

Do season and distribution affect thermal energetics of a hibernating bat endemic to the tropics and subtropics?

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Stawski C, Geiser F. Do season and distribution affect thermal energetics of a hibernating bat endemic to the tropics and subtropics? *Am J Physiol Regul Integr Comp Physiol* 301: R542–R547, 2011. First published June 1, 2011; doi:10.1152/ajpregu.00792.2010.—Although many tropical and subtropical areas experience pronounced seasonal changes in weather and food availability, few studies have examined and none have compared the thermal physiology and energetics of a hibernating mammal that is restricted to these regions. We quantified thermal energetics of northern long-eared bats (*Nyctophilus bifax*; body mass ~10 g) during summer, winter, and spring from a subtropical habitat, and also during winter from a tropical habitat, to determine how *N. bifax* cope with climate and seasonal changes in weather. We captured bats in the wild and measured metabolic rates via open-flow respirometry. The basal metabolic rate of subtropical bats at an ambient temperature (T_a) of $32.6 \pm 0.7^\circ\text{C}$ was $1.28 \pm 0.06 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ during both summer and winter, similar to other species of *Nyctophilus*. Resting metabolic rates below the thermoneutral zone increased similarly with decreasing T_a during all seasons and in both regions. All individuals showed a high proclivity to enter torpor at T_a values below the thermoneutral zone. Metabolic rates in torpid thermoconforming bats fell with T_a and body temperature, and mean minimum metabolic rates during torpor were similar during all seasons and in both regions and as predicted from body mass in temperate zone hibernators. At very low T_a , torpid *N. bifax* thermoregulated, and this threshold T_a differed significantly between subtropical ($T_a = 3.5 \pm 0.3^\circ\text{C}$) and tropical ($T_a = 6.7 \pm 0.7^\circ\text{C}$) individuals, but not between seasons. Our data show that thermal energetics of *N. bifax* do not vary seasonally and in many aspects are similar in tropical and subtropical bats; however, torpid individuals from the subtropics allow body temperature to fall to significantly lower values than those from the tropics.

hibernation; metabolic rate; *Nyctophilus bifax*; thermoneutral zone; thermoregulation

INSECTIVOROUS BATS ARE SMALL and consequently are strongly affected by the thermal conditions of their environment, which also affects their supply of food. Whereas thermal biology and physiological adaptations of temperate zone bats have been well documented (8, 11, 13, 18, 29, 32), few studies have examined in detail the thermal physiology of the very large number of tropical and subtropical bat species. In Australia, tropical and subtropical habitats form a large part of the continent's landmass, which fosters diverse and numerous bats. Even though ambient temperatures (T_a) are mild throughout most of the year in these regions, they are not devoid of periods of adverse conditions. Many subtropical regions in Australia can reach T_a values below 5°C during winter and even the tropical regions of Australia experience cool and dry winters

during which insect numbers are reduced greatly (21). Insectivorous bats in these regions must be able to cope with these thermal and energetic challenges.

The most effective energy-conserving mechanism available to mammals is torpor (3, 10). Reductions in body temperature (T_b) and metabolic rate (MR) characterize torpor and result in significant energy savings, particularly when T_a is low (24). Small mammals, such as bats in particular, often make use of torpor to compensate for their large surface area-to-volume ratio, which increases heat loss and thus energy requirements. Whereas in the past multiday torpor (hibernation) in bats was thought to be an adaptation specifically to cold climates (17), recent data show that it may be employed frequently by mammals, even in mild tropical and subtropical habitats. For example, primates hibernate for prolonged periods during winter in tropical Madagascar (6), and bats are able to hibernate in subtropical Australia, South Africa, and Taiwan (5, 19, 27). Compared with temperate regions, T_a is mild in the tropics and subtropics, and it appears that seasonal reductions in metabolism are employed mainly in response to decreases in food or water rather than thermal stress (4) and that, therefore, the characteristics of torpor use may differ from that in cold climates.

