Cold and alone? Roost choice and season affect torpor patterns in lesser short-tailed bats

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Abstract Seasonal changes in weather and food availability differentially impact energy budgets of small mammals such as bats. While most thermal physiological research has focused on species that experience extreme seasonal temperature variations, knowledge is lacking from less variable temperate to subtropical climates. We quantified ambient temperature (T_a) and skin temperature (T_{sk}) responses by individuals from a population of New Zealand lesser short-tailed bats (*Mystacina tuberculata*) during summer and winter using temperature telemetry. During summer, communal roosts were more thermally stable than T_a . During winter, solitary roosts were warmer than T_a indicating significant thermal buffering. Communal roost trees were used on 83 % of observation days during summer, and individuals occupying them rarely entered torpor. Solitary roosts were occupied on 93 % of observation days during winter, and 100 % of individuals occupying them used torpor. During summer and winter, bats employed torpor on 11 and 95 % of observation days, respectively. Maximum torpor bout duration

was 120.8 h and winter torpor bout duration correlated negatively with mean T_a . Torpor bout duration did not differ between sexes, although female minimum T_{sk} was significantly lower than males. The summer Heterothermy Index varied, and was also significantly affected by T_a . Mean arousal time was correlated with sunset time and arousals occurred most frequently on significantly warmer evenings, which are likely associated with an increased probability of foraging success. We provide the first evidence that torpor is used flexibly throughout the year by *M. tuberculata*, demonstrating that roost choice and season impact torpor patterns. Our results add to the growing knowledge that even small changes in seasonal climate can have large effects on the energy balance of small mammals.

Keywords Torpor · *Mystacina tuberculata* · Thermoregulation · Microhabitat · Seasonal weather

Introduction

All organisms must maintain a positive daily energy balance or they will perish. Energy balance is influenced by precipitation, reproductive state, circannual cycles, photoperiod, food/water availability, and ambient temperature (T_a) (Csada and Brigham 1994; Song and Geiser 1997; Körtner and Geiser 2000a; b; McNab 2002; Doucette et al. 2012). Ambient temperature has fundamental impacts on metabolism, particularly in small endotherms (i.e. mammals and birds). Maintaining a high and stable body temperature (T_b) requires large amounts of energy, particularly for small mammals that quickly lose heat to the environment due to their high surface area to volume ratios.

Though individuals living in highly variable temperate climates face the most drastic changes in seasonal

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We show exciting flexibility in seasonal behaviour of a warm temperate mammal. New Zealand bats used a heterothermic continuum, like cold temperate bats, despite mild changes in ambient temperature.

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environment, warm temperate areas also expose individuals to seasonal changes in T_a and presumably energy availability. For most temperate and subtropical endotherms, summer is a period of positive energy balance. During summer, food is usually more abundant than in winter and the costs of thermoregulation at higher T_a are lower. In cold-temperate areas, winter is challenging because endotherms must cope with energy shortages and greater heat loss to the environment. However, the influence of T_a variability in subtropical and warm temperate habitats has been less thoroughly explored.

To minimize energy loss during periods of prolonged energy scarcity, many clades of vertebrates employ daily or multiday torpor (Wang 1989; Grigg et al. 2004; Ruf and Geiser 2015). Torpor is a physiological state characterized by decreases in metabolic rate (MR) leading to reduced T_b (Geiser 2004). Some hibernators accumulate a fat store or food cache large enough to balance energy costs (e.g., Lyman 1982; Geiser 2004). During winter, many of these species decrease energy expenditure so that their reserves are large enough to survive, as even small increases in energy expenditure may negatively impact survival (Speakman et al. 1991; Boyles and Brack 2009; although see Geiser (2007)).

Most species that hibernate periodically arouse, via metabolic heat production to a high, stable T_b (i.e. normothermia), and while periodic arousals are brief, this can account for up to 90 % of overwinter energy expenditure (Wang 1989; Thomas et al. 1990; Geiser 2004). The “torpor optimization hypothesis” postulates that expression of torpor should reflect a balance between the benefits of reduced MR and arousal costs (Humphries et al. 2003; Jonasson and Willis 2011). Furthermore, the torpor optimization hypothesis predicts differences in sex-specific energy budgets for species with differential timing of reproductive investment (Michener 1992; Humphries et al. 2003; Jonasson and Willis 2011).

