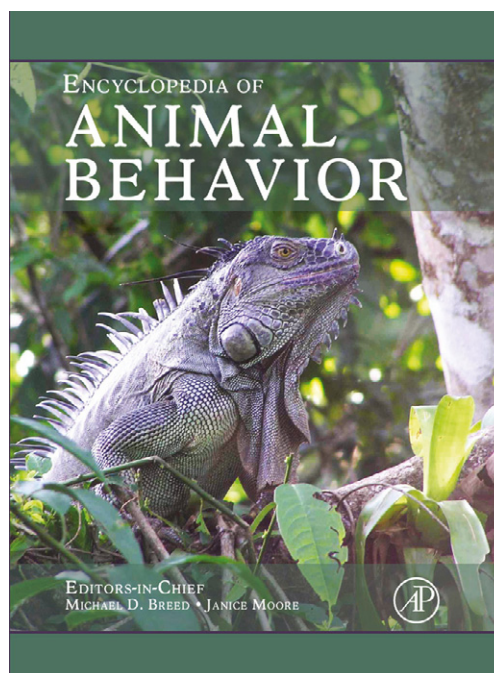


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Hibernation, Daily Torpor and Estivation in Mammals and Birds: Behavioral Aspects

F. Geiser, University of New England, Armidale, NSW, Australia

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Introduction

Mammals and birds are endothermic (within heating). They differ from ectothermic organisms, which rely on external heat for thermoregulation and comprise most animals and plants, primarily in their ability to regulate body temperature (T_b) by a generally high but adjustable internal production of heat generated by the combustion of fuels. Because the surface area in relation to the volume of heat-producing tissues of animals increases with decreasing size, many small endotherms must produce an enormous amount of heat to compensate for heat loss over their relatively large body surface. While heat loss is especially pronounced during cold exposure, even exposure to mild ambient temperatures (T_a) of 25–30 °C, considered to be warm by humans, causes mild cold stress in many small species.

Obviously, prolonged periods of high metabolic rates (MR) for heat production can only be sustained by regular food intake. During adverse environmental conditions and/or food shortages, energetic costs for thermoregulation may exceed those that can be obtained via food uptake. High energy expenditure and food uptake also require substantial foraging times and consequently exposure to predators even when food is abundant. Therefore, not all mammals and birds are permanently homeothermic (i.e., maintain a constant high normothermic T_b), but many, especially small species, enter a state of torpor during certain times of the day or the year. Torpor in these 'heterothermic endotherms' is characterized by a controlled reduction of T_b , energy expenditure, and other physiological processes and functions.

Torpor is by far the most effective means for energy conservation available to mammals and birds. Torpor conserves energy because no thermoregulatory heat for maintenance of a high normothermic T_b of around 37–40 °C is required. Moreover, because many torpid animals are thermoconforming over a wide range of T_a , T_b falls with T_a , and the substantial fall of T_b reduces MR via temperature effects. Further, in some species, inhibition of metabolism (in addition to temperature effects) can substantially lower energy expenditure to only a small fraction of the basal metabolic rate (BMR) or maintenance MR of normothermic, resting individuals under thermoneutral conditions.

Although MR and T_b during torpor in heterothermic endotherms are very low and often similar to those in

ectotherms, torpid endotherms can rewarm from low T_b during torpor by using internally generated heat, whereas ectotherms, such as lizards, must rely on uptake of heat from external sources for raising T_b . Moreover, unlike in ectotherms, T_b in torpid endotherms is regulated at or above a species-specific minimum by a proportional increase in heat production that compensates for heat loss to prevent T_b from falling to critically low levels, likely to prevent tissue or organ damage, or to maintain the ability for endothermic arousal.

Torpor is often confused with 'hypothermia,' which also is characterized by reduced T_b and MR. However, torpor is a precisely controlled physiological state, whereas hypothermia is pathological and nothing but a failure of thermoregulation often due to depletion of energy reserves, excessive cold exposure, or from the influence of certain drugs.

