

# Roost use and thermoregulation by female Australian long-eared bats (*Nyctophilus geoffroyi* and *N. gouldi*) during pregnancy and lactation<sup>1</sup>

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**Abstract.** Small insectivorous bats commonly use torpor while day-roosting, even in summer. However, reproductive female bats are believed to benefit from avoiding torpor because a constant, elevated body temperature maximises the rate of offspring growth, which could increase offspring survival. We used temperature-sensitive radio-transmitters to locate roosts and document the thermal biology of pregnant and lactating females of *Nyctophilus geoffroyi* (9 g) and *N. gouldi* (11 g) at a woodland in a cool temperate climate. Unlike males, reproductive female *Nyctophilus* spp. roosted as small groups (<25) within insulated tree cavities. Roost switching occurred every  $3.7 \pm 1.5$  (*N. geoffroyi*) or  $1.7 \pm 0.8$  days (*N. gouldi*), and radio-tagged individuals roosted together and apart on different days. Skin temperature during roosting was most often between 32 and 36°C, and torpor was used infrequently. Male *Nyctophilus* have been shown in previous studies to use torpor daily during summer. These contrasting torpor patterns likely reflect the warmed cavities occupied by maternity colonies and the thermally unstable shallow crevices occupied by individual males. Our results support the hypothesis that availability of thermally suitable roosts will influence thermoregulatory patterns of reproductive females and hence the growth rates and survival of their offspring. Thus, it is important to conserve woodland habitat with trees in a range of decay stages to provide opportunities for selection and movement among roost trees by reproductive female bats.

**Keywords:** bats, body temperature, roost, thermoregulation, torpor, tree-roosting.

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## Introduction

For small insectivorous bats, maintenance of a constant elevated body temperature during resting requires a steep increase in rate of metabolic heat production with decreasing air temperature below ~30°C (Hock 1951; Geiser and Brigham 2000). Thermoregulation during the daytime roosting period therefore can require high mass-specific energy costs. Consequently, small insectivorous bat species that inhabit cool temperate climates routinely use torpor during roosting (Speakman and Thomas 2003; Geiser 2006; Stawski *et al.* 2014; Ruf and Geiser 2015). Torpor is used even by species in subtropical (Turbill *et al.* 2003b; Geiser and Stawski 2011) and tropical climates (Geiser *et al.* 2011; Czenze and Dunbar 2017; O'Mara *et al.* 2017). Torpor is defined as a controlled, reversible decrease in body temperature and resting metabolic rate below normal levels (Geiser 2004; Geiser *et al.* 2014).

Field studies have demonstrated the frequent and remarkably dynamic use of torpor by small insectivorous bats. Because small bats cool rapidly when entering torpor and have relatively small energy costs for rewarming relative to basal metabolic rates (Thomas *et al.* 1990; Turbill *et al.* 2008), even short bouts of torpor can provide these bats with substantial energy savings. Even during summer, insectivorous bats can also employ long bouts of torpor of up to two days at low body temperature and metabolic rates (Turbill *et al.* 2003a). Overall, it is clear that torpor and its energy savings are integral to the biology and ecology of small insectivorous bats, which comprise a diverse and abundant component of fauna in woodland habitats throughout the world.

The use of torpor during reproduction is not uncommon among mammalian orders (McAllan and Geiser 2014) and can provide an important mechanism for reducing daily energy

<sup>1</sup>This article is dedicated to the memory of Les Hall.

expenditure (McLean and Speakman 1999). However, a low body temperature and metabolic rate during torpor by reproductive female bats has been shown to slow offspring growth during gestation (Racey 1969; Racey and Susan 1981) and to interfere with the production of milk during lactation (Wilde *et al.* 1999). For bats breeding in cool temperate-zone climates, it has been hypothesised, therefore, that pregnant and lactating females should prefer to maintain an elevated body temperature and high rate of resting metabolism. In most temperate-zone vespertilionid bat species studied the use of torpor during summer is reduced in reproductive females, and particularly during lactation, compared with males (Chruszcz and Barclay 2002; Pretzlaff *et al.* 2010; Dzal and Brigham 2013; Klug and Barclay 2013; Rintoul and Brigham 2014). In a subtropical climate, pregnant *Nyctophilus bifax* used torpor less frequently than males during spring (Stawski 2010). The avoidance of torpor by reproductive female bats coincides with a change in their roosting behaviour during the maternity season that reduces their thermoregulatory energy costs. Reproductive females of bat species that roost singularly during the maternity season use torpor more frequently than those species that roost in groups (Chruszcz and Barclay 2002; Willis *et al.* 2006; Klug and Barclay 2013). In either case, reproductive females typically select roost sites that are warmer than the average of available sites (Chruszcz and Barclay 2002; Willis and Brigham 2005). Cave-roosting bats congregate in large maternity colonies in caves with a dome-shaped roof that traps emitted body heat to raise the local air temperature by up to 10°C (Dwyer and Harris 1972). Similarly, females of many tree-roosting species roost during spring and summer in maternity colonies and select relatively warm and well insulated tree cavities (Kerth *et al.* 2001; Sedgeley 2001) that trap their released body heat (Willis and Brigham 2007). The availability of thermally suitable tree roosts and social factors affecting group-roosting are important in allowing reproductive females to minimise the energy costs of maintaining an elevated body temperature (Speakman and Thomas 2003).

