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SHORT COMMUNICATION

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Deep, prolonged torpor by pregnant, free-ranging bats

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Abstract Many mammals save energy during food shortage or harsh weather using controlled reductions in body temperature and metabolism called torpor. However, torpor slows offspring growth, and reproductive individuals are thought to avoid using it because of reduced fitness resulting from delayed offspring development. We tested this hypothesis by investigating torpor during reproduction in hoary bats (*Lasiurus cinereus*, Vespertilionidae) in southern Canada. We recorded deep, prolonged torpor bouts, which meet the definition for hibernation, by pregnant females. Prolonged torpor occurred during spring storms. When conditions improved females aroused and gave birth within several days. Our observations imply a fitness advantage of torpor in addition to energy conservation because reduced foetal growth rate could delay parturition until conditions are more favourable for lactation and neonatal survival.

Introduction

Maintaining high body temperatures (T_b) during cold exposure is energetically costly for small endotherms (i.e. mammals and birds), and this problem may be compounded for many species because food availability is often reduced during cold weather (Geiser 2004; Wang 1989). Therefore, many species employ controlled reductions in T_b and metabolism known as torpor to survive periods of food shortage and inclement weather when they might otherwise starve (Dausmann et al. 2004; Geiser 2004; Wang 1989). Species which use only shallow, short-term torpor bouts lasting hours are known as daily heterotherms, while those capable of deep, prolonged torpor bouts lasting days or weeks are defined as hibernators (Geiser and Ruf 1995). Torpor results in enormous energy savings for endotherms, but it is widely viewed as a disadvantage for reproductive individuals because it slows offspring development (Geiser 1996; Racey 1973; Racey and Swift 1981). In mammals, torpor delays parturition (Racey and Swift 1981) and inhibits lactation (Wilde et al. 1999). For temperate species these costs may be especially pronounced because offspring must grow quickly during a short warm season to survive the winter (Geiser 1996). Consistent with this hypothesis are observations that free-living reproductive mammals tend to avoid torpor, especially long, deep bouts, relative to non-reproductive individuals (Geiser 1996; Lausen and Barclay 2003). However, even during relatively warm months of the year, reproductive individuals of many temperate species may be exposed to unpredictable periods of cold and food shortage, especially in spring. Mammalian lactation results in particularly high energetic costs (Thompson and Nicoll 1986) so during harsh weather it could be difficult, if not impossible, for lactating mammals to maintain rapid offspring growth and still avoid starvation.

To test the hypothesis that reproductive mammals avoid deep prolonged torpor, we investigated torpor use during reproduction by hoary bats (*Lasiurus cinereus*; Fig. 1) in the Cypress Hills of Saskatchewan, Canada. Hoary bats are migratory and pregnant females return to Saskatchewan in late May when the weather can be harsh. This species roosts in open foliage, which offers little protection from thermal extremes, and the hoary bat's highly insulating pelage appears to be an adaptation to foliage roosting (Shump and Shump 1980). In the Cypress Hills, reproductive females roost in white spruce trees (*Picea glauca*; (Willis and Brigham 2005)).

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Fig. 1 Pregnant hoary bat (*Lasiurus cinereus*) in torpor

Materials and methods

We measured skin temperatures (T_{sk}) of four pregnant bats (mass=35.8±1.6 g) over 24 bat days during three spring rain/snow storms in early June of 2001 and 2002. Daily ambient temperature (T_a) maxima during these storms averaged 11.9±4.5°C, and minima averaged 5.4±2.7°C. Bats were captured in mist nets when they were foraging on unseasonably warm spring nights prior to the storms. Pregnancy was assessed by gentle palpation of the abdomen, and all four bats were heavily pregnant. Our protocol for transmitter attachment, radiotracking and monitoring of roost T_a is described by (Willis and Brigham 2005).

We recorded T_{sk} at 10-min intervals using 1-g temperature-sensitive radiotransmitters calibrated to ±0.1°C (BD-2T, Holohil Systems Limited, Carp, ON, Canada). We used T_{sk} rather than core T_b because the transmission range of small implanted transmitters is insufficient for following wide-ranging animals (Körtner et al. 2001). However, T_{sk} is correlated with T_b and metabolic rate during torpor and normothermia and thus allows for accurate measurement of torpor bout depth and duration (Willis and Brigham 2003; Willis et al. 2004). We observed bats from the base of trees with binoculars each morning to determine parturition dates. Even early postnatal hoary bats are large relative to their mother, and pups were readily visible after parturition.

