SHORT COMMUNICATION

Heterothermy in free-ranging male Egyptian Free-tailed bats (*Tadarida aegyptiaca*) in a subtropical climate

Dawn Cory Toussaint, Andrew E. McKechnie*, Mac van der Merwe

Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

Bats, like many other small endotherms, often use facultative reductions in metabolic rate and body temperature (T_b) to decrease their daily energy expenditure (Lyman 1970). The lower energy requirements associated with heterothermy offset the high mass-specific rates of heat loss of most microchiropterans, allowing them to maintain energy balance even in environments where the availability of food fluctuates temporally and/or spatially. Heterothermic responses in bats and other mammals are thought to be broadly divisible into two categories, namely daily torpor and hibernation, which are distinguishable primarily on the basis of bout length (Geiser and Ruf 1995). Daily torpor typically involves periods of reduced T_b lasting less than 24 hours, whereas hibernation involves multi-day bouts that may last as long as several months (Geiser and Ruf 1995).

Hibernation is widespread in temperate-zone bat species that experience low environmental temperatures and reduced food availability during winter (Lyman et al. 1982; Arlettaz et al. 2000; Humphries et al. 2002). Bats often hibernate in thermally stable microsites such as caves and buildings during winter, which allows them to maintain more-or-less constant T_b between interbout normothermic periods (Lyman et al. 1982; Arlettaz et al. 2000; Humphries et al. 2002; Boyles and Willis 2009). In contrast, daily torpor appears to be a more common response in species inhabiting lower latitudes (Geiser and Brigham 2000; Turbill et al. 2003; Willis et al. 2005; Jacobs et al. 2007; Vivier and van der Merwe 2007). Several recent studies of thermoregulation during winter in Australian tree-roosting bats, however, suggest that hibernation may in fact be more common in tropical and subtropical species than previously thought, with at least three *Nyctophilus* species (Vespertilionidae) exhibiting heterothermic bouts lasting for several days (Turbill and Geiser 2008; Stawski et al. 2009). In these species, the T_b of torpid individuals fluctuates widely (up to ∼10 °C) on a daily basis, reflecting the fact that they roost in relatively thermolabile sites in tree cavities and under bark (Turbill and Geiser 2008; Stawski et al. 2009).

Recent studies suggest that heterothermy may be more important in the thermal energetics of bats from tropical and subtropical regions than currently appreciated. We hypothesized that similar patterns of heterothermy to those recently reported for Australian tree-roosting vespertilionids occur in the Egyptian Free-tailed Bat (*Tadarida aegyptiaca*), a ∼16 g molossid that is widespread in southern Africa and which roosts in buildings, rock crevices, as well as in tree cavities and under bark (Skinner and Chimimba 2005). We selected *T. aegyptiaca* for this study on account of the fact that it occurs in Pretoria year-round, and likely experiences substantial reductions in food availability during the cool, dry winter months (Ashdown and McKechnie 2008).

---

*Corresponding author. Tel.: +27 12 4203232; fax: +27 12 3625242.
E-mail address: aemckechnie@zoology.up.ac.za (A.E. McKechnie).

The study was conducted during June and July 2008 at the Groenkloof educational campus (25°46′9″S, 28°12′33″E) of the University of Pretoria in Pretoria, South Africa, at approximately 1,200 m a.s.l.. Pretoria is in a subtropical area that receives rainfall during the austral summer and is characterized by hot, moist summers and cool, dry winters. The dominant vegetation type in the vicinity of Pretoria is deciduous savannah, with a suburban mix of indigenous and exotic tree species at the study site.

We recorded roost temperatures (T_{roost}) by attaching miniature data loggers (Thermochron iButtons, model 1922L, Dallas Semiconductor) in shaded, well-ventilated locations close to roosting bats. Before deployment, the iButtons were calibrated in a water bath over the full range of roost temperatures experienced during the study using a mercury thermometer, with accuracy traceable to the US National Bureau of Standards. The iButtons were recalibrated at the end of the study to account for any long-term drift that may have occurred.

At Groenkloof, T. aegyptiaca typically roosts in vertical gaps between walls and roof overhangs. We captured bats on 28 June and 1 July 2008 as they emerged from their roosts to forage by suspending a 16-mesh mist net (4 × 10 m) across the roost openings. Only male T. aegyptiaca were caught. Skin temperature (T_{skin}) was measured using 0.8 g (equivalent to 4.4–5.5% of body mass) temperature-sensitive transmitters (model BD-2 T, Holohil Systems, Carp, Ontario). The mean body mass of the individuals we attached transmitters to was 16.9 ± 1.1 g (n = 6, range 14.6-18.1 g). Before attachment, the transmitters were calibrated in a water bath against a mercury thermometer over a range of temperatures from 5 °C to 45 °C. The transmitters were attached to the skin between the scapulae by clipping the fur away and using latex-based adhesive (Osto-Bond, M.O.C., Vaudreuil QC, Canada). The bats roosted between vertical surfaces, without any obstructions below them. Had any of the transmitters become detached, they would have fallen to the ground below the roost and been readily detectable, and we are thus confident that they remained securely attached to the bats throughout the study period. Each transmitter emitted a unique frequency between 150.083 and 150.203 MHz that allowed us to identify individual bats.