In this study, we investigated the use of day-roost sites and regulation of body temperature by female Australian long-eared bats (*Nyctophilus geoffroyi* (9 g) and *N. gouldi* (11 g); family Vespertilionidae) during pregnancy and lactation. The study was conducted at a woodland field site on the Northern Tablelands of New South Wales, Australia, where we have previously studied the roosting behaviour and thermoregulatory physiology of males and non-reproductive females of both species (Geiser and Brigham 2000; Turbill *et al.* 2003a; Turbill 2006). These small insectivorous bats forage by flying relatively slowly under the canopy (Brigham *et al.* 1997), often listening passively to glean invertebrates from surfaces, as well as taking them in flight (Grant 1991). Males of these species roost during the day singularly under exfoliating bark and in narrow crevices, whereas females during the maternity season roost in small groups of less than 30 individuals in more substantial tree cavities (Lunney *et al.* 1988; Lumsden *et al.* 2002; Turbill *et al.* 2003a; Webala *et al.* 2010; Threlfall *et al.* 2013; Law *et al.* 2018; Rueegger *et al.* 2018). The female annual reproductive cycle of *Nyctophilus* at the field site resembles that of many other

temperate-zone vespertilionids: mating occurs in late autumn and winter, females store sperm until ovulation and fertilisation in late August and September (early spring), birth, often of twins, occurs in late October and November, and juveniles are suckled until about late January (Phillips and Inwards 1985; Hosken 1997).

## Methods

This study was conducted between November and December in 2002, 2003 and 2004 at Imbota Nature Reserve (151.73°S, 30.58°E, 1000 m above sea level), a 215-ha area of eucalypt woodland located 10 km south-east of Armidale on the Northern Tablelands of New South Wales, Australia.

Bats were captured using harp traps (Austbat, Faunatech) and mist nets (14 mm, Ecotone) set along tracks and around a dam. Pregnancy was determined by gentle palpation of the bat's abdomen and lactation indicated by bare patches around nipples and the expression of milk. Skin temperature was measured by gluing (Skinbond, Smith & Nephew) temperature-sensitive radio-transmitters (Titley Electronics, model LTM, and Holohil, model LB-2T, both 0.55 g) to a shaved patch of skin on the bat's dorsal side between the shoulder blades. Transmitters were precalibrated to the nearest 0.1°C in a water bath between 5 and 40°C against a high-precision mercury thermometer. Bats were released on the same night as capture and radio-tracked each day thereafter to find the location of their daytime roost. Receiver/logger stations (Körtner and Geiser 1998) were deployed within 100 m of roost locations to automatically record the pulse interval every 10 min for each transmitter within reception range (i.e. mostly during the daytime rest phase). The exact location of roosting bats was identified, where possible, by reducing the signal gain on the receiver to increase directionality during radio-tracking, by observing the bats or transmitter antenna inside the roost during careful inspection during the day or by watching the roost after sunset for exiting bats. Air temperature at the field site was recorded using a temperature logger (T-TEC, Temperature Technology, resolution: 0.2°C) placed in the shade 1 m above the ground. Roost trees were marked and later measured for diameter at breast height (DBH), height (estimated) and stage of decay using a categorical index from 1 (alive, no dead branches) to 7 (dead, trunk only).

Torpor was defined by skin temperature decreasing below a threshold of 28°C for at least 30 min. This threshold was chosen because a body temperature of 31°C is often considered a threshold for torpor (Hudson and Scott 1979; Geiser 2004) and skin temperature in these small bats is expected to be within 3°C of core body temperature (Barclay *et al.* 1996). For these reasons, this threshold had also been used previously in published studies for these species at the same study site (Turbill *et al.* 2003a; Turbill 2006; Turbill and Geiser 2008). We appreciate that a threshold definition of torpor is somewhat arbitrary and biologically important energy savings could have been gained by smaller reductions in body temperature (Willis 2007). Relatively low sample sizes precluded a statistical analysis of among-group comparisons. Data are presented as mean  $\pm$  1 s.d.

## Results

We recorded body temperature during roosting for a single pregnant female of both *N. geoffroyi* (3 days) and *N. gouldi* (4 days) and for three lactating female bats of *N. geoffroyi* (up to 10 days per individual; 14 total bat-days) and five lactating female *N. gouldi* (up to 6 days per individual; 12 total bat-days). Minimum daily air temperature during the recorded days for pregnant bats was  $8.6 \pm 2.2^\circ\text{C}$  and for lactating bats was  $10.9 \pm 4.2^\circ\text{C}$ . Information about roosting behaviour was recorded only for lactating female bats and included five different roosts occupied over >13 bat-days for *N. geoffroyi* and 16 different roosts occupied over >32 bat-days for *N. gouldi* (Table 1).

