Use of Torpor in Chiroptera

Caitlin Barale

* * *

Writer's Comment: I have been fascinated by torpor since I first learned about it while working with tenrecs at the Oakland Zoo. This paper allowed me to expand my knowledge of torpor by exploring its use among a totally different set of organisms, bats. I read many articles analyzing torpor in a variety of bat species, then worked to synthesize my findings. I learned a lot about cost and benefit analysis in the process, and tried hard to communicate what I had learned with my readers. In the process, I discovered both consequences and benefits of decreased metabolic rate that I had not anticipated. I was particularly fascinated about the potential of torpor to increase longevity. I find physiological ecology to be a fascinating topic, so it was a pleasure to learn more about it and share my enthusiasm for the subject with others.

—Caitlin Barale

Instructor's Comment: Physiological ecology of wildlife is a difficult class, delving into a convoluted realm of environmental science, biochemistry, physics, behavior, and ecology. To further a class's frustration, it is taught across a wide range of taxa: invertebrates, fish, amphibians, reptiles, birds, and mammals. The instructor's challenge is to guide students through an obstacle course of materials, leaving them with an expanded toolbox for the future. One of their assignments was really quite vague: create a physiological ecology website that would engage readers and would allow future classes to add onto it. Each student was assigned the task of writing a scientific review paper to synthesize the current knowledge of a physiological mechanism and *relate it to ecology, or to compare and contrast a mechanism across various taxa. The assignment allowed the students in the class to take reins and write about whatever piqued their interests. Caitlin embraced this assignment. Her interest, acquired knowledge, and strong writing skills allowed her to craft an in-depth review on torpor in Chiroptera, a family of bats. Caitlin begins her review by explaining torpor and then assessing the physiological benefits and costs associated with torpor. As the review progresses, she relates each mechanism back to behavioral and ecological interactions. Her approach allows readers less savvy in physiological ecology to understand complex processes and their implications on Chiroptera's way of life. Well done, Caitlin!*

—Christa Woodley, Center for Watershed Sciences

◆

Chiroptera (bats) are among many species of small mammals that use a thermoregulatory mechanism called torpor to cope with adverse environmental conditions (Malatesta et al. 2007; Willis et al. 2005a). Torpor is the daily or seasonal lowering of an organism's body temperature and metabolic rate in order to survive environmental perturbations such as cold or a diminished food supply (Hosken & Withers 1999; Warnecke et al. 2008). It is a particularly useful strategy for small endotherms, which must withstand high rates of heat and water loss due to physiological constraints. Bats are endotherms and the second most numerous order of mammals, comprising 20% of all mammalian species (Turbill 2006). Additionally, their order has the greatest diversity in morphology, diet, and behavior among mammals (Dixon & Rose 2003). Despite their enormous variety in lifestyle functions (food preference, body size, habitat selection), bats worldwide use torpor as a key physiological survival tactic (Dietz & Kalko 2006). This paper will examine the basis of torpor among bats, as well as its costs and benefits, from both a physiological and an ecological perspective.

Torpor occurs when bats regulate their body temperature below normothermic levels, which can take place on a daily and/or seasonal scale (Wojciechowski et al. 2007). Common characteristics of a hypothermic state include a substantial reduction in metabolic rate, heart rate and energy demands. The torpid state may last from a few hours to a few weeks, thus allowing survival when environmental conditions are suboptimal (Malatesta et al. 2007). The average minimum body temperature for bats in torpor is 17° C (a 24° C difference from their average active body temperature); metabolic rate typically is decreased by 80–99% (Kortner & Geiser 2000). This metabolic reduction occurs as a result of significantly reduced or completely eliminated thermoregulatory requirements and a drastic change in the effects of temperature on the rates of biological activity (Humphries et al. 2003). Additional metabolic inhibition is obtained through respiratory acidosis (Humphries et al. 2003). The metabolic depression that results from these changes means that the bat needs to expend less energy to survive and can thus weather periods of environmental stress.

