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SHORT COMMUNICATION

Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals?

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Abstract Bats are most diverse in the tropics, but there are no quantitative data on torpor use for energy conservation by any tropical bat in the wild. We examined the thermal biology, activity patterns and torpor use of two tree-roosting long-eared bats (*Nyctophilus geoffroyi*, 7.8 g) in tropical northern Australia in winter using temperature telemetry. Bats commenced activity about 20 min after sunset, ended activity about 2.5 h before sunrise and entered torpor everyday in the early morning even when minimum ambient temperatures (T_a) were as high as 23°C. On average, bats remained torpid for almost 5 h, mean minimum skin temperature (T_{skin}) measured was 22.8± 0.1°C and daily T_{skin} minima were correlated with T_a. Our study shows that even in the tropics, torpor is frequently employed by bats, suggesting that worldwide most bat species are heterothermic and use torpor for energy conservation. We propose that the ability of employing torpor and the resulting highly plastic energy requirements may partially explain why these small insectivorous bats can inhabit almost the entire Australian continent despite vastly different climatic and likely trophic conditions. Reduced energy requirements also may permit survival in degraded or modified habitats, reduce the need for foraging and reduce exposure to predators. Thus, the ability to employ torpor may be one important reason for why most Australian bats and other heterothermic mammals have not gone extinct whereas many obligatory homeothermic mammals that cannot employ torpor and have high energy and foraging requirements have suffered high rates of extinctions.

Keywords Body temperature · Energy conservation · Bat heterothermy · Mammal distribution · Mammal extinctions

Abbreviations

T_a	Ambient temperature
T_b	Body temperature
T_{skin}	Skin temperature
TNZ	Thermo-neutral zone

Introduction

In recent years, the traditional view that daily torpor and hibernation are adaptations that are mainly employed to overcome adverse weather and food shortages during cold northern winters has been challenged (Bieber and Ruf 2009; Stawski and Geiser 2010; Levy et al. 2011; Smit et al. 2011). Torpor, characterised by pronounced reductions in metabolism and body temperature (T_b), has now been recorded in free-ranging tropical dwarf lemurs and tenrecs from Madagascar, small dasyurid marsupials from a tropical Australian desert, as well as in subtropical insectivorous bats (Turbill et al. 2003a; Vivier and van der Merwe 2007; Dausmann 2008; Lovegrove and Genin 2008; Schmid and Speakman 2009; Stawski et al. 2009; Körtner et al. 2010; Cory Toussaint et al. 2010; Liu and Karasov 2011). These studies indicate that despite mild ambient conditions, torpor is widely used for energy and water conservation in tropical

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and subtropical mammals. Whereas in tropical fat-tailed and mouse lemurs, tenrecs and dasyurid marsupials, torpor use appears to be in response primarily to lack of or limited food and occurs mainly in winter (Fietz et al. 2003; Dausmann 2008; Lovegrove and Genin 2008; Schmid and Speakman 2009; Körtner et al. 2010), in subtropical Australian insectivorous tree-dwelling bats, torpor is frequently employed even during summer when insect prey is plentiful (Turbill et al. 2003a; Stawski and Geiser 2010). It is likely that these subtropical bats use torpor because the low ambient temperature (T_a) of around 15°C in the morning followed by passive rewarming with T_a around midday (Turbill et al. 2008) permit substantial energy savings that reduce foraging requirements and exposure to nocturnal predators. Passive rewarming requires only a small fraction of the energy that is needed for active rewarming by endogenous heat production and is widely employed by heterothermic endotherms (Geiser et al. 2004).