Lactating female bats roosted in tree cavities inside branches and dead sections of the trunk (Table 1). Roost trees varied in decay stage from completely alive with few dead branches to standing dead trunks, including tree stumps. Roost trees used by lactating *N. geoffroyi* were  $28.1 \pm 8.9$  cm DBH and  $11.2 \pm 10.5$  m high ( $n = 6$  roosts) and by lactating *N. gouldi*  $42.8 \pm 17.2$  cm DBH and  $20.4 \pm 5.5$  m high ( $n = 15$ ).

**Table 1. Characteristics of roosts occupied by maternity colonies of *Nyctophilus geoffroyi* and *N. gouldi***

Means  $\pm$  1 s.d. (min., max.) of all observations (1–3 observations per individual) are shown

	<i>N. geoffroyi</i> ( $n = 6$ roosts)	<i>N. gouldi</i> ( $n = 17$ roosts)
Occupancy (days) <sup>A</sup>	$3.7 \pm 1.5$ (2, 5)	$1.7 \pm 0.8$ (1, 3)
Tree species	<i>E. caliginosa</i> ( $n = 5$ )	<i>E. caliginosa</i> ( $n = 16$ ), <i>E. viminalis</i> ( $n = 1$ )
Decay stage <sup>B</sup>	$4.7 \pm 2.9$ (1, 7)	$2.0 \pm 1.1$ (1, 5)
Tree height (m)	$11.2 \pm 10.5$ (1.3, 22)	$20.4 \pm 5.5$ (10, 28)
Tree DBH (cm)	$28.1 \pm 8.9$ (15.9, 38.2)	$42.8 \pm 17.2$ (19.1, 82.8)
Roost height	$7.3 \pm 6.7$ (0.7, 14)	$8.5 \pm 4.3$ (4, 20)
Group size <sup>C</sup> (exit counts)	3, 5 and 20	24

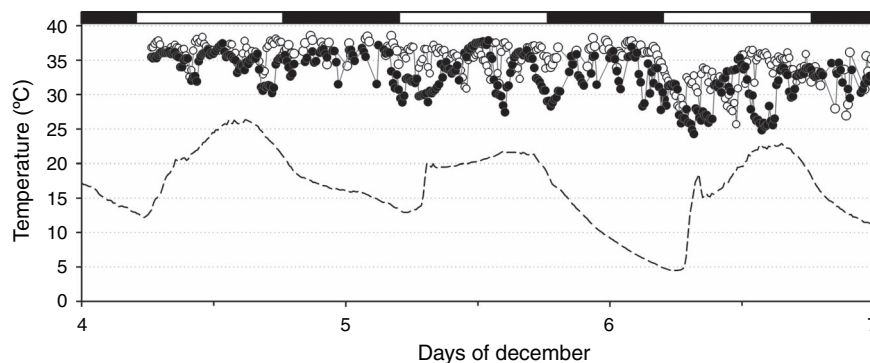
<sup>A</sup>Number of consecutive days an individual occupied the same roost; occupancy unknown for some roosts.

<sup>B</sup>A continuous scale of tree age and decay varying between 1 (alive, no dead branches) and 7 (dead, trunk only).

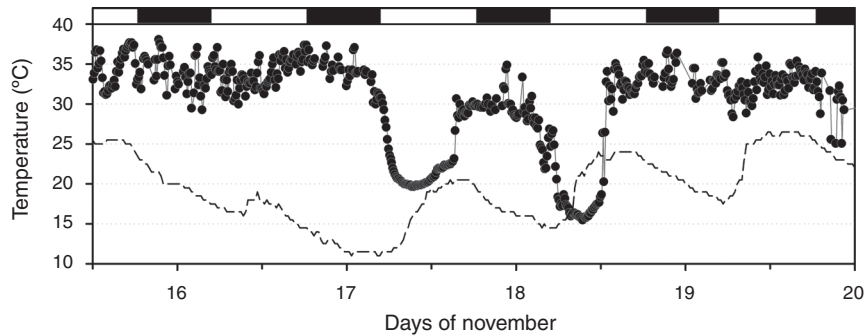
<sup>C</sup>All roost exit counts were at roosts of lactating females.

Roosts were often located below the canopy: average roost height for *N. geoffroyi* was  $7.3 \pm 6.7$  m ( $n = 6$ ) and for *N. gouldi* was  $8.5 \pm 4.3$  m ( $n = 15$ ), with one roost only 0.7 m above ground. Lactating *N. geoffroyi* occupied the same roost on average for  $3.7 \pm 1.5$  days and a maximum of five days ( $n = 3$  observed occupancy durations). Lactating *N. gouldi* occupied the same roost on average for  $1.7 \pm 0.8$  days and a maximum of three days ( $n = 15$  observed occupancy durations), with roost occupancy of just one day on 44% of observations. In one case, a lactating *N. gouldi* occupied four different roosts over six recorded days. Bats were not observed to reoccupy a previously used roost during the relatively short period of tracking. During one seven-day period when three lactating female *N. gouldi* were tracked simultaneously, all three bats roosted together on one day, two out of three bats roosted together on three of the days, and all three bats roosted in different roosts on the remaining three days. In one of the roosts occupied by only one tracked bat, we counted 24 bats exiting at dusk; no other roost exit counts were made for *N. gouldi*. Observations of dusk emergence at roosts of radio-tracked lactating *N. geoffroyi* counted between 3 and 20 individuals (Table 1).