Lesser short-tailed bats (*Mystacina tuberculata*) are the only extant species of family *Mystacinidae*, and this family is endemic to New Zealand. *Mystacina tuberculata* provide a good model to examine energetic flexibility in small mammals, as they live in areas with more subtle seasonal variations than most temperate mammals. Lesser short-tailed bats roost throughout the year in tree cavities, which may or may not be thermally stable (Sedgeley 2006). Reproductive activity by males peaks during late summer and females give birth the following spring (Daniel 1990). Winter behaviour is generally characterized by inactivity within a tree roost, however, activity is positively correlated with T_a (Daniel 1979; Christie 2003, 2006; Christie and Simpson 2006). Notably, mild winter weather (i.e. above 10 °C) increases the abundance of flying insects (Paige 1995), and although *M. tuberculata* are omnivorous, insects make up the majority of their diet (Arkins et al. 1999).

We used temperature-sensitive radio transmitters on individuals to address thermoregulatory patterns of free-ranging *M. tuberculata* in Pureora Forest Park, in the central North Island of New Zealand. Our first hypothesis was that differences in seasonal energy budgets, due to changes in T_a , would affect roost choice, and we predicted that individuals would choose thermally buffered roost microclimates to save energy. Our second hypothesis was that seasonal variation in T_a influence the frequency, duration, and depth of torpor bouts, and we predicted that warmer T_a during summer would lead individuals to use torpor less than during winter. Furthermore, we predicted that when torpor was used, it would be more frequent, prolonged, and/or deeper during colder days when prey availability is presumably lower. Finally, we examined the hypothesis that timing differences in reproductive investment lead to intersexual differences in winter skin temperature (T_{sk}) patterns. Specifically we predicted females, whose reproductive investment comes after winter would be more conservative and exhibit longer and/or deeper torpor bouts than males.

Methods

All procedures were approved by the University of Auckland Animal Ethics Committee (AEC-R1374) and were conducted under New Zealand Department of Conservation Wildlife Act Authorization Number 39083-FAU. Our study was conducted in the Pikiariki Ecological Area of Pureora Forest Park (38°26'S, 175°39'E), central North Island, New Zealand, during the Austral “summer” (January–March) and “winter” (June–October). Pikiariki consists of approximately 450 ha of native, mature podocarp–hardwood forests and is home to approximately 700 *M. tuberculata* (Wallace 2006). Bats occupied 15 solitary roosts (housing only one individual), and four communal roosts (housing upwards of 400 individuals at a time).

We caught bats in harp traps and mist nets. Individuals were sexed, aged, weighed to the nearest 0.5 g using a spring pesola, forearm length was measured to the nearest 1 mm, and we calculated body condition index (BCI), mass (g) forearm length (mm)^{−1}. Young of the year were distinguished from adults by the lack of ossification of the metacarpal-phalangeal joint on the third digit (Davis and Hitchcock 1965).

For small bats, T_{sk} provides a good approximation of T_b (Audet and Thomas 1996; Barclay et al. 1996; Willis and Brigham 2003). We clipped a small patch (<1 cm²) of fur between the shoulders and attached a temperature-sensitive radio-transmitter (0.9–1 g, BD-2NT; Holohil Systems Ltd, Carp, Ontario) using a latex cement (TORBOT Group, Inc., Cranston RI, USA). On average the body mass of bats affixed with transmitters was 14.5 ± 1.5 g and transmitters

represented between 5.6 and 7.5 % of body mass. Individual bats were radio-tracked each morning to find day roosts using a scanning receiver (Australis 26K Scanning Receiver, Titley Electronics, Ballina, Australia) connected to a 3-element Yagi antenna. A data-logging receiver (Lotek SRX_800; Lotek Engineering Inc. Newmarket, Ontario, Canada) was deployed at roosts and recorded individual T_{sk} at 10-min intervals whenever a radio-tagged bat was present.

