Metabolism during winter in a subtropical hibernating bat, the Formosan leaf-nosed bat (*Hipposideros terasensis*)

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The 60-g subtropical Formosan leaf-nosed bat, *Hipposideros terasensis*, hibernates in the wild at warm roost (and hence body) temperatures up to 23°C. For small hibernators, torpid metabolic rate is temperature dependent and thus hibernation in warm hibernacula is predicted to be energetically costly. This species, however, rarely feeds during the hibernation season to offset the expected high energetic costs. In this study we used a respirometry system to quantify physiological characteristics of euthermic and torpid *H. terasensis* in winter. We tested the hypothesis that *H. terasensis* exhibits metabolic inhibition during torpor. Our results showed that *H. terasensis* saved 94.6% energy by using torpor at air temperatures of 15°C, compared with its euthermic metabolic rate at that air temperature. Torpor metabolic rate declined with declining air temperature to around 14°C, but then increased at lower air temperatures of 10–14°C. Above 14°C, the slope of $-13.0^\circ K \pm 1.4^\circ K$ between metabolic rates and body temperatures in an Arrhenius plot (or $Q_{10} = 4.4$) suggests that, in addition to direct temperature effects, *H. terasensis* exhibited metabolic inhibition during torpor. A model used to evaluate energy expenditure of *H. terasensis* showed that at 20°C and 23°C a 55-g bat needs 194 kJ (4.9 g fat) and 273.2 kJ (6.9 g fat), respectively, to survive a 70-day hibernation period.

Key words: energy expenditure, subtropical bats, torpid metabolic rate

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Torpor is a physiological adaptation that some endotherms use for energy savings during periods of cold and food shortage. During torpor, body temperature ($T_b$) and metabolic rate (MR) of animals are substantially reduced. Animals that exhibit daily torpor reduce their torpor metabolic rate (TMR) to, on average, 29.5% of basal metabolic rate, whereas animals that exhibit multiday torpor (hibernation) reduce TMR to 5.1% of basal metabolic rate on average (Geiser and Ruf 1995). The reduction of metabolism below basal metabolic rate during torpor can be explained by 2 mechanisms. As animals cool, many chemical reactions, including those involved in metabolism, decline exponentially by a factor of 2–3 for each 10°C decrease in $T_b$ (i.e., a $Q_{10}$ effect—Schmidt-Nielsen 1997). Gillooly et al. (2001, 2006) have advocated the application of the Boltzmann–Arrhenius relation used in physical chemistry to characterize the effect of temperature on biochemical reaction rates, although it is not clear that it offers definite benefits over the $Q_{10}$ approach (Clarke 2004, 2006). In either case, however, the metabolic reduction in some hibernators is much more pronounced than the assumed temperature effects alone can explain (Hosken and Withers 1999; Tsien et al. 2011; Willis et al. 2005). For example, at air temperature ($T_a$) of 4.6°C ($T_b = 7.5°C$) the little forest bat (*Vespodelus vulturnus*) had a TMR at only 1.4% of the basal metabolic rate when $T_b = 33.3°C$ (Willis et al. 2005), whereas a $Q_{10}$ of 3 leads to a higher predicted value of 5.9% (more than 4 times higher). Such a reduction in TMR in excess of that predicted for the reduction in temperature has been called metabolic inhibition (or metabolic depression), and it has been suggested to play an important role in lowering TMR (Geiser 1988; Geiser and Brigham 2000; Malan 1993; Storey and Storey 1990).

Daily torpor and hibernation are widely used by temperate-zone bats to cope with seasonal cold and food shortages (Speakman and Thomas 2003). Although the weather is relatively mild in the tropics and subtropics, several microbats and relatively small pteropodids are capable of entering torpor (Bartels et al. 1998; Coburn and Geiser 1998; Geiser et al. 1996; Genoud 1993; Jacobs et al. 2007). Only recently has hibernation by subtropical bats been demonstrated (Liu and
Karasov 2011; Stawski et al. 2009). A number of studies have quantified physiological characteristics during torpor in temperate hibernating bats (e.g., Hosken and Withers 1999) and tropical and subtropical bats (Geiser et al. 1996; Genoud 1993). However, knowledge is scarce about energetics and thermal biology of subtropical hibernating bats and to what extent they differ from temperate hibernating bats.