When examining the roots of torpor in the order Chiroptera, it is important to consider the physiological limitations bats face. First, they are small in body size, with at least 50% of known species weighing less than 10 g (Smith 2003; Willis et al. 2005c). Having such a small body is problematic because it means bats have a high surface area-to-volume ratio relative to larger bodied mammals (Malatesta et al. 2007). This high ratio leads to an increased rate of water and heat loss to the environment, particularly at low ambient temperatures (Willis 2007), compounded by the relatively high basal metabolic rates (BMR) small mammals have. The relationship between BMR, body size, body temperature, and water loss is explained by the organism's mass-specific metabolic rate (MSMR), a measure of the metabolic rate per unit tissue. MSMR values increase steeply with decreasing body mass, and consequently heat loss increases for small mammals when ambient temperatures fall below their thermoneutral zone. The average lower critical value for bats is approximately 30° C (French 1985; Kortner & Geiser 2000). The high rate of heat loss experienced by bats means that the cost of maintaining normothermic body temperature increases rapidly with decreasing ambient temperature—a problem for an organism which is primarily active at night, when ambient temperatures can be extremely low (Cryan & Wolf 2003). The result of these physiological constraints is that bats spend much of their daily energy budget on thermoregulation (Cryan & Wolf 2003; Kortner & Geiser 2000). Thus, lowering body temperature during times of inactivity can be an excellent energy conservation strategy (Kortner & Geiser 2000).

Another consequence of small body size is that bats have minimal fat reserves, making it difficult for bats to insulate themselves when air temperatures are low (French 1985). Bats have little extra fuel to burn, which can be problematic because their foraging mechanism—flight—is energetically costly, and having extra fuel can make the difference between successful feeding and failure (Kelm & Helversen 2007; Soriano et al. 2002). Fat stores are also useful when the available food supply diminishes unexpectedly, an event that occurs periodically as temperature and other environmental conditions change (Turbill 2006). The result is that bats have little available stored energy and thus have difficulty meeting the increased demands of thermoregulation dictated by their body size and behavioral strategies (aerial foraging). This is particularly the case for bats living in areas where climate and food supply vary seasonally (Solick & Barclay 2006). In order to conserve their energy for vital tasks such as growth, reproduction, and foraging, many bats minimize energy expenditure by entering torpor when ambient temperature is low or when food and/or water shortages occur (Park et al. 2000; Solick & Barclay 2007).

Torpor therefore has many benefits for bats. Depth and duration of torpor varies extensively from species to species, with some northern bats entering winter hibernation and equatorial bats utilizing shallow daily torpor (Kortner & Geiser 2000). Evaporative water loss is reduced by torpor, so bats that spend time in torpor are at a much lower risk for dehydration than bats that don't (Maloney et al. 1999). Another benefit of torpor is the maintenance of osmoregulatory homeostasis, which reduces evaporative water loss to the environment so that water can be conserved for essential metabolic and cellular processes (Maloney et al. 1999). Saving water allows bats to spend less time obtaining water from the environment, thus reducing their predation risk as well.

Another benefit of torpor is the potential for increased longevity (Humphries et al. 2003). Bats as an order are incredibly long-lived relative to other mammals of similar body mass. This longevity is particularly surprising given their small body size and extremely high mass-specific metabolic rate (Filho et al. 2007). Long life span for small mammals is unusual and is thought to be the result of reduced somatic damage rate and daily modulation of key antioxidants (Filho et al. 2007). Hypothetically, antioxidants reduce the oxidative stress experienced by tissues during the transition from torpor to normothermy; thus, the combination of antioxidants with energy savings from daily torpor increases longevity (Filho et al. 2007). Additionally, the dramatic decrease in body temperature—from an active body temperature of 40° C or greater to an average torpid body temperature of 17° C (Hock 1951; Kortner & Geiser 2000)—may slow down cellular damage to somatic cells (Humphries et al. 2003). There is little empirical support for this hypothesis in bats, but studies on other animals (Solick & Barclay 2006) show that reduced metabolism and caloric intake increase longevity (Shanley & Kirkwood 2000; Speakman 2000).