Signals from the transmitters were recorded using a broad-band communications receiver (IC-R10, Icom, Bellevue, WA) and a three-element Yagi antenna, either by timing pulse intervals manually with a stopwatch, or using a custom-built data logger to record pulse intervals following McKechnie et al. (2004). For manual measurements, a minimum of 20 pulse intervals per reading were timed using a stopwatch (McKechnie et al. 2007). Skin temperatures were estimated from the pulse intervals measured manually or with the data logger using the calibration curve obtained for each transmitter.

To account for variation in $T_{skin} - T_b$ gradients, we used a relatively conservative threshold of $T_{skin} \leq 25$ °C to define torpor. A T_{skin} value of 25 °C is approximately 10 °C lower than typical normothermic T_{skin} values (see results). Rewarming rates during arousals were estimated by fitting least-squares linear regression models to T_{skin} data during rewarming periods that preceded normothermy. Data are presented as mean $\pm$ SD.

We were able to obtain T_{skin} data from only four of the seven male T. aegyptiaca that we attached transmitters to, and assume that the remaining three individuals moved to roost sites beyond reception range. All four individuals exhibited heterothermy, with the three individuals that we obtained most of our data from regularly exhibiting reduced T_{skin} during the study period (Fig. 1), with bout duration (i.e., time between arousals during which $T_b \leq 25$ °C) ranging from 2 to >84 hours (Fig. 1). In addition, one individual remained heterothermic for more than nine days at the end of the study (Fig. 1A). The three individuals exhibited three distinct thermoregulatory patterns during the study period, best illustrated by an individual for whom we obtained T_{skin} traces with high temporal resolution using a data logger (Fig. 1A). This individual left its roost site only twice during the study. For approximately 10 hr on the evening of 4 July, and for 24 hr starting on the evening of 9 July, the signal from its transmitter was not detectable at the roost (Fig. 1). Thereafter, it remained in the roost for 11 days until the end of the study on 20 July. Before the arrival of a cold front on 11 July, this individual displayed daily torpor (periods of normothermy interspersed with deep torpor bouts), with a bimodal T_{skin} distribution, in which the lower T_{skin} peak reflects periods of heterothermy and the upper T_{skin} peak is associated with arousal and normothermy (Fig. 1). The pronounced drop in daytime roost temperatures associated with the cold front coincided with a switch to hibernation, and a unimodal T_{skin} distribution with the majority of values between 13-19 °C (Fig. 1). Once the cold front passed and daytime temperatures increased again on 16 and 17 July, this individual did not resume the daily torpor pattern evident early in the study period, but instead exhibited large (~10 °C) daily fluctuations in T_{skin} until the end of the study (Fig. 1). During this period, the T_{skin} distribution was unimodal, reflecting the lack of active arousals and normothermy, even though $T_{skin} \geq 25$ °C occurred on some days (Fig. 1). Although we were unable to obtain T_{roost} data for this individual, the T_{skin} of two other bats closely tracked T_{roost} (Fig. 1B,C).