The 81 species in the family Hipposideridae, the Old World leaf-nosed bats, are primarily distributed in tropical and subtropical areas (Simmons 2005). The few measurements available showed that hipposiderids either regulate their T_b at a high and stable level or only allow their T_b to fall slightly lower than 30°C at low T_a (Baudinette et al. 2000; Bonaccorso and McNab 2003; McNab 1989). Detailed work on energetics and temperature regulation for hipposiderids in torpor has never been conducted. The Formosan leaf-nosed bat, Hipposideros terasensis (Yoshiyuki, 1991), is a 60-g, insectivorous, cave-dwelling bat inhabiting primarily lowland areas (<1,000 m) of subtropical Taiwan. In a previous study, we found that in winter this species enters hibernation at roost temperature and T_b of 14–24°C (Liu and Karasov 2011), which is higher than a typical 6–12°C for temperate hibernating bats (Webb et al. 1996). For small hibernators, TMR is temperature dependent and thus hibernation in warm hibernacula is presumably energetically costly compared to hibernation in cooler hibernacula. Unlike in temperate areas, winter temperatures in subtropical Taiwan are mild and insects are likely to be available on warm nights. It is reasonable to suggest that H. terasensis might arouse from hibernation and feed frequently to offset energetic costs. However, H. terasensis rarely feeds during the hibernation period but relies mainly on body fat as an energy source. It has been suggested that H. terasensis might have a particularly low TMR (i.e., metabolic inhibition) to meet its winter energetic budget (Liu and Karasov 2011). H. terasensis is one of the few bats known to hibernate in the subtropic and, to our knowledge, it is also the largest species of bat to employ hibernation. There is a need to obtain data from species spanning the full range of body sizes and climatic zones for a better understanding of physiological adaptations in bats.

In this study we quantified physiological characteristics of euthermic and torpid H. terasensis in winter and tested the hypothesis that its TMR would be reduced to an extent greater than predicted simply from the direct effect of low temperature on biochemical reaction rates, an operational definition of metabolic inhibition. We predicted that its TMR declines with declining T_b to a significantly greater extent than predicted based on the Arrhenius equation. For the purposes of species management and conservation, it is important to understand the energetic budget of a species during its critical periods, for example, hibernation. Thus, we used empirical data on the relationship between TMR and T_b during torpor, along with measures of expenditure during periodic arousal, to simulate energy expenditure and use of fat by H. terasensis during the hibernation period at various temperatures. We predicted that our simulations would reconcile the observed overwinter fat mobilization of white adipose tissue of free-ranging H. terasensis (Liu and Karasov 2011) with the patterns of T_b and metabolism of hibernating bats.

**Materials and Methods**

**Animals.—**From 5 December 2008 to 27 January 2009, 12 adult male (mass X±SE = 53.9 ± 1.3 g), 34 adult female (54.2 ± 0.8 g), and 9 juvenile (47.0 ± 1.4 g) H. terasensis were captured at the entrances of 3 hibernacula when bats returned to the hibernacula within 3 h after sunset. Detailed information about locations of the hibernacula and the characteristics we used to distinguish juveniles and adults were described in Liu and Karasov (2011). Bats were immediately transported to the Taiwan Endemic Species Research Institute and kept individually in bell-shaped nylon netted cages (50 x 50 x 50 cm) housed in a 20°C dark room with water ad libitum, but no food for 1 night prior to metabolic trial. Bats were used for measurements only on the day following capture and were fasted at least 12 h to be postabsorptive before measurements (Genoud 1993; Morris et al. 1994). No feces were found during measurements. After metabolic trials, bats were banded on the forearm with numbered aluminum bands (5.2 x 5.5 mm; Lambournes Ltd, Birmingham, United Kingdom) and released to their roosts. Each individual was used in only 1 metabolic trial at a single T_a. The experimental procedures with bats in this study followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and the animal use protocol was approved by the Institutional Animal Care and Use Committee of the Taiwan Endemic Species Research Institute (IACUC Approval 95001).