In the wet–dry tropics of the Australian Northern Territory, daily and seasonal fluctuations in temperature are small. Winters are dry and warm and precipitation is usually restricted to the monsoonal summer period. The average yearly T_a is approximately 28°C (Bureau of Meteorology, Darwin), which is only about 1°C below the lower critical temperature of the thermo-neutral zone (TNZ, 29.1 to 33.2°C) of the lesser long-eared bat, *Nyctophilus geoffroyi* (Geiser and Brigham 2000), a tree-roosting species found over almost the entire Australian continent (Lumsden and Turbill 2008). Because these bats in the tropical part of their range are often exposed to thermo-neutral or near thermo-neutral conditions even in winter (i.e. require little energy for thermoregulation) and because there are no quantitative data on torpor in free-ranging tropical bats in the literature, the first aim of our study was to examine whether torpor is still employed in the wild and, if so, whether torpor and activity patterns are related to environmental variables. The study was conducted at a site where large carnivorous ghost bats (*Macroderma gigas*), a species known to prey on small bats (Richards et al. 2008) are abundant, therefore the second aim of our study was to examine whether torpor and activity might be affected by the presence of these nocturnal predators.

Methods

The study was conducted south of Darwin near Pine Creek (13°49′ S, 131°49′ E, 202 m altitude), Northern Territory, in the wet–dry tropics of Australia in winter (9 June to 11 July 2010), when *N. geoffroyi* are nonreproductive. T_a was measured at two sites at 30-min intervals in the shade ~1 m above the ground with temperature data loggers (±0.5°C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, CA, USA); however, only the data from one logger within 1 km of roosts were used. During the study, T_a ranged from 16.5°C to 34.0°C.

We netted bats in open Eucalypt woodland within 2 km of Pine Creek. Mist nets (2 ×12 m, 1×9 m) were opened approximately 20 min after sunset for 2 to 3 h on 16 evenings. We captured one black flying fox (*Pteropus alecto*), five ghost bats (*M. gigas*), one hoary wattled bat (*Chalinolobus nigrogriseus*), one northern long-eared bat (*Nyctophilus bifax*), and two lesser long-eared bats (*N. geoffroyi*). The two adult *N. geoffroyi* (one male, one female, body mass 7.8±1.1 g SD) were used for our study, under permits from the University of New England Animal Ethics Committee and the Parks and Wildlife Service of the Northern Territory.

Skin temperature (T_{skin}) of bats was measured using temperature-sensitive radio transmitters (0.6 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada). Before attachment to bats, transmitters were calibrated to the nearest 0.1°C against a precision thermometer between 10°C and 40°C in a water bath. Equations derived from these calibrations (r^2=0.999) were used to calculate the T_{skin} of bats. Transmitters were attached to the skin of bats between the shoulder blades using a latex adhesive (SkinBond, Smith and Nephew United, Mount Waverley, VIC, Australia), after removal of a small patch of fur. External transmitters were used to maximise transmitter range because they can be quickly attached without the need for surgery, and because T_{skin} of resting or torpid bats is typically within 2.0°C of core T_b (Barclay et al. 1996). Therefore, T_{skin} is a reliable measure for quantifying torpor patterns especially when daily fluctuations in T_b are pronounced.

Tagged bats were released within 1 h after capture at the capture site. Bats were tracked daily to locate roosts in the early morning. Transmitters remained attached for 9 days on the female and >8 days on the male (it was still attached when the study concluded). The T_{skin} of both bats was recorded once every 10 min by a remote receiver/logger (Körtner and Geiser 2000) when bats were in reception range. Receiver/loggers were moved to maintain reception range and data were downloaded every 2 to 4 days. Manual readings (TR-4, Telonics, Mesa, AZ, USA, and Yagi antennae, Sirtrack Havelock North, New Zealand) were made over ten transmitter pulse intervals using a stop watch when bats were foraging and out of range of the receiver/loggers. Manual readings were also made near the time bats began to forage to determine short-term changes in T_{skin} before and during departure from the roost and the exact time when bats left the roost, based on fluctuating transmitter signal strength. The end of the activity phase was considered to be the time of the bats' final return to the roost based on continuous transmitter reception on the receiver/logger.

