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Thermal biology and roost selection of free-ranging male little forest bats, *Vespadelus vulturnus*, during winter

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Insectivorous bats are particularly susceptible to heat loss due to their relatively large surface area to volume ratio. Therefore, to maintain a high normothermic body temperature, bats require large amounts of energy for thermoregulation. This can be energetically challenging for small bats during cold periods as heat loss is augmented and insect prey is reduced. To conserve energy many bats enter a state of torpor characterized by a controlled reduction of metabolism and body temperature in combination with selecting roosts based upon thermal properties. Our study aimed to quantify torpor patterns and roost preferences of free-ranging little forest bats (*Vespadelus vulturnus*) during winter to identify physiological and behavioral mechanisms used by this species for survival of the cold season. All bats captured were male (body mass 4.9 ± 0.7 g, n = 6) and used torpor on every day monitored, with bouts lasting up to 187.58 h (mean = 35.5 ± 36.7 h, n = 6, total number of samples [N] = 61). Torpor bout duration was significantly correlated with daily minimum and maximum ambient temperature, mean skin temperature, insect mass, and body mass of individuals and the multiday torpor bouts recorded in the cold qualify as hibernation. The lowest skin temperature recorded was 5.2°C, which corresponded to the lowest ambient temperature measurement of −5.8°C. Most bats chose tall, large, live *Eucalyptus* trees for roosting and to leave their roost for foraging on warmer days. Many individuals often switched roosts (every 3–5 days) and movements increased as spring approached (every 1–2 days). Our data suggest that *V. vulturnus* are capable of using the environmental temperature to gauge potential foraging opportunities and as a cue to reenter torpor when conditions are unsuitable. Importantly, frequent use of torpor and appropriate roost selection form key roles in the winter survival of these tiny bats.

Key words: body temperature, conservation, endotherm, heterothermy, roost selection, torpor

Mammals and birds are endothermic and can adjust their high metabolic rate (MR) for physiological and/or behavioral thermoregulation (Withers et al. 2016), allowing them to inhabit a wide array of climates by using many unique combinations of physiological and behavioral traits. Since temperatures can vary drastically across seasons, a species' physiology and behavior can vary substantially, especially regarding fat and water storage, foraging, migration schedules, reproduction, and thermal biology (Nieminen et al. 2013; Stawski et al. 2014). Many endothermic animals deal with unfavorable environmental fluctuations by employing torpor, a controlled reduction in MR and body temperature (T_b) to well below normothermic levels (Ruf and Geiser 2015; Levesque et al. 2016). Prolonged multiday bouts of torpor during winter, in contrast to daily torpor with minimum T_bs around 18°C and lasting <24 h, are often referred to as hibernation, with T_b of some hibernators even reaching 0°C or less when ambient temperature (T_a) is low (Geiser 2021). Due to high rates of heat loss, small insectivorous bats often use torpor as a crucial survival mechanism for dealing with food shortages and cold periods (Stawski et al. 2014).

Insectivorous bats can find winter particularly challenging as food resources are often reduced (Paclík and Weidinger 2007; Stawski et al. 2014). Their prey, ectothermic invertebrates, have an array of mechanisms to deal with winter, such as migration (Zhan et al. 2014; Wu et al. 2015) and reduced activity and dormancy during the cold season (Cáceres 1997; Walther and Gosler 2001; Schröder 2013), decreasing their availability to bats. Many insectivorous bats cope with the reduction in prey and T_a by hibernating throughout much of the winter, especially

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those from temperate regions, but even subtropical bats or bats in hot caves are known to hibernate (Stawski et al. 2009; Levin et al. 2015). Some bats are also known to employ torpor when conditions are favorable, and they are in good body condition, possibly to avoid predation and/or to conserve fat reserves for more lenient times (Stawski and Geiser 2010).