**Measurements of physiological characteristics.—**The TMR and resting metabolic rates were determined by measuring whole-animal rates of oxygen consumption (VO_2, in ml O_2/h) and carbon dioxide production (VCO_2) in an open-flow respirometry system. Each bat was weighed to the nearest 0.1 g before and after measurement and the average body mass (M_b) was used for calculation of mass-specific metabolic rate. At the end of each trial, the bat was removed from the metabolic chamber and its T_b was measured to the nearest 0.1°C within 40 s by inserting a paraffin wax–coated digital thermocouple 2 cm into the rectum (our results showed that in the beginning of arousal handling for 40 s would not increase T_b > 0.2°C). Bats were considered euthermic if T_b ≥ 30°C and torpid if T_b < 30°C (Geiser et al. 1996). For each trial, 1 animal channel and 1 reference channel (air) were operated simultaneously. A bat was placed in a 1,100-ml transparent plastic metabolic chamber fitted with plastic mesh on the top for hanging. The chamber was placed in a temperature-controlled cabinet (Peltier controller PElt-4; Sable Systems, Las Vegas, Nevada) and kept dark during experiments to minimize the effect of thermal radiation (Porter 1969). T_b within the cabinet was measured by a digital thermocouple thermometer and kept between 10°C and 28°C. The temperature range covered winter maximum and minimum hibernacula temperatures (Liu and Karasov 2011), and included the thermal neutral zone (26–
of 0.96% ± 0.03% (n = 55). All values were corrected to standard temperature and pressure for dry air, and also adjusted to mass-specific values for comparison to the values of other bat species in the literature.

In order to construct a model of energy expenditure during torpor we needed to characterize how MR changes per unit temperature differential (Tb – T). This is calculated for each individual as C = VO2/(Tb – T) and is referred to as wet thermal conductance (C—Hosken and Withers 1997). To examine rewarming rate during arousal, which is part of the model, Tb of 5 arousing individuals (body mass = 53.1 ± 2.0 g) were measured at room temperature (20–22°C) at 5-min intervals until Tb reached 34°C. Within the thermal neutral zone euthermic bats maintain a Tb of approximately 34°C (J.-N. Liu, pers. obs.). Maximum rates of rewarming were presented in 5-min as well as 10-min intervals to be comparable with other studies.

All data are presented as mean (X) ± 1 SE. N and n indicate number of observations and number of individuals measured, respectively. Least-squares linear regression was used to analyze several relationships: between log MR and Tb, rewarming rate and Tb, and MR of thermoregulating bats and the Tb – Ta differential. Accordingly, we used the Arrhenius equation to evaluate the impact of body temperature on MR:

\[ K(T) = K_0 e^{-\frac{E_i}{kT}} \]

in which T is absolute temperature (in °K), K(T) is a rate of reaction at some temperature, K0 is a rate constant independent of temperature (relating to molecular collision frequency), Ei is the activation energy (has units eV and averages about 0.65 eV among biochemical reactions—Gillooly et al. 2001), and k is Boltzmann’s constant (k = 8.62 × 10^-5 eV/K—Karasov and Martínez del Rio 2007). If changes in MR with changing Tb (i.e., values of K(T)) are governed by this model, in which changes in reaction rate are due to changes in temperature, then a graph of ln(MR) versus 1/T should yield a straight line with slope equal to -Ei/k (Gillooly et al. 2001; Karasov and Martínez del Rio 2007). The expected slope for Ei = 0.65 eV is -7.5, and slopes in hibernating mammals and birds and many other organisms bracket that value, ranging from -5.02 to -9.15 (Gillooly et al. 2001). Hence, we used that as a standard for comparison. The P-value for statistical significance was set at P < 0.05.

**RESULTS**

During winter, Tb of *H. terasensis* was thermally labile. Bats showed different patterns of temperature and thermal regulation in response to Ta; 12 bats remained euthermic (Tb > 30°C), 31 bats showed thermoconforming torpor (Tb – Ta < 5°C), and 12 bats exhibited thermoregulating torpor (MR or Tb or both elevated; Fig. 1). We consider respective patterns of Tb and metabolism for each group below.