Thermoregulatory stages were classified following Jonasson and Willis (2011). Warming: an abrupt increase in torpid T_{sk} (three consecutive recordings) that eventually stabilized at a normothermic level. Normothermic: the time between the end of the warming phase and the initiation of cooling. Cooling: readily obvious as a decline in T_{sk} (three consecutive recordings) preceding steady-state torpor. Torpid: stable T_{sk} (three consecutive recordings) following the cooling phase and preceding the warming phase. We excluded data from the first 24 h after releasing the bats to avoid the influence of disturbance on our results. We recorded the date and time of each arousal from the T_{sk} trace and converted the time of arousal to radians. We then used Rayleigh's test for circular distributions to determine if the daily distribution of arousal times was significantly different from random.

We recorded regular drops in T_{sk} during the normothermic phase which we refer to as shallow heterothermy, and did not meet our criteria for torpor (i.e. more than 30 min). To compare normothermic bouts we calculated the Heterothermy Index: $\sqrt{\frac{\sum (\text{mean modal } T_{sk} - T_{sk})^2}{n-1}}$ (HI; Boyles et al. 2011). HI provides a single value for daily fluctuations in T_{sk} , and can be used to quantify, and compare highly variable T_{sk} data.

To estimate energy savings associated with drops in T_{sk} during normothermia, we estimated power (energy consumption; W) of maintaining mean modal active T_{sk} (E_{mm}), and estimated energy consumption of recorded T_{sk} (E_{obsv}). We assumed bat mass was 80 % water, and estimated kilojoules using: $\text{kJ} = (\text{Mass}) (\text{specific heat capacity of water}) (T_{sk} - T_a)$. We assumed that T_{sk} and T_a remained constant during the 10 min recording interval, and then estimated energy consumption using: $W = (\text{kJ s})^{-1} 1000$, and daily energy consumption as the sum of these values. We subtracted daily E_{obsv} from daily E_{mm} (E_{diff}) to estimate energy savings.

We recorded T_a , barometric pressure (P_{bar}), and roost temperature (T_{roost}) of one communal roost using data loggers (HOBO Micro Station Data Logger—H21-002, Onset Computer Corporation, Cape Cod, MA, USA). Ambient temperature was recorded in the shade, 2 m above the ground, and the logger inside the communal roost was placed 1 m inside the tree hole in a part of the cavity known to be used by bats.

To determine which bat-specific, and weather-specific variables best predict thermoregulatory strategy we used

linear mixed effect models (LMEM). In bat-specific models, we used torpor bout duration ($\log_{10}$) (to decrease the spread of residuals) and minimum T_{sk} as response variables, sex as a fixed effect, and individual as a random effect. In weather-specific models we used torpor bout duration ($\log_{10}$), minimum T_{sk} , or HI as response variables, and three variables which have been associated with bat activity in past studies: (1) T_a ; (2) T_{roost} , which may be buffered and less variable compared to T_a ; (3) change in P_{bar} , which reflects passing weather fronts and is correlated with both insect and bat activity (Jones et al. 1995). Temperature and especially P_{bar} should rapidly equilibrate inside and outside the roost, and could be used by bats to assess relative levels of insect abundance.

All analyses were conducted in R studio version 0.98.945 (R Development Core Team 2009) and values are reported as the mean $\pm$ SD with n representing the number of animals and N the number of events/arousals. We assessed significance at the $P < 0.05$ level.

Results

We attached transmitters to 8 individuals (5 males, 3 females) and recorded 61 bats-days of T_{sk} data from 7 individuals (4 males, 3 females). Neither body mass ($P = 0.65$, $t = -0.47$, $n = 8$ individuals) nor BCI ($P = 0.74$, $t = -0.35$, $n = 8$) differed between sexes. Individuals caught in the summer were heavier (16 ± 0.0 g; $n = 3$; $P < 0.01$, $t = 5.7$) than those caught during winter (14 ± 0.8 g; $n = 5$), and had higher BCI ($P < 0.01$, $t = 6.1$).