Daily minimum T_{skin} ranged from 6.2 °C to 26.2 °C, and our data suggest that during most of the study period, the bats were thermoconforming (Fig. 1). Periods of normothermy generally coincided with
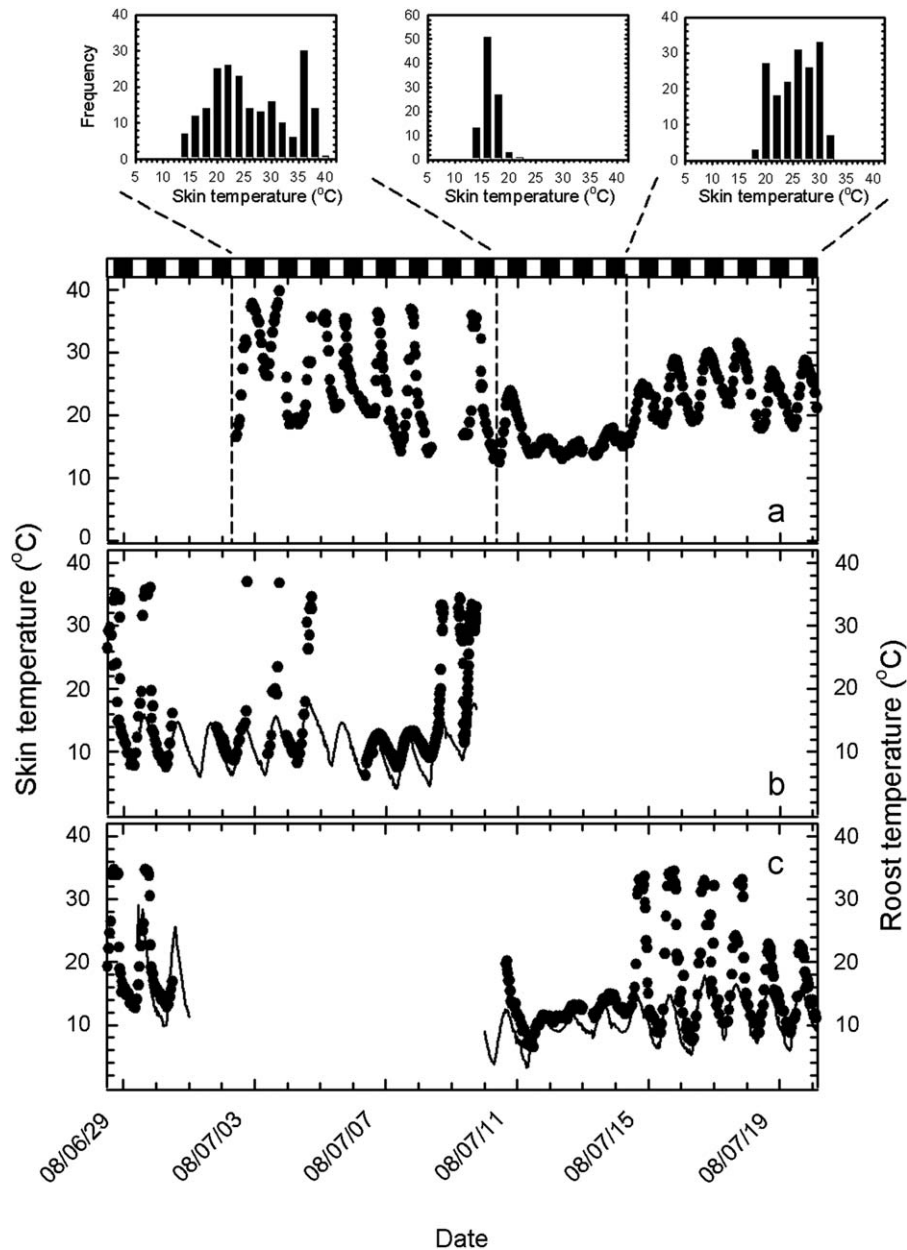
Fig. 1. Skin temperatures (black dots) in three male *Tadarida aegyptiaca* during July 2008 in Pretoria, South Africa. In panels B and C, roost temperature is indicated by a solid line. No roost temperature data are available for the roost occupied by the individual shown in panel A. The three histograms above panel A show the distributions of T_{skin} during three patterns of heterothermy exhibited by this individual, with each period delineated by dashed vertical lines.

warmer evenings, and maximum T_{roost} values on days when at least one bat aroused ($T_{roost} = 15.7 \pm 4.8\,°C$) were higher than days on which all study individuals remained torpid ($T_{roost} = 11.5 \pm 1.6\,°C$). Rewarming rates for three individuals during active arousal averaged $0.30 \pm 0.12\,°C\,min^{-1}$ ($n = 3$), and ranged from 0.17–$0.39\,°C\,min^{-1}$.

Our data confirm that hibernation occurs in a southern African molossid. These observations are similar to those made for Australian vespertilionids (Turbill and Geiser 2008; Stawski et al. 2009), and provide further evidence that hibernation is an important component of winter thermoregulation in bats inhabiting subtropical latitudes. Previous telemetric studies of thermoregulation in southern African bats have documented daily torpor, but not hibernation (Jacobs et al. 2007; Vivier and van der Merwe 2007). The range of bout lengths in our study, from 2 hours to more than 9 days, is greater than that for other subtropical bats, such as *Nyctophilus bifax* ($<$ 24 hr to 128.5 hr)

(Stawski et al. 2009), but similar to male *N. geoffroyi* (up to 9 days) and *N. gouldi* (up to 11 days) (Turbill and Geiser 2008). We did not catch any female *T. aegyptiaca* during the study period, although it is possible that they were roosting at other sites in the vicinity. Whether or not females of this species undertake seasonal movements is unknown (Skinner and Chimimba 2005).

The roosts used by *T. aegyptiaca* displayed daily cycles of environmental temperature, mirrored by cycles of cooling and heating in torpid individuals (Fig. 1). The large circadian cycles of T_{skin} during hibernation are quantitatively similar to those in tree-roosting Australian species (Turbill and Geiser 2008; Stawski et al. 2009), some of which actively selected north-facing sunlit roost sites, and contrast with the approximately stable T_b of many temperate species that spend the winter in caves (Arlettaz et al. 2000; Humphries et al. 2002). The selection of thermally labile roost sites that are warmed by solar radiation may provide energetic benefits to heterotherms by ameliorating the energetic cost of periodic arousals (Turbill and Geiser 2008).