The skin temperature of reproductive female bats of both species was often elevated substantially above external air temperature (Fig. 1), although torpor bouts were observed in pregnant and lactating bats of both species (e.g. Fig. 2). Transmitter pulses and hence skin temperature were recorded during the day from roosting bats and also to a lesser extent during the night (i.e. during the bat's active phase of the day). It was not known what proportion of the body temperature data collected at night represented bats resting at the roost (e.g. because of suckling) or bats foraging within the range of reception (<200 m) of the receiver/datalogger stations, which were positioned close to the roost(s). The frequency distribution of all skin temperature data had a broad mode for both species between  $32$  and  $36^\circ\text{C}$  (Fig. 3). During pregnancy, torpor was used by a *N. geoffroyi* on all four roost days (100%), and by a *N. gouldi* on two out of three days (66%). Torpor bouts (i.e. a sequence of skin temperature  $<28^\circ\text{C}$ , excluding occasional data points) were recorded only during the daytime. For each pregnant bat, skin temperature  $\leq 28^\circ\text{C}$  (threshold for torpor) comprised 47.6% (*N. geoffroyi*) and



**Fig. 1.** Skin temperature of two lactating female *Nyctophilus gouldi* recorded over three days in December (closed and open symbols and solid lines) while both roosted together in a tree cavity. External air temperature is also shown (dashed line). The dark bars at top represent timing of the scotophase.



**Fig. 2.** Skin temperature of a lactating female *Nyctophilus geoffroyi* recorded over four days in November (symbols and solid lines). External air temperature is also shown (dashed line). The dark bars at top represent timing of the scotophase. Note that the lag in skin temperature during torpor relative to the daily increase in external air temperature likely reflects some insulation of the roost cavity.

10.8% (*N. gouldi*) of observations, whereas skin temperature  $\leq 31^{\circ}\text{C}$  (equivalent to a body temperature of  $32\text{--}34^{\circ}\text{C}$ , which is above our conservative threshold for torpor but nevertheless below what might be considered a normothermic body temperature of  $36^{\circ}\text{C}$ : Geiser and Brigham 2000) comprised 74.1% (*N. geoffroyi*) and 25.1% (*N. gouldi*) of observations (Fig. 3). During lactation, torpor was used by *N. geoffroyi* ( $n = 3$ ) on 65% of 14 bat-days and by *N. gouldi* ( $n = 5$ ) on 45% of 12 bat-days. For lactating bats, skin temperature  $\leq 28^{\circ}\text{C}$  (threshold for torpor) comprised 16.1% (*N. geoffroyi*) and 7.8% (*N. gouldi*) of observations, whereas skin temperature  $\leq 31^{\circ}\text{C}$  comprised 33.8% (*N. geoffroyi*) and 18.0% (*N. gouldi*) of observations (Fig. 3). Overall, minimum skin temperature during torpor tended to be lower during pregnancy than during lactation, and also lower for lactating *N. geoffroyi* than for lactating *N. gouldi* (Fig. 4). However, average minimum daily air temperature was also several degrees lower during the recorded days for pregnant *N. geoffroyi* compared with the recorded days for pregnant *N. gouldi* and lactating bats.

