	Carnivora, carnivores

(Burrmyidae) and feathertail gliders (Acrobatidae). In the placental mammals, hibernation occurs in armadillos (Superina and Boily, 2007), rodents (dormice, marmots, chipmunks, ground squirrels and hamsters), some small primates (fat-tailed lemur) (Dausmann *et al.*, 2004; Dausmann, 2008), bats (Microchiroptera), and the insectivores (hedgehogs, tenrecs) (Lovegrove and Genin, 2008). **See also:** Chiroptera (Bats); Insectivora (Insectivores); Macroscelidea; Marsupialia (Marsupials); Monotremata; Rodentia (Rodents)

Hibernation in bears is often referred to a 'winter sleep' because it differs somewhat from small hibernators with regard to the body temperature. In bears body temperature falls only by 3–5°C rather than by >30°C as in small hibernators. However, the metabolic rate in bears is as low as in small hibernators suggesting a similar physiology (Toien *et al.*, 2011). Nevertheless, in contrast to small hibernators in deep torpor, which are cold and stiff, bears are capable of coordinated movements and females may even suckle their young during the winter denning period. Other relatively large carnivores (badgers) also have relatively high body temperatures and short torpor bouts. **See also:** Carnivora (Carnivores)

Daily torpor is known from a very large number of small marsupial and placental mammals. It occurs in several marsupial families from South America (e.g. mouse opossums, Didelphidae) and Australia (e.g. carnivorous marsupials, Dasyuridae; small possums, Petauridae; honey possum, Tarsipedidae). In placentals, daily torpor occurs in rodents (deermice, gerbils and small Siberian hamsters), some primates (mouse lemurs and bush babies) (Nowak *et al.*, 2010; Schmid and Speakman, 2009), bats (e.g. small fruit bats), the insectivores (shrews) (Nagel, 1977), and some small carnivores (skunk) (Geiser and Ruf, 1995; Hwang *et al.*, 2007). **See also:** Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes)

Whereas most mammals appear to fit into one of these two groups (i.e. the hibernators or the daily heterotherms), not all species conform. For example elephant shrews (Macroscelidea) have low body temperatures and metabolism during torpor similar to those of hibernators, however, their torpor bouts last only for a few hours up to about 2 days (Lovegrove *et al.*, 2001; Mzilikazi *et al.*, 2002).

## Preparation for Hibernation

The time of hibernation in many species is controlled by a seasonal change in photoperiod. Shortening of the photoperiod in late summer or autumn often induces involution of reproductive organs and initiates physiological and behavioural changes in preparation for hibernation. However, not all species are photoperiodic. For example, many ground squirrel species show a strong innate circannual (yearly) rhythm that controls hibernation largely irrespective of photoperiod. Other species from unpredictable habitats show opportunistic hibernation and seem to enter prolonged torpor irrespective of season or

photoperiod, but at any time of the year when environmental conditions deteriorate (Körtner and Geiser, 2000).

**See also:** Circadian Rhythms

Preparation for hibernation involves primarily fattening and/or hoarding of food and selection of an appropriate hibernaculum. Selection of appropriate hibernacula is crucial especially in cold regions. Hibernators often use underground burrows, boulder fields, piles of wood or leaves, tree hollows, caves or mines. Hibernacula provide shelter not only from potential predators, but also from temperature extremes and potential desiccation. Many hibernacula in cold regions show temperatures a few degrees above the freezing point of water even when outside air temperature minima are well below freezing. Snow often acts as an additional thermal blanket. However, in tropical and subtropical regions temperatures of hibernacula are much higher, often around 20°C and may even show strong daily fluctuations (Dausmann *et al.*, 2004; Stawski *et al.*, 2009; Cory Toussaint *et al.*, 2010; Liu and Karasov, 2011). In tropical and subtropical regions exposure to freezing temperatures is rare so animals may hibernate in trees under leaves or bark, but also in houses or caves.

As many daily heterotherms enter torpor throughout the year they have to be able to do so without major preparation. However, in those species that show seasonal changes in torpor use, photoperiod, food availability and ambient temperature appear the major factors that affect the seasonal changes in physiology.