Ambient temperature during summer varied between a mean minimum of 10.2 ± 1.6 °C ($N = 18$, absolute minimum = 2.7 °C) and mean maximum of 18.6 ± 1.7 °C ($N = 18$, absolute maximum = 22.3 °C), with a mean daily range of 8.4 ± 1.5 °C ($N = 18$, absolute range = 11.5 °C). During winter, T_a varied between a mean minimum of 5.6 ± 2.3 °C ($N = 43$, absolute minimum = -2.2 °C) and a mean maximum of 10.3 ± 2.3 °C ($N = 43$, absolute maximum = 15.9 °C), with a mean daily range of 4.7 ± 2.1 °C ($N = 43$, absolute range 10.1 °C; Fig. 1).

During summer, mean minimum communal T_{roost} (13.2 ± 1.5 °C) was higher than mean minimum T_a (10.2 ± 1.6 °C), and mean T_{roost} range (3.8 ± 0.9) was smaller than mean T_a range (8.4 ± 1.5 ; Table 1). Mean daily solitary T_{roost} ($n = 3$ roosts, $N = 12$ days; 14.2 ± 3.4 °C) was higher than mean T_a (10.2 ± 1.6 °C), and the mean T_{roost} range (2.8 ± 1.2) was less than the mean T_a range (4.6 ± 1.5).

During summer and winter, 97.6 % of torpor bouts occurred in solitary roosts (42/43) and only once in a communal roost. The HI for all bats was significantly higher (i.e. more heterothermic) when they roosted in solitary roosts (19.5 ± 4) compared to communal roosts (3.2 ± 3.6 ,

Fig. 1 Differences in temperature between summer (black bars) and winter (white bars). Max. T_a and Min. T_a are the means of all respective daily maximum and minimum ambient temperature (T_a); day T_a and night T_a are the means of all day and night T_a (sunrise to sunset, and sunset to sunrise); range T_a is the mean of all daily ranges in T_a (max. T_a –min. T_a); Min. T_{skin} is the mean of all individuals mean minimum skin temperature. Values represent mean $\pm$ SD, asterisks represents a significant difference between seasons (Student's t test; $P < 0.05$)

Table 1 Communal and solitary roost thermal characteristics compared to corresponding ambient conditions in Pureora Forest Park

	Mean T_a (°C)	Max T_a (°C)	Min T_a (°C)	Range T_a (°C)
Communal roost	14.7 $\pm$ 1.4	17.2 $\pm$ 1.7	13.2 $\pm$ 1.5	3.8 $\pm$ 0.5
Communal ambient	15.6 $\pm$ 1.5 [#]	18.6 $\pm$ 1.7*	10.2 $\pm$ 1.6*	8.4 $\pm$ 1.5*
Solitary roost	14.2 $\pm$ 3.4	15.4 $\pm$ 3.0	12.8 $\pm$ 3.5	2.8 $\pm$ 1.1
Solitary ambient	6.8 $\pm$ 4.7*	8.8 $\pm$ 4.5*	4.2 $\pm$ 4.6*	4.6 $\pm$ 1.5*

Mean T_a is the average of all mean ambient temperatures (T_a); Max T_a and Min T_a are the mean of all respective daily maxima and minima T_a ; Range T_a is the mean of all daily ranges in T_a (max. T_a –min. T_a). Values are mean $\pm$ SD, communal $N = 18$ days, solitary $N = 12$

* Significant difference between values (Student's t test; $P < 0.01$), [#] = 0.098

$P < 0.01$, $t = -15.7$, $df = 35.8$). During winter, bats used torpor on 95.3 % of days and on 11.1 % of observation days during summer (Fig. 2). Every individual entered torpor at least once in winter, while only one individual did so during summer. Torpor bout durations ranged from 0.9 to 2.2 h in summer and 6.7 to 120.8 h in winter.