Hibernation and Daily Torpor

The two most common patterns of torpor are hibernation (prolonged multiday torpor) and daily torpor. Hibernation often is seasonal and usually lasts from autumn to spring; however, 'hibernators' do not remain torpid continuously throughout the hibernation season (Figure 1). 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 <1 day) resting periods with high normothermic T_b and high energy turnover, apparently to recuperate from the prolonged time at low T_b . Hibernating mammals (with the exception of bears and some other large carnivores that reduce T_b only by about 5–8 °C) are generally small (<10 kg), and most weigh between 10 and 1000 g with a median mass of 85 g. Many hibernators fatten extensively before the hibernation season and rely to a large extent on stored fat for an energy source in winter, whereas fewer species store food for the hibernation season.

Hibernating species usually reduce their T_b to below 10 °C, with a minimum of –3 °C in arctic ground squirrels and most have minimum T_b of around 5 °C. The MR in torpid hibernators is on average reduced to about 5% of the BMR, but can be as low as 1–2% of BMR in small hibernators and often is <1% of that in

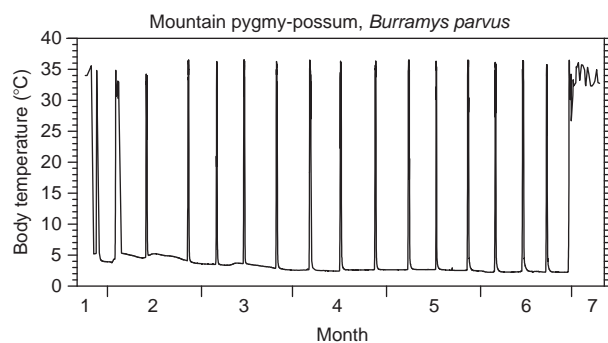
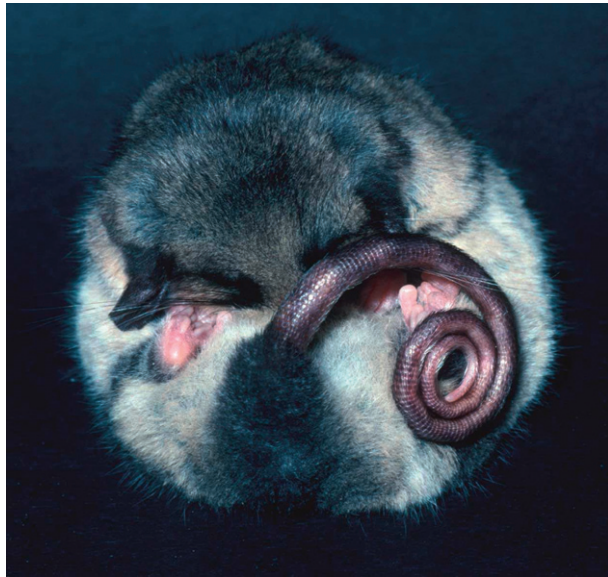


Figure 1 Body temperature (T_b) fluctuations during the hibernation season of a free-ranging mountain pygmy possum, *Burramys parvus* (body mass: 50 g). The hibernation season lasts for ~6 months, but torpor bouts when T_b and other functions are reduced to a minimum last only for up to about 2 weeks and are interrupted by periodic endothermic arousals.

active individuals. Energy expenditure during the mammalian hibernation season is reduced by ~85–95% in comparison to that of an animal that would have remained normothermic throughout winter, even if the high cost of periodic arousals is considered, which consume most of the energy required during the hibernation season. This enormous reduction in energy expenditure is perhaps best illustrated by the fact that many hibernating mammals can survive for 6–8 months or even longer entirely on body fat that has been stored prior to the hibernation season.