*Euthermic bats.*—At Tb within 26–28°C (thermal neutral zone), all 8 bats remained euthermic with an average Tb of 32.6°C ± 0.5°C (range, 30.4–34.8°C; Fig. 1a) and an average
conductance of Hipposideros terasensis of 10–28 

tially declined with decreasing Tb. When we plotted these data (h

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2
on an Arrhenius plot (Fig. 2), we found that the slope,

In the plot the data on euthermic bats in the thermal neutral

zone (above), the slope was steeper, 

5
14
2
C from 6 December 2008 to 28 January 2009. Open circle,

ranged from 0.6
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C). Tb 

6
C (Figs. 1a and 1b). For those torpid

thermoregulating bats, MR was a function of Tb

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approximately 4.5 times the average lowest TMR (above).

Elevated MR or increased Tb – Ta differential, or both, was

found in 9 of 12 individuals at Ta < 14°C and in all 6

individuals at Ta < 12.5°C (Figs. 1a and 1b). For those torpid

thermoregulating bats, MR was a function of Tb – Ta
differential; the equation was MR = 0.06(Tb – Ta) + 0.049

(R² = 0.78, P < 0.001, n = 12).

Respiratory quotient.—Average RQ value was 0.78 ± 0.02

(range, 0.67–0.88, n = 15) for torpid thermoconforming bats,
similar to values in other torpid bats (Hosken and Withers

1997, 1999) and consistent with catabolism of a combination

of fat and protein during torpor. RQ values were 0.89 and 0.87

for 2 euthermic bats and 0.87 for a thermoregulating bat.

Thermal conductance.—The C of torpid thermoconforming bats

ranged from 0.02 to 0.09 ml O₂ h⁻¹ g⁻¹ °C⁻¹ and was

independent of Tb (P = 0.4) or Tb (Fig. 1c). The average C

of torpid thermoconforming bats (0.05 ± 0.004, n = 31) was

significantly lower than that of euthermic bats below the

thermal neutral zone (0.09 ± 0.005, n = 4). The average C

of torpid thermoregulating bats (0.07 ± 0.004, n = 12) also

was significantly lower than that of euthermic bats below the

thermal neutral zone (P < 0.05) but higher than that of torpid

thermoconforming bats (P < 0.01).

Five bats rewarmed from torpor (Tb range, 13–24°C) to a Tb

of 34–37°C in 20–50 min (Fig. 3a), with an average rate of

0.51 ± 0.04°C/min (N = 28 five-minute intervals). Calculated

rates over 5-min intervals increased with increasing Tb

(Fig. 3b) and reached a maximum of 0.76 ± 0.07°C/min (or
mean Tb during the interval. Filled and open circles indicate Tb below and above 34°C, respectively. y = 0.003x, R² = 0.56, P < 0.001, N = 28.

maximum of 0.72 ± 0.06°C/min over 10-min intervals; n = 5 individuals).

**DISCUSSION**

**Metabolic rates and energy savings.**—Formosan leaf-nosed bats hibernate in winter in caves at roost temperature and Tb of 14–24°C (Liu and Karasov 2011). A comparison of their metabolic rate with that of euthemic bats over the same temperature range provides one kind of assessment of their energy savings. Based on results in Fig. 1b, bats torpid at Ta of 15°C reduced metabolic rate 94.6% in contrast to euthemic bats at the same temperature. The value is similar to a 90–99% savings in energy expenditure in several bat species torpid at Ta or Tb of 5–15°C (Cryan and Wolf 2003; Geiser and Brigham 2000; Hosken and Withers 1997; Willis et al. 2005). Considering the higher hibernation temperatures of *H. terasensis*, this finding supports our hypothesis that this species exhibits metabolic inhibition during winter torpor.

Accordingly, we used the Arrhenius equation and plot to evaluate the impact of body temperature on MR. A graph of ln(MR) versus 1,000/T should yield a straight line with an expected slope of −7.5°C. Slopes of these plots of metabolism versus 1,000/T in hibernating mammals and birds and many other organisms range from −5.02°C to −9.15°C (Gillooly et al. 2001). For comparison, simulations based on Q₁₀ values of 2–3 yield slopes of −6.1°C to −9.7°C, respectively. When we plotted our data on an Arrhenius plot (Fig. 2) we found that the slopes, −11.1°C and −13.0°C (depending upon data set), were significantly steeper than these slopes. Thus, metabolism of *H. terasensis* declines with declining temperature more rapidly than expected, based on the effect of temperature on molecular collision frequency. This is consistent with our hypothesis that in addition to lowered MR due to the direct effect of lower Tb, *H. terasensis* also exhibits metabolic inhibition during torpor.