Though energy savings and other benefits gained from torpor are clearly substantial, there are associated costs as well. Reduced responsiveness in emergency situations and accumulation of sleep debt are two such examples (Kelm & Helversen 2007; Wojciechowski et al. 2007). When torpid, bats have limited sensory and motor function and need ample time to return to normothermic conditions before they can adequately respond to emergency situations, specifically predatory threats (Humphries et al. 2003; Jacobs et al. 2007). Since constant alertness and the ability to fly at a moment's notice are necessary for successful evasion of predators, the costs of predation associated with regularly entering torpor may be enormous (Kelm & Helversen 2007). Many bat species that roost during times when predators are around rely on camouflage as an alternative strategy for avoiding predation (Kelm & Helversen 2007).

In addition, the energetic cost of arousal from torpor can be high if the bat actively has to warm itself using metabolic heat (Thomas et al. 1990). Arousal costs are a problem because most bat species undergo daily torpor rather than seasonal torpor and consequently must return to normothermia regularly to forage. Daily torpor usually occurs for a few hours at night after the bats return from foraging. The costs of regaining normothermia can thus be offset by passive warming within roost sites as the rising sun heats the area (Lausen & Barclay 2003). Species that do undergo seasonal torpor or hibernation must still regain normothermia periodically to replenish diminished fat reserves (Dunbar & Tomasi 2006). Avery (1985) studied this periodic arousal in pipistrelle bats (*Pipistrellus pipistrellus kuhl*) and discovered that activity and feeding during the winter months occurs primarily on warm, calm nights. Only on such nights are enough insects present to make the energetic costs of arousal and foraging worthwhile (Avery 1985). This selective activity maximizes energetic gain from feeding while minimizing the cost of regaining normothermia on nights when insects are not abundant.

A novel hypothesis on why torpid animals must return to normothermy is based on observations that hibernating ground squirrels spend much of their arousal time sleeping.Daan et al. (1991) suggest that the need for sleep slowly accumulates during prolonged torpor, and that returning to euthermy (the condition in which body temperature is maintained at a near-constant value by changes in metabolism and heat loss) is periodically required before sleep can occur. A related study suggests that the extremely low body temperatures experienced by torpid or hibernating animals inhibit the restorative functions of sleep from taking place (Trachsel et al. 1991). This sleep-debt accumulation problem could be a substantial cost for hibernating bats not only because of the physiological effects of sleep debt, but also because of the costs associated with returning to euthermia.

A final, extremely important cost of torpor is related to reproduction. Many studies have been conducted on the effects of torpor in pregnant and lactating females, empirically demonstrating that regular and/or deep torpor can lead to prolonged pregnancy, reduced milk production, and slowed fetal and juvenile development (Solick & Barclay 2007; Willis et al. 2005a; Wojciechowski et al. 2007). Unsurprisingly, these effects have many repercussions for pregnant females. They must cope with the enormous thermoregulatory demands related to their body size and foraging mechanisms, as well as with the energetic demands associated with carrying the fetus, giving birth, and providing milk, but cannot rely on torpor to the same extent as their nonpregnant counterparts.

In one study of torpor use by pregnant, lactating, and postlactating (nonpregnant) female big brown bats (*Eptesicus fuscus*), the depth and duration of torpor and the ambient temperature of roosts varied significantly (Lausen & Barclay 2003). Both pregnant and lactating females used torpor to the same extent in terms of degree-minutes, but with very different thermoregulatory patterns. Pregnant females entered torpor infrequently but spent an unusually high percentage of their torpor time in deep torpor (Lausen & Barclay 2003). Lactating females used torpor very frequently but rarely entered deep torpor—they spent an unusually high percentage of their torpor time in shallow torpor (Lausen & Barclay 2003). Lactating females also preferentially roosted in deeper cavities with higher and more stable ambient temperatures, thus reducing their need to enter deep torpor (Lausen & Barclay 2003). These differences are logical from a cost-benefit perspective in that the lactating females could gain the energy-saving benefits of shallow torpor while avoiding the cost of inhibited milk production incurred by deep torpor (Solick & Barclay 2007). Postlactating females who had already weaned their young used torpor more extensively than either of the other groups (Lausen &