Daily torpor is the other widely used pattern of torpor in mammals and also in birds. This form of torpor in the ‘daily heterotherms’ 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. Daily heterotherms are unable to express multiday torpor bouts. Many daily heterotherms are less seasonal than hibernators, may employ torpor throughout the year, although

torpor use often increases in winter. While daily torpor in many species occurs predominantly as a response to acute energy shortages, in other species, it appears to be used regularly to balance energy budgets even when environmental conditions appear favorable. For example, in hummingbirds, daily torpor is not only used to lower energy expenditure during adverse conditions, but may be employed to conserve energy during migration when birds are relatively fat. The marsupial Mulgara (*Dasycercus cristicauda*) appears to use daily torpor during pregnancy to store fat for the energetically demanding period of lactation. On average, daily heterotherms are even smaller than hibernators and most weigh between 5 and 100 g with a median of 19 g.

In contrast to hibernators, many daily heterotherms do not show extensive fattening before the season torpor is most commonly employed, and often only enter torpor when their body mass is low. The main energy supply of daily heterotherms even in their main torpor season remains food, often gathered during daily foraging, rather than stored body fat. In daily heterotherms, T_b usually fall to 10–20 °C with an average minimum T_b of 18 °C. However, in some hummingbirds, T_b below 10 °C have been reported, whereas in other, mainly large species, such as Tawny frogmouths (*Podargus strigoides*), T_b just below 30 °C are maintained. The MR 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 T_a is used as point of reference, reductions of MR during daily torpor to about 10–20% of that in normothermic individuals at the same T_a are common. Overall, daily energy expenditure is usually reduced by 10–50% and in extreme cases by up to 90% on days when daily torpor is employed in comparison to days when no torpor is used, primarily depending on the species, the duration of the torpor bout, torpor depth, whether or not basking is employed during rewarming and rest, and how long animals are active.

As stated earlier, torpor bouts in the daily heterotherms are shorter than 1 day, independent of food supply or prevailing ambient conditions. Hibernators also can show brief torpor bouts lasting <1 day early and late in the hibernation season or at high T_a . However, it appears that physiologically these are nothing but brief bouts of hibernation with MR well below those of the daily heterotherms even at the same T_b . Thus, the term ‘daily torpor’ seems inappropriate for describing short torpor bouts of hibernators.

Often contrasted with hibernation and daily torpor, ‘estivation’ describes a period of torpor in summer or under warm conditions, which appears to be induced to a large extent by a reduced availability of water and consequently lack of food due to high T_a . In some ground squirrels, the hibernation season begins in the hottest part of the year and therefore qualifies as estivation. Many hibernating bats

enter short bouts of torpor in summer and therefore estivate. Small arid zone marsupials regularly express daily torpor in summer, which not only reduces energy expenditure, but also water loss. However, it appears that there is no physiological difference between estivation and hibernation/daily torpor, apart from the higher T_b and thus MR during estivation because of the relative high T_a experienced in summer. It also appears that estivation is often not directly induced by heat because animals still employ torpor during the coolest part of the day, and it is likely that heat affects torpor use indirectly by reducing supply of food and water. However, reduced foraging opportunities because of heat may also result in torpor use.

Torpor in Mammals and Birds

Over recent years, the number of known heterothermic mammals and birds has increased substantially. Contrary to what was widely believed in the past, these are found in a wide diversity of taxa and in a variety of climatic regions ranging from arctic and alpine areas to the tropics.

In mammals, hibernation occurs in many species from all three mammalian subclasses. Hibernators include the egg-laying short-beaked echidna (*Tachyglossus aculeatus*) of Australia (Monotremata) and several marsupials including the Chilean opossum (*Dromiciops gliroides*, Microbiotheriidae), several pygmy-possums (Burramyidae), and feather-tail glider (*Acrobates pygmaeus*, Acrobatidae). In the placental mammals, hibernation occurs in rodents (dormice, marmots, chipmunks, ground squirrels, hamsters), armadillos (*Zaedyus pichii*), perhaps in some elephant shrews (Macroscelidea), some small primates (*Cheirogaleus medius*, fat-tailed lemur; *Microcebus murinus*, mouse lemur), many bats (Microchiroptera), and the insectivores (e.g., *Erinaceus europaeus*, hedgehogs; *Echinops telfairi*, tenrecs).