One possible explanation for metabolic inhibition is that during hibernation pH value of blood and intracellular fluids is reduced, which might cause acidosis and reduce rates of metabolic reactions (Hand and Somero 1983; Malan 1993; Malan et al. 1988; Storey and Storey 1990). The reduction in pH might result from accumulation of CO₂ during entry into hibernation. Snapp and Heller (1981) found that in golden-manated ground squirrels (*Spermophilus lateralis*) the RQ declines during entry into hibernation and rises during arousal. Whether *H. terasensis* uses this mechanism to achieve metabolic inhibition needs further investigation.

The minimum TMR for some temperate bats hibernating at Tb of 0–10°C is about 0.02 ml O₂ h⁻¹ g⁻¹ (Hock 1951; Thomas et al. 1990; Willis et al. 2005). A slightly higher minimum TMR ranging from 0.03 to 0.05 ml O₂ h⁻¹ g⁻¹ has been reported in some other bats at a Ta < 10°C (Geiser and Brigham 2000; Genoud 1993; Szewczak and Jackson 1992). In the present study, the absolute lowest TMR of 0.02 ml O₂ h⁻¹ g⁻¹ and the average lowest TMR of 0.046 ± 0.003 ml O₂ h⁻¹ g⁻¹ in *H. terasensis* were similar to the values in the literature despite this bat’s relatively large body size and high torpid Tb. Our result supports the viewpoint that the minimum TMR in hibernators is independent of body size (Geiser and Ruf 1995; Heldmaier and Ruf 1992). It seems that there are no general differences in minimum TMR between subtropical and temperate-zone hibernators.

**Body temperature and roost selection.**—The majority of *H. terasensis* elevated their MR or Tb, or both, at a Ta < 14°C (Figs. 1a and 1b), suggesting that below this temperature torpid *H. terasensis* increases metabolism and defends its Tb above a threshold (~13.3°C in this study). This threshold Tb is referred to as Tb_min, and in most temperate bats ranges between 0°C and 10°C (Geiser and Brigham 2000; Geiser and Ruf 1995; Willis et al. 2005). Relatively high Tb_min of 17–30°C were reported in some tropical and subtropical bats that exhibit torpor (Bartels et al. 1998; Bartholomew et al. 1970; Coburn and Geiser 1998; Geiser et al. 1996; Genoud et al. 1990). The Tb_min of *H. terasensis* lies between that of temperate hibernating bats and tropical–subtropical bats. Geiser and Ruf (1995) showed that the Tb_min in hibernators is independent of Mb. Taken together, examination of these data suggests that Tb_min of bats is likely related to the thermal
environment exposed during torpor (Geiser and Brigham 2000). Because bats will be forced to increase thermoregulatory costs or arousal frequency, or both, at a $T_b$ below $T_{b_{min}}$, bats should select hibernacula with temperatures above $T_{b_{min}}$ for most, if not all, of the hibernation season. Our result could explain our observations that free-ranging $H. terasensis$ hibernates at hibernacula with temperatures $> 14\, ^\circ C$ (Liu and Karasov 2011). Field observations show that caves in winter that possess cooler temperatures than $14\, ^\circ C$ are available, but apparently are not chosen by $H. terasensis$ (Liu and Karasov 2011).

For bats, hibernaculum selection or geographical distribution, or both, is likely related to their physiological regulatory capacities (Arlettaz et al. 2000; Henshaw 1970; Webb et al. 1990). For example, in comparison to temperate vespertilionids that have $T_{b_{min}}$ of 1–5 $^\circ C$ (Duban and Tomasi 2006; Geiser and Brigham 2000; Hock 1951), a relatively high $T_{b_{min}}$ of 7.5–10 $^\circ C$ in Tadarida teniotis has been suggested for the reason why this species is excluded from high latitudinal areas (Arlettaz et al. 2000). Additionally, an inability to allow $T_b$ to fall below approximately $15\, ^\circ C$ in some small tropical species has been used to explain the biogeography of bats (Bonaccorso and McNab 1997; Geiser et al. 1996). In winter, $H. terasensis$ does not migrate to higher elevational areas to seek cooler roosts. We suspect that the relatively high $T_{b_{min}}$ might limit $H. terasensis$ to lower elevation areas. Some other hipposiderids, Asellia tridens and Coelops frithii, extend their northern range into warm temperate areas and it has been suggested that they employ hibernation (Nowak 1999; Quinseyh 1988). It would be of interest to investigate whether and how the thermal physiology of those hipposiderids differs from that of $H. terasensis$ and whether these differences explain their successful penetration into colder climates.