Thermal energetics differ among species and are often affected by season, habitat, and food supply. However, although seasonal patterns of torpor vary enormously in free-ranging cool-temperate bats of the genus *Nyctophilus* (29, 30), these seasonal changes appear to be governed largely by changes in T_a , rather than seasonal physiological adjustments because MRs during torpor (TMR) do not vary seasonally under the same thermal conditions (11, 13). In contrast, subtropical nectarivorous blossom bats (*Syconycteris australis*) measured under the same thermal conditions had lower TMRs during summer than in winter, suggesting a seasonal physiological change does occur, likely to deal with decreased nectar availability during the subtropical summer (4).

Patterns of torpor and thermal energetics also differ among regions. Woodchucks (*Marmota monax*) from northern temperate populations hibernate for longer periods than those from southern populations (34), and TMRs of two species of temperate bats (*Eptesicus fuscus* and *Lasiurus borealis*) varied between northern and southern populations (8). Hibernating primates from tropical Madagascar differ from those of temperate hibernating species, especially in regard to TMR at mild T_a values, which seem to be higher than in temperate hibernators (7). Importantly, torpid mammals can thermoregulate to defend T_b , often between 0 and 10°C , to prevent critically low values that may cause tissue damage (2, 9). This T_b threshold appears to be population-specific because torpid feathertail gliders (*Acrobates pygmaeus*) from a cool montane region

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defend a lower T_b than those from a subtropical coastal region (14).

Bats of the genus *Nyctophilus* (Vespertilionidae) are found all over Australia. Whereas data on torpor patterns and thermal energetics of several species of *Nyctophilus* from temperate Australia are available (13, 29), they are almost entirely lacking for subtropical/tropical species. We therefore examined the thermal energetics of northern long-eared bats (*Nyctophilus bifax*), a subtropical/tropical endemic. Regional comparisons between tropical and subtropical populations were made in winter when torpor in the latter is most pronounced (25). Seasonal comparisons were undertaken on a subtropical population of *N. bifax* to determine whether thermal energetics vary seasonally because torpor use by free-ranging bats in this population differs between summer and winter (25). We tested the following hypotheses: 1) thermal energetics differ between tropical and subtropical bats and also from their temperate congeners and 2) thermal energetics of subtropical bats differ among seasons, since it is widely assumed that hibernators have distinct summer and winter phenotypes (20).

Such comparative studies are important to understand how thermal physiology is shaped by environmental factors and why species are restricted to certain habitats.

MATERIALS AND METHODS

Northern long-eared bats were captured using mist nets at two field locations. Bats were captured during the austral summer (February–March 2008, $n = 7$; February 2009, $n = 4$), spring (October–November 2008, $n = 4$), and winter (June 2009, $n = 3$) at the southern subtropical field site, which was located at Iluka Nature Reserve on the north coast of New South Wales in Australia (29°24'S, 153°22'E). During winter, T_a at Iluka Nature Reserve ranges from a mean minimum of 6.3°C to a mean maximum of 20.5°C, and, during summer, T_a ranges from a mean minimum of 19.7°C to a mean maximum of 30.1°C (Australian Bureau of Meteorology). At the northern tropical field site, located at Djiru National Park in Queensland, Australia (17°50'S, 146°03'E), bats were captured during winter (July–August 2009, $n = 8$). During winter, T_a at Djiru National Park ranges from a mean minimum of 11.1°C to a mean maximum of 19.5°C, and, during summer, T_a ranges from a mean minimum of 19.1°C to a mean maximum of 27.9°C (Australian Bureau of Meteorology). Metabolic measurements were undertaken at the field sites in a field laboratory and also in a laboratory setup at the University of New England (UNE) in Armidale, Australia. In the field, captive bats were kept for no longer than 2 days; mealworms and water were provided daily. Bats transferred to UNE from Iluka were kept for 2 wk in a large mesh tent where they were able to fly freely when not being measured. Once bats had accepted mealworms as a food source, they were fed daily with a plate of mealworms and a shallow dish of water. Body mass recorded on a daily basis was stable and suggested that bats were remaining in good condition.