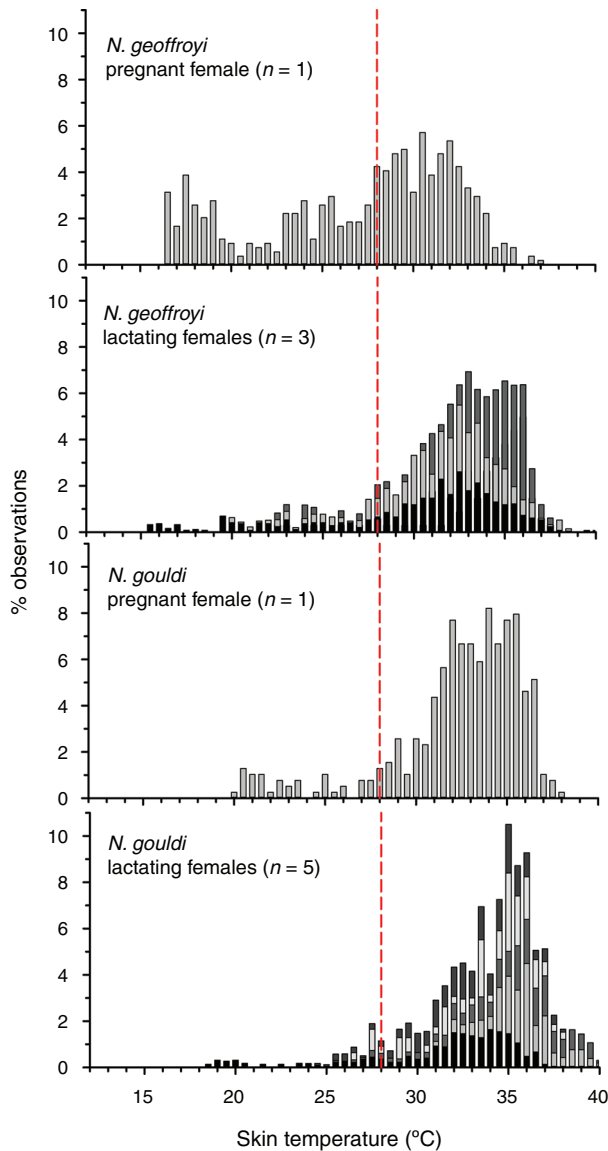
## Discussion

The roosting behaviour and thermoregulatory patterns of reproductive female Australian long-eared bats (*Nyctophilus*) differed from that exhibited by males during spring and summer at this location (Turbill *et al.* 2003a). Reproductive females roosted in small colonies within tree cavities and often maintained a normothermic body temperature (as indicated by skin temperature). When torpor was used by reproductive females, minimum body temperature was typically at least  $10^{\circ}\text{C}$  above the external daily air temperature minima, and typically higher in the larger *N. gouldi* than in *N. geoffroyi*. However, deep torpor bouts were used occasionally during pregnancy and early lactation. A larger dataset would be desirable to better understand the range of thermoregulatory patterns used by reproductive female *Nyctophilus*. In contrast to reproductive females, males roost individually in exposed locations, such as under exfoliating bark, and enter torpor every day in summer, with torpor lasting most of the photophase on cooler days (Turbill *et al.* 2003a; Turbill 2006). The skin temperature of males during torpor often decreased to within a few degrees of external air temperature minima, and

skin temperature reached as low as  $9^{\circ}\text{C}$  during summer at the same field site.

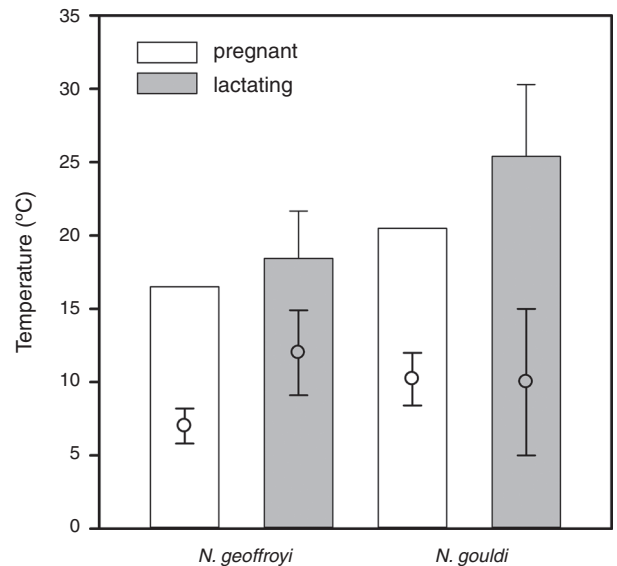
The reduced frequency and depth of torpor by roosting reproductive females compared with males could be explained by the propensity of either sex to enter torpor and/or differences in their roosting conditions in the field. However, when male, pregnant and lactating female *N. geoffroyi* and *N. gouldi* were exposed to  $15^{\circ}\text{C}$  overnight in respirometry chambers in the laboratory, all individuals entered torpor and we found no significant difference in duration, minimum body temperature, and minimum metabolic rate during torpor (Turbill and Geiser 2006). The results of that experiment suggest that, when faced with the same thermoregulatory costs as males, reproductive females do not exhibit an aversion to torpor. Hence, avoidance of torpor by reproductive females in the wild might not indicate excessively higher energy expenditure for thermoregulation compared with male bats. Rather, it seems that huddling (Hayes *et al.* 1992), warming of the roost microclimate by released body heat (Willis and Brigham 2007) and selection of relatively insulated tree cavities (Kurta 1985; Sedgeley 2001) are important mechanisms allowing reproductive females to reduce the energetic cost of normothermic thermoregulation during roosting. Nevertheless, even if thermoregulatory costs were nullified (i.e. reduced to basal metabolic levels), resting energy expenditure of normothermic reproductive female bats would still be substantially greater than that of male bats using torpor extensively during roosting (Geiser and Brigham 2000).