**Thermal conductance.**—There are contradictory results on whether $C$ changes or not when animals enter torpor. Some studies have reported a lower $C$ in torpid than in euthermic bats (Cryan and Wolf 2003; Hosken and Withers 1997, 1999; Morris et al. 1994; Willis et al. 2005) and rodents (Snyder and Nestler 1990), whereas others did not find significant differences in $C$ between torpid and euthermic animals (Bonaccorso and McNab 1997; Heldmaier and Ruf 1992). Our results showed that $C$ in torpid thermoconforming $H. terasensis$ was only 59% of $C$ in euthermic bats below the thermal neutral zone (Fig. 1c). The lower $C$ in torpid bats might result from a reduction of TMR and peripheral vasoconstriction in association with the low $T_b$ (Geiser 2004).

**Rewarming rate.**—The maximum rewarming rate in $H. terasensis$ ($0.72\, ^\circ C/min$ over 10-min intervals) was higher than that in other hipposiderids ($0.32\, ^\circ C/min$ for 9-g Hipposideros speoris and $0.42\, ^\circ C/min$ for 15-g A. tridens—Geiser and Baudinette 1990) and higher than the allometrically predicted value ($0.5\, ^\circ C/min$) for a 53-g heterothermic mammal using the equation log rewarming rate (in $^\circ C/min$) = $0.295 - 0.345 \log M_b$, where $M_b$ is body mass in grams (Geiser and Baudinette 1990). Why $H. terasensis$ has a higher average rewarming rate remains unknown. However, Willis (2008) found that tropical and subtropical species of bats with stable roost microenvironments and small colony size have higher rewarming rates, presumably to compensate for less opportunity to exploit passive rewarming. It is possible that the solitary roosting behavior and stable roost temperature of $H. terasensis$ to some extent contribute to its high rewarming rate.

**Energy expenditure.**—We used our data on $T_b$, MR, $C$, and rate of rewarming to simulate energy expenditure during the hibernation period, based on earlier models (Cryan and Wolf 2003; Humphries et al. 2002). The total energetic expenditure ($E_{total}$, in J) during the hibernation period can be described as:

$$E_{total} = E_{tor} + E_{ar},$$

where $E_{tor}$ and $E_{ar}$ denote total energy expenditures during torpor and arousals, respectively. We further calculated $E_{tor}$ and $E_{ar}$ by:

$$E_{tor} = TMR \times k \times t_{tor} \times M_b$$

and

$$E_{ar} = a \left[ s (T_{eu} - T_{tor}) M_b + \int_{t_1}^{t_2} (Q + RMR \times M_b \times k \times t_{eu}) \right],$$

where $k$ is the caloric equivalent for oxygen ($19.02\, J/ml\, O_2$ was taken, $RQ = 0.78$), $t_{tor}$ is total time that bats remain in torpor, $a$ is number of arousals during the hibernation period, $s$ is specific heat capacity of tissues ($3.9\, J\, g^{-1}\, ^\circ C^{-1}$ was taken—Withers 1992), $T_{eu}$ and $T_{tor}$ are euthermic and torpid $T_b$s, and $t_1$ and $t_2$ are times of start and end of rewarming. $Q$, which is the metabolic heat production needed to balance heat loss to the environment (Cryan and Wolf, 2003), was calculated as $Q = C (T_{eu} - T_{tor}) \times M_b \times k$, where $C$ is thermal conductance ($0.09\, ml\, O_2\, h^{-1}\, g^{-1}\, ^\circ C^{-1}$ was taken). $RMR$ ($ml\, O_2\, h^{-1}\, g^{-1}$) is euthermic metabolic rate at a specific $T_a$, and $t_{eu}$ is duration that bats maintain euthermia during each arousal episode.