The rate of oxygen consumption was used as a measure of MR and was obtained via open-flow respirometry. Various experimental procedures were used to obtain basal MR (BMR), resting MR (RMR), and TMR. For most experiments, bats were measured from a few hours before sunset until the same time the following day, remaining in the chamber for up to 24 h. These experiments included the following T_a changes: 30–10°C, 20–2°C, 15–2°C, and 10–6°C. The maximum number of T_a changes during a day was six, and each T_a was maintained for a minimum of 2 h. Changes in T_a between 30 and 10°C were done in increments of 5°C, whereas any changes in T_a below 10°C were done in increments of 2°C to precisely detect the T_a where torpid bats thermoregulated. To measure BMR, bats were placed in chambers in the morning and remained for ~8 h with T_a

increasing from 26°C up to 34°C in increments of 2°C. This T_a range to measure BMR was selected from the thermoneutral zone (TNZ) of *N. geoffroyi* and *N. gouldi* (13). BMR was only measured for subtropical bats at UNE during summer and winter, and bats were considered postabsorptive, since they were fed >12 h before BMR was measured. At UNE, each individual was measured three times, whereas, in the field laboratory, each individual was measured only one time. Bats were weighed immediately before and after each measurement period, and a linear mass loss throughout measurements was used for calculation of mass-specific MR values.

Three different oxygen-analyzing systems were used for our study. All produced statistically indistinguishable results at the same T_a values (ANOVA, $P > 0.2$). Consequently, data collected in the field laboratory and at UNE during summer from the subtropical region were combined. In the field laboratory, a portable oxygen analyzer was used (output resolution 0.002%; David Bishop Instruments, Heathfield E. Sussex, UK), which was housed in a cooler bag and a Styrofoam box to maintain a stable temperature. The field analyzer was a single-channel system that took readings from an animal channel and a reference channel (outside air) every 3 min in sequence. At UNE, two different analyzers were used, either a FOX analyzer (resolution 0.001%; Sable Systems International, Las Vegas, NV) or a FC-1B analyzer (resolution 0.001%; Sable Systems International). The FOX analyzer system switched in sequence between three animal channels and a reference channel every 3 min; the FC-1B analyzer system switched between two animal channels and a reference channel every 3 min. MR values were derived from times when oxygen consumption was minimal and stable for more than three consecutive readings (i.e., over >27 min). Rotameters (Aarlborg 7908) were used to control the rate of airflow in the chambers, and mass flowmeters (model FMA-5606; Omega, Stamford, CT) were used to measure the rate of airflow. Flow rates of 65–200 ml O₂/min were used throughout the experiments; flow rates <100 ml O₂/min were restricted to torpid bats to improve the accuracy of measurements. Voltage outputs from flowmeters and oxygen analyzers were recorded on a computer via a 14-bit analog-to-digital (A/D) converter card. Air samples were dried using silica gel.

Cylindrical, clear Perspex tubes (~160 ml) were used as respirometry chambers for the bats. These tubes were lined inside with a plastic mesh to allow the bats to roost while in the chambers and were large enough to allow free movement. Both ends of the chamber were sealed with rubber stoppers that contained the inlet/outlet for air. Once the bat was placed inside the chamber, it was hung vertically within a temperature-controlled unit. In the field laboratory, T_a inside the chamber was measured every 10 min with temperature data loggers ($\pm 0.5^\circ\text{C}$; DS 1921G Thermochron iButtons; Maxim Integrated Products, Sunnyvale, CA). At UNE, T_a was measured at the time of MR readings by a calibrated thermocouple ($\pm 0.1^\circ\text{C}$, Omega DP116 digital thermocouple thermometer) that was inserted in the air space of the chamber; data were transferred to the computer via the A/D converter card. Rectal T_b was measured with a thermocouple thermometer (HH-71T; Omega) within 20 s after removal from the chambers by inserting the thermocouple probe ~1 cm. For rewarming measurements, the thermocouple was taped to the bats' tail, and T_b was recorded every minute.