Multiday torpor bouts made up 47.6 % of torpor bouts (10/21) during winter and were not recorded during summer. Mean daily torpor bout duration during winter was 10.1 ± 3.7 h ($n = 4$, $N = 11$) while mean multiday torpor duration was 60.7 ± 27.5 h ($n = 4$, $N = 10$). Torpor bout duration ($\log_{10}$) decreased with increasing T_a during winter ($P = 0.02$, $t = -2.6$, ordinary least square (OLS)

Fig. 2 Skin temperature (T_{sk} , upper trace, dotted line) and ambient temperature data (T_a , lower trace, dashed line) for two different *M. tuberculata* individuals, monitored over 3 days in **a** a communal roost during summer and **b** a solitary roost during winter. Black and white bars denote night and day, respectively

Fig. 3 Torpor bout duration (hours) of *M. tuberculata* as a function of mean T_a during torpor bout in summer (black circles) and winter (white circles). Winter torpor bout duration ($\log_{10}$) decreased with increasing T_a (linear mixed effect model; $P = 0.02$, $t = -2.6$, $N = 3$ individuals, $n = 16$ torpor bouts), dashed line represents ordinary least square regression of winter only torpor bouts $r^2 = 0.23$. Summer and winter torpor bout duration ($\log_{10}$) decreased with increasing T_a (linear mixed effect model; $P < 0.001$, $t = -4.7$, $N = 4$, $n = 18$), solid line represents ordinary least square regression of summer and winter torpor bouts $r^2 = 0.49$. Note log scale used on y-axis

$r^2 = 0.23$; Fig. 3). When torpor bout duration ($\log_{10}$) and T_a from summer and winter were pooled and regressed together the r^2 value of this relationship was stronger ($P < 0.001$, $t = -4.7$, OLS $r^2 = 0.49$) compared to data from the winter-only.

Torpor bout duration did not differ between males and females ($P = 0.8$, $t = -0.2$, $df = 9.6$). During winter, females had lower minimum torpid T_{sk} 11.9 °C than

males $14.8\text{ }^{\circ}\text{C}$ ($P = 0.03$, $t = -2.3$, $df = 17$), but were not exposed to significantly colder T_a ($P = 0.7$, $t = 0.3$, $df = 32.7$). The HI during days when bats did not use torpor was negatively correlated with the mean T_a ($P < 0.01$, $t = -5.9$, $df = 13$, OLS $r^2 = 0.69$, slope = -0.44) and the previous night's mean T_a ($P < 0.01$, $t = -4$, $df = 13$, OLS $r^2 = 0.53$, slope = -0.54 , $n = 4$, $N = 18$). However, when removing the two winter days when bats did not enter torpor and analysing data for summer only, the relationship between mean T_a ($P = 0.01$, $t = -2.9$, $df = 12$, OLS $r^2 = 0.37$, slope = -0.37) remained significant but not the relationship between previous night's mean T_a ($P = 0.067$, $t = -2$, $df = 12$, OLS $r^2 = 0.23$, slope = -0.32 , $n = 3$, $N = 16$).

We found that E_{diff} was positively correlated with HI ($P < 0.01$, $t = 3.8$, $df = 13$, $n = 4$, $N = 18$, $r^2 = 0.45$), i.e. more heterothermic behaviour lead to greater energy savings. The r^2 of this relationship increased when we analysed just the summer data ($P < 0.01$, $t = 5.1$, $df = 13$, $n = 3$, $N = 16$, OLS $r^2 = 0.65$). We found that E_{diff} increased with decreasing mean T_a ($P = 0.02$, $t = -2.6$, $df = 13$, $n = 4$, $n = 18$, OLS $R^2 = 0.3$) and the r^2 of this relationship increased when we analysed summer only data ($P = 0.01$, $t = -3.0$, $df = 12$, $n = 3$, $n = 16$, OLS $r^2 = 0.39$).