## Fat Stores and Dietary Lipids

Pre-hibernation fattening is common in many hibernators. Fat stores are important quantitatively because in many species they are the main source of energy throughout the prolonged hibernation season. Some species roughly double their body mass largely due to fat storage in autumn, but increases in body mass on the order of 10–30% are more common.

Although the quantity of fat is important as it is the main energy source in winter, the pattern of hibernation is also affected by the composition of body lipids. Function at low body temperature during mammalian torpor obviously requires physiological adaptations (Carey *et al.*, 2003). In ectothermic organisms one of the major adaptations for function at low temperatures appears to be an increase of polyunsaturated fatty acids in tissues and cell membranes. These lower the melting point of fats and increase the fluidity of cell membranes apparently to allow function at low temperatures. Although not as clear cut as in ectotherms, polyunsaturated fatty acids also show significant increases in depot fat and some membrane fractions of torpid hibernators. However, as vertebrates are unable to synthesise most polyunsaturated fatty acids, their proportion in tissues and cellular membranes can only be raised by dietary uptake. Polyunsaturated fatty acids are required not only as building blocks for cellular membranes but also

for synthesis of some hormones. **See also:** [Fatty Acids: Structures and Properties](#); [Lipids](#)

Dietary polyunsaturated fatty acids have been shown to enhance torpor in hibernators as well as in daily heterotherms (Geiser and Kenagy, 1987; Frank, 1994; Florant, 1999). Ground squirrels and chipmunks fed on a diet rich in polyunsaturated fatty acids have lower body temperatures and metabolic rates and longer torpor bouts than conspecifics on a diet rich in saturated fatty acids. This should increase the chance of winter survival because energy expenditure is reduced. Short photoperiod also affects the selection of polyunsaturated fatty acids (Hiebert *et al.*, 2003), but even without the availability of different dietary fats, incorporation of unsaturated fatty acids is increased under short photoperiod apparently by selective uptake for the preparation of the apparently imminent winter (Geiser *et al.*, 2007). In the wild, ground squirrels select food rich in polyunsaturated fatty acids during pre-hibernation fattening apparently to enhance winter survival (Frank, 1994). In alpine marmots the increase in polyunsaturated fatty acids in cellular membranes during pre-hibernation appears to occur without diet selection and may be controlled by photoperiod or a circannual rhythm (Arnold *et al.*, 2011). However, it appears that monounsaturated fatty acids, which can be synthesised by vertebrates, may be used to some extent for function at low temperatures to compensate for lack of dietary polyunsaturates (Falkenstein *et al.*, 2001; Fietz *et al.*, 2003). In large hibernators, such as marmots, some ground squirrels and echidnas, feeding on a diet of appropriate composition and consequently minimal energy use in winter may also increase fitness. This is because the chance of successful mating in males, which usually emerge from hibernation before females in early spring when food is still limited, is dependent on sufficient stored fat having been accumulated in the previous autumn and spared during hibernation.

## Body Size and its Implications

Deep torpor is currently known to occur only in endotherms that are smaller than 10 kg. Nevertheless, the range of body mass from about 2 g in shrews and bats to 10 000 g in marmots and echidnas has profound implications on thermoenergetics. A small 2 g heterotherm will have much higher heat loss and much lower capacity of fat storage than a large 10 000 g heterotherm and consequently should be more energetically challenged. It is therefore important that small heterotherms enhance energy savings during torpor if they are to survive periods of limited energy supply. Hibernators and daily heterotherms appear to have different approaches to overcome size-dependent energy challenges. **See also:** [Ecological Consequences of Body Size](#)