Barclay 2003). These results suggest that the costs of using torpor during pregnancy and lactation are significant enough to warrant a decrease in torpor during those times. Similar results were confirmed on free-ranging Daubenton's bats (*Myotis daubentonii*) (Dietz & Kalko 2006) and on hoary bats (*Lasisurus cinereus*) (Cryan & Wolf 2003).

As mentioned in the analysis of torpor use by females in varying reproductive stages, habitat selection also plays a role in torpor. The issue of torpor is not merely physiological—it has a behavioral component as well. Many species of bats choose roosts based on their thermoregulatory needs (Jacobs et al. 2007). The type of roost chosen varies significantly depending on species. Popular roost locations include the eaves of buildings, tree cavities, cellars or attics, and protected caves (Lausen & Barclay 2006; Nagel & Nagel 1991; Soriano et al. 2002; Turbill 2006). The amount of energy saved in torpor varies according to the minimum body temperature achieved by the torpid bat, which is in turn dependent on the ambient temperature in the roost (Nagel & Nagel 1991). Lower body temperatures yield greater reductions in metabolism and consequently increased energy savings. Thus, it follows that bats using torpor as an energy-saving mechanism would choose cooler roosts so they could have the greatest possible metabolic reduction (Solick & Barclay 2007). All of the roosts listed above are in some way shaded or otherwise protected from direct solar heating. On the other hand, bats that use torpor less frequently, such as reproductive females, are likely to choose roosts that have warmer ambient temperatures (Solick & Barclay 2007). Individuals choose roosts with a thermal gradient so they can move to areas of higher or lower ambient temperature as needed throughout the day (Solick & Barclay 2007).

Bats may also regulate the internal microclimate of the roost by clustering with conspecifics (Dixon & Rose 2003; Maloney et al. 1999). According to Dixon and Rose (2003), clustering can substantially decrease an individual's thermal conductance by diminishing its exposed body surface by up to 60%. Clustering can also reduce the risks of predation associated with torpor, as shown in neotropical nectar-feeding bats (*Glossophaga soricina*), which roost openly during the day in large groups (Kelm & Helversen 2007). Researchers have discovered that some individuals within the group are torpid, but many are not. The torpid individuals rely on their nontorpid conspecifics for protection (Alvarez et al. 1991; Kelm 2006) This group dynamic allows individuals to reap the rewards of torpor without incurring as much predation risk to themselves.

While the majority of bats use cool roosts as a way of increasing torpor benefits, some species rely on roosts whose ambient temperature is extremely high. An example of this is the Angolan free-tailed bat (*Mops condylurus*), which preferentially roosts under corrugated metal roofs in sub-Saharan Africa, where the temperature regularly exceeds 40° C (104° F) (Maloney et al. 1999). Generally, small mammals cannot survive at body temperatures in excess of 43° C (Cossins & Bowler 1987), but *M. condylurus* actively seeks out these lethally hot roosts. Living in such a hot area limits the ability of bats to enter torpor, as their body temperature is directly related to the ambient temperature (Maloney et al. 1999). However, the loss of torpor-related energy savings is offset by other energetic advantages. According to Maloney et al. (1999), warm roosts may decrease the reproductive costs associated with torpor, increase energy availability for activities such as foraging and reproduction, and increase the speed of juvenile growth and development.