Nevertheless, torpor is a crucial adaptation, especially for small bats facing climatic constraints on feeding activities (Soriano et al. 2002; Stawski et. 2014). Saving energy and fat stores during winter may be particularly important for male bats, as some species undergo spermatogenesis and mate with females in autumn and continue to do so throughout winter (Tidemann 1993; Dietz and Kalko 2006). While torpor is efficient in conserving energy, it does have potential negative physiological effects (Luis and Hudson 2006; Vuarin et al. 2015), and to minimize these an adequate balance between torpor duration, activity, and foraging is required to ensure survival. As insect activity increases with the T_a, assessing the T_a allows bats to sense an opportunity to forage when food may be more abundant (Turbill 2008; Johnson et al. 2012). Shifting between deep torpor and activity has been found in some bat species from different climates (Dietz and Kalko 2006; Johnson et al. 2012).

To further reduce energy loss some bats also employ behavioral strategies (often in conjunction with torpor), such as huddling (Boratynski et al. 2015) and/or altering roost preferences (Willis and Brigham 2005; Turbill 2006a; Czenze et al. 2017). Behavioral selection of a particular roost type can offset thermoregulatory energetic costs (Turbill et al. 2008, 2020). For example, tree hollows in large trees are buffered from the T_a, whereas caves are largely independent of daily external T_a variations, which may aid in saving energy by permitting long torpor bouts due to a stable microclimate (Soriano et al. 2002; Coombs et al. 2010). Roosting in trees can also be energetically beneficial as they are subject to solar radiation, which can enable passive rewarming and reduce the costs of arousals from torpor (Halsall et al. 2012; Stawski and Currie 2016). Appropriate selection of roosts affects rates of survival, reproduction (Kerth et al. 2001), and risk of predation (Willis and Brigham 2005; Clement and Castleberry 2012). For bats in particular, it appears that females often form large maternity colonies that likely aid in preventing heat loss during critical reproductive periods, whereas males are often found to roost solitarily (Turbill et al. 2020)—behaviors that have implications for thermal biology.

Despite the ecological importance of understanding how bats alter their behavior and physiology to survive low T_a, food abundance, and habitat loss, data on small (<6 g) free-ranging tree-roosting species from cool-temperate regions are not available. Previous studies often have focused on females and the importance of thermal biology in relation to reproduction, while few studies have investigated males (Stawski et al. 2014). This is particularly so for the little forest bat (*Vespadelus vulturnus*), one of Australia's smallest bats weighing ~6 g or less (Churchill 2008). A laboratory study on *V. vulturnus* reported a maximum torpor bout duration (TBD) of 16.7 h (Willis et al. 2005), substantially less than for other bats living in similar areas, and it is also known that torpor expression in captive mammals and birds is typically less pronounced than in free-ranging individuals (Geiser et al. 2000).

Therefore, our study aimed to quantify roost preferences, thermal biology, and insect availability to gain a better understanding of how free-ranging male *V. vulturnus* cope with winter in a small nature reserve surrounded by agricultural areas in comparison to other animals inhabiting the same location (Vuarin et al. 2015). Agricultural landscapes can be subject to reduced foraging patches (Park 2015; Put et al. 2019) that can lead to detrimental energetic constraints. To cope with these challenging conditions and to minimize possible energy loss from mating during autumn and throughout winter, we hypothesized that (1) low T_as will prolong TBD of *V. vulturnus* as in other mammals, and (2) bats will favor warmer roosts and change roosts when T_a increases to permit foraging.

Materials and Methods

Study area and ambient conditions.—Bats were captured and studied during July to August 2017 at Imbota Nature Reserve (30°34′39.1″S, 151°42′45.6″E), Australia. Elevations of the remnant woodlands range from 980 to 1,050 m above sea level. The reserve consists of approximately 218 hectares of native vegetation, containing 179 plant species (55 families and 132 genera; Hunter 2007). The climate of Imbota is likely to be similar to that of the nearby city (~6 km), Armidale, which has a highly variable rainfall of 549.8–1,060.4 mm (annual data from 1997 to 2016) with temperatures ranging from −6.0 to 26.8°C (winter data only from 1997 to 2016; AG BOM 2017).

Two temperature loggers (±0.5°C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, California), protected from direct sunlight in an upside-down styrofoam cup, were placed on tree branches 2–3 m above the ground at two separate sites where *V. vulturnus* were captured, to record T_a at 10-min intervals.