In daily heterotherms, the minimum body temperature that is metabolically defended during torpor is a function of body mass (Geiser and Ruf, 1995). Small daily heterotherms (<10 g; e.g. shrews, hummingbirds) commonly have minimum body temperatures that are around or

below 15°C, whereas large daily heterotherms (approximately 1000 g; e.g. quolls) commonly have minimum body temperatures around 25°C. The greater reduction in body temperatures will enhance energy savings in the small species because their lower body temperatures will further reduce the metabolic rate during torpor via temperature effects (**Figure 1** and **Figure 2**). Moreover, the low minimum body temperature during torpor will lower the likelihood of reaching the body temperature set point and requiring thermoregulation during torpor. As predicted from the relationship of body temperature and body mass, the reduction of metabolism during daily torpor in comparison to BMR is also a function of body mass. On average, species weighing around 50–100 g (e.g. mice, *mulgara*) reduce their metabolic rate during torpor to about 50% of BMR whereas species weighing around 10 g (e.g. mouse opossums, *planigales* and *ningauis*) reduce the metabolic rate during torpor to about 10–30% of BMR, reflecting the greater reduction of body temperature in the smaller species.

In hibernators the minimum body temperature is not a function of body mass (Geiser and Ruf, 1995). Most likely because of the implication of the freezing of body fluids, most hibernators have minimum body temperatures around 5°C no matter if they weigh 5 or 5000 g. Obviously it is not possible to lower body temperatures much below 0°C and the common values slightly above the freezing point of water suggest that many species have been selected for some safety margin. How then do small hibernators survive on limited energy stores with essentially the same body temperature as large hibernators? Although both large and small hibernators appear to use metabolic inhibition in addition to temperature effects to lower energy expenditure during torpor, the reduction of metabolism in small species is more pronounced. Thus, the reduction of energy metabolism during torpor in species weighing about 10 g can be as little as 1% of the BMR whereas in hibernators weighing around 1000 g it is about 10% of BMR. The greater reduction of energy metabolism in small in comparison to large hibernators is one of the reasons why the former are able to survive a prolonged hibernation season despite limited fat stores. However, other factors may further lower energy expenditure of small hibernators during torpor. It has been suggested that, on average, small species display longer torpor bouts than large species (French, 1985) and the lower arousal frequency would further reduce energy requirements during the hibernation season. Moreover, hoarding of food as in chipmunks or foraging during winter as in some bats provides small hibernators with additional avenues to supplement internal energy stores.

The variation of body temperature and metabolic rate during torpor is of course not exclusively affected by body mass. Not surprisingly, the variation around the regression lines or the averages (Geiser and Ruf, 1995) appears also to be affected by the climate of the habitat of a particular species. Similar-sized species from cold climates tend to have lower minimum body temperatures than those from

the tropics. In species that have a wide distribution range with different populations exposed to different climates, the minimum body temperature can show intraspecific variations reflecting the thermal conditions of the habitat to at least some extent.

## Periodic Arousals

Periodic arousals consume most of the energy during the hibernation season and, from an energetic point of view, it would be advantageous if the animals remained torpid throughout winter. The possible reasons for these periodic arousals are poorly understood, but several hypotheses have been developed to explain their regular occurrence (Körtner and Geiser, 2000). One hypothesis states that physiological imbalances develop during hibernation that are rectified during normothermic periods. This could involve depletion of nutrients, as for example, blood glucose, that have to be resynthesised, or loss of body water during torpor that has to be replenished. Arousals could also be caused by accumulation of noxious substances that cannot be excreted because of the reduced blood pressure during torpor, high pressure in the urinary bladder that has to be relieved, or to catch up with slow wave sleep which is abolished at low body temperatures. Another hypothesis postulates that torpor bouts may be controlled by a biological clock and that animals arouse according to this internal signal to check their surroundings periodically.

The thermal dependence of torpor bout duration of hibernators supports the view that periodic arousals are determined by both metabolic processes and the body temperature experienced during torpor (Geiser and Kenagy, 1988). The duration of torpor bouts in hibernators increases with decreasing ambient temperature above the body temperature set point (i.e. when animals are thermoconforming and metabolic rates and body temperatures fall), but decreases at ambient temperatures below the body temperature set point (i.e. when metabolic rates increase, but body temperature is maintained at a minimum). This suggests that the metabolic processes responsible for production of noxious products or depletion of nutrients provide the stimulus for arousal, but this appears to be modulated by body temperature as the sensitivity to such stimuli should decline with a lowering of body temperature (Geiser and Kenagy, 1988). However, as the predictable seasonal changes of torpor bout duration during the hibernation season even under constant thermal conditions (long bouts in the middle, short bouts at the beginning and end) are likely to be controlled by a biological clock, the two hypotheses do not appear to be mutually exclusive, but may function together to control different aspects of the timing of arousals.