Torpor entries and arousals and the duration of torpor bouts were calculated from the time T_{skin} of inactive bats fell below and subsequently rose above 30.0°C (Barclay et al. 2001; Willis and Brigham 2003; Geiser and Mzilikazi 2011) because the T_{skin} of normothermic and active bats (Fig. 1) was similar or greater than the T_{b} measured rectally for normothermic individuals of the same species (Geiser and Brigham 2000). On one occasion, the male rewarmed passively around midday to 30.6°C, but after this peak, T_{skin} fell again below 30°C. The period of passive rewarming was included into the torpor bout.

Insects were abundant during our study. We regularly captured moths, grasshoppers and some beetles in the nets, which are major prey items of *N. geoffroyi* (Lumsden and Turbill 2008). Moreover, many flying insects that were attracting foraging bats were seen under streetlights in the nearby town.

Minitab Statistical Software (Minitab version 13.1, 2000) and StatistiXL (V1.8, 2007) were used for statistical analyses. Numerical values are reported as means±SD for "*n*" the number of individuals; "*N*" is the number of measurements. Mean values for each individual were used to calculate group means to account for repeated measures in individuals; alpha<0.05 was considered to be significant. Linear regressions were fitted by the least squares method. Times of entry and arousal from torpor and beginning and end of activity were examined using Rayleigh tests to determine whether they differed from random distribution.

Results

During the time we were able to measure T_{skin} of the two bats (29 June to 11 July), the weather was mild and mainly sunny, with some cloud cover on several days; light rain fell briefly in the early afternoon on 6 July and the afternoon of that day was cool and windy. The mean T_{a} was 24.4±4.3°C, the mean minimum T_{a} was 19.2±1.8°C, and the mean maximum T_{a} was 31.6±1.6°C. The lowest and highest T_{a} measured was 16.5°C and 34.0°C, respectively.

Both bats roosted, apparently individually, in trees (*Eucalyptus* spp.) with hollows and/or peeling bark. Both bats reused a single roost tree over several days in sequence, but changed roost trees once (female) or twice (male). All roosts were within 1 km of the capture site and transmitter signals of bats were regularly heard at night when they appeared to be foraging near the capture site. Activity of both bats commenced predictably (Rayleigh test, $p<0.001$) during twilight, about 20 min after sunset (1827 hours) at 1848±0018 hours (mean vector for female, $N=8$) and at 1852±0005 hours (mean vector for male, $N=5$) (Fig. 2). Both bats regularly returned to or near to the roost at night for brief periods. The overall foraging time, including these brief visits to the roosts, was similar for the two individuals ($p=0.72$, $t_8=0.37$) and the overall mean was 0952±0056 h ($n=2$, $N=10$). Activity ended at 0432±0050 hours (mean vector for female, $N=7$) and 0457±0041 hours (mean vector for male, $N=6$), about 2.5 h before sunrise (0707 hours).

Despite the mild thermal conditions, both bats entered torpor every day T_{skin} was measured, as is shown for the female (Fig. 1). Even on days when minimum T_{a} was as high as 23°C, both bats employed torpor, usually in the morning. Time of torpor entry for morning bouts occurred non-randomly (Rayleigh test, $p<0.001$) before sunrise at a mean of 0517±0056 hours (mean vector for female, $N=9$) and 0645±0120 hours (mean vector for male, $N=7$). Arousal from torpor, during which T_{skin} usually passively