Trapping and radio-tracking.—Bats were captured using harp traps and mist nets over 66 nights. Once bats were captured they were transported ~14 km in a cloth bag to the University of New England (UNE) for processing. Temperature-sensitive radio transmitters with individual transmission frequencies (~0.3 g, Holohil Systems, Inc., Carp, Ontario, Canada) were used to track the bats. To determine skin temperature (T_{skin}) of bats, transmitter pulse rates were calibrated to the nearest 0.1°C for temperatures ranging between 5 and 45°C. After a small patch of fur was clipped, the transmitters were glued between the bats' shoulder blades using adhesive surgical glue (B-520; Factor2, Lakeside, Arizona) and the bats were kept until the next night to ensure that the transmitters were still attached. Our research followed American Society of Mammalogists guidelines (Sikes et al. 2016) and was approved by the UNE Animal Ethics Committee (AEC17-038) and NSW National Parks and Wildlife Service (SL100791).

On the following day, 1 h after dusk, bats were released at their capture site. The next morning bats were radio-tracked using a handheld receiver and a three-element Yagi antenna (Titley Scientific, Brendale, QLD, Australia). Once bats were successfully located to a tree, locations were marked on a GPS

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(Garmin Inc., Olathe, Kansas). Roosting trees were described, the circumference (m) of the tree measured at chest height. A receiver/logger system (designed and built by Dr. Gerhard Körtner) with a H-frame antenna (Titley Scientific, Brendale, QLD, Australia) was placed near the roost, recording the pulse interval of the transmitters, and therefore T_{skin}, every 10 min. Radio-tracking continued each morning until either the signal became too weak from a fading battery or the signal was no longer detectable.

Insect sampling.—Insects were sampled using a light trap, which was only activated on nights that bats were being monitored. The light trap consisted of a 12-V ultraviolet light protected by a clear plastic tube, powered by a 12-V battery (Turbill 2008). The bulb was suspended over a funnel so that insects would fall into a plastic collecting container. The trap was then mounted onto a metal frame to raise the trap above the ground to attract aerial insects. Each day the collecting container was thoroughly sprayed with commercial insect spray, to ensure insects were deceased by the next morning. The insect trap was light-sensitive and automatically operated at night. The battery was replaced daily and insects were retrieved and placed into vials. Insects were identified to order, counted, measured, and placed into one of four respective size categories: <5 mm, 5≥ × <15 mm, 15≥ × <25 mm, and ≥25 mm. After being dried in an oven for 8 h at 70°C, insects from each day were weighed using an analytical scale (0.01 g resolution, OHAUS, Pioneer, Parsippany, New Jersey), then dried again for a further 8 h and reweighed, to ensure there were minimal mass differences between the duration of drying times.

Data analysis.—Torpor bout entry of bats was defined by a decrease in T_{skin} below a torpor threshold of 28°C; this threshold has previously been used for T_{skin} measurements in other small bats (e.g., Stawski et al. 2009). This torpor threshold was deemed appropriate, as many other studies define the torpor threshold of T_b as <30°C and the T_{skin} of small bats is usually within 2°C of T_b (Barclay et al. 1996; Brigham et al. 2011). TBD was calculated based on the time bats remained below the 28°C threshold.

Statistical analyses were conducted with "R" Studio (Version 1.1.414; R Development Core Team 2009–2018). An analysis of variance (ANOVA) was used to compare insect count and mass against T_a variables (minimum, maximum, and mean T_a). To determine whether there were differences in insect mass, insect count, and mean and minimum T_a on days when bats remained torpid versus days that bats aroused, a Welch two-sample *t*-test was performed. Generalized linear mixed-effects models (lme, also referred to as a GLM) were fitted (package "nlme") to test which variables affected TBD and minimum T_{skin}, using individual bats as a random effect. Results were deemed significant when $P < 0.05$. Numeric values are expressed at means ± *SD*, "*n*" is the number of individuals, "*N*" is the number of measurements.