The circular distribution of arousal times after torpor bouts was significantly non-random (Rayleigh $Z = 19.8$, $P < 0.001$, mean vector = 0.93 , $n = 5$, $N = 23$). Mean time of arousal was $18:13 \pm 1:31$ h and arousals began 8.2 ± 102.8 min ($n = 5$, $N = 23$) before sunset. During winter, mean T_a on nights when bats aroused from torpor was higher ($7.9 \pm 2.1\text{ }^{\circ}\text{C}$) than on nights when bats remained torpid ($6.7 \pm 1.7\text{ }^{\circ}\text{C}$, $P = 0.045$, $t = -2.1$, $df = 40$). None of the other weather variables we recorded differed between days bats remained torpid or aroused.

Discussion

We demonstrate that *M. tuberculata* exhibit seasonal roost choice, with a preference for communal roosts during summer and solitary roosts during winter. This agrees with our first hypothesis. We also found support for our second hypothesis, providing the first evidence that *M. tuberculata* is flexible in its seasonal energetic strategy, using prolonged torpor during winter and short bouts of torpor during summer and winter. In addition, torpor bout duration correlates negatively with mean T_a . We found mixed support for our final hypothesis, as we did not find that females performed longer torpor bouts than males, but we did observe that females had lower minimum torpid T_{sk} . Our data indicate that individuals are more energetically stressed during winter than summer and suggests that they use buffered roosts and torpor to cope with presumed energy shortages.

Roost choice changed seasonally with 83 % of nights spent in communal roosts during summer compared to 7 % during winter. The thermal characteristics we recorded indicate that communal roosts are more thermally stable than T_a and buffer against extreme cold. In other parts of New Zealand *M. tuberculata* prefer thermally buffered communal roosts with large cavities during summer (Sedgeley 2003, 2006). Large cavities may allow for more conspecifics and the potential for greater social thermoregulation (Willis et al. 2006; although see Dausmann and Glos 2014). Roosts that are buffered and large enough for social thermoregulation may be ideal for reproductive females to leave young of the year which may be more susceptible to drastic T_a fluctuations. However, disturbance by roost mates can be detrimental, and impromptu arousals by roost mates may lead to unwanted energy expenditure which may be especially dangerous when energy reserves are low (Speakman et al. 1991; Turner et al. 2015). The preference for solitary roosts during winter may be driven by energetically stressed individuals avoiding the potential costs associated with communal living.

The preference by bats for solitary roosts during winter may reflect a need for buffered microclimates. For all hibernating animals there is a “set-point” temperature (T_{set}) below which thermoregulation is initiated, metabolic rate increases and torpor bout duration decreases, and therefore, energy costs increase (Heller and Hammel 1972). In response to freezing T_a some hibernating individuals must perform costly emergency arousals (Humphries et al. 2003). To protect against temperatures below T_{set} many species use insulated nests/roosts (Casey 1981; Schmid 1998; Buck and Barnes 1999). It is likely that during winter, individuals must seek out roosts to facilitate and enhance energy savings from torpor, but buffered against T_a below T_{set} . Although we could not determine the T_{set} of *M. tuberculata*, we did record minimum torpid T_{sk} of $8.6\text{ }^{\circ}\text{C}$. We recommend future studies using open-flow respirometry to determine *M. tuberculata*'s T_{set} and behavioural tests to examine preferences in roost microclimate.

To balance the physiological costs of torpor with the energetic benefits, the torpor optimization hypothesis predicts that individuals with large energy stores should express less torpor than those with limited reserves. *Myotis tuberculata* seem to employ both short and multi-day torpor bouts during winter. During winter, bats used torpor more often, and these torpor bouts are deeper and more prolonged compared to summer. Similar to other insectivorous bats (Stawski and Geiser 2010; Park et al. 2000) torpor bout duration during winter correlated with T_a and individuals performed longer torpor bouts in response to colder T_a . Temperatures $<10\text{ }^{\circ}\text{C}$ are likely to constrain

insect abundance which reduces foraging success and makes torpor a less risky energetic strategy compared to foraging (Park et al. 2000; Hope and Jones 2012). Despite relatively cold T_a during winter in 2015, warmer mean night T_a between 9 and 10 °C were not uncommon, which may provide conditions for greater insect abundance, and therefore, the opportunity to forage successfully. During summer, individuals likely have larger fat stores compared to winter, and therefore, do not need to rely on torpor due to improved fuel availability and insulation.

