Winter climate affects torpor patterns and roost choice in New Zealand lesser short-tailed bats

Z. J. Czenze¹ , R. M. Brigham², A. J. R. Hickey¹ & S. Parsons^{1,*}

¹ School of Biological Sciences, University of Auckland, Auckland, New Zealand

² Department of Biology, University of Regina, Regina, SK, Canada

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Correspondence

Zenon J. Czenze, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand. Tel: +64 022 185 1060

Email: czenze@hotmail.com

*Current address: School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane, QLD, Australia

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Abstract

Variation in winter conditions differentially impacts thermoregulation of endotherms, with some species using torpor as an energy-saving strategy during periods of negative energy balance. We evaluated how differences in energy balance due to winter ambient temperatures (T_a), would lead to differing torpor expression and roost choice between populations. Here, we monitored T_a and skin temperatures (T_{sk}) of New Zealand lesser short-tailed bats (*Mystacina tuberculata*) using temperature telemetry from an inland population from Pureora, North Island and another from Hauturu/Little Barrier Island (Hauturu), an offshore island. Relative to Pureora, all recorded T_a variables were higher in Hauturu. Hauturu bats used short torpor (<24 h) more frequently (51% of observational days) than their Pureora conspecifics (33%). Furthermore, minimum T_{sk} of Hauturu bats correlated positively with mean T_a and Hauturu bats were more likely to arouse on nights with warmer sunset T_a . No correlation was found for Pureora bats. Torpor bout duration did not differ between sites. On Hauturu, bats preferred thermally unstable roosts and preferentially roosted inside dead punga/silver fern-trees (*Cyathea dealbata*). As punga thermal characteristics did not differ from T_a , Hauturu bats may take advantage of warm T_a to reduce rewarming costs. We did not observe differences in any thermoregulatory variables between sexes in Hauturu. Differences in winter T_a may differentially impact populations across a latitudinal gradient. Although bat populations in warmer climates are under less thermoregulatory stress, site and climate specific adaptations appear to be employed that affect roost choice and torpor patterns.

Introduction

Metabolic energy is a principal currency for all living things, and balancing food intake versus metabolic output is critical for survival. An individual's energy balance is affected by biotic and abiotic factors such as photoperiod, food/water availability, and ambient temperature (T_a) (Song & Geiser, 1997; Körtner & Geiser, 2000; McNab, 2002; Doucette *et al.*, 2012).

Subtle changes in T_a can dramatically impact endotherms' (i.e. many mammals and birds) energetic balance (Boyles *et al.*, 2007). Small mammals, with high surface to volume ratios, rapidly lose heat to the environment and many clades of small temperate, subtropical and tropical mammals decrease energy expenditure through torpor (Wang, 1989; Geiser, 2004; Grigg, Beard & Augee, 2004; Ruf & Geiser, 2015). Torpor is a physiological state characterized by controlled depression in metabolic rate which leads to a lower T_b that in turn further reduces metabolism (Geiser, 2004).

Ambient temperature influences thermoregulatory behaviour and hibernation traits among populations of hibernators

(Dunbar & Brigham, 2010; Zervanos *et al.*, 2010; Stawski & Geiser, 2011). Although temperate hibernators tend to use deep torpor to deal with prolonged low T_a and minimize energy use (e.g., Barnes, 1989), subtropical winters can be less thermally challenging and subtropical species may use shorter or shallower torpor bouts (Geiser & Stawski, 2011). Indeed, tropical populations of the eastern long eared bat, *Nyctophilus bifax*, exposed to warmer T_a , exhibit shorter torpor bouts, and defend higher skin temperatures (T_{sk}) than subtropical individuals (Stawski, 2012). Although torpor patterns of temperate species are relatively well-known, fewer studies have examined the use of winter torpor by subtropical species and species that inhabit both temperate and subtropical climates (e.g., Stawski, Turbill & Geiser, 2009; Stawski, 2012; Levin *et al.*, 2015).