G. Körnter wrote the data acquisition software, and MR was calculated by using equation 3a of Withers (33). The following equation was used to calculate Q_{10} : $Q_{10} = (\text{MR}_1/\text{MR}_2)^{10/(T_{b1} - T_{b2})}$. StatistixXL (version 1.8, 2007) was used to analyze data, which are reported as means \pm SD for the number of individuals (n). Means are represented by the means of each individual. Null hypotheses were rejected if the significance level was $P < 0.05$. ANOVA was used to examine statistical differences among individuals, seasons, and regions. All linear regressions were compared via ANCOVA to determine whether slopes/intercepts differed among individuals, seasons, and regions. Long-term data for the mean of the lowest 10% of minimum T_a from areas near each of the field locations were obtained

from the Australian Bureau of Meteorology. Permits to undertake this research were approved by the University of New England Animal Ethics Committee (AEC08/046 and AEC09/058), New South Wales National Parks and Wildlife Service (no. S12448), and Queensland Parks and Wildlife Service (WITK04955708).

RESULTS

Body mass of *N. bifax* did not differ among seasons and regions, and the overall mean was 9.8 ± 1.1 g ($n = 26$).

During summer and winter in the T_a range of 30.7 – 34.6°C , BMR of subtropical bats was 1.28 ± 0.06 ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($n = 6$; $T_a = 32.6 \pm 0.7^\circ\text{C}$; body mass = 9.9 ± 0.7 g), with no difference between seasons. During summer, T_b in the TNZ (T_a 30.7 – 34.6°C) was $37.4 \pm 1.1^\circ\text{C}$ ($n = 4$). RMR of subtropical bats during summer, winter, and spring was negatively correlated with T_a in the range of 10.3 – 29.9°C [RMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $11.2 - 0.3T_a$ ($^\circ\text{C}$), $r^2 = 0.9$, $P < 0.001$, $F(1,81) = 908.9$], with no difference among seasons for either slope or intercept. Furthermore, RMR during winter in both regions was negatively correlated with T_a in the range of 10.5 – 29.6°C [RMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $11.2 - 0.3T_a$ ($^\circ\text{C}$), $r^2 = 0.9$, $P < 0.001$, $F(1,38) = 755.8$], with no difference between regions for either slope or intercept. Finally, this relationship remained when all seasons and both regions were combined into one regression [RMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $11.2 - 0.3T_a$ ($^\circ\text{C}$), $r^2 = 0.9$, $P < 0.001$, $F(1,104) = 1,273.7$; Fig. 1], and again there were no differences among all experimental groups for either slope or intercept.

At T_a below the TNZ ($<30.7^\circ\text{C}$), bats readily entered torpor during all seasons. Mean TMR of subtropical bats measured at T_a values between 6.5 and 11.4°C was 0.048 ± 0.006 ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($n = 9$, $T_a = 8.9 \pm 0.5^\circ\text{C}$), and TMRs for all seasons were statistically indistinguishable (Fig. 2). Mean TMR of tropical bats measured at T_a values between 6.5 and 11.4°C was 0.046 ± 0.007 ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($n = 8$, $T_a = 9.0 \pm 0.8^\circ\text{C}$) and did not differ from that in subtropical bats (Fig. 2).

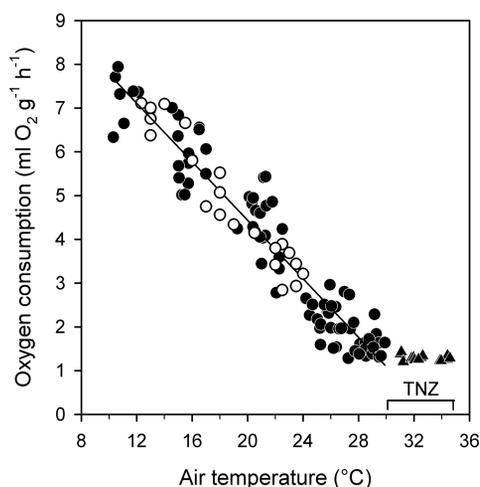


Fig. 1. Oxygen consumption as a function of ambient temperature (T_a) in *Nyctophilus bifax* from all seasons and both regions. Each symbol represents one individual measurement. ●, Resting metabolic rate (RMR) in the subtropical region; ○, RMR in the tropical region; ▲, basal metabolic rate (BMR) in the subtropical region. RMR of all individuals was negatively correlated with T_a , and the following equation is representative of all seasons and both regions: RMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $11.2 - 0.3 T_a$ ($^\circ\text{C}$), $r^2 = 0.9$. TNZ, thermoneutral zone.