We used an energetic model, based on laboratory respirometry measurements of metabolic rate during torpor and normothermia (Cryan and Wolf 2003; Willis et al. 2004), and predicted energetic costs during rewarming (Eq. 3 in McKechnie and Wolf 2004) to estimate energy savings afforded by torpor bouts in hoary bats. We divided each torpor bout into an entry period (starting when T_{sk} declined sharply and ending when it stabilised at low T_a), a period of steady-state torpor (when T_{sk} was stable and closely correlated to T_a) and an arousal period (beginning when T_{sk} increased sharply and ending when it stabilised at normothermic levels). One torpid bat defended T_{sk} when T_a declined below 4°C, but we accounted for the corresponding increase in energy use based on measurements of metabolic rate by torpid hoary bats (Cryan and Wolf 2003). We did not observe the other two individuals at T_a <6°C, and they were obviously thermoconforming throughout their prolonged torpor bouts, so we calculated their energy use based on the relationship between torpid metabolic rate and T_a (Cryan and Wolf 2003). We compared the model-predicted energy expenditure of bats using prolonged torpor to the predicted energy expenditure of bats maintaining a constant T_b under the same T_a conditions. The model provides a conservative estimate of energy savings during torpor because it does not incorporate radiant heat gain during passive warming nor the energetic cost associated with convective cooling due to wind exposure during normothermia (Willis and Brigham 2003).

Results

Three of the four pregnant bats used deep, prolonged torpor during harsh weather, employing torpor bouts lasting 4.3±1.3 days. Daily T_{sk} minima during these torpor bouts fell as low as 5.5°C and averaged 7.6±3.9°C, and bats remained torpid until T_a increased markedly with sun exposure (Fig. 2). The longest torpor bout lasted 5.6 days, but this individual remained inactive at the roost without foraging for a total of 9.1 days. For 3.5 days after her prolonged torpor bout, she aroused briefly following passive warming each morning and immediately re-entered torpor (Fig. 2a).

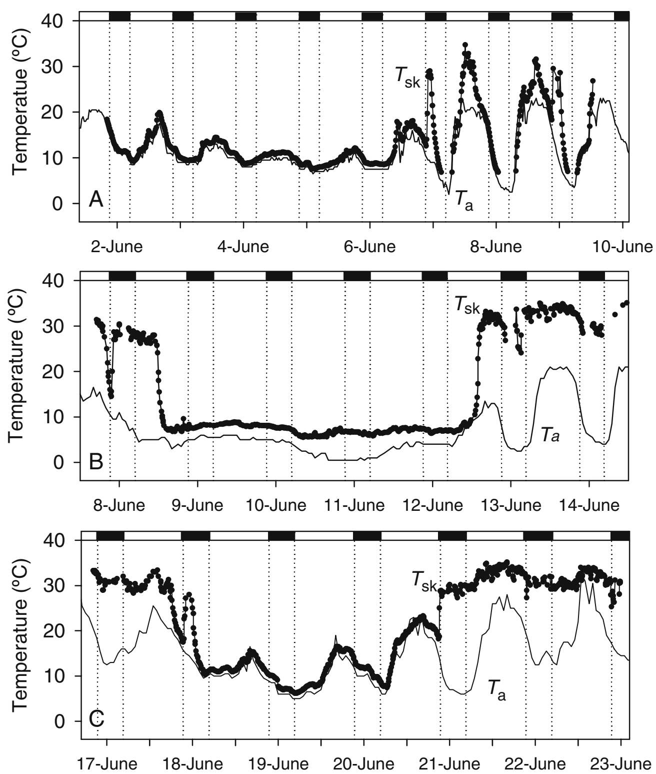

Fig. 2 Representative patterns of skin temperature (*filled symbols*) for three pregnant hoary bats during periods of cold and wet/snowy spring weather from **a** 2–10 June 2001, **b** 8–12 June, and **c** 18–21 June 2002. *Dotted lines* represent sunrise and sunset times, and *dark bars* represent the dark phase. The *solid black line* indicates ambient temperature recorded at each bat's roost site. Bats gave birth within 3.1±1.3 days of final arousal from prolonged torpor

The fourth pregnant bat did not use multi-day torpor but it did respond to harsh weather between 18–21 June 2002 with two short torpor bouts lasting 0.9 and 0.6 days, during which T_{sk} fell as low as 8.5°C. The first storm in 2002 involved a heavy snowfall of about 15 cm, and the foliage roost of one torpid bat was snow-covered for approximately 2 days. Based on our initial observations of pups, parturition in the three bats which used prolonged torpor occurred 3.1±1.3 days after the final arousals we observed. The fourth bat, which used two shorter torpor bouts, was never observed with pups, which means that sometime after being released she either gave birth and abandoned her young or resorbed the embryos.