In our model, values of all the variables were made based on data in this study and Liu and Karasov (2011). We assumed that the hibernation period was 70 days, bats aroused 8 times, and $M_b$ linearly decreased with time as they catabolized mainly fat. During hibernation, adult males, adult females, and juveniles lost 13.7% 12.9%, and 15% $M_b$, respectively. For each arousal episode, bats took 0.75, 0.5, and 0.33 h ($t_2 - t_1$) to rewarm from $T_{tor}$ of 15°C, 20°C, and 25°C to $T_{eu}$ (34°C was taken), respectively. Once aroused, bats remained euthermic for 2 h ($t_{eu} = 2$). Total time that bats remained in torpor at different $T_{tor}$ was then calculated as $t_{tor} = 70 	imes 24 - 8[2 + (t_2 - t_1)]$. TMRs and RMRs that were reported in this study were for standard temperature and pressure for dry air conditions. Considering oxygen transport within the body, in our model simulations we converted all TMRs and RMRs to body temperature at ambient pressure and saturated with water vapor. Although in our study the rewarming rates varied with $T_b$, we assumed that rewarming rate was constant. Because temperature of natural hibernacula is very stable and we did not find evidence that $H. terasensis$ uses passive rewarming to facilitate arousals (Liu and Karasov 2011), heat gain or loss due to passive rewarming was neglected.
Our model showed that total energy expenditure during the hibernation period increased with increasing $T_b$ (Fig. 4). This result is consistent with simulation of winter energy requirements of little brown bat (Myotis lucifugus—Humphries et al. 2002). In a previous study, we found that female adult $H.\ \text{terasensis}$ ($M_b = 54.9 \pm 0.5\ \text{g}$) lost an average of 7.1 g of $M_b$ during the hibernation period (Liu and Karasov 2011). If we assume all the mass that was lost was fat, and the energy content of chiropteran fat stores is 39.41 kJ/g (Ewing 2011). If we assume all the mass that was lost was fat, and the energy content of chiropteran fat stores is 39.41 kJ/g (Ewing 2011), the energy of 7.1 g of fat permits a 55-g bat to survive the same period at the same temperature in a 23°C. This result could explain why $H.\ \text{terasensis}$ did not fatten itself in autumn and why this species did not feed frequently in winter (Liu and Karasov 2011).

Our model demonstrated the important role that metabolic inhibition plays in $H.\ \text{terasensis}$. When a $Q_{10}$ value of 2.5 is assumed, $H.\ \text{terasensis}$ needs 1.8–2.2 times more energy to survive the same period at the same temperature in comparison to the simulations based on our metabolic measurements (Fig. 4).

At a $T_b$ of 15°C, each arousal costs 7.4 kJ of energy. As a direct consequence, a total of 8 arousals accounts for 44.8% of total energy expenditure during the hibernation period. The percentage decreases to 21.8% when bats hibernate at a $T_b$ of 20°C. For comparison, little brown bats (M. lucifugus) hibernating at 5°C spent 90% of total energy expenditure on arousals (Thomas et al. 1990b). The energetic costs for arousals are substantially reduced in species that hibernate at a warmer temperature. Studies have shown that human disturbances provoke bats to arouse from hibernation and might result in a “cascade effect,” which means a few aroused individuals arouse others by flying (Speakman et al. 1991; Thomas 1995). Arousals caused by human disturbances, which increase the energetic demands of hibernating bats and may result in death due to depletion of energy reserves, should be avoided.

This is the 1st study describing energetics in hipposiderids in torpor. Our results confirm our expectations that $H.\ \text{terasensis}$ exhibits metabolic inhibition during torpor. Torpid $H.\ \text{terasensis}$ increased metabolism and defended its $T_b$ at a relatively high $T_{b\ \text{Min}}$, compared with temperate hibernating bats. Thus, $H.\ \text{terasensis}$ might have less physiological capability to tolerate low temperature, which could be the reason why free-ranging $H.\ \text{terasensis}$ does not inhabit high-elevation areas and did not choose cooler caves as hibernacula. Our previous field study shows that adult $H.\ \text{terasensis}$ accumulated 13–14% $M_b$ (fat) before hibernation (Liu and Karasov 2011). With a markedly low TMR supported by metabolic inhibition, those stored fats permit bats to hibernate at temperature as high as 23°C.

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