The selection of thermally appropriate hibernacula is important, because, at an ambient temperature close to the body temperature set point, metabolic rates are lowest and arousals are least frequent and therefore energy expenditure will be minimal. Selection of a hibernaculum with a

temperature below the body temperature set point for much of the hibernation season should be detrimental because of the increased energy expenditure. However, it is likely that there is also a strong selective pressure to lower the set point to values below those experienced within hibernacula, as individuals hibernating at ambient temperatures below their body temperature set point will have a reduced chance of winter survival because energy stores will be depleted well before spring, whereas individuals with a low set point will survive and reproduce. Interestingly, alpine marmots do successfully hibernate at ambient temperatures below their body temperature set point for some of the winter. But this species is very large and uses social hibernation to enhance the chance of winter survival, particularly that of juveniles (Arnold, 1993). Social thermoregulation in relatively large skunks allows a reduction in torpor use (Hwang *et al.*, 2007).

In daily heterotherms the function of arousals is more obvious than in hibernators. Time of arousal often shows little flexibility and coincides with the time of the beginning of the subsequent activity period (i.e. late afternoon in nocturnal species, such as blossom-bats, and late night in diurnal species, such as hummingbirds). In some nocturnal species arousal from daily torpor is common around midday, most likely because in the wild these species experience at least partial passive rewarming when ambient temperature rises (Körtner and Geiser, 2000). In contrast to arousals, the timing of torpor entry is often a function of ambient temperature and/or food availability. When food is plentiful and ambient temperatures are high, entry into daily torpor in nocturnal species, such as small dasyurid marsupials, is usually delayed toward the beginning of the rest phase, whereas entry occurs in the activity phase when ambient temperatures are low or food is restricted. Thus, the duration of torpor bouts is lengthened and energy expenditure is reduced appropriately by shifting the time of torpor onset.

Heat for endogenous rewarming at the end of a torpor bout is generated by muscle shivering and, in placental mammals, to some extent from nonshivering thermogenesis in brown fat. Rewarming rates are mass-dependent. Small species (approximately 10 g, such as bats) can rewarm at maximum rates of over 1°C per minute, whereas large species (approximately 5000 g, such as marmots or echidnas) manage only around 0.1°C per minute. However, maximum rewarming rates are not sustained throughout the entire arousal process, which usually lasts less than 1 h in small species, several hours in large hibernators, and, in elephants, would require several days. Thus, as with most facets of hibernation and daily torpor, rate of rewarming is affected by body size and provides a further explanation as to why deep torpor is restricted to small species.

## Passive rewarming

As we have seen above, endothermic rewarming from torpor is energetically expensive requiring most of the energy used during hibernation. It reduces the savings

accrued from daily torpor and may cause death of light individuals during hibernation if they arouse too frequently. To reduce these costs, desert dasyurid marsupials in the field, which use daily torpor in winter on up to 100% of days, use basking in the sun during rewarming from torpor in late morning (Geiser *et al.*, 2002; Warnecke *et al.*, 2008). Basking during torpor also appears to occur in elephant shrews (Mzilikazi *et al.*, 2002). Body temperatures in basking dasyurids in the wild can be extremely low, and often are between 15 and 20°C. Basking during rewarming from torpor can reduce rewarming costs by up to 85% (Geiser *et al.*, 2004). Rewarming costs can also be reduced using daily fluctuations of ambient temperature to passively raise body temperature. This approach appears to be widely used by free-ranging primates, bats and other mammals (e.g. Dausmann 2008; Stawski *et al.*, 2009), and, as for basking, reduces costs of rewarming enormously (Lovegrove *et al.*, 1999).