We found that maternity colonies of *N. geoffroyi* and *N. gouldi* roosted in cavities in dead wood that were often within the trunk of eucalypt trees. Roosts of female *N. gouldi* were in relatively large and alive trees with dead sections on the main trunk, whereas roosts of *N. geoffroyi* tended to be in smaller and often dead trees. These observations mostly concur with previous observations of roosting behaviour for maternity colonies of both species (Lunney *et al.* 1988; Lumsden *et al.* 2002; Webala *et al.* 2010; Threlfall *et al.* 2013; Ruegger *et al.* 2018); however, at a woodland site where large, hollow-bearing trees were uncommon reproductive female *N. gouldi* roosted in relatively small, dead trees (Law *et al.* 2018). Differences in physical characteristics of tree roosts used by maternity colonies of the two species in the



**Fig. 3.** Frequency distribution of skin temperature measurements (predominantly rest phase) recorded for pregnant and lactating *Nyctophilus geoffroyi* and *N. gouldi*. Data from different individuals are indicated by shading of bars ( $n$  = individuals). Vertical dashed line represents the threshold used for delineating torpor.

current study might have influenced internal thermal conditions and might partly explain the higher minimum skin temperature during torpor and higher, more narrow, range of normothermic skin temperature measured for *N. gouldi* compared with *N. geoffroyi*. Reproductive females of both species moved frequently among different roost sites, not necessarily as a cohesive group, and roost-switching might function to reduce parasite load or probability of predation (Lewis 1995). This behaviour suggests that maternity colonies of *N. geoffroyi* and *N. gouldi* would require a large number of tree cavities with favourable thermal properties over the summer maternity season, and the density of tree cavities



**Fig. 4.** Minimum skin temperature recorded for pregnant and lactating *Nyctophilus geoffroyi* and *N. gouldi* (columns; mean  $\pm$  1 s.d.) and daily minimum air temperature over the recorded days (symbols; mean  $\pm$  1 s.d.). See Fig. 3 for sample sizes.

suitable for roosting might limit their occupation of woodland habitats. Negative effects of thermally suboptimal roosts that induce greater torpor use or higher thermoregulatory costs would be a greater threat to reproductive success (Racey 1982; Kunz 1987) in colder portions of the ranges of these widespread species. Hence, reductions in the abundance and diversity of available tree cavity roosts, resulting, for example, from clearing for agricultural development, wildfire, timber harvesting and competition from overabundant hollow-dependent species, might have negative effects on the population growth rate of bats, especially in colder climates. However, despite this concern, populations of these two species of *Nyctophilus* persist in wooded habitats with varying levels of disturbance. Group size will also impact the thermoregulatory cost of an individual and reproductive females roosting in small groups could be forced to enter torpor more frequently (Pretzlaff *et al.* 2010). Our observations that reproductive individuals sometimes roosted together and sometimes roosted separately matched the ‘fission–fusion’ pattern of social cohesion described for maternity colonies of several other tree-roosting bats (Kerth and König 1999; Willis and Brigham 2004) and these social dynamics might also determine the energetic costs of roosting for a female on a particular day.

Our field observations show that, even though reproductive female *Nyctophilus* use torpor no differently from males under identical laboratory conditions, in the wild, when roosting as part of a maternity colony, lactating and to, a lesser extent, pregnant females typically maintain a relatively high body temperature and use torpor less than males in summer (Turbill *et al.* 2003a; Turbill 2006). Interpretation of these results should take account of the relatively small sample size, especially for pregnant females. Nevertheless, our findings support the hypothesis that thermal conditions of roosts

occupied by maternity colonies are important for enhancing offspring growth rates and hence reproductive success in temperate climates where the growing season is limited and bats must also fatten before winter hibernation (Racey 1982). Further research is needed to understand how availability and use of tree roost sites with different thermal and other properties (Kunz and Lumsden 2003; Goldingay 2009) interact with the roosting behaviour and thermal physiology of female maternity colonies to influence the population dynamics of vespertilionid bats. This knowledge would enable more accurate evaluation of habitat quality for tree-roosting bats in the context of ongoing loss and degradation of woodland in Australia and elsewhere around the world.

### Conflicts of interest

The authors declare no conflicts of interest.