Interactive Akaike information criterion (AIC) models were then used to find the best-predictor variables that explain TBD and minimum T_{skin}. When logging insect count data for the AIC model, if there were values of zero, this was changed to one as log 1 = 0; a value of one represents zero for logarithmic distributions. The best-fit model was determined when all variables were significant and by the lowest AIC value. Rayleigh tests (package "circular") were performed to assess the uniformity of times of entry and arousal of each torpor bout occurrence. A significant *P*-value indicated a nonrandom distribution of entry and arousal times and that these events occurred at clustered times. If that was the case, mean arousal and entry times were calculated.

Results

Study animals.—A total of six male bats were captured and radio-tracked between 7 July and 1 September 2017. The body mass of the bats was similar, with a mean body mass of 4.9 ± 0.7 g ($n = 6$; range: 4.0–5.8 g). Transmitters remained detectable for 17.9 ± 6.9 days ($n = 6$; range: 7–26 days). Free-ranging bats were exposed to naturally fluctuating T_a. The daily mean T_a was 8.3 ± 3.2°C ($N = 67$; range: 2.9–19.9°C), daily mean minimum T_a was 1.2 ± 4.6°C ($N = 67$; range: −5.8 to 12.8°C), and daily mean maximum T_a was 15.5 ± 3.1°C ($N = 67$; range: 7–23.8°C). The overall daily mean range of T_a for the duration of the study was 6.9 ± 5.9°C ($N = 67$; range: −5.8 to 23.8°C).

Arthropod abundance and mass.—An average of 234.7 ± 1,107.2 insects ($N = 50$ nights; range: 0–6,810 insects) were captured each night and the average insect mass was 0.2 ± 0.6 g ($N = 50$ nights; range: 0–3.9 g). Of the total insects caught, 96.7% were <5 mm ($n = 11{,}344$ insects) in length, 2.3% between 5 and 15 mm ($n = 275$ insects), 1.0% between 15 and 25 mm ($n = 116$ insects), and one insect ≥25 mm. The minimum T_a was positively correlated with insect abundance ($P < 0.01$, $F_{1,63} = 10.2$; ANOVA; Fig. 1A) and mass ($P < 0.001$, $F_{1,63} = 11.9$; ANOVA; Fig. 1B). Insect abundance increased substantially on nights above 7°C and ranged from 4,048 to 6,810 insects, with no insects captured when T_a was below −3.5°C ($N = 3$ days; Fig. 1A). On warmer nights above T_a 7°C insect mass increased considerably from 1.3 to 3.9 g in dry mass (Fig. 1B).

Roost choice.—Roosts were predominantly in live, tall (approximately >12 m), *Eucalyptus* trees (distance between roosts mean = 218.9 ± 118.0 m; $n = 17$ roosts; range 37.9–469.9 m). Individuals were often detected high up within the canopy. Only two of the six individuals were sighted leaving their roost of a night, and both individuals emerged out of the canopy. No other bats were sighted leaving the same roost for up to 15 min after their emergence; therefore, we assumed these bats were roosting on their own. Bats roosted in live trees 73.3% of the time ($n = 11$ trees), and the mean circumference breast height of all roost trees was 150.6 ± 59.9 cm ($n = 21$ trees; range: 46–264 cm).

One individual bat showed strong roost fidelity and did not change roost site during the entire time (26 days) of the transmitter attachment. Other individuals switched roosts every 3–5 days, particularly the last bat monitored up until late August, which had the highest recorded level of roost switching with a roost change every 1.3 ± 0.6 days ($n = 1$, $N = 3$ roost switches; range: 1–2). Overall individuals stayed at a roost for