The 'winter sleep' of the large Carnivores (bears; European badger, *Meles meles*) appears to differ somewhat from deep hibernation in small mammals since T_b falls only by $\sim 5^\circ\text{C}$ rather than by $>30^\circ\text{C}$, as in most of the small species. This type of dormancy, especially in bears, is often referred to as 'winter anorexia.'

Daily torpor (Figure 2) is known from a very large number of small marsupial and placental mammals. It occurs in several marsupial families from Australia (e.g., insectivorous/carnivorous marsupials, e.g., *Sminthopsis* spp. or *Pseudantechinus macdonnellensis*, Dasyuridae; small possums, *Petaurus breviceps*, Petauridae; honey possum, *Tarsipes rostratus*, Tarsipedidae) and South America (e.g., mouse opossums, *Thylamys elegans*, Didelphidae). In placentals, daily torpor occurs in rodents (deermice, *Peromyscus* spp., gerbils, *Gerbillus* spp., small siberian hamsters, *Phodopus sungorus*), some elephant shrews (*Elephantulus* spp., Macroscelidea), some primates (*Microcebus* mouse lemurs), bats (some Microchiroptera and small Megachiroptera), the

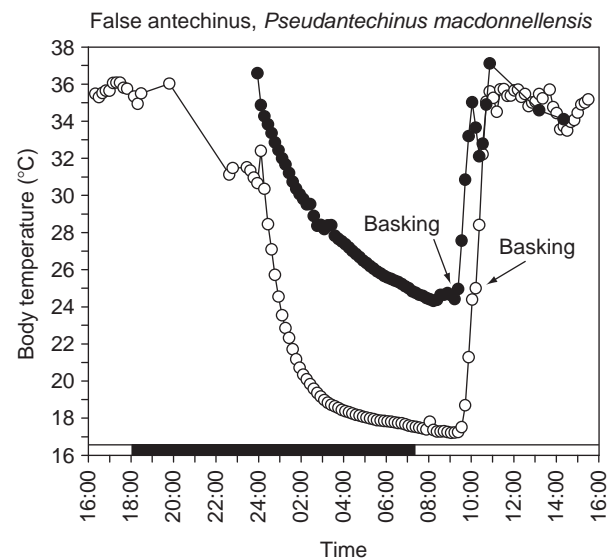


Figure 2 Daily torpor in two free-ranging false antechinus, *Pseudantechinus macdonnellensis* (31 g). The species is generally active with high T_b of about 36°C for the first half of the night, enters torpor around midnight (characterized by a rapid reduction of T_b), and in the morning employs basking in the sun (arrows indicate visual observations) for rewarming from torpor (rapid rise of T_b) to minimize energy expenditure.

insectivores (shrews, e.g., *Crocodyra* spp.), and some small carnivores (e.g., skunk, *Mephitis mephitis*).

In birds, daily torpor also is common. Many birds have normothermic T_b around 40°C , whereas during daily torpor, T_b are usually in the range of $10\text{--}30^\circ\text{C}$, 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. Daily torpor is known from several avian orders including todies (*Todus mexicanus*) and kookaburras (*Dacelo novaeguineae*, Coraciiformes), mouse birds (*Colius* spp., Coliiformes), swifts (e.g., *Apus apus*, Apodiformes), hummingbirds (e.g., *Calyptra* spp., Trochiliformes), nightjars (e.g., *Caprimulgus* spp., Caprimulgiformes), pigeons (e.g., *Drepanoptila holosericea*, Columbiformes), and martins (*Delichon urbica*), woodswallows (*Artamus cyanopterus*), chickadees (*Parus* spp.), and

sunbirds (*Nectarinia* spp.) (Passeriformes). The largest bird presently known to enter daily torpor is the Australian tawny frogmouth (500 g), a nightjar relative. In contrast to mammals, multiday hibernation is presently known only for one bird, the common poorwill (*Phalaenoptilus nuttallii*) from North America.