Regardless of climate, species employing torpor appear to choose specific microclimates (i.e., roost, nest or burrow), and regularly arouse to a stable T_b (i.e. normothermia). Although arousals are brief, they form the most energetically expensive phase of the torpor/arousal cycle, and increased T_a significantly reduces energetic costs of arousals (Wang, 1989; Thomas,

Dorais & Bergeron, 1990; Geiser, 2004; Currie, Noy & Geiser, 2015). Temperate species appear to preferentially choose microclimates that buffer them from large fluctuations in T_a (Schmid, 1998; Buck & Barnes, 1999; Sedgeley, 2001). Although thermally buffered microclimates may protect from extreme low T_a , they insulate individuals from beneficial increases of T_a . Tropical species, which are less likely to experience dangerously low T_a , appear to occupy shelters that are less insulated, and harness the thermoregulatory benefits of increased T_a (Turbill, 2006; Bondarenko, Körtner & Geiser, 2016).

The timing, duration and frequency of arousals is critically important to an individual's energy budget, and a balance between the energetic savings from torpor, and costs of arousals must be met (Humphries, Thomas & Kramer, 2003; Jonasson & Willis, 2011). In addition, species with differential timing of reproductive investment exhibit differences in sex-specific winter energy budgets (Michener, 1992; Humphries *et al.*, 2003; Jonasson & Willis, 2011).

The New Zealand lesser short-tailed bat (*Mystacina tuberculata*) is the only extant species of family *Mystacinidae*, and is endemic to New Zealand. *Mystacina tuberculata* range from the top of New Zealand's North Island to the bottom of the South Island, as well as being found on several offshore islands, including Hauturu/Little Barrier Island (Hauturu). *Mystacina tuberculata* provide a good model to examine the variation of energetic strategies in small mammals, as their range includes both subtropical and temperate habitats with more subtle seasonal variation in climate than faced by most temperate mammals. *Mystacina tuberculata* roost in tree cavities that vary in thermal stability (Sedgeley, 2006). Winter activity, presumably for foraging, is positively correlated with T_a and likely reflects periods with increased prey availability (Daniel, 1979; Christie, 2003, 2006; Christie & Simpson, 2006). Males sing during summer, females give birth the following spring (Toth, 2016), and some populations of *M. tuberculata* exhibit sex differences in seasonal thermoregulatory behaviour (Czenze *et al.*, 2017). Although thermoregulatory behaviour varies between seasons in the central North Island, no work has evaluated population differences during winter in subtropical and temperate populations.

We used temperature-sensitive radio transmitters to assess differences in winter thermoregulatory patterns between free-ranging *M. tuberculata* from an inland and offshore island population. Our first hypothesis was that differences in energy balance, due to winter T_a , would lead to varying torpor expression and roost choice between populations. Specifically, we predicted that higher T_a in Hauturu would cause individuals to use torpor less frequently and bouts would either be shorter or shallower. Second, we predicted that, similar to other subtropical bats, individuals from Hauturu would prefer roosts with thermally unstable microclimates to reduce costs of arousals, and would be more responsive to T_a to take advantage of warmer evenings for foraging. Finally, we examined the hypothesis that the timing of reproductive investment would lead to intersexual differences in winter T_{sk} patterns. Specifically, we predicted females, whose reproductive investment occurs after winter, would use deeper or longer torpor bouts than males.

Materials and methods

All procedures were approved by the University of Auckland Animal Ethics Committee (AEC-R1374) and were conducted under permit 39083-FAU issued by the New Zealand Department of Conservation. Our offshore island site is located was Hauturu/Little Barrier Island (Hauturu) (36°19' S, 175°07' E), an island 80 km off the East Coast of the North Island, New Zealand during the 2016 Austral 'winter' (May–July). Our inland site was located in the Pikiariki Ecological Area of Pureora Forest Park (Pureora) (38°26' S, 175°39' E), central North Island, New Zealand; we used data on T_{sk} and T_a collected during May–July 2015 by Czenze *et al.* (2017).

At both sites bats occupied mainly solitary roosts (housing only one individual) and occasionally communal roosts (housing more than one individual at a time). Roosts were classified by recording the number of individuals who emerged for 1 h after dusk.

We caught bats in harp traps. Individuals were weighed to the nearest 0.5 g using a Pesola spring scale (Pesola AG, Schindellegi, Switzerland), and sex was determined. Forearm length was measured to the nearest 1 mm.