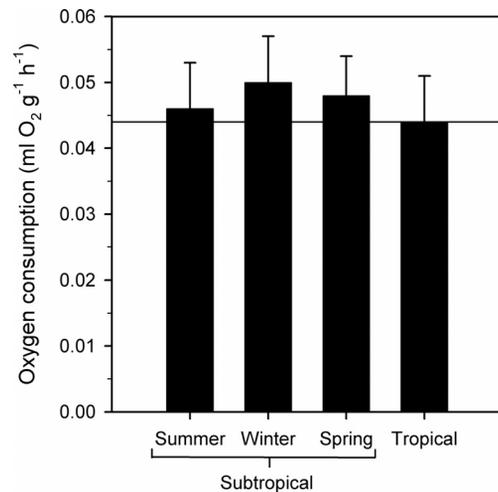


Fig. 2. Mean oxygen consumption of thermoconforming *N. bifax* within a range of T_a values (6.5 – 11.4°C) during each season and from each region. The horizontal line is the predicted TMR for a 10-g hibernator at a body temperature (T_b) of 0 – 10°C (10).

As T_a decreased below the TNZ, TMR decreased exponentially during all seasons and in both regions [TMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $0.0102 \times 1.169^{T_a}$ ($^\circ\text{C}$), $r^2 = 0.9$; Fig. 3], with no differences among seasons and regions.

Torpid bats thermoregulated once T_a decreased below a population-specific threshold. During summer and winter, subtropical bats began to increase TMR sevenfold at a population-specific threshold T_a of $3.5 \pm 0.3^\circ\text{C}$ ($n = 7$; Fig. 3), and the T_a at which the increase occurred did not differ between seasons. Tropical bats increased TMR 14-fold at a population-specific threshold T_a of $6.7 \pm 0.7^\circ\text{C}$ ($n = 7$; Fig. 3), which differed significantly from subtropical bats ($P < 0.001$, $T = 7.4$, degrees of freedom = 8; Fig. 3). Population-specific threshold T_a values of *Nyctophilus* species were positively correlated

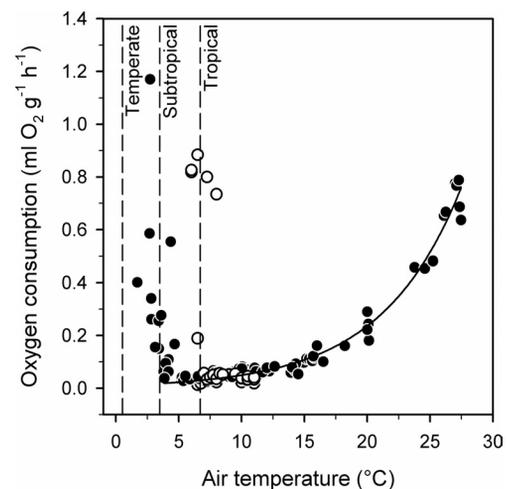


Fig. 3. Oxygen consumption as a function of T_a in torpid *N. bifax* from all seasons and both regions. Each circle represents one individual measurement. ●, the subtropical region; ○, the tropical region. The vertical broken lines represent the mean T_a at which tropical ($6.7 \pm 0.7^\circ\text{C}$), subtropical ($3.5 \pm 0.3^\circ\text{C}$), and temperate ($0.4 \pm 0.3^\circ\text{C}$, obtained from Ref. 13) torpid bats thermoregulated. The metabolic rate during torpor (TMR) decreased exponentially with T_a in thermoconforming bats, and the following equation is representative of all seasons and both regions: TMR (ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $0.0102 \times 1.169^{T_a}$ ($^\circ\text{C}$), $r^2 = 0.9$.

with the ambient conditions of the specific habitat in which each population resided. Specifically, when data from subtropical and tropical *N. bifax* were compared with temperate *N. geoffroyi* (13), the population-specific threshold T_a was strongly correlated with the mean of the lowest 10% of minimum T_a of the area where each population resided [population-specific threshold T_a ($^{\circ}\text{C}$) = $-2.9 + 1.2 T_a$ ($^{\circ}\text{C}$), $r^2 = 0.9$, $P = 0.05$, $F(1,2) = 144.32$].