Torpor is characterized by reduced activity, and traditionally, lack of movement or poor coordination has even been used for defining torpor. However, in recent years, new evidence has emerged showing that even torpid individuals can move at low T_b , for example, to basking sites, expressing behaviors that minimize energy expenditure for rewarming from torpor. Other species employ social torpor in groups and must behaviorally interact to maximize energetic outcomes. Some species are reproductively active even during the torpor season, which obviously will entail some behavior. Moreover, before they commence to employ torpor, many species prepare for the torpor season by selecting sites for torpor use or hibernacula, hoarding food, or accumulating fat, and this usually is accompanied by a change in behavior. The aim of this summary is to synthesize these behaviors.

Preparation for Hibernation

Shortening of photoperiod in late summer or autumn initiates physiological and behavioral changes of many species in preparation for hibernation. In other species, as for example ground squirrels, a strong innate circannual rhythm controls the seasons of activity and torpor use largely irrespective of photoperiod. Other species, for example, those from unpredictable habitats, may 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, or perhaps to avoid predation.

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 express seasonal changes in torpor use, photoperiod, food availability, and T_a appear the major factors that affect the seasonal adjustments in physiology.

Selection of Hibernacula and Torpor Sites

Selection of an appropriate hibernaculum or torpor site is of vital importance. Hibernators often use underground burrows, boulder fields, piles of wood or leaves, tree hollows, caves, or mines. Hibernacula do not only provide shelter from potential predators, but also from temperature extremes and potential desiccation. Most hibernacula show temperatures a few degrees above the freezing point

of water even when outside T_a are well below freezing. Snow often acts as additional thermal blanket.

The selection of thermally appropriate hibernacula or sites where torpor is expressed is important, because at T_a close to the minimum T_b that is defended during torpor, MR are lowest and arousals are least frequent and therefore energy expenditure is minimal. Selection of a hibernaculum with a T_a below the minimum T_b for much of the hibernation season can be detrimental for small and solitary species because of the increased thermoregulatory energy expenditure and more frequent arousals. Therefore, it is likely that the minimum T_b is subject to strong selective pressure for adjustments that result in approximating the minimum T_b to the minimum T_a experienced. Arctic ground squirrels (*Spermophilus parryi*) do hibernate solitary at a T_a that is well below their minimum T_b (-2 to -3 °C); however, this species supercools and is rather large (~ 1 kg), is likely to use insulated nests, and obviously there is a limit how far T_b can be reduced, without causing freezing of tissues.

There is also some evidence that the selection of hibernacula may change during winter during periodic arousals apparently when the thermal conditions change due to, for example, rainfall or seasonal T_a change in caves. Mountain pygmy possums select different torpor sites after rain, which decreases T_a in sub-nivean spaces, whereas bats are known to select appropriate hibernacula sites along thermal gradients in caves that generally change with season.

Some species such as bats or fat-tailed lemurs enter torpor under bark, in trees hollows, or even under leaves with little physical protection. In blossom bats, roosts selection changes with season with bats selecting forest centers in summer to avoid heat exposure and forest edges in winter likely to allow bats to rewarm passively from torpor with the increasing T_a in the late morning. Long-eared bats (*Nyctophilus* spp.) enter torpor under bark that will be exposed to sun on the following morning to also take advantage of passive rewarming.

Fat Stores and Dietary Lipids

Preparation for hibernation involves primarily fattening and/or hoarding of food. Prehibernation 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 approximately double their body mass largely due to fat storage in autumn, but increases in body mass the order of 10–30% are more common. Fattening often is achieved by a combination of hyperphagy and a reduction in activity.