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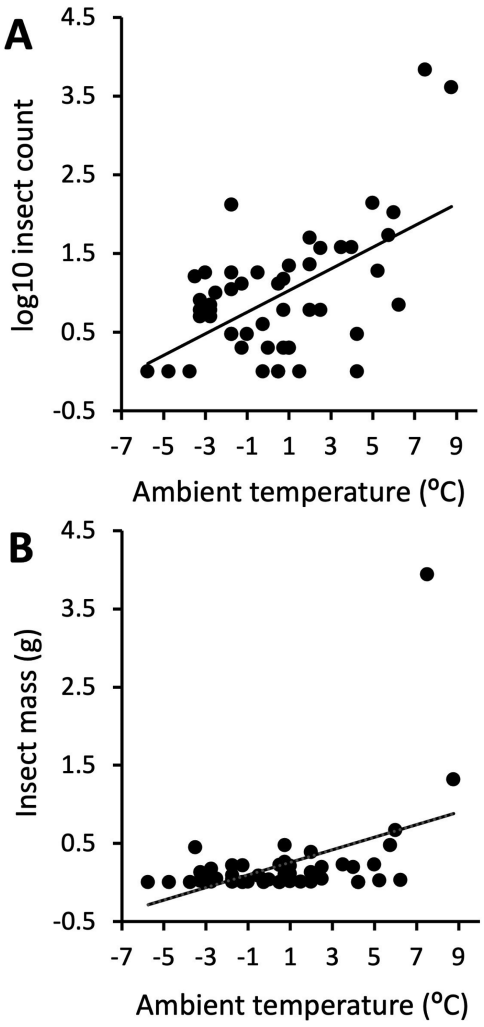


Fig. 1.—The relationship between minimum ambient temperature (T_a) and (A) Log_{10} insect count ($P = 0.002$, $F_{1,63} = 10.2$, $R^2 = 0.33$, Log_{10} insect count = 0.14 * minimum T_a + 0.87) and (B) insect mass (g) ($P < 0.001$, $F_{1,63} = 11.9$, $R^2 = 0.21$, insect mass = 0.08 * minimum T_a + 0.18) throughout the study period (July–August 2017).

an average of 5.1 ± 5.1 days ($n = 6$, $N = 21$; range: 1–22) and all individuals showed roost area fidelity with an average distance of 209.0 ± 127.8 m ($n = 6$, $N = 15$; range: 16.4–406.5 m) between consecutive roosts.

The bats were also roosting near the closest water source (which was situated next to the capture site), at an average distance of 206.6 ± 109.3 m ($N = 21$; range: 37.9–469.9 m) between the lake and the roost. On three occasions, after using a new roost, individuals returned to previously used roosting locations. Bats were more likely to switch roosts during warmer days ($P < 0.0001$, $t_{-12.35} = 101.81$; t-test) with a mean T_a of 9.7 ± 4.1°C ($N = 14$) instead of cooler days with a mean T_a of 8.3 ± 3.4°C ($N = 49$).

Torpor use.—Bats rarely were normothermic while resting and expressed bouts of torpor on every day, with torpor bouts strongly affected by T_a and T_{skin} typically remaining above or closely tracking the T_a (Fig. 2A and B). Bats often passively rewarmed by thermoconforming with the T_a around midday. Winter T_b patterns most often consisted of torpor bouts from after midnight to around sunset with short normothermic periods in the evening or no normothermic periods of up to several days (Fig. 2A). Without the consideration of external factors influencing TBD, on any given night bats had a mean of 49.6 ± 43.9% chance of arousal ($N = 55$).

Times of torpor entry and arousal were not uniformly distributed, and bats entered and aroused from torpor at clustered times (entry: $t = 0.6$, $P < 0.001$; arousal: $t = 0.5$, $P < 0.001$; Rayleigh's test). Arousals were significantly clustered around 17:08 ± 1.1 h ($n = 6$, $N = 64$) and bats mostly aroused from 0 to 1 h ($n = 6$, $N = 57$) after sunset, with most bats on many occasions arousing half an hour after sunset ($n = 6$, $N = 31$); bats then either reentered torpor after arousal or left the roost. A few arousals occurred during the middle of the day ($n = 2$, $N = 3$) and no arousals occurred more than 1.5 h after sunset (Fig. 3). On average torpor entry occurred at 18:56 ± 0.1 h ($n = 6$, $N = 55$), with most entries occurring 1.5–2.5 h after sunset ($n = 6$, $N = 34$; Fig. 3). Bats spent a large proportion of time in torpor, although the TBD varied greatly, lasting for a mean 35.5 ± 36.7 h ($n = 6$, $N = 61$; range: 2.0–187.58 h). Activity was restricted to brief periods with normothermic periods lasting on average for 1.7 ± 1.1 h ($n = 6$, $N = 57$; range: 1.2–5.3 h).