For small bats, T_{sk} provides a reasonable approximation of core temperature and is a reliable index for the study of torpor in field conditions (Audet & Thomas, 1996; Barclay *et al.*, 1996; Willis & Brigham, 2003). We clipped a small (<1 cm²) patch of fur between the shoulders and attached a temperature-sensitive radio-transmitter (0.9–1 g, BD-2NT; Holohil Systems Ltd, Carp, Ontario, Canada) using a latex cement (TORBOT Group, Inc., Cranston, Rhode Island, USA). On average, the body mass of bats fitted with transmitters was 12.6 g ± 1.5 g and thus transmitters represented between 6.0 and 8.6% of body mass. Individual bats were tracked to day roosts each morning using a scanning receiver (Australis 26K Scanning Receiver, Titley Electronics, Ballina, New South Wales, Australia) connected to a 3-element Yagi antenna. A data-logging receiver (Lotek SRX_400, SRX_600, or SRX_800; Lotek Engineering Inc. Newmarket, Ontario, Canada) was deployed at roosts and recorded individual T_{sk} at 10-min intervals whenever a tagged bat was present. Unsafe terrain prevented travel to one specific roost, however, we were still able to record T_{sk} for the individual who inhabited it. In Hauturu, we recorded roost temperature (T_{roost}) of a pohutukawa (*Metrosideros excelsa*) from a functional transmitter that an individual bat had shed inside the tree. After inspection, we determined the transmitter had been shed inside the tree approximately 1.5 m above cavity entrance.

Thermoregulatory phases were readily identifiable from visual inspection of T_{sk} traces. Although we did not use specific T_b cut-offs (i.e. 30°C) to identify thermoregulatory stages, we did use objective guidelines derived from Jonasson & Willis (2011) and previously used for *M. tuberculata* (Czenze *et al.*, 2017): (1) warming: an abrupt increase in torpid T_{sk} (three consecutive recordings) that eventually stabilized at a 'normothermic' level; (2) normothermic: the time between the end of the warming phase and the initiation of cooling; (3) cooling: readily obvious as a decline in T_{sk} (three consecutive

Table 1 Ambient thermal characteristics in Pureora Forest compared to Hauturu/Little Barrier Island during winter 2015 and 2016, respectively

	Mean max T_a	Mean min T_a	Mean day T_a	Mean night T_a	Mean range T_a	Max T_a	Min T_a	Max range T_a
Pureora	9.3 $\pm$ 2.6	4.4 $\pm$ 2.8	7.6 $\pm$ 2.5	6.2 $\pm$ 2.7	4.9 $\pm$ 2.1	10.1	-1.2	10.1
Hauturu	15.4 $\pm$ 1.8	11.6 $\pm$ 2.3	14 $\pm$ 2	12.1 $\pm$ 2.4	6.9 $\pm$ 4.1	18.2	6.8	6.4

Winter T_a was higher in Hauturu than Pureora. Mean max T_a and Mean min T_a are the mean of all respective daily maxima and minima T_a ; Mean Day T_a and Mean night T_a are the mean of all respective mean T_a from sunrise-sunset and sunset-sunrise; Mean range T_a is the mean of all daily ranges in T_a (max. T_a -min. T_a); Max T_a and Min T_a are the respective absolute maxima and minima T_a ; Max range T_a is the largest recorded daily range in T_a . Values are in ($^{\circ}$ C), means $\pm$ sd $N = 64$ (days).

recordings) preceding steady-state torpor; And (4) torpid: T_{sk} (three consecutive recordings) following the cooling phase and preceding the warming phase. We excluded data from the first 24 h after releasing tagged bats to avoid the influence of disturbance to individuals on our results.

In Hauturu, we recorded T_a , barometric pressure (P_{bar}), and T_{roost} of a punga/silver fern-tree (punga; *Cyathea dealbata*), previously inhabited by a solitary individual, using data loggers (HOBO Micro Station Data Logger - H21-002, Onset Computer Corporation, Bourne, Massachusetts, USA). Ambient temperature was recorded in the shade, 2 m above the ground, and the logger inside the punga was placed 1 m inside the entrance.

We performed logistic regression using a generalized linear mixed effect model (GLME; packages 'nlme' version 3.1-127, 'lme4' version 1.1-10 and 'MuMIn' version 1.15.6 in R version 3.1.0; R Development Core Team 2009) to analyse data with a dichotomous response variable while controlling for pseudoreplication associated with multiple recordings from individuals. We used a GLME to examine differences in the proportion of torpor bouts which were or were not >24 h with site and sex as explanatory variables, and individual as a random effect. We also used a GLME to determine whether individuals would or would not arouse from torpor in response to weather variables that have been associated with bat activity in past studies: T_a and change in P_{bar} , which reflects passing weather fronts and is correlated with both insect and bat activity (Jones, Duvergé & Ransome, 1995), and individual as a random effect. Finally, we used a GLME to determine if T_a and change in P_{bar} predicted roost type (i.e. tree cavity or punga) used by bats, with individual as a random effect.