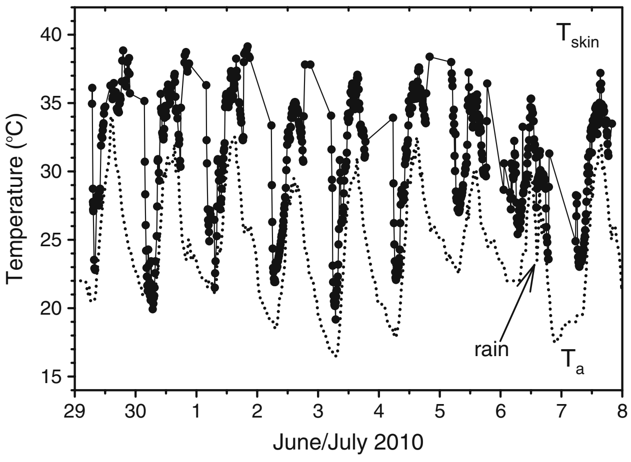

Fig. 1 Fluctuations of skin temperature (T_{skin}, *dots* and *solid lines*) of the female *N. geoffroyi* and ambient temperature (T_{a}, *dotted line*) over 9 days during the tropical winter. The period of rain is indicated by an *arrow*

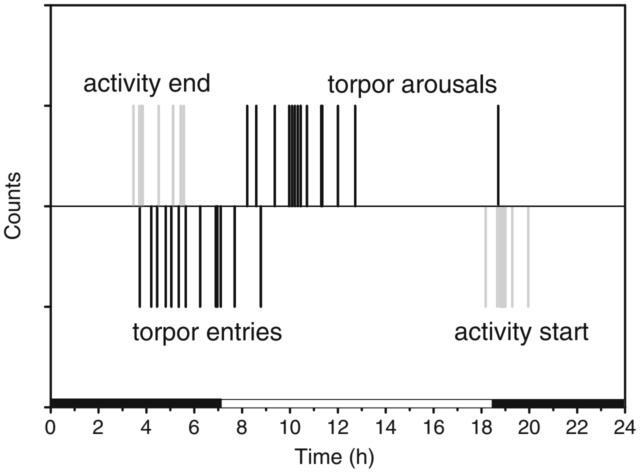

Fig. 2 The times of activity start and end (*grey bars*) and torpor entries and arousals (*black bars*) of two *N. geoffroyi* during the tropical winter. Each *vertical bar* represents an individual observation, *black horizontal bars* indicate the period between sunset and sunrise

tracked T_a for much of the arousal process, occurred at 0957±0055 hours (mean vector for female, $N=9$) and 1228±259 hours (mean vector for male, including the bout lasting till afternoon, $N=6$) (Figs. 2 and 3). On one occasion on 6 July when light rain fell after midday and the afternoon was cool and windy, the female re-entered torpor for 0510 h in the afternoon after a morning torpor bout of 0538 h (Fig. 1). On the same day, the male did not rewarm actively to normothermic T_b at midday, but rather showed passive rewarming with T_{skin} almost exactly tracking T_a to a maximum T_{skin} of 30.6°C (Fig. 3). After this peak, T_a and T_{skin} of the male fell during and after the rain period, but a second passive rewarming phase was observed at ~1530 hours after which T_{skin} again declined with T_a; active arousal occurred at 1835 hours, 8 min after sunset.

Mean torpor bout duration for morning bouts was 0440±0054 h (female) and 0520±0240 h (male, including the bout lasting till afternoon, Fig. 3). Torpor bout duration did not differ between individuals ($p=0.49$; $t_{14}=0.71$) and the overall torpor bout duration, including the afternoon bout was 0457±0142 h ($n=2$, $N=16$).

Likely because of the consistent thermal conditions during our study, torpor bout duration was not correlated with the maximum and minimum daily T_a or the average daily T_a. The total time during a day bats remained torpid was also not correlated with T_a.

Mean minimum T_{skin} during morning torpor of the two bats did not differ statistically ($p=0.88$; $t_{15}=0.15$) and was 22.8±0.1°C ($n=2$, $N=17$). The minimum individual T_{skin} measured was 20.2°C (female) and 19.8°C (male). The T_{skin} maxima, measured during nightly foraging were 39.1°C (female, Fig. 1) and 40.3°C (male, Fig. 3). The minimum T_{skin} was strongly correlated with the minimum T_a measured near the same time of day in both individuals and the regression lines were very similar (female: $y=6.60+0.81x$, $F_{1,\,7}=7.26$, $r^2=0.51$, $p=0.031$; male: $y=6.24+0.82x$, $F_{1,\,6}=15.17$, $r^2=0.72$, $p=0.008$). Over the entire T_a range, minimum T_{skin} was on average about 2°C above minimum T_a.

