

Roosting and thermoregulatory behaviour of male Gould's long-eared bats, *Nyctophilus gouldi*: energetic benefits of thermally unstable tree roosts

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Abstract. Information about the thermal biology of bats in relation to their roosting behaviour is scant. I used temperature telemetry to locate roosts and record the thermoregulatory behaviour of male long-eared bats, *Nyctophilus gouldi* (9 g), during late spring in the Northern Tablelands of New South Wales. Bats roosted under bark and in tree cavities, where they typically experienced wide daily fluctuations in ambient temperature (T_a). On 13 out of 16 days, bats employed two torpor bouts per day, during the early morning and late afternoon, coinciding with times of low T_a . Heating of roosts during the day resulted in up to 20°C of passive re-warming before active arousal and provided high T_a around midday when bats were normothermic. By switching between torpor and normothermic thermoregulation according to the daily T_a cycle, male *N. gouldi* appear to gain an energetic advantage from choosing poorly insulated and often sun-exposed roosts.

Introduction

The thermal physiology of small bats is linked closely to prevailing environmental conditions. During resting, the energetic cost of maintaining an elevated, normothermic body temperature (T_b) increases steeply for bats as ambient temperature (T_a) decreases below thermoneutrality (i.e. <30°C: Speakman and Thomas 2003). However, many bats are able to avoid this cost by temporarily lowering their T_b and entering torpor for short or prolonged periods (Lyman 1970; Geiser 2006). Torpor results in a substantial reduction in metabolic rate and energy expenditure, even at T_a close to thermoneutrality (Hock 1951; Studier 1981; Thomas *et al.* 1990; Geiser 2004).

During summer, female tree-roosting bats typically roost in maternity colonies within well insulated tree cavities (Sedgeley 2001; Lumsden *et al.* 2002), whereas males often roost alone in shallow tree cavities or under exfoliated bark (Law and Anderson 2000; Kunz and Lumsden 2003). For females, a warm, thermally stable environment minimises the energetic cost of normothermic thermoregulation, which is beneficial to reproductive output (Racey 1973). In contrast, the tree roosts of solitary males often appear to provide little thermal insulation from external daily fluctuations in T_a (Hosken 1996; Lumsden *et al.* 2002; Turbill *et al.* 2003a, 2003b). However, few studies have examined the thermoregulatory behaviour and energy use of bats exposed to variable daily T_a . Therefore, I used temperature telemetry to investigate the roosting and thermoregulatory behaviour of free-ranging male Gould's long-eared bats (*Nyctophilus gouldi*) in south-eastern Australia.

Materials and Methods

Bats were captured using mist nets in Imbota Nature Reserve (30°35'S, 151°44'E; elevation 1000 m) ~10 km south-east of Armidale, Australia, fitted with pre-calibrated temperature radio-transmitters (Holohil, LB-2T, 0.55 g) and released on the night of capture. Transmitters were calibrated in a water bath at T_a between 5 and 40°C against a precision thermometer ($\pm 0.2^\circ\text{C}$) to derive an equation relating pulse rate to temperature ($R > 0.99$). Transmitters were glued (Skinbond; Smith and Nephew, Mount Waverley, Vic., Australia) to the bat's skin after first clipping a small patch of mid-dorsal fur. Skin temperature (T_{skin}) is a close surrogate for core T_b during resting in small bats, when $T_b - T_{\text{skin}}$ differentials are <3°C (Audet and Thomas 1996; Willis and Brigham 2003). Bats were located during day-roosting using radio-telemetry and T_{skin} was recorded (via interpulse interval) every 10 min in the field using receiver/dataloggers (details in Körtner and Geiser 1998). At the same time, T_a was recorded every 10 min with another datalogger (T-Tec; resolution $\pm 0.2^\circ\text{C}$) placed at 1-m elevation in the shade.