During bouts of torpor, bats exhibited large passive daily fluctuations in T_{skin}. The mean daily T_{skin} was 12.6 ± 2.6°C ($n = 6$, $N = 67$; range: 8.6–22.7°C) and minimum daily T_{skin} was 8.7 ± 2.4°C ($n = 6$, $N = 67$; range: 5.2–17.9°C). The lowest T_{skin} recorded was 5.2°C with a corresponding T_a of −5.8°C, which was the minimum measured T_a throughout the study. Minimum T_{skin} was positively correlated with minimum T_a ($P < 0.01$, $t_{1.8,58} = 2.94$; AIC; Fig. 4) and an increase in T_a was positively correlated with insect count ($P = 0.03$, $t_{1.8,58} = -2.19$; AIC).

The duration of torpor bouts was significantly affected by a range of variables. In an interactive model, TBD was best explained by the model that contained minimum T_a, maximum T_a, mean T_{skin}, body mass of individual bats, and insect mass (Table 1). As the minimum T_a decreased TBD increased ($P < 0.0001$, $t_{0.5,56} = -5.12$; Fig. 5A), similar to the correlation with the mean T_{skin} ($P < 0.001$, $t_{0.5,56} = -3.53$; Fig. 5B). The maximum T_a also had a significant negative effect on TBD ($P = 0.0002$, $t_{0.5,56} = 3.95$). Insect mass also was significantly correlated with TBD ($P = 0.02$, $t_{0.5,56} = -2.29$), such that bats were more likely to arouse from torpor when insect biomass was greater. Body mass of individual bats also had a significant influence on TBD in the final model ($P = 0.04$, $t_{0.5,4} = -2.99$), with smaller bats often exhibiting multiday hibernation instead of brief torpor bouts of <24 h ($n = 2$, $N = 5$; range: 102.16–187.58 h or 7.8 days, which was the longest bout recorded).

Mean T_a significantly differed between days that bats aroused from torpor ($N = 65$; 8.3 ± 2.7°C) and days that bats remained torpid ($N = 51$; 6.2 ± 1.7°C; $P < 0.0001$, $t_{105.31} = 4.57$; t-test). Therefore, T_a had a substantial impact on the likelihood of arousal from torpor. On nights when >130 insects were captured, 100 ± 0% ($N = 5$) of bats aroused from torpor. In contrast, when <130 insects were caught a mean of 45.1 ± 42.1% ($N = 45$) of bats aroused from torpor.