## Torpor and extinctions in mammals

Whereas torpor is effective in reducing energy and water needs during adverse conditions it appears to have other functions in relation to survival. Recent analyses have proposed that species capable of using torpor appear less threatened by extinction and fewer have suffered extinction than obligate homeotherms (Geiser and Turbill, 2009; Liow *et al.*, 2009). Of the 61 worldwide confirmed extinct mammal species over the past 500 years (American Museum for Natural History, Committee on Recently Extinct Organisms, <http://creo.amnh.org>), only four species likely were heterothermic (Geiser and Turbill, 2009). Obviously, more work is needed in this area because we cannot be certain that thermoregulatory patterns in extant taxa adequately predict those that are extinct.

Nevertheless, it has been suggested that the ability of using torpor with its enormous scope for adjusting energy requirements may allow long-term survival of adverse environmental conditions, habitat modification and degradation, and avoidance of introduced or native predators (Bieber and Ruf, 2009; Stawski and Geiser, 2010; Geiser and Stawski, 2011), likely to be the major causes of extinctions. Thus, the use of opportunistic torpor appears to have permitted small mammals to deal with anthropogenic disturbances better than is the case for homeothermic species.

## Perspectives

With the aid of modern telemetry and miniature data logging equipment, our knowledge of torpor use has improved substantially in recent years and the number of known heterothermic endotherms has been ever increasing. Since the majority of mammals and birds are small and therefore could benefit by entering torpor, the question arises whether strict homeothermy still qualifies as a general characteristic of mammals and birds as widely claimed in

textbooks. Further, some of the major questions in regard to torpor, such as why torpid animals have to arouse periodically or why heterotherms have a much greater thermal tolerance than homeotherms remain to be resolved. Thus future work on torpor provides many opportunities for tackling unresolved questions on the diversity and evolution, ecology and behaviour, physiology, biochemistry and molecular biology of heterothermic mammals and birds.

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## Further Reading

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## Key Concepts:

- Hibernation and daily torpor are the most effective means of energy conservation available to mammals and birds and are crucial for survival of adverse conditions of many species.
- Use of torpor often is enhanced by low ambient temperatures and limited food.
- Because torpor reduces energy requirements, its opportunistic use allows extension of gestation, nutrient sparing during development, and permits survival in modified and degraded habitats and also reduces the need for foraging and thus exposure to predators.
- As the rate of extinction in heterothermic mammals is much lower than in homeotherms, thermal energetics are of concern to conservation biologists because mammals and birds that can use and cannot use torpor differ enormously in their energy requirements and thus foraging needs.

## Glossary:

### Daily torpor

A period of controlled reduction of body temperature and metabolism in daily heterotherms lasting for less than one day.

### Ectotherm

An organism whose metabolic heat production is low and therefore its body temperature is usually close to that of the environment. Ectotherms generally lack insulation.

### Endotherm

An organism with the capacity of high metabolic heat production by the use of shivering and/or nonshivering thermogenesis. Endotherms generally have good insulation in the form of fur, feathers, and/or fat.

### Heterothermic endotherm

An organism that is capable of homeothermic thermoregulation, but, at certain times of the day or the year, enters a state of torpor.

### Hibernation or prolonged torpor

A sequence of multiday torpor bouts, during which metabolism and often body temperature are extremely low, interrupted by periodic arousal periods.

### Homeotherm

An organism that maintains a more or less constant body temperature either *via* appropriate heat production or heat loss, or by living in a thermally stable environment.

### Hypothermia

An uncontrolled pathological reduction of body temperatures often due to drugs or extreme cold-exposure.

### Metabolic rate

A measure of the total metabolic energy use. Can be quantified indirectly by measuring oxygen consumption or carbon dioxide production or directly by measuring metabolic heat production.

### Normotherm (=eutherms)

The physiological state during which a heterothermic endotherm displays homeothermic thermoregulation.

### Torpor

A period of a controlled reduction of body temperature, metabolism and other physiological processes. Torpor is a general term and can be daily or prolonged.