T_a and \log_{10} TMR of thermoconforming bats were positively correlated [\log_{10} TMR ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $-1.86 + 0.06 T_a$ ($^{\circ}\text{C}$), $r^2 = 0.9$, $F(1,90) = 813.8$; Fig. 4], and this regression intersected with BMR in the TNZ. Q_{10} values were constant at 4.0 if calculated from the \log_{10} TMR regression line (Fig. 4) over the entire T_b range. However, at $T_a \sim 27^{\circ}\text{C}$, TMRs were consistently above the regression line.

The T_b of torpid thermoconforming bats decreased with T_a (Fig. 5). In contrast, the $T_b - T_a$ differential of torpid bats was not influenced by T_a . Normothermic bats in the TNZ showed a larger $T_b - T_a$ differential ($4.3 \pm 1.1^{\circ}\text{C}$, $n = 4$) compared with thermoconforming torpid individuals ($1.6 \pm 0.8^{\circ}\text{C}$, $n = 34$). The lowest T_b recorded in subtropical bats during summer was 3.7°C ($T_a = 2.8^{\circ}\text{C}$), and, during winter, it was 3.4°C ($T_a = 1.8^{\circ}\text{C}$). The lowest T_b recorded in tropical bats during winter was 7.3°C ($T_a = 4.0^{\circ}\text{C}$).

Rates of rewarming from torpor did not differ between summer and winter, and the mean overall rate of rewarming was $0.8 \pm 0.3^{\circ}\text{C}/\text{min}$ ($n = 4$). The maximum rate of rewarming (over 3 min) occurred ~ 30 min after the beginning of the rewarming process and was $1.8 \pm 0.4^{\circ}\text{C}/\text{min}$ ($n = 4$), and the mean maximum rate of rewarming over a period of 10 min was $1.2 \pm 0.3^{\circ}\text{C}/\text{min}$ ($n = 4$).

DISCUSSION

Our study on thermal energetics of captive *N. bifax* tested the hypotheses that 1) thermal energetics differ between regions and 2) that thermal energetics in the subtropics differ among seasons.

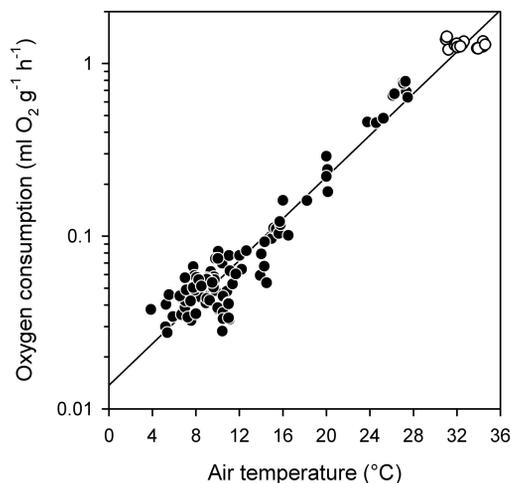


Fig. 4. Oxygen consumption of torpid thermoconforming *N. bifax* (●) and of normothermic *N. bifax* (○) as a function of T_a . Each circle represents one individual measurement. As T_a increased, \log_{10} TMR also increased, and this linear relationship is represented by the following equation: \log_{10} TMR ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) = $-1.86 + 0.06 T_a$ ($^{\circ}\text{C}$), $r^2 = 0.9$. BMR values are not included in this regression.

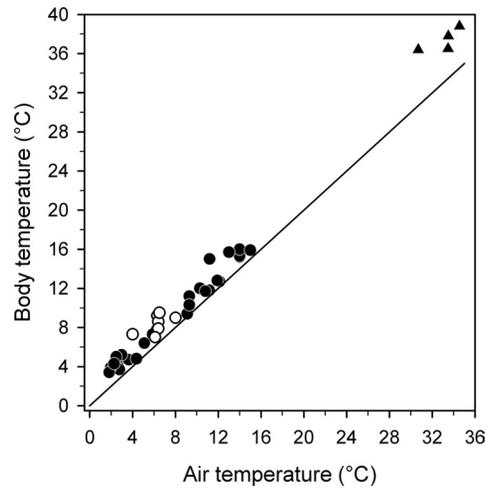


Fig. 5. T_b as a function of T_a in *N. bifax* from all experiments. Each circle represents one individual measurement. ●, Torpid subtropical individuals; ○, torpid tropical individuals; ▲, normothermic subtropical individuals. The diagonal line represents $T_b = T_a$.