Most bats will preferentially select warmer ambient temperatures even if temperatures mimicking their natural roost are offered (Kelm 2006; Lausen & Barclay 2003; Neubaum et al. 2006; Solick & Barclay 2006; Wojciechowski et al. 2007). Thermal preference for roosting, at least in *Myotis myotis*, is based on the maximum temperature available rather than on a fixed ambient temperature set point (Wojciechowski et al. 2007). The bats tend to prefer ambient temperatures about 30% lower than the maximum available temperature in the roost, suggesting that bats choose environments (at least in terms of ambient temperature and humidity) that guarantee optimal conditions for both hibernation and overall survival (Wojciechowski et al. 2007). Once again, it comes down to maximizing the cost-benefit ratio of energy gains, which do not increase linearly with decreases in temperature. Conversely, the costs do—the physiological costs of metabolic depression and the energetic costs of arousal get higher as the ambient temperature in the roost drops. It is more cost-efficient to enter torpor at a higher ambient temperature to obtain the energy-saving benefits of torpor while avoiding as much as possible the physiological costs of subsisting at and recovering from low temperatures (Maloney et al. 1999).

Given their average small body size, high mass-specific metabolic rate, high surface area-to-volume ratio and subsequent high rates of water and heat loss, bats must conserve as much energy as possible to survive not only environmental perturbations but also day-to-day life. When torpor is analyzed as a thermoregulatory strategy, we can see that though substantial costs are associated with torpor, the benefits outweigh those costs, or the costs can at the very least be mitigated by behavioral choices. Thus it follows that bats would use torpor as a physiological energy-saving mechanism, as demonstrated by the worldwide use of torpor among species of *Chiroptera*.

◆

References

Alvarez, J., M. R. Willig, J. K. Jones, and D. Webster. 1991. *Glossophaga soricina*. *Mammal Species* **379**:1–7.

Avery, M. I. 1985. Winter activity of pipistrelle bats. *Journal of Animal Ecology* **54**:721–738.

Cossins, A. R., and K. Bowler 1987. *Temperature Biology of Animals.* Chapman & Hall, London.

Cryan, P. M., and B. O. Wolf. 2003. Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *The Journal of Experimental Biology* **206**:3381–3390.

Daan, S., B. Barnes, and A. Strijkstra. 1991. Warming up for sleep - ground squirrels sleep during arousals from hibernation. *Neuroscience Letters* **128**:265–268.

Dietz, M., and E. K. V. Kalko. 2006. Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiological Biology* **176**:223–231.

Dixon, K. J., and R. W. Rose. 2003. Thermal energetics of *Nyctophius geoffroyi* (Chiroptera : Vespertilionidae) at the southern limits of its distribution. *Australian Journal of Zoology* **51**:43–50.

Dunbar, M. B., and T. E. Tomasi. 2006. Arousal patterns, metabolic rate, and an energy budget of Eastern red bats (*Lasiurus borealis*) in winter. *Journal of Mammalogy* **87**:1096–1102.

Filho, D. W., S. L. Althoff, A. L. Dafré, and A. Boveris. 2007. Antioxidant defenses, longevity and ecophysiology of South American bats. *Comparative Biochemisty and Physiology* **146**:214–220.

French, A. R. 1985. Allometries of the duration of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. *Journal of Comparative Physiology* **156**:13–19.

Hock, R. J. 1951. The metabolic rates and body temperatures of bats. *The Biological Bulletin* **101**:289–299.

Hosken, D. J., and P. C. Withers. 1999. Metabolic physiology of euthermic and torpid lesser long-eared bats, *Nyctophilus geoffroyi* (Chiroptera: Vespertillionidae). *Journal of Mammalogy* **80**:42–52.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiological and Biochemical Zoology* **76**:165–179.

Jacobs, D. S., E. J. Kelly, M. Mason, and S. Stoffberg. 2007. Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertillionidae). *Canadian Journal of Zoology* **85**:883–890.

Kelm, D. H. 2006. Roosting ecology of neotropical bats: communal roosting, the energetics interface and applications in restoration ecology. Dissertation. University of Erlangen-Nuremberg, Germany.