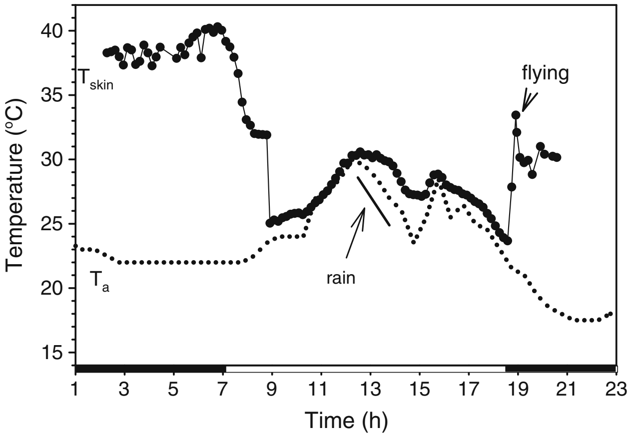

Fig. 3 Fluctuations of skin temperature (T_{skin}, *dots* and *solid lines*) of the male *N. geoffroyi* and ambient temperature (T_a, *dotted line*) on the day light rain fell in the early afternoon (*bar* and *arrow*). T_{skin} tracked T_a for much of the daytime, active arousal occurred after sunset before the bat began to fly. *Black horizontal bars* indicate the period between sunset and sunrise

Discussion

Our study shows that during winter in the wet–dry tropics of the Australian Northern Territory, even under thermal conditions that approximate the TNZ of *N. geoffroyi*, both bats entered torpor on every day. This provides further evidence that torpor may be expressed over a wide range of distribution and climates in bats (Dunbar and Brigham 2010). Torpor in tropical *N. geoffroyi* was employed at minimum T_as (16.5°C to 23°C) that were well above those at which the species expressed torpor in summer in a cool temperate region (minimum T_a ~7°C to 17°C; Turbill et al. 2003b), and despite the apparent abundance of insects. However, with the exception of a single afternoon bout, torpor entry always occurred in the early morning when T_a was lowest and usually lasted till late morning or midday, and once into the late afternoon. Torpor bouts lasting longer than 10 h were not recorded.

Although our data are based on only two individuals, we contend that they are representative because torpor was used every day over many days and differences between the individuals were small. Further, non-reproductive individuals of the same species from a cool temperate habitat exhibit similar torpor patterns under similar environmental conditions (Turbill et al. 2003b). We predict that *N. geoffroyi* will use torpor for most of the year including summer in many tropical areas because the thermal conditions show little seasonal change and considering the positive effect of rain, which substantially increases in summer, on torpor duration. Our data on frequent use of torpor in a tropical bat also suggests that the majority of the world's approximately 1,100 bat species, most of which are small and insectivorous and are found in the tropics/subtropics, will be heterothermic and employ torpor for energy conservation.

The frequent use of torpor we observed raises the question as to why torpor should be employed at all by a tropical bat and why it is used so regularly. At a T_b of 23°C, near the average minimum T_{skin} measured, the metabolic rate during torpor would be only 5% of the resting metabolic rate at T_a 23°C and only 13% of the basal metabolic rate of *N. geoffroyi* (Geiser and Brigham 2000). This pronounced reduction of metabolic rate is due to a large extent to the small size of the bat. Thus, even the small reduction of T_b results in a substantial reduction of energy expenditure that over the average bout duration of about 5 h/day and the ability to largely rewarm passively results in substantial reductions in the need to forage.