Our first hypothesis was supported, since the T_b that was defended by torpid bats was 3.3°C lower in the subtropics than in the tropics. Our second hypothesis was not supported because TMR did not differ seasonally in the subtropical region. Data from our current study agree with previous field data and show that *N. bifax* is a subtropical/tropical hibernator (27). Additionally, our data demonstrate that *N. bifax* have MRs during both normothermia and torpor that are similar to other similar-sized temperate hibernators, illustrating that hibernation is important in many bat species, even those occupying regions with mild weather.

BMR of subtropical *N. bifax* did not change seasonally, and mass-specific BMR was similar to previous values recorded in similar-sized temperate *N. geoffroyi* and *N. gouldi* (13). Furthermore, BMR of *N. bifax* closely conforms (112%) to the allometric prediction from the body mass of vespertilionid bats (32). It is well established that body mass is the main variable that influences BMR of mammals and other endotherms (31, 32). This suggests that the minimum energy required for basic maintenance in normothermic bats is similar within similar-sized vespertilionid bats, regardless of the habitat they occupy and the season it is measured. The low BMR of *Nyctophilus* species and other vespertilionids ensures minimal energy expenditure while normothermic in their TNZ.

RMR of *N. bifax* and therefore energy expenditure below the TNZ increased as T_a decreased, and this relationship did not differ among seasons and regions and was very similar to that of their temperate congeners (13). This suggests that energy use as a function of T_a in normothermic *Nyctophilus* below the TNZ is similar among seasons and regions and suggests similar insulation/heat loss despite different thermal environments. This clearly differs from what was previously assumed to be the rule for large mammals (22) and supports the view that seasonal changes in thermoenergetics in *Nyctophilus* are not pronounced (13).

Many Australian bats employ torpor regularly throughout the year and in a variety of habitats (11, 15, 26). Multiday torpor has even been documented in *N. bifax* in a subtropical region (27). In our current study, *N. bifax* entered torpor readily

at T_a below the TNZ, and the minimum TMR, measured near T_a 9°C, did not differ among seasons and was essentially identical to both *N. geoffroyi* and *N. Gouldi* and also fell in the range of minimum TMR for most other hibernating temperate bats (1, 11, 13, 18, 29). Furthermore, the minimum TMR of *N. bifax* was only 3.8% of BMR and ~0.7% of RMR at the same T_a . Clearly, employment of torpor can save these tropical/subtropical bats enormous amounts of energy, which is important during times of low T_a and low food availability.

Similarly to other heterotherms, TMR of thermoconforming *N. bifax* decreased exponentially with T_a , and this relationship did not vary seasonally or regionally. At $T_a > 20^\circ\text{C}$, TMR of *N. bifax* were relatively high, similar to the hibernating tropical primate *Cheirogaleus medius* (7). However, low values of TMR as measured for *N. bifax* at $T_b/T_a < 10^\circ\text{C}$ were not provided for *C. medius* (7). Dausmann et al. (7) suggested from their results that torpor in tropical regions differs thermoenergetically from temperate regions because of higher T_a experienced during torpor, and our data at high T_a support this interpretation to some extent. However, our data also show that, at low T_a/T_b values, subtropical and tropical *N. bifax* express TMR similar to those of temperate hibernators (13), suggesting that the mechanisms of MR reduction in subtropical/tropical hibernators do not categorically differ from those in temperate hibernators.