We used linear regression using linear mixed effect models (LME; packages 'nlme' version 3.1-127, 'lme4' version 1.1-10 and 'MuMIn' version 1.15.6 in R version 3.1.0; R Development Core Team 2009) to analyse data with a continuous response variable while controlling for pseudoreplication. We conducted model selection by comparing models, starting with a saturated model including the interaction of all explanatory variables (sex, T_a , and site), using maximum likelihood tests until only significant variables remained. We used LMEs with torpor bout duration or minimum T_{sk} as response variables, sex, T_a , and site as explanatory variables, and individual as a random effect. In all linear mixed models, P represents the significance of the full model and R^2 represents the total proportion of variance described by explanatory variables and random effects (*sensu* Nakagawa & Schielzeth, 2013).

All analyses were conducted in R version 3.1.0 (R Development Core Team 2009) and values are reported as

means $\pm$ 1 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

All T_a variables we recorded, except daily T_a range, were higher in Hauturu compared to Pureora (Table 1).

In total, we attached transmitters to 11 individuals (Pureora=3 males, 2 female; Hauturu = four males, two females) and recorded 104 bats-days of T_{sk} data from nine individuals (five males, four females; we did not record data from 1 Pureora and 1 Hauturu individual, both males).

We recorded short (<24 h) and multiday torpor bouts in Hauturu and Pureora. Bats in Hauturu used torpor on 98% of observation days (60/61), and on 95% of observation days (41/43) in Pureora. Bats used short torpor more often in Hauturu [51% (31/61 days)] compared to Pureora [33% (14/43 days); $Z = 2.1$, $n = 9$, $N = 59$, $P = 0.04$]. In Hauturu, torpor bout duration ranged from 6.2 to 128.4 h. Mean short torpor bout duration was 9.1 ± 3.4 h ($n = 5$, $N = 28$), and mean multiday torpor bout duration was 68.1 ± 30.2 h ($n = 4$, $N = 9$; Fig. 1),

Figure 1 Representative traces for skin temperature (T_{sk} , upper trace, dotted line) and ambient temperature (T_a , lower trace, dashed line) for two individual *M. tuberculata* in Hauturu/Little Barrier Island.

Table 2 Significant predictors (site, mean ambient temperature (T_a), and the interaction between the two) from a linear mixed effect model of minimum skin temperature (T_{sk}) of torpid lesser short-tailed bats (*Mystacina tuberculata*) from Pureora and Hauturu/Little Barrier Island, New Zealand

Predictor variable	Regression coefficient	d.f.	T value	P value
(Intercept)	-6.43 ± 2.85	48	-2.26	0.03
Site (Pureora)	16.87 ± 3.99	7	4.23	<0.01
Mean T_a	1.23 ± 0.188	48	6.55	<0.01
Site (Pureora): mean T_a	-1.0 ± 0.36	48	-2.76	<0.01

Decreasing T_a during winter was associated with decreased minimum T_{sk} in Hauturu but not in Pureora. Regression coefficient is $\pm$ SE; d.f. represents degrees of freedom; n (individuals) = 9; N (observations) = 59.

which was not different than multiday torpor bout duration in Pureora [60.7 ± 27.5 h ($n = 4$, $N = 10$); $T = -0.6$, d.f. = 5, $P = 0.6$]. Further, when we combined short and multiday torpor bouts we found no difference in torpor bout duration between Hauturu (22 ± 28.9 h) and Pureora (34.2 ± 32.9 ; $T = 1.5$, d.f. = 5, $P = 0.17$).