While the quantity of fat is important as it is the main energy source in fat-storing hibernators during winter, patterns of hibernation are also affected by the composition

of dietary fats and body lipids. Function at low T_b during mammalian torpor obviously requires some physiological adjustments. In ectothermic organisms, increases of unsaturated polyunsaturated fatty acids in tissues and cell membranes form an important role in facilitating function at low T_b because unsaturated fatty acids lower the melting point of depot fats and increase the fluidity of cell membranes at low temperatures. In torpid endotherms, polyunsaturated fatty acids increase only slightly in depot fat and some membrane fractions. However, dietary polyunsaturated fatty acids have been shown to enhance torpor in hibernators as well as in daily heterotherms. Ground squirrels and chipmunks fed on a diet rich in polyunsaturated fatty acids, in comparison to conspecifics on a diet rich in saturated fatty acids, have lower T_b and MR and longer torpor bouts substantially reducing energy requirements during winter. In the wild, ground squirrels and marmots select food rich in polyunsaturated fatty acids during prehibernation fattening apparently to enhance winter survival, and perhaps to retain fat for the mating season immediately after hibernation. Further, recent evidence shows that selection of dietary fats is affected by photoperiod exposure with hamsters exposed to short photoperiod increasing their preference for diets rich in unsaturated fatty acids. These observations support the view that uptake of appropriate dietary fats form part of the winter preparation of many heterothermic mammals.

Behavior During Torpor or the Torpor Season

Social Torpor

Interestingly, alpine marmots (*Marmota marmota*) do successfully hibernate at T_a below their minimum T_b for some of the winter despite increased thermoregulatory energy expenditure. However this species, like other marmots, is very large and uses social hibernation to enhance the chance of winter survival. To achieve this, individuals huddle closely in their hibernacula to decrease the exposed surface area and to limit heat loss. Moreover, torpid marmots synchronize entry and arousals from torpor to minimize heat loss to the environment. Especially during endothermic rewarming, large adults typically commence to rewarm first and their endogenously produced heat can be shared by other, particularly small juveniles, minimizing their rewarming costs. Other species that are known to enter torpor socially are sugar gliders and feathertail gliders; however, although it is known that arousals in the former can be highly synchronized and that huddling in normothermic groups reduces energy expenditure, there are no data on whether or not huddling reduces rewarming costs.

Reproduction and Torpor

Social torpor and also solitary torpor do not prevent some heterothermic species to undertake some important reproductive behaviors. Whereas torpor and reproduction often are seen to be mutually exclusive, recent evidence has shown that both pregnant and lactating females may use torpor for energy conservation. For example, hoary bats (*Lasiurus cinereus*) employ torpor during pregnancy during cold spells in spring, which in addition to energy conservation may be used to reduce growth rates of young to delay parturition until conditions are more favorable for lactation and neonatal survival. Moreover, mating may occur during the hibernation season in bats and echidnas. Short-beaked echidnas mate in late winter when promiscuous males appear to seek out torpid females and mate with these either while torpid or during brief normothermic periods of females. A large proportion of torpid females were pregnant, suggesting that mating during hibernation is a common practice in this species, and perhaps may be employed by females for selection of males. Another group of mammals that is known to mate during the hibernation season are bats. In little brown bats (*Myotis lucifugus*), mating occurs frequently early in the hibernation season when bats are active. However, later in the hibernation season when the number of torpid females increases, adult males often force copulation with torpid individuals (females and males).