If torpor is employed, energy savings increase with a fall of T_{sk} . We found no sex differences in torpor bout duration during winter. However, we did find that female minimum torpid T_{sk} was lower than males despite no significant differences in the mean or minimum T_a they experienced. This agrees with predictions of the torpor optimization hypothesis for species with sex specific life history differences. Jonasson and Willis (2011) showed that male bats use their energy stores more rapidly than females during hibernation and their body mass declined (by as much as 130 %) faster relative to that of females. Male *M. lucifugus*, unlike females, do not need to conserve fat to fuel post-emergence pregnancy (Jonasson and Willis 2011). Female *M. tuberculata* are likely under greater pressure to enter the reproductive season with larger fat reserves to initiate pregnancy. Conversely, males are likely under less pressure to conserve energy during winter, and spend more energy than females during torpor, and potentially decrease costs of torpor by maintaining higher minimum T_{sk} .

Weather conditions appear to influence the thermal strategies of normothermic individuals and our data lend further support to the torpor optimization hypothesis. We found that the HI for normothermic individuals correlated with mean T_a , indicating that individuals were more heterothermic during colder days. Moreover, HI positively correlated with daily E_{diff} . Individuals using a greater degree of heterothermy would save more energy compared to individuals maintaining a stable T_b . Though only an estimate, our model predicts that a 15 g individual in a 10 °C day-roost defending a T_b of 39.4 °C would spend 1.4 kJ while at 25.5 °C it would spend only 0.78 kJ. It would be useful for further studies in the laboratory to calculate metabolic rate under controlled conditions to better calculate the precise energy savings.

During winter, arousals from torpor were significantly non-random and occurred on significantly warmer nights. This suggests that individuals, while torpid, are able to use environmental cues from within their roost to assess ambient conditions. Greater horseshoe (*Rhinolophus ferrum-equinum*) and Natterer's bats (*Myotis nattereri*) maintained a circadian pattern to arousals and synchronized arousals with sunset, likely to take advantage of mild winter nights

and potential prey abundance (Hope and Jones 2012; Park et al. 2000). Aerial insect abundance can increase dramatically with mild T_a (Jones et al. 1995), providing opportunities to forage especially near dusk when flying insects are most abundant (Racey and Swift 1985). Our results suggest that during winter, individuals may track T_a passively and arouse in response to nights which provide lower thermoregulatory costs and higher probability of successful foraging.

Conclusions

We show that *M. tuberculata* has a highly flexible seasonal energetic strategy despite relatively low seasonal variation in T_a . During summer and winter, roosts are used that buffer against T_a fluctuations, and this is most important during winter. Our data suggest that, in the wild, *M. tuberculata* are facultative torpor users. While we cannot definitively state that *M. tuberculata* are hibernators, they clearly employ a continuum of heterothermic responses during summer and winter; from shallow heterothermy to multi-day torpor bouts. Longer torpor bouts were correlated with colder T_a and were interrupted by arousals at sunset during significantly warmer evenings presumably for individuals to take advantage of milder conditions. These data agree with the torpor optimization hypothesis and it appears that individuals attempt to balance the physiological costs associated with torpor induction and cessation against energy savings of metabolic suppression in torpor. Our data also indicate that small mammals in warm temperate climates respond to relatively small changes in seasonal T_a with a similar energetic strategy as more cold temperate species. It will be interesting to compare populations of *M. tuberculata* from the cold temperate South Island of New Zealand to determine roost preference and thermoregulatory response to more extreme seasonal changes in T_a , and the extent of the species' phenotypic plasticity and energetic flexibility.

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Author contribution statement ZJC, RMB and SP conceived and designed the study. ZJC conducted fieldwork, analysed the data, and wrote the manuscript; RMB, SP and AJRH provided editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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