Kelm, D. H., and O. v. Helversen. 2007. How to budget metabolic energy: torpor in a small neotropical mammal. *Journal of Comparative Physiological Biology* **177**:667–677.

Kortner, G., and F. Geiser. 2000. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. Chronobiology International: *The Journal of Biological and Medical Rhythm Research* **17**:103–128.

Lausen, C. L., and R. M. R. Barclay. 2003. Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *Journal of Zoology*, London **260**:235–244.

Lausen, C. L., and R. M. R. Barclay. 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings.

Journal of Mammalogy **87**:362–370.

Malatesta, M., M. Biggiogera, and C. Zancanaro. 2007. Hypometabolic induced state: a potential tool in biomedicine and space exploration. *Review of Environmental Science and Biotechnology* **6**:47–60.

Maloney, S. K., G. N. Bronner, and R. Buffenstein. 1999. Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: a small mammal that uses hot roosts. *Physiological and Biochemical Zoology* **72**:385–396.

Nagel, A., and R. Nagel. 1991. How do bats choose optimal temperatures for hibernation? *Comparative Biochemisty and Physiology* **99**:323–326.

Neubaum, D. J., T. J. O'Shea, and K. R. Wilson. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. *Journal of Mammalogy* **87**:470–479.

Park, K. J., G. Jones, and R. D. Ransome. 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumquinum*). *Functional Ecology* **14**:580–588.

Shanley, D. P., and T. B. L. Kirkwood. 2000. Calorie restriction and aging: a life-history analysis. *Evolution* **54**:740–750.

Smith, F. A. 2003. Body mass of quaternary mammals. *Ecology* **84**:12.

Solick, D. I., and R. M. R. Barclay. 2006. Thermoregulation and roosting behaviour of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. *Canadian Journal of Zoology* **84**:589–599.

Solick, D. I., and R. M. R. Barclay. 2007. Geographic variation in the use of torpor and roosting behaviour of female western long-eared bats. *Journal of Zoology* **272**:358–366.

Soriano, P. J., A. Ruiz, and A. Arends. 2002. Physiological responses to ambient temperature manipulation by three species of bats from Andean cloud forests. *Journal of Mammalogy* **83**:445–457.

Speakman, J. R. 2000. The cost of living: field metabolic rates of small mammals. *Advances in Ecological Research* **30**:177–297.

Thomas, D. W., M. Dorais, and J.-M. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis* *lucifugus*. *Journal of Mammalogy* **71**:475–479.

Trachsel, L., D. Edgar, and H. Heller. 1991. Are ground squirrels sleep deprived during hibernation? *American Journal of Physiology* **260**:1123–1129.

Turbill, C. 2006. Thermoregulatory behavior of tree-roosting chocolate wattled bats (*Chalinolobus morio*) during summer and winter. *Journal of Mammalogy* **87**:318–323.

Warnecke, L., J. M. Turner, and F. Geiser. 2008. Torpor and basking in a small arid zone marsupial. *Naturwissenschaften* **95**:73–78.

Willis, C. K. R. 2007. An energy-based body temperature threshold between torpor and normothermia for small mammals. *Physiological and Biochemical Zoology* **80**:643–651.

Willis, C. K. R., R. M. Brigham, and F. Geiser. 2005a. Deep, prolonged torpor by pregnant, free-ranging bats. Naturwissenschaften **93**:80–83.

Willis, C. K. R., J. E. Lane, E. T. Liknes, D. L. Swanson, and R. M. Brigham. 2005b. Thermal energetics of female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology* **83**.

Willis, C. K. R., C. Turbill, and F. Geiser. 2005c. Torpor and thermal energetics in a tiny Australian verpertilionid, the little forest bat (*Vespadelus vulturnus*). *Journal of Comparative Physiological Biology* **175**:479–486.

Wojciechowski, M. S., M. Jefimow, and E. Tegowska. 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). *Comparative Biochemisty and Physiology* **147**:828–840.