In Hauturu, the lowest T_{sk} of torpid bats we recorded was 4.7°C compared to 8.6°C in Pureora. Mean minimum T_{sk} of torpid bats was not affected by sex. However, mean minimum T_{sk} of torpid bats was related to the interaction between site and mean T_a (Table 2; Fig. 2), so we analysed sites separately. In Hauturu, minimum T_{sk} of torpid bats ($T = 7.1$, d.f. = 32, $P < 0.01$, $R^2 = 0.71$, $n = 5$, $N = 38$) was positively correlated with corresponding T_a , but this was not true in Pureora ($T = 1.0$, d.f. = 16, $P = 0.3$, $R^2 = 0.02$, $n = 4$, $N = 21$; Fig. 2). Mean minimum T_{sk} of torpid bats was lower in Hauturu ($11.1 \pm 3.0^\circ\text{C}$) compared to Pureora ($12.3 \pm 2.4^\circ\text{C}$).

In Hauturu, sunset T_a best predicted whether or not an individual would arouse from torpor ($Z = 3.5$, $n = 5$, $N = 61$, $P < 0.01$) but not in Pureora ($Z = 1.6$, $n = 4$, $N = 43$, $P = 0.12$).

In Hauturu, multiday torpor bout duration increased with decreasing mean T_a ($T = -4.2$, d.f. = 7, $P < 0.01$, $R^2 = 0.76$; Fig. 3). However, short torpor bout duration was not correlated with mean T_a ($T = 1.9$, d.f. = 26, $P = 0.08$, $R^2 = 0.27$).

Bats in Pureora roosted exclusively in tree cavities, but Hauturu bats roosted in tree cavities on 20% of days (11/56), non-tree roosts, such as sloughed nīkau palm (*Rhopalostylis sapida*) fronds, on 7% of days (4/56), and hollow punga on 73% of days (41/56). In Hauturu, none of the temperature variables we recorded, except T_{range} , differed between the punga roost and T_a . Only max T_{roost} and T_{range} differed between data collected from pohutakawa (tree roost) and punga (non-tree roost) (Table 3).

In Hauturu, torpor bout duration was not different between tree and non-tree roosts ($T = 1.4$, d.f. = 32, $P = 0.2$). However, minimum T_{sk} was lower in non-tree roosts ($T = 4.0$, d.f. = 50, $P < 0.01$) than tree roosts.

In Hauturu, multiday torpor bout duration ($T = 3.3$, d.f. = 2, $P = 0.08$), and minimum T_{sk} of torpid bats did not differ between the sexes ($T = 0.6$, d.f. = 3, $P = 0.6$), and females did not use multiday torpor bouts more than males ($Z = -1.7$, $n = 5$, $N = 39$, $P = 0.09$).

Figure 2 Minimum skin temperature (T_{sk}) for days bats used torpor as a function of T_a for individuals from Hauturu/Little Barrier Island (white circles) and Pureora (black circles). Minimum T_{sk} decreased with decreasing T_a for days bats used torpor in Hauturu (white circles; $T = 7.1$, d.f. = 32, $P < 0.01$, $R^2 = 0.71$, $n = 5$, $N = 38$) but not Pureora (black circles; $T = 1.0$, d.f. = 16, $P = 0.3$, $R^2 = 0.02$, $n = 4$, $N = 21$). Solid line represents the regression of Hauturu/Little Barrier Island individuals, and dashed line represents regression of Pureora individuals.

Discussion

Although the sites are only 232 km away from each other, mean winter T_a in Hauturu was 6.2°C higher than in Pureora, and *M. tuberculata* differed in expression of torpor between sites. We found mixed support for our first prediction that expression of torpor should vary between sites. We did not record differences in frequency of torpor, or torpor bout duration between sites. However, Pureora bats were more likely to use multiday torpor bouts than Hauturu bats. In accord with our second prediction relating to roost choice, Hauturu bats preferentially chose roosts that did not differ from ambient conditions. Unlike Pureora bats, we found that the minimum T_{sk} positively correlated with corresponding T_a for Hauturu bats. Furthermore, multiday torpor bout duration was negatively correlated with mean T_a for Hauturu bats. Sunset T_a was the best predictor of arousal for Hauturu bats, but not for Pureora bats. In Hauturu, we found no evidence of sex differences in any thermoregulatory behaviour. Although bats did

Figure 3 Multiday torpor bout duration (h) as a function of T_a for individuals from Hauturu/Little Barrier Island. Torpor bout duration decreased with increased T_a ($T = -4.2$, d.f. = 7, $P < 0.01$, $n = 4$, $N = 12$, $R^2 = 0.76$) dashed line represents regression of days bats remained torpid.