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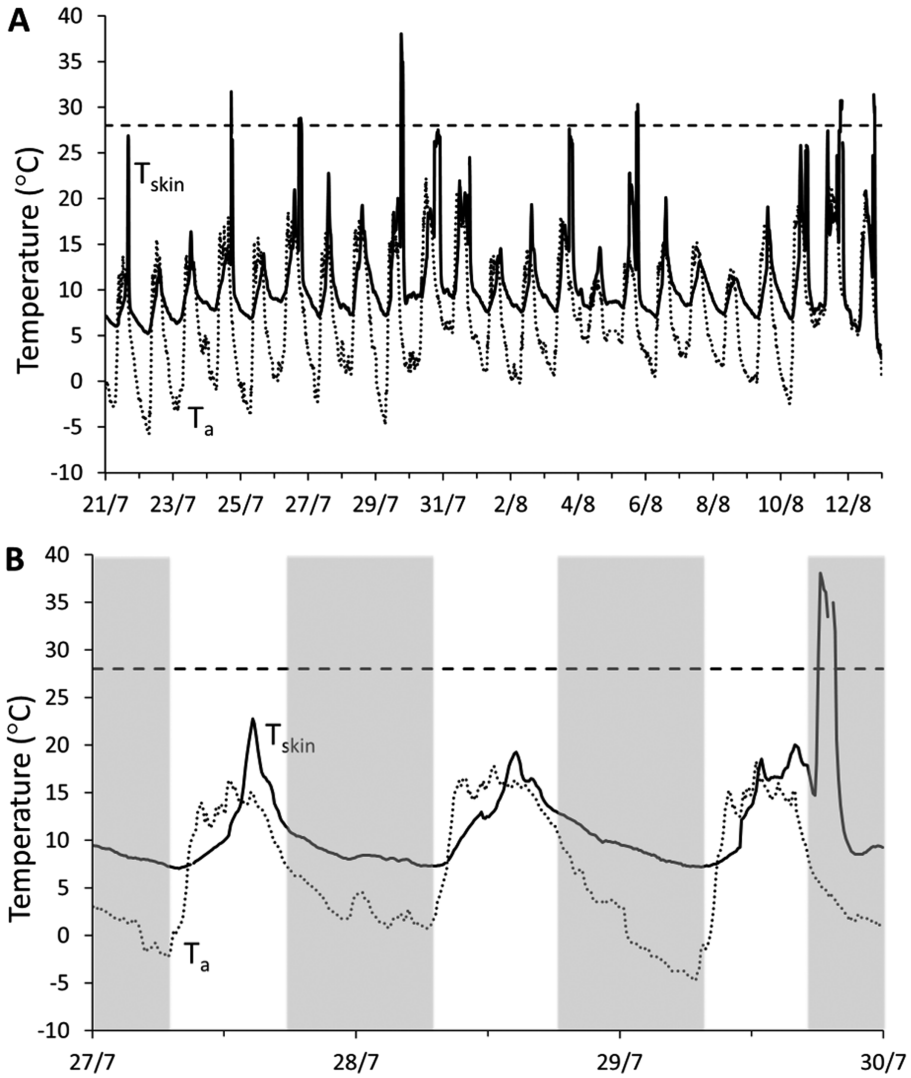


Fig. 2.—A) Skin temperature (T_{skin}, solid line) fluctuations of a male free-ranging *Vespadelus vulturnus* throughout the study (July–August 2017), including ambient temperature (T_a, dotted line); the dashed line indicates the torpor threshold, 28°C. B) Three consecutive days (27–29 July 2017) during winter of T_{skin} fluctuations of a male free-ranging *V. vulturnus*; the black line indicates T_{skin} and the gray bars indicate night (17:00 to 07:00 h). The gray dotted line indicates T_a and the black dashed line indicates the torpor threshold, 28°C.

Discussion

We found that tiny male *V. vulturnus* bats use a number of physiological and behavioral approaches to survive cold winters in nature. Physiological mechanisms included short as well as multiday torpor bouts of hibernation to cope with winter conditions. Behavior and activity patterns were influenced by increased food supply, and bats often aroused from torpor when conditions were more suitable for foraging and at specific times following sunset. The male *V. vulturnus* in our study were found to roost mostly in tall, live *Eucalyptus* trees with a large circumference, which were limited to the small reserve due to the surrounding agricultural landscape. These combinations of physiological and behavioral mechanisms likely enable males to manage their daily energy budgets throughout winter and to recover from the autumn mating period and continuation of mating throughout winter.

Bats employed torpor on all days during winter using a combination of brief and multiday torpor bouts by reducing their T_{skin} by about 12–30°C, resulting in substantial energetic savings, important at times when T_a is low and insect abundance is reduced. Arousals occurred on days the T_a was on average warmer compared to days they remained torpid. Normothermic periods were typically short (~1.7 h), likely to minimize thermoregulatory energy expenditure. These thermal biology data are similar to those of other free-ranging bats within the reserve and also from other areas in Australia (Turbill 2006a; Turbill and Geiser 2008; Geiser et al. 2019) but differ from cave-roosting cold-climate bats which can display TBDs of several weeks (Jonasson and Willis 2012). Torpor use has also been recorded in nocturnal insectivorous birds during winter in Imbota, although unlike the insectivorous bats in this reserve, these birds always aroused on a daily basis (Körtner et al. 2001; Doucette et al. 2012). Further, an arboreal mammal, the sugar glider (*Petaurus breviceps*), was found to employ daily torpor rarely at Imbota and typically on particularly cold and wet days (Körtner and Geiser 2000). Importantly, despite widely