Bats were considered to be torpid when T_{skin} was below 28°C, which effectively delineated torpor bouts from normothermic thermoregulation (Hudson and Scott 1979; Willis and Brigham 2003; Geiser 2004). All times are Australian Eastern Standard Time (UTC + 10 h). Owing to multiple observations within each individual, means ± 1 s.d. were calculated from average values for individuals. N = number of observations from n individuals.

Results

Roosting and thermoregulatory behaviour of four male *N. gouldi* (body mass 8.8 ± 0.1 g) were recorded over a total of 16 days (1–7 days per bat) during November (late spring) 2002. During this time, T_a varied daily from a minimum of $11.9 \pm 2.6^\circ\text{C}$ (range: 9–16°C) to a maximum of $27.0 \pm 3.6^\circ\text{C}$ (range: 25–32°C).

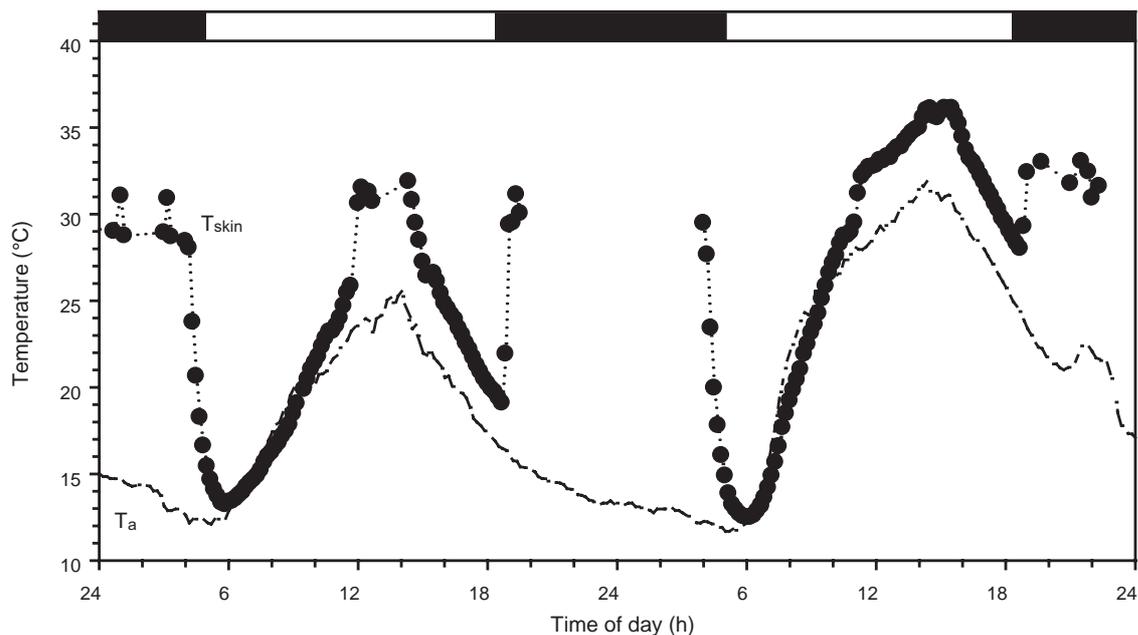


Fig. 1. Skin temperature (symbols and dotted line) of a male *Nyctophilus gouldi* roosting under exfoliated bark on the northern (sunny) side of a dead tree and external ambient temperatures (dashed line) during November (late spring). Dark/light horizontal bars at top represent the photoperiod.

Male *N. gouldi* roosted under exfoliated bark of dead trees ($N = 4$, $n = 4$), within fissures in the trunk of dead trees ($N = 2$, $n = 2$) and within a hollow in a dead branch of a live tree ($N = 1$). Roosts were at a height of 4.0 ± 0.6 m. Of six roosts under bark or in fissures, five had a northerly (sunny) aspect, while one had a southerly aspect. The location of the

first roost of each bat was 675 ± 562 m (range: 200–1300 m) from the trap site. Bats occupied roosts for 3.4 ± 2.5 days (range: 1–7+ days; $N = 5$, $n = 3$) and consecutive roosts were 457 ± 284 m apart ($N = 4$, $n = 2$).