Relative to a hypothetical normothermic bat, the energetic model predicted that the three individuals using multi-day torpor bouts saved 70.3±11.1 kJ day^{-1} on average, which equates to a savings of 84.8% at the same T_a, or the energetic equivalent of approximately 13 g of fresh insects (Bell 1990). Total energy savings resulting from the longest torpor bout (5.6 days) were enormous at 376 kJ, or the equivalent of approximately 68 g of insects (Bell 1990).

Discussion

We report the first direct observations of multi-day torpor, which meet the definition of hibernation (Geiser and Ruf 1995), in any free-living reproductive mammal. Our findings contrast with the widely held view that prolonged torpor necessarily reduces fitness to reproductive individuals. Model-predicted energy savings for these bats were very large compared to energetic costs of defending normothermic T_b. By reducing the immediate risk of death by starvation for mother and pups, the benefits of prolonged torpor during pregnancy for these bats clearly outweighed any long-term fitness costs of slower offspring growth.

The three individuals using prolonged torpor were thermoconforming throughout almost all of their torpor bouts, even at very low T_a (>4°C), which suggests that they were not attempting to regulate T_b to increase offspring growth rate. They also gave birth within a few days of arousal. The fourth bat, which did not enter prolonged torpor, was not successful in rearing pups. Together these observations suggest that, in addition to immediate energetic benefits, torpor during pregnancy could also be advantageous not in spite of slow offspring development but because of it. Prolonged torpor during unpredictable harsh weather would represent a benefit if it delayed parturition until food availability and ambient conditions were more favourable for offspring survival.

Lactation is more energetically demanding than pregnancy (Thompson and Nicoll 1986), so lactating females defending T_b during harsh weather could easily exhaust their energy reserves, resulting in starvation for mother and offspring. In addition, early postnatal young may not survive if exposed to periods of harsh weather lasting several days. Therefore, using torpor to delay parturition until after harsh weather could improve the likelihood of mother and offspring survival and increase fitness. We hypothesize that the ability to enter prolonged torpor while pregnant allows females to be more flexible in scheduling mating and gestation and, for migratory species, reduces the risk of returning early to summer roosting areas.

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References

Bell GP (1990) Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Stud Avian Biol 13:416–422

Cryan PM, Wolf BO (2003) Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. J Exp Biol 206:3381–3390

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Geiser F (1996) Torpor in reproductive endotherms. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: 10th international hibernation symposium. University of New England Press, Armidale, pp 81–86

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Körtner G, Brigham RM, Geiser F (2001) Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). Physiol Biochem Zool 74:789–797

Lausen CL, Barclay RMR (2003) Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. J Zool (1987) 260:235–244

McKechnie AE, Wolf BO (2004) The energetics of the rewarming phase of avian torpor. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanisms, adaptation and application. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 265–267

Racey PA (1973) Environmental factors affecting the length of gestation in heterothermic bats. J Reprod Fertil Suppl 19:175–189

Racey PA, Swift SM (1981) Variation in gestation length in a colony of pipistrelle bats (*Pipistrellus pipstrellus*) from year to year. J Reprod Fertil 61:123–129

Shump KA Jr, Shump AU (1980) Comparative insulation in vespertilionid bats. Comp Biochem Physiol A 66:351–354

Thompson SD, Nicoll ME (1986) Basal metabolic rate and energetics of reproduction in therian mammals. Nature 321:690–693

Wang LCH (1989) Ecological, physiological and biochemical aspects of torpor in mammals and birds. In: Wang LCH (ed) Advances in comparative and environmental physiology. Springer, Berlin Heidelberg New York, pp 361–401

Wilde CJ, Knight CH, Racey PA (1999) Influence of torpor on milk protein composition and secretion in lactating bats. J Exp Zool 284:35–41

Willis CKR, Brigham RM (2003) Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. J Comp Physiol B 173:379–389

Willis CKR, Brigham RM (2005) Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). J Mammal 86:85–94

Willis CKR, Lane JE, Liknes ET, Swanson DL, Brigham RM (2004) A technique for modeling thermoregulatory energy expenditure in mammals and birds. In: Barnes BM, Carey HV (eds) Life in the cold: evolution, mechanism, adaptation, and application. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 209–220