Basking During Rewarming from Torpor

Endothermic rewarming from torpor is energetically expensive and reduces the savings accrued from daily torpor and often results in death of light individuals during hibernation if they arouse too frequently. Small insectivorous/carnivorous dasyurid marsupials living in Australian deserts use daily torpor in winter frequently in the field and frequently employ basking during rewarming apparently to lower energy expenditure during arousal. Elephant shrews are the only other group of mammals for which data strongly suggest they may bask when rewarming from torpor. Basking during rewarming from torpor in dasyurids can reduce rewarming costs by up to 85% and consequently is highly significant to small mammals with high thermoregulatory energy expenditure, especially for those living in resource-poor environments such as deserts.

Arid zone dasyurids known to employ basking during rewarming are two dunnarts and a planigale living on sandy or clay substrate, and the rock-dwelling false antechinus (Table 1). In these species, torpor occurs frequently (~60–100% of days) in the wild in autumn and winter. Basking was observed in individuals that moved from their rest site, where they apparently had entered torpor, to a basking site in the sun at T_b ranging between 13.8 and 19.7 °C, well below the T_b often used for defining torpor

Table 1 Basking in torpid mammals

Species	Basking T_b minimum ($^{\circ}\text{C}$)	Source
<i>Marsupials</i>		
Planigale <i>Planigale gilesi</i> (8 g)	13.8	Geiser et al. (2008)
Dunnart <i>Sminthopsis</i> <i>crassicaudata</i> (10 g)	14.6	Warnecke et al. (2008)
Dunnart <i>Sminthopsis</i> <i>macroura</i> (15 g)	19.3	Geiser et al. (2008)
False Antechinus <i>Pseudantechinus</i> <i>macdonnellensis</i> (31 g)	19.3	Geiser et al. (2002)
<i>Placentals</i>		
Elephant shrew <i>Elephantulus myurus</i> (55 g)	–	Mzilikazi et al. (2002)

in mammals (i.e., $T_b < 30^{\circ}\text{C}$). Basking often commenced about 3 h after sunrise when the sun reached openings of rock crevices or soil cracks employed by torpid individuals to expose themselves to sun. Basking often lasted throughout the entire rewarming process. When an observer approached too closely, animals rapidly retreated into their shelter, demonstrating that these individuals are fully alert and well enough coordinated even at low T_b .

In Elephant shrews, rewarming from torpor was tightly linked with changes in T_a . The T_b rose from low values at the same time T_a in the sun increased, strongly suggesting that the animals were basking, as basking was also observed independently in normothermic individuals.

Detailed behavioral observation on basking are available for free-ranging false antechinus, which typically basked with the back oriented toward the sun and less commonly with the flanks facing the sun. Both exposure of the entire body and exposure of only parts of the body were observed. Basking animals did not remain stationary for long periods and regularly changed body position or posture. These changes included altering orientation toward the sun by as much as 180° , and small movements of the body to increase or decrease the amount of sun exposure. Usually, a change of body posture or position occurred every ~ 5 min, suggesting that the animals were seeking to maximize heat uptake depending on their internal thermal condition. In the laboratory, torpid dunnarts (*Sminthopsis crassicaudata*) actively moved from a shaded area where they entered torpor to a heat lamp on 100% of observations to passively rewarm from low T_b .

Summary

While in the past lack of activity and movement were widely used to define periods of torpor, it is now clear that torpid animals at low T_b often are well aware of their

surroundings and even express a number of complex behaviors either while torpid or during normothermic periods between torpor bouts. These behaviors likely contribute to maximize survival of the torpor season or the survival of a species in general as heterothermic species are more resistant to extinction than homeotherms. It thus appears that torpor, although widely viewed as the 'physiological option,' in contrast the 'behavioral option' as for example migration, for survival/avoidance of adverse conditions, also involves several important behavioral components that form an crucial role in enhancing a species' fitness.

See also: Behavioral Endocrinology of Migration; Caching; Circadian and Circannual Rhythms and Hormones; Conservation and Anti-Predator Behavior; Female Sexual Behavior and Hormones in Non-Mammalian Vertebrates; Group Living; Habitat Selection; Internal Energy Storage; Seasonality: Hormones and Behavior.

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