At least one torpor bout was exhibited by male *N. gouldi* during roosting on 15 out of 16 days in summer. One indi-

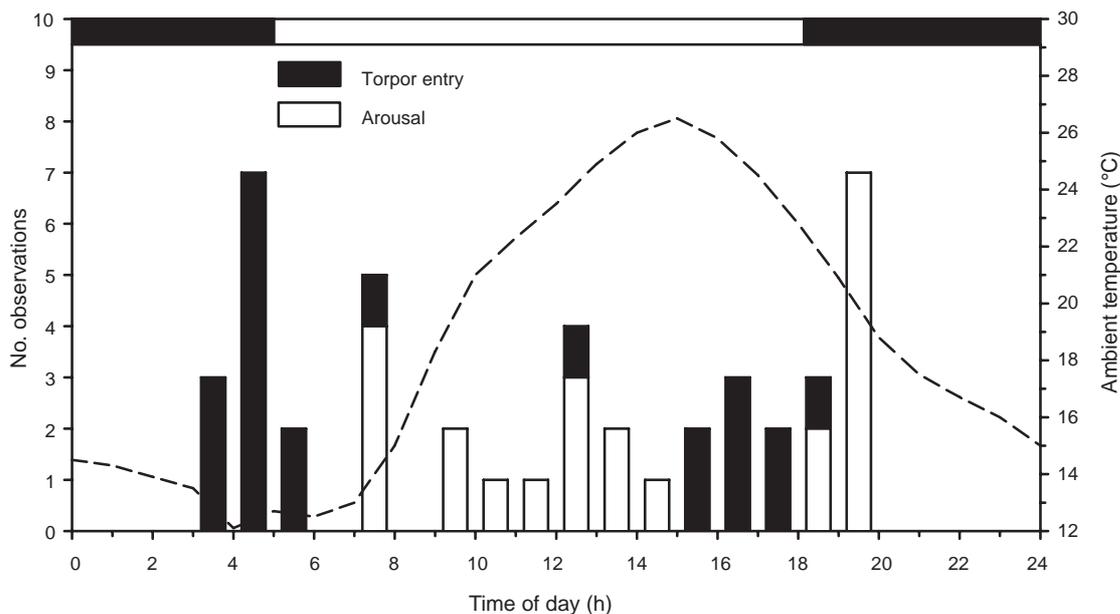


Fig. 2. Time of entry into torpor (dark bars) and arousal from torpor (open bars) by *Nyctophilus gouldi* ($n = 4$) during roosting and average daily external ambient temperatures (dashed line) during November 2002. Dark/light horizontal bars at top represent the photoperiod.

vidual did not enter torpor on one day with a relatively warm minimum T_a of 14°C. On 13 out of 16 days (81%), bats ($n = 4$) entered two torpor bouts per day, with one bout in the morning and another in the late afternoon (Fig. 1). Bats entered torpor between 03:45 and 05:45 hours, shortly after they were first recorded to return to their roost, or on one occasion later at 07:41 hours (average time of entry: 04:36 \pm 0:29 hours) (sunrise 04:58 to 04:48 hours) (Fig. 2). Arousals occurred between 07:34 and 14:59 hours (average time of arousal: 10:33 \pm 2:47 hours) and morning torpor bouts lasted 5.6 \pm 2.1 h (range: 3.4–8.3 h). On average, minimum T_{skin} ($\sim T_b$) during morning torpor bouts reached 14.3 \pm 1.6°C, which was 0.9 \pm 1.2°C above external T_a at the same time. After a period of high normothermic T_{skin} coinciding with high T_a during the middle of the day, bats re-entered a second torpor bout in the afternoon at between 12:34 and 18:10 hours (average time of re-entry: 16:07 \pm 1:59 hours), which lasted 3.8 \pm 1.9 h. On 2 out of 16 days, one individual exhibited only a single torpor bout during the morning on each day. All torpid bats aroused between 18:38 and 19:30 hours (average time of second arousal: 19:04 hours) (sunset: 18:16 to 18:29 hours) (Fig. 2).