### Acknowledgements

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### References

- Barclay, R. M. R., Kalcounis, M. C., Crampton, L. H., Stefan, C., Vonhof, M. J., Wilkinson, L., and Brigham, R. M. (1996). Can external radiotransmitters be used to assess body temperature and torpor in bats? *Journal of Mammalogy* **77**, 1102–1106. doi:10.2307/1382791
- Brigham, R. M., Francis, R. L., and Hamdorf, S. (1997). Microhabitat use by two species of *Nyctophilus* bats: a test of ecomorphology theory. *Australian Journal of Zoology* **45**, 553–560. doi:10.1071/ZO97026
- Chruszcz, B. J., and Barclay, R. M. R. (2002). Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Functional Ecology* **16**, 18–26. doi:10.1046/j.0269-8463.2001.00602.x
- Czenze, Z. J., and Dunbar, M. B. (2017). Hot bats go cold: heterothermy in neotropical bats. *Canadian Journal of Zoology* **95**, 909–912. doi:10.1139/cjz-2016-0318
- Dwyer, P. D., and Harris, J. A. (1972). Behavioral acclimatization to temperature by pregnant *Miniopterus* (Chiroptera). *Physiological Zoology* **45**, 14–21. doi:10.1086/physzool.45.1.30155922
- Dzal, Y. A., and Brigham, R. M. (2013). The tradeoff between torpor use and reproduction in little brown bats (*Myotis lucifugus*). *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **183**, 279–288. doi:10.1007/s00360-012-0705-4
- 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 A. Zubaid, G. F. McCracken, and T. H. Kunz.) pp. 5–22. (Oxford University Press: New York.)
- 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/s0036000050270
- Geiser, F., and Stawski, C. (2011). Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integrative and Comparative Biology* **51**, 337–348. doi:10.1093/icb/icr042
- Geiser, F., Stawski, C., Bondarenko, A., and Pavey, C. (2011). Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals? *Naturwissenschaften* **98**, 447–452. doi:10.1007/s00114-011-0779-y
- Geiser, F., Currie, S. E., O'Shea, K. A., and Hiebert, S. M. (2014). Torpor and hypothermia: reversed hysteresis of metabolic rate and body temperature. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology* **307**, R1324–R1329. doi:10.1152/ajpregu.00214.2014
- Goldingay, R. L. (2009). Characteristics of tree hollows used by Australian birds and bats. *Wildlife Research* **36**, 394–409. doi:10.1071/WR08172
- Grant, J. D. A. (1991). Prey location by Australian long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*. *Australian Journal of Zoology* **39**, 45–56. doi:10.1071/ZO9910045
- Hayes, J. P., Speakman, J. R., and Racey, P. A. (1992). The contributions of local heating and reducing exposed surface area to the energetic benefits of huddling by short-tailed field voles (*Microtus agrestis*). *Physiological Zoology* **65**, 742–762. doi:10.1086/physzool.65.4.30158537
- Hock, R. J. (1951). The metabolic rates and body temperatures of bats. *The Biological Bulletin* **101**, 289–299. doi:10.2307/1538547
- Hosken, D. J. (1997). Reproduction and the female reproductive cycle of *Nyctophilus geoffroyi* and *N. major* (Chiroptera: Vespertilionidae) from south-western Australia. *Australian Journal of Zoology* **45**, 489–504. doi:10.1071/ZO96060
- Hudson, J. W., and Scott, I. M. (1979). Daily torpor in the laboratory mouse, *Mus musculus* var. *albino*. *Physiological Zoology* **52**, 205–218. doi:10.1086/physzool.52.2.30152564
- Kerth, G., and König, B. (1999). Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteini*). *Behaviour* **136**, 1187–1202. doi:10.1163/156853999501711
- Kerth, G., Weissmann, K., and König, B. (2001). Day roost selection in female Bechstein's bats (*Myotis bechsteini*): a field experiment to determine the influence of roost temperature. *Oecologia* **126**, 1–9. doi:10.1007/s004420000489
- Klug, B. J., and Barclay, R. M. R. (2013). Thermoregulation during reproduction in the solitary, foliage-roosting hoary bat (*Lasiurus cinereus*). *Journal of Mammalogy* **94**, 477–487. doi:10.1644/12-MAMM-A-178.1
- Körtner, G., and Geiser, F. (1998). Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burrhamys parvus*). *Oecologia* **113**, 170–178. doi:10.1007/s004420050365
- Kunz, T. H. (1987). Post-natal growth and energetics of suckling bats. In 'Recent Advances in the Study of Bats'. (Eds M. B. Fenton, P. A. Racey, and M. V. Rayner.) pp. 395–420. (Cambridge University Press: Cambridge.)
- 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.)
- Kurta, A. (1985). External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comparative Biochemistry and Physiology. Part A, Physiology* **82**, 413–420. doi:10.1016/0300-9629(85)90876-X
- Law, B., Gonsalves, L., Brassil, T., and Hill, D. (2018). Does thinning homogenous and dense regrowth benefit bats? Radio-tracking, ultrasonic detection and trapping. *Diversity* **10**, 45. doi:10.3390/d10020045
- Lewis, S. E. (1995). Roost fidelity of bats: a review. *Journal of Mammalogy* **76**, 481–496. doi:10.2307/1382357
- Lumsden, L. F., Bennett, 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/S095283690200081X