Two activity peaks, one in the evening and one in the morning are often observed in bats especially during mild thermal conditions (Pavey et al. 2001). The use of torpor well before sunrise and the resulting lack of a pre-dawn activity peak in our study, despite the mild climate, suggest that *N. geoffroyi* restricts nocturnal activity in the second half of the night. Thus, the regular return to the roost at night and early entry into torpor suggest that bats were limiting their foraging at night perhaps to avoid predation by carnivorous ghost bats (*M. gigas*, 100 g). Our trap location and general study area were located within 2 km of the largest known roost of ghost bats, with up to 1,000 individuals. Individual ghost bats in the Pine Creek colony capture large numbers of birds and bats, including members of several families of microchiropterans (Tidemann et al. 1985; Schulz 1986; Richards et al. 2008). These microbats are captured in flight by aerial pursuit (Pettigrew et al. 1986) similar to what has been observed for diurnal avian raptors preying on bats (Fenton et al. 1994). Ghost bats were the most common species captured in our nets and radio-tracked ghost bats from the Pine Creek colony flew a mean of 1.9 km to the centre of their foraging areas (Tidemann et al. 1985), indicating that our *Nyctophilus* foraged in an area with high predator activity. The regular torpor use and relative short foraging times we observed in *N. geoffroyi* support the view that torpor in bats may not only be employed to minimise energy expenditure, but also to avoid nocturnal predators when bats have good or sufficient energy stores and are not required to feed (Stawski and Geiser 2010). *N. geoffroyi* departed their roosts about 1 h and returned about 80 min before ghost bats radio-tagged in late autumn began/ceased activity (Tidemann et al. 1985), suggesting *N. geoffroyi* minimized overlap with ghost bat activity times. This provides evidence of potential survival benefits of torpor in an area with abundant prey, but with a high risk of predation.

Use of torpor also appears to affect the distribution of *N. geoffroyi*, a fact that has been overlooked in the past. Increases in geographic distribution ranges often (not always) correlate with an increase in body size (Gaston and Blackburn 1996). Interestingly, despite its small size, *N. geoffroyi* is only one of three of the approximately 300 native Australian mammals that are distributed over most of the continent. One may argue that this is due to its ability to fly, as for another species with a similar distribution, Gould's wattled bat (*Chalinolobus gouldii*). However, the third species with an Australia-wide distribution, the echidna (*Tachyglossus aculeatus*), is a slow-moving non-volant monotreme. The shared traits of these three species, phylogenetically separated by 160 million years, are a diet of insects, opportunistic use of roosting/resting sites and the ability to employ torpor in many habitats (Hosken and Withers 1997; Brice et al. 2002; Morrow and Nicol 2009). These three species have to cope with vastly different thermal environments ranging from alpine to arid to tropical and consequently different energy requirements and trophic conditions. Although large geographic ranges are not a general attribute of all heterothermic mammals because distribution is affected by a multitude of factors, it appears the ability of using torpor for adjusting energy and water requirements to the prevailing local conditions may permit these three small Australian species to invade and persist in such a variety of habitats.

Recently, the ability to use torpor has been implicated in the context of mammalian extinctions (Geiser and Turbill 2009). Although Australia has suffered almost half of all worldwide mammal extinctions over the last 200 years, Australian bats, unlike many homeothermic marsupials and rodents, have been almost entirely spared (Johnson 2006; Geiser and Turbill 2009). It has been suggested that, in addition to the ability to fly, the ability to use torpor with its enormous scope for phenotypic plasticity with regard to energy requirements may allow long-term survival of adverse conditions, habitat modification and degradation, as well as avoidance of introduced or native predators, which likely are the major causes of extinctions (Geiser and Turbill 2009; Canale and Henry 2010; Hallam and Mzilikazi 2011). Thus, conservation biologists cannot continue to ignore thermal energetics because animal species are not defined simply by their size, numbers or the environment they live in, but also by vastly different energy requirements and abilities to survive depending on whether they can or cannot employ torpor.

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