Roosts appeared to be poorly insulated from external T_a , as T_{skin} during torpor was typically close to T_a and followed passively with heating of T_a in the morning and cooling of T_a during the late afternoon. Passive fluctuation of T_{skin} during torpor was substantial for one individual that roosted over seven days under bark on the northern side of a small dead tree (see Fig. 1). In this bat, T_{skin} was passively rewarmed by up to 20°C from a daily minimum T_{skin} of 9–15°C to a maximum of 24–29°C before active arousal from morning torpor bouts each day.

Discussion

Male *N. gouldi* were poorly insulated from the daily T_a cycle during roosting in summer, and torpor bouts coincided with times of minimum T_a in the early morning and cooling of T_a in the late afternoon. A similar pattern of torpor has been observed during summer in male *Nyctophilus geoffroyi* (8 g), which also roosts under bark (Turbill *et al.* 2003a), and for pregnant *Eptesicus fuscus* (18 g) while roosting in shallow rock crevices (Lausen and Barclay 2003). Even in a subtropical climate, males of another tree-roosting vespertilionid, *Vespadelus pumilus* (5 g), regularly exhibited a similar W-shaped diurnal pattern of torpor during summer (Turbill *et al.* 2003b).

Exposure of *N. gouldi* to low daily minimum T_a resulted in a large reduction in T_b during torpor in the early morning (by $\sim 20^\circ\text{C}$). Energy savings from torpor were further increased because arousals were partly or solely achieved by passive rewarming from rising roost T_a (Lovegrove *et al.* 1999; Geiser *et al.* 2004). In addition, a period of high roost T_a during the middle of the day provided the opportunity for normothermic thermoregulation at a much-reduced cost. Normothermia and

high T_b allow the normal functioning of physiological and behavioural activities that are likely to be beneficial during resting. However, normothermic periods were limited to the time of elevated T_a , when thermoregulatory costs were relatively low, and bats re-entered torpor in response to cooling of T_a in the late afternoon. Hence, even during late spring, when insect food is usually abundant, the thermoregulatory behaviour of male *N. gouldi* is linked closely to changes in T_a and thermoregulatory energy expenditure.

Owing to their small body mass, bats cool quickly on entering torpor and rewarm rapidly and at a reduced energetic cost relative to larger heterotherms during arousal from torpor. Furthermore, bats achieve a large reduction in metabolic rate and energy expenditure with only a small decrease in T_b during torpor (Studier 1981; Geiser and Brigham 2000). Therefore, even short torpor bouts (i.e. >0.5 h) at T_a below thermoneutrality provide energy savings to small bats. Thus, by switching between torpor and normothermic thermoregulation according to the daily T_a cycle during roosting, male *N. gouldi* appear to gain an energetic advantage from choosing poorly insulated and sun-exposed tree roosts.