Table 3 Ambient versus non-tree roost ($N = 40$ days) and tree versus non-tree ($N = 8$) roost thermal characteristics in Hauturu/Little Barrier Island

	Mean T_a	Max T_a	Min T_a	Range T_a
Ambient	13.2 $\pm$ 1.9	15.1 $\pm$ 1.7	11.3 $\pm$ 2.1	3.7 $\pm$ 1.2
Non-tree	13.2 $\pm$ 2.4	14.8 $\pm$ 2.4	11.6 $\pm$ 2.5	3.1 $\pm$ 1.1
T -value	0.1	-0.6	0.7	-2.3
d.f.	74	70.0	76.4	77
P -value	0.9	0.5	0.5	0.03 ^a
Tree	8.3 $\pm$ 2.1	9.3 $\pm$ 2.2	7.4 $\pm$ 2.0	1.9 $\pm$ 1.0
Non-tree	10.9 $\pm$ 3.0	12.7 $\pm$ 2.7	9.4 $\pm$ 3.1	3.4 $\pm$ 0.8
T -value	0.06	2.7	1.4	3.4
d.f.	12.3	13.1	11.7	13.3
P -value	0.2	0.02 ^a	0.2	<0.01 ^a

Punga roosts did not differ from ambient temperatures (T_a). Mean T_a is the average of all mean 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 in ($^{\circ}$ C), means $\pm$ sd.

^aRepresent significant differences based on Student's T test.

not use torpor (short and multi-day combined) more in Pureora than Hauturu, Hauturu bats used multiday torpor less frequently, suggesting that Hauturu bats have less need to suppress metabolism to cope with elevated thermally induced energetic demands.

Hauturu bats were exposed to a mean winter T_a nearly double that of their Pureora counterparts. Although we did not observe any differences in torpor variables, we did find that Hauturu bats used short torpor more often than Pureora bats. Prolonged torpor is associated more with physiological costs like dehydration stress and accumulation of metabolic wastes (Thomas & Cloutier, 1992; Thomas & Geiser, 1997; Németh *et al.*, 2010; Ben-Hamo *et al.*, 2013). Shorter torpor bouts are associated with warmer/unpredictable climates (Lovegrove, 2000), and individuals can save energy during rest phases and take advantage of milder conditions during active phases. During winter, Hauturu bats may prefer short torpor due to higher T_a , and therefore lower energy constraints, compared to Pureora bats, which are exposed to predictably lower T_a and face greater pressure to employ prolonged torpor bouts and risk the accumulation of physiological costs. Alternatively, or in addition to, higher night T_a in Hauturu may provide conditions for increased prey availability, foraging success, and therefore decreased demands for multiday torpor.

Minimum T_{sk} correlated positively with T_a in Hauturu but not in Pureora. Energy savings are negatively correlated with T_{sk} until a minimum 'set-point' temperature (T_{set}) below which thermoregulation is initiated, metabolic rate increases, torpor bout duration decreases, and energetic costs increase (Heller & Hammel, 1972). In free ranging Australian Gould's wattled bat (*Chalinolobus gouldii*), minimum T_{sk} was positively correlated with T_a (Stawski & Currie, 2016). Ambient temperature may be a signal of food availability for insectivorous species as aerial insect abundance increases with T_a , especially when T_a exceeds 10° C (Jones *et al.*, 1995). In some climates, increased thermoregulatory costs, in concert with decreased prey availability, make torpor a better strategy compared to foraging

(Park, Jones & Ransome, 2000; Hope & Jones, 2012). In Pureora, mean night $T_a > 10^{\circ}$ C occurred on only 7% of observation nights (3/43) compared to 92% of observation nights (56/61) in Hauturu. Below a threshold T_a , insects likely become predictably absent and, therefore, foraging success decreases. Although the notion of temperature mediated effects on prey availability and bat behaviour is speculation, bats captured at Hauturu regularly defecated during handling, suggesting they were foraging and well fed.