Rewarming rates during daily torpor in three male *T. aegyptiaca* were lower than those reported for other molossids (0.73–1.40 °C min^{-1}, Willis 2008), which is consistent with the idea that selection for rapid rewarming is likely to be more pronounced in bats that roost in thermally stable microsites than in species that occupy thermally labile sites (Willis 2008).

Previous studies of thermoregulation in free-ranging southern African vespertilionids and molossids have reported daily torpor, but not hibernation (Jacobs et al. 2007; Vivier and van der Merwe 2007). In the latter study, T_b was measured between 06:00 and 18:00 in *Mops condylurus* held in a cage; the absence of hibernation may simply reflect the fact that T_b measurements lasted for only 12 hr. Our data for *T. aegyptiaca* reveal, as predicted by Stawski et al (2009), that prolonged, multiday heterothermic bouts occur in at least one subtropical species outside of Australia. This is further evidence that hibernation is not restricted to species from temperate latitudes. Recent observations of hibernation in subtropical species are not surprising; for instance, night-time air temperatures in Pretoria during winter can approach freezing, and the availability of aerial insects decreases exponentially with air temperature (Ashdown and McKechnie 2008). The heterothermy exhibited by *T. aegyptiaca*, like other subtropical bat species, is likely a response to a combination of increased energy requirements and reduced food availability on cool nights.

Acknowledgements

References

Arlettaz, R., Ruchet, C., Aeschimann, J., Brun, E., Genoud, M., Vogel, P., 2000. Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. Ecology 81, 1004–1014.

Ashdown, R.A.M., McKechnie, A.E., 2008. Environmental correlates of Freckled Nightjar activity in a seasonal, subtropical habitat. J. Ornithol. 149, 615–619.

Boyles, J.G., Willis, C.K.R., 2009. Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? Front. Ecol. Environ. doi:10.1890/080187.

Geiser, F., Brigham, R.M., 2000. Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). J. Comp. Physiol. B 170, 153–162.

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.

Humphries, M.M., Thomas, D.W., Speakman, J.R., 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418, 313–316.

Jacobs, D.S., Kelly, E.J., Mason, M., Stoffberg, S., 2007. Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae). Can. J. Zool. 85, 883–890.

Lyman, C.P., 1970. Thermoregulation and metabolism in bats. In: Wimsatt, W.A. (Ed.), Biology of Bats. Academic Press, New York pp. 301–330.

Lyman, C.P., Willis, J.S., Malan, A., Wang, L.C.H., 1982. Hibernation and Torpor in Mammals and Birds. Academic Press, New York.

McKechnie, A.E., Ashdown, R.A.M., Christian, M.B., Brigham, R.M., 2007. Torpor in an Afrotropical caprimulgid, the Freckled Nightjar (*Caprimulgus tristigma*). J. Avian Biol. 38, 261–266.

McKechnie, A.E., Körtner, G., Lovegrove, B.G., 2004. Rest-phase thermoregulation in free-ranging white-backed mousebirds. Condor 106, 144–150.

Skinner, J.D., Chimimba, C.T., 2005. The Mammals of the Southern African Subregion, 3rd ed. Cambridge University Press, Cambridge.

Stawski, C., Turbill, C., Geiser, F., 2009. Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). J. Comp. Physiol. B 179, 433–441.

Turbill, C., Geiser, F., 2008. Hibernation by tree-roosting bats. J. Comp. Physiol. B 178, 597–605.

Turbill, C., Körtner, G., Geiser, F., 2003. Natural use of heterothermy by a small, tree-roosting bat during summer. Physiol. Biochem. Zool. 76, 868–876.

Vivier, L., van der Merwe, M., 2007. The incidence of torpor in winter and summer in the Angolan free-tailed bat, *Mops condylurus* (Microchiroptera: Molossidae), in a subtropical environment, Mpumulanga, South Africa. Afr. Zool. 42, 50–58.

Willis, C.K.R., 2008. Do roost type or sociality predict warming rate? A phylogenetic analysis of torpor arousal. In: Lovegrove, B.G., McKechnie, A.E. (Eds.), Hypometabolism in Animals: Hibernation, Torpor and Cryobiology. University of KwaZulu-Natal, Pietermaritzburg pp. 373–384.

Willis, C.K.R., Turbill, C., Geiser, F., 2005. Torpor and thermal energetics in a tiny Australian vespertilionid, the little forest bat (*Vespadelus vulturnus*). J. Comp. Physiol. B 175, 479–486.