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References

- Audet, D., and Thomas, D. W. (1996). Evaluation of the accuracy of body temperature measurement using external radio transmitters. *Canadian Journal of Zoology* **74**, 1778–1781.
- Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology* **66**, 239–274. doi:10.1146/annurev.physiol.66.032102.115105
- Geiser, F. (2006). Energetics, thermal biology, and torpor in Australian bats. In 'Functional and Evolutionary Ecology of Bats'. (Eds T. H. Kunz, A. Zubaid and G. F. McCracken.) pp. 5–22. (Oxford University Press: Oxford.)
- Geiser, F., and Brigham, R. M. (2000). Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **170**, 153–162. doi:10.1007/s003600050270
- Geiser, F., Drury, R. L., Körtner, G., Turbill, C., Pavey, C. R., and Brigham, R. M. (2004). Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In 'Life in the Cold: Evolution, Adaptation and Application'. (Eds B. M. Barnes and C. H. Carey.) pp. 51–62. (University of Alaska: Fairbanks, AK.)
- Hock, R. J. (1951). The metabolic rates and body temperatures of bats. *Biological Bulletin* **101**, 289–299.
- Hosken, D. J. (1996). Roost selection by the lesser long-eared bat, *Nyctophilus geoffroyi*, and the greater long-eared bat, *N. major* (Chiroptera: Vespertilionidae) in *Banksia* woodlands. *Journal of the Royal Society of Western Australia* **79**, 211–216.

- Hudson, J. W., and Scott, I. M. (1979). Daily torpor in the laboratory mouse *Mus musculus* var. albino. *Physiological Zoology* **52**, 205–218.
- Körtner, G., and Geiser, F. (1998). Ecology of natural hibernation in the marsupial mountain pygmy possum (*Burramys parvus*). *Oecologia* **113**, 170–178. doi:10.1007/s004420050365
- Kunz, T. H., and Lumsden, L. F. (2003). Ecology of cavity and foliage roosting bats. In 'Bat Ecology'. (Eds T. H. Kunz and M. B. Fenton.) pp. 3–89. (University of Chicago Press: Chicago.)
- Lausen, C. L., and Barclay, R. M. R. (2003). Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *Journal of Zoology* **260**, 235–244. doi:10.1017/S0952836903003686
- Law, B. S., and Anderson, J. (2000). Roost preferences and foraging ranges of the eastern forest bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecology* **25**, 352–367. doi:10.1046/j.1442-9993.2000.01046.x
- Lovegrove, B. G., Körtner, G., and Geiser, F. (1999). The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **169**, 11–18. doi:10.1007/s003600050188
- Lumsden, L. F., Bennet, A. F., and Silins, J. E. (2002). Selection of roost sites by the lesser long-eared bat (*Nyctophilus geoffroyi*) and Gould's wattled bat (*Chalinolobus gouldii*) in south-eastern Australia. *Journal of Zoology* **257**, 207–218. doi:10.1017/095283690200081X
- Lyman, C. P. (1970). Thermoregulation and metabolism in bats. In 'Biology of Bats'. (Ed. W. A. Wimsatt.) pp. 301–330. (Academic Press: New York.)
- Racey, P. A. (1973). Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility. Supplement* **19**, 175–189.
- Sedgeley, J. A. (2001). Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* **38**, 425–438. doi:10.1046/j.1365-2664.2001.00607.x
- Speakman, J. R., and Thomas, D. W. (2003). Physiological ecology and energetics of bats. In 'Bat Ecology'. (Eds T. H. Kunz and M. B. Fenton.) pp. 430–492. (University of Chicago Press: Chicago.)
- Studier, E. H. (1981). Energetic advantages to slight drops in body temperature in little brown bats, *Myotis lucifugus*. *Comparative Biochemistry and Physiology* **70A**, 537–540.
- Thomas, D. W., Dorais, J., and Bergeron, J. M. (1990). Winter energy budgets and costs of arousal for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* **71**, 475–479.
- Turbill, C., Körtner, G., and Geiser, F. (2003a). Natural use of heterothermy by a small, tree-roosting bat during summer. *Physiological and Biochemical Zoology* **76**, 868–876. doi:10.1086/378915
- Turbill, C., Law, B. S., and Geiser, F. (2003b). Summer torpor in a free-ranging bat from sub-tropical Australia. *Journal of Thermal Biology* **28**, 223–226. doi:10.1016/S0306-4565(02)00067-0
- Willis, C. K. R., and Brigham, R. M. (2003). Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **173**, 379–389. doi:10.1007/s00360-003-0343-y

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