If the thermal response of TMR is examined using Q_{10} , the overall Q_{10} between BMR and minimum TMR was four, similar to other small-hibernating mammals (10, 13). However, at high T_a , TMRs were consistently above that predicted by the regression line (Fig. 4) despite the increased $T_b - T_a$ differential in the TNZ (Fig. 5). At T_a values $> 27^\circ\text{C}$, Q_{10} is ~2, suggesting a largely passive process because of cooling of T_b , similar to that in daily heterotherms (10). In contrast, the Q_{10} between BMR and TMR at $T_b/T_a < 27^\circ\text{C}$ is ~4, suggesting an additional physiological inhibition as in other hibernators (10). The reason for different approaches to TMR reduction at different T_b/T_a may be related to the thermal requirements of subtropical/tropical bats to passively enter torpor at high T_b to allow for frequent, rapid arousals with minimum energy expenditure from T_a values $> 20^\circ\text{C}$, as is often experienced during summer (25). This may also explain the higher TMRs in hibernating subtropical/tropical *N. bifax* compared with temperate hibernating species. However, at T_a values $< 20^\circ\text{C}$, as experienced in winter when prolonged torpor is employed in the wild (27), they appear to use additional physiological inhibition to minimize energy expenditure like their temperate congeners. The biochemical mechanisms involved in the additional physiological inhibition to reduce MR are largely unknown, but it has been suggested that it may involve inhibition of enzymes (10, 16, 28).

Surprisingly, differences between the tropical and subtropical population of *N. bifax* were few. However, one important aspect, the population-specific threshold T_a at which torpid individuals thermoregulated, differed between tropical and subtropical bats. We show that tropical torpid *N. bifax* thermoregulated, on average, at a 3.3°C higher T_a than those from the subtropics, similar but more extreme than in a regional comparison of feathertail gliders (14). Interestingly, the population-specific threshold T_a values of subtropical and tropical *N. bifax* and temperate *N. geoffroyi* (13) were strongly correlated ($r^2 = 0.9$) with the mean of the lowest 10% of minimum

T_a of the area where each population resided. Therefore, it appears that, while much of the thermal physiology between the northern and southern populations is similar, there are long-term thermal adaptations to the habitat that they occupy. It is likely that the threshold T_a for thermoregulation during torpor is under strong selection pressure because regulation of T_b at low T_a requires a large increase in TMR, which is relaxed in the tropics because extremely low T_a are not experienced.

Torpid *N. bifax* allowed T_b to approximate T_a over a wide T_a range, and this small $T_b - T_a$ differential remained constant, demonstrating that bats were thermoconforming and thus saved large amounts of energy. This is also the case for many other hibernating mammals that show $T_b - T_a$ differentials of ~1–2°C when thermoconforming during steady-state torpor (17, 23). When rewarming from these low T_b values, the overall rewarming rates were also comparable to other small heterothermic mammals (12) and also did not differ among seasons. However, the maximum rewarming rates measured here are among the highest recorded in mammals and are comparable to some other similarly sized temperate bats (12). These high rewarming rates in *N. bifax* require a high thermogenic capacity, which may be unexpected, since they only occupy subtropical/tropical habitats and are not exposed to extremely low T_a often associated with high heat production. Therefore, high rewarming rates may be an adaptation to allow rapid arousal when foraging conditions are favorable or to evade predation.

Perspectives and Significance

Our study provides strong evidence that the thermal physiology of subtropical and tropical *N. bifax*, a species that is capable of both short and multiday torpor bouts with a pronounced reduction in metabolism, is in many aspects similar to that of temperate hibernators. However, the population-specific T_a thresholds of torpid subtropical and tropical bats were significantly higher than in temperate bats, and this almost certainly reflects selection due to the exposure to lower minimum T_a during winter in the latter. Our data substantially advance the knowledge of the thermal physiology of torpor in subtropical and tropical regions. Because bats are most diverse in the tropics/subtropics, the minimum TMRs measured here together with information on prolonged torpor in the field, both similar to those of hibernators in temperate regions, suggest that torpor is crucial for energy conservation by many tropical and subtropical bats. Thus torpor, a physiological adaptation that is widely employed and often viewed to be exclusively used by cold climate mammals, also appears to play a key role in the survival strategies of small mammals living in tropical and subtropical regions.

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DISCLOSURES

No conflicts of interest are declared by the authors.

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