- Lunney, D., Barker, J., Priddel, D., and O'Connell, M. (1988). Roost selection by Gould's long-eared bat, *Nyctophilus gouldi* Tomes (Chiroptera, Vespertilionidae), in logged forest on the south coast of New South Wales. *Wildlife Research* **15**, 375–384. doi:10.1071/WR9880375
- McAllan, B. M., and Geiser, F. (2014). Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. *Integrative and Comparative Biology* **54**, 516–532. doi:10.1093/icb/icu093
- McLean, J. A., and Speakman, J. R. (1999). Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. *Functional Ecology* **13**, 360–372. doi:10.1046/j.1365-2435.1999.00321.x
- O'Mara, M. T., Rikker, S., Wikelski, M., Ter Maat, A., Pollock, H. S., and Dechmann, D. K. N. (2017). Heart rate reveals torpor at high body temperatures in lowland tropical free-tailed bats. *Royal Society Open Science* **4**, 171359doi:10.1098/rsos.171359
- Phillips, W. R., and Inwards, S. J. (1985). The annual activity and breeding cycles of Gould's long-eared bat, *Nyctophilus gouldi* (Microchiroptera: Vespertilionidae). *Australian Journal of Zoology* **33**, 111–126. doi:10.1071/ZO9850111
- Pretzlaff, I., Kerth, G., and Dausmann, K. H. (2010). Communally breeding bats use physiological and behavioural adjustments to optimise daily energy expenditure. *Naturwissenschaften* **97**, 353–363. doi:10.1007/s00114-010-0647-1
- Racey, P. A. (1969). Diagnosis of pregnancy and experimental extension of gestation in the pipistrelle bat, *Pipistrellus pipistrellus*. *Reproduction* **19**, 465–474. doi:10.1530/jrf.0.0190465
- Racey, P. A. (1982). Ecology of bat reproduction. In 'Ecology of Bats'. (Ed. T. H. Kunz.) pp. 57–104. (Plenum Press: New York.)
- Racey, P. A., and Susan, M. S. (1981). Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *Reproduction* **61**, 123–129. doi:10.1530/jrf.0.0610123
- Rintoul, J. L. P., and Brigham, R. M. (2014). The influence of reproductive condition and concurrent environmental factors on torpor and foraging patterns in female big brown bats (*Eptesicus fuscus*). *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **184**, 777–787. doi:10.1007/s00360-014-0837-9
- Ruegger, N., Goldingay, R., and Law, B. (2018). Physical and microclimate characteristics of *Nyctophilus gouldi* and *Vespadelus vulturnus* maternity-roost cavities. *Wildlife Research* **45**, 611–619. doi:10.1071/WR18101
- Ruf, T., and Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biological Reviews of the Cambridge Philosophical Society* **90**, 891–926. doi:10.1111/brv.12137
- 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. 430–490. (University of Chicago Press: Chicago.)
- Stawski, C. (2010). Torpor during the reproductive season in a free-ranging subtropical bat, *Nyctophilus bifax*. *Journal of Thermal Biology* **35**, 245–249. doi:10.1016/j.jtherbio.2010.05.009
- Stawski, C., Willis, C. K. R., and Geiser, F. (2014). The importance of temporal heterothermy in bats. *Journal of Zoology* **292**, 86–100. doi:10.1111/jzo.12105
- Thomas, D. W., Dorais, M., and Bergeron, J.-M. (1990). Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* **71**, 475–479. doi:10.2307/1381967
- Threlfall, C. G., Law, B., and Banks, P. B. (2013). Roost selection in suburban bushland by the urban sensitive bat *Nyctophilus gouldi*. *Journal of Mammalogy* **94**, 307–319. doi:10.1644/11-MAMM-A-393.1
- Turbill, C. (2006). Roosting and thermoregulatory behaviour of male Gould's long-eared bats, *Nyctophilus gouldi*: energetic benefits of thermally unstable tree roosts. *Australian Journal of Zoology* **54**, 57–60. doi:10.1071/ZO05068
- Turbill, C., and Geiser, F. (2006). Thermal physiology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **176**, 165–172. doi:10.1007/s00360-005-0038-7
- Turbill, C., and Geiser, F. (2008). Hibernation by tree-roosting bats. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **178**, 597–605. doi:10.1007/s00360-007-0249-1
- 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 subtropical Australia. *Journal of Thermal Biology* **28**, 223–226. doi:10.1016/S0306-4565(02)00067-0
- Turbill, C., Körtner, G., and Geiser, F. (2008). Timing of the daily temperature cycle affects the critical arousal temperature and energy expenditure of lesser long-eared bats. *The Journal of Experimental Biology* **211**, 3871–3878. doi:10.1242/jeb.023101
- Webala, P. W., Craig, M. D., Law, B. S., Wayne, A. F., and Bradley, J. S. (2010). Roost site selection by southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* in logged jarrah forests, south-western Australia. *Forest Ecology and Management* **260**, 1780–1790. doi:10.1016/j.foreco.2010.08.022
- Wilde, C. J., Knight, C. H., and Racey, P. A. (1999). Influence of torpor on milk protein composition and secretion in lactating bats. *The Journal of Experimental Zoology* **284**, 35–41. doi:10.1002/(SICI)1097-010X(19990615)284:1<35::AID-JEZ6>3.0.CO;2-Z
- 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. doi:10.1086/521085
- Willis, C. K. R., and Brigham, R. M. (2004). Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission–fusion model. *Animal Behaviour* **68**, 495–505. doi:10.1016/j.anbehav.2003.08.028
- Willis, C. K. R., and Brigham, R. M. (2005). Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). *Journal of Mammalogy* **86**, 85–94. doi:10.1644/1545-1542(2005)086<0085:PAEAOR>2.0.CO;2
- Willis, C. K. R., and Brigham, R. M. (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology and Sociobiology* **62**, 97–108. doi:10.1007/s00265-007-0442-y
- Willis, C. K. R., Brigham, R. M., and Geiser, F. (2006). Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* **93**, 80–83. doi:10.1007/s00114-005-0063-0

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