In Hauturu, like in Pureora, bats employ short and multiday torpor bouts during winter (Czenze *et al.*, 2017). Similar to other insectivorous bats (Park *et al.*, 2000; Stawski & Geiser, 2010), torpor bout duration during winter is negatively correlated with T_a . Further, in Hauturu, but not in Pureora, arousals from torpor occurred on evenings with significantly warmer sunset T_a . Thermoregulatory behaviour is influenced by food availability (see Vuarin & Henry, 2014 for a review), and torpid individuals use environmental cues to assess ambient conditions and food availability (Wojciechowski, Jefimow & Tęgowska, 2007). Sunset T_a may provide cues regarding foraging opportunities as insect prey is likely more abundant soon after dusk (Racey & Swift, 1985; Rydell, Entwistle & Racey, 1996). Indeed, Natterer's (*Myotis nattereri*) and Greater horseshoe bats (*Rhinolophus ferrumequinum*) synchronize arousals with sunset to take advantage of warm T_a and increased prey availability (Park *et al.*, 2000; Hope & Jones, 2012). We observed that bats track T_a passively and arouse in response to nights that likely provide lower thermoregulatory costs and higher probability of successful foraging. We are unable to say what an individual did during the time we lost its signal after an arousal, however, the presence of faeces suggests individuals were foraging. Therefore, it seems likely that individuals may be arousing on warmer nights, to take advantage of presumably higher prey availability.

In Hauturu, individuals preferentially chose thermally unstable roosts. In Pureora, bats use roosts buffered against sub-zero T_a (Czenze *et al.*, 2017). Roosting difference is likely a preference by Hauturu bats for dead hollowed punga trunks and, despite their availability, punga roosts were never used by Pureora bats. Hauturu punga roosts were cylindrical 'chimney' structures with an exposed top. Punga T_{roost} variables did not differ from T_a , except for mean daily T_{range} which was 0.5° C lower. Furthermore, the tree cavity roost we recorded had higher mean T_{roost} , maximum T_{roost} , and T_{range} relative to punga. Roost choice facilitates thermoregulatory behaviour and, to defend against temperatures below T_{set} , many species prefer insulated nests/roosts (Casey, 1981; Schmid, 1998; Buck & Barnes, 1999; Humphries *et al.*, 2003). Although thermally stable roosts prolong torpor, thermally variable roosts may enhance arousals via passive rewarming and reduce costs during the most demanding phase of torpor (Chrushcz & Barclay, 2002; Stawski *et al.*, 2009; Rintoul & Brigham, 2014; Currie *et al.*, 2015). In a comparison of three sympatric bats, brown long-eared bats (*Plecotus auritus*), a heterothermic species, prefer roosts with low thermal stability and low mean minimum T_{roost} , whereas the other species use more thermally stable roosts (Otto, Becker & Encarnacao, 2016). During winter, Pureora individuals seek warm, thermally stable roosts to avoid dangerously low T_a (Czenze *et al.*, 2017). Hauturu

bats, which experience less extreme T_a , can choose more thermally variable roosts and harness the benefits of faster cooling rates or reduced arousal costs.

In cold climates, energetically constrained individuals may be thriftier with fat reserves (Jonasson & Willis, 2011). During winter, in colder parts of their range, female *M. tuberculata* have lower minimum T_{sk} than males, presumably to conserve fat to fuel post-emergence pregnancy (Czenze *et al.*, 2017). In contrast, bats from warmer climates forage more regularly during winter, and sex differences in thermoregulatory behaviour are not apparent (Hope & Jones, 2012; Park *et al.*, 2000; In Hauturu, we did not detect differences between the sexes in any of the thermoregulatory variables, yet we did at Pureora. The mean winter night T_a in Hauturu was 12.1°C, almost double that of the Pureora, likely increasing the probability of successful foraging. If Hauturu females can augment their fat reserves via winter foraging, they would be under less pressure to save energy.

Conclusions

Mystacina tuberculata has a varied strategy for conserving energy at different latitudes during winter. Although many of the thermoregulatory variables did not differ between sites, bats from Hauturu appear to be more influenced by ambient conditions than Pureora bats. This is most evident in their minimum T_{sk} , and arousal times, all of which are influenced by T_a . Population differences in roost choice are apparent. Individuals from Hauturu chose thermally unstable roosts and we show the first evidence that *M. tuberculata* prefer punga roosts in their more northern offshore island range. Finally, in this warmer location, the less severe demands on energy removes sexual differences in torpor behaviour observed at other sites. Our data provide further evidence that differences in seasonal T_a at sites separated by latitude impact the energetic strategies within populations of small mammalian species.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Author contributions

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.

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