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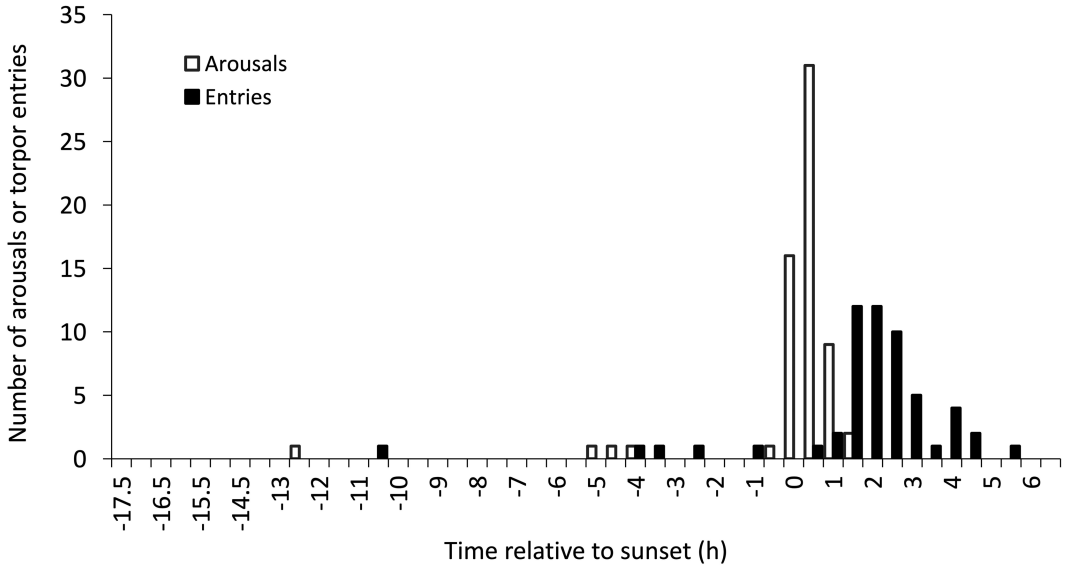


Fig. 3.—Timing of torpor arousals ($N = 64$) and entries ($N = 55$) of free-ranging *Vespadelus vulturnus* relative to sunset (17:00 h) throughout the study (July–August 2017). The black bars depict torpor entry times and the white bars depict torpor arousal times.

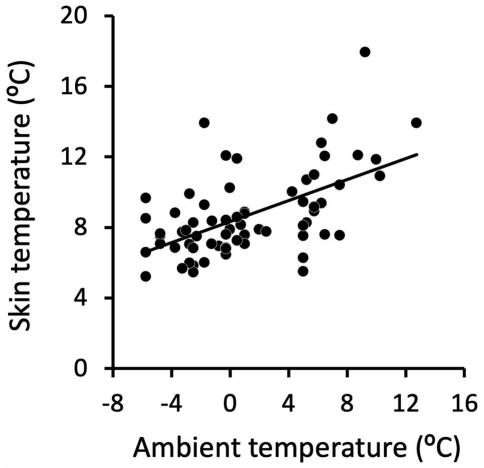


Fig. 4.—The relationship between minimum skin temperature (T_{skin}) of free-ranging *Vespadelus vulturnus* and minimum ambient temperature (T_a) ($P < 0.01$, $R^2 = 0.31$, minimum $T_{skin} = 0.29$ * minimum $T_a + 8.33$) throughout the study period (July–August 2017).

fluctuating daily T_a bats were capable of prolonged torpor bouts of up to 187.58 h (almost 8 days) during cold periods, confirming that this southern hemisphere temperate bat is capable of hibernation. The maximum duration of torpor measured in our study was more than 10-fold of the 16.7 h previously reported in captive *V. vulturnus* (Willis et al. 2005).

Interestingly, a previous study conducted at Imbota found that while female chocolate wattled bats (*Chalinolobus morio*; ~8 g) employed torpor bouts lasting up to 15 days during winter, males of the same species aroused from torpor on most days (Turbill 2006a). It is likely that males of this species search for and copulate with females during the winter period, which is also probable for *V. vulturnus* that primarily mate during autumn but have also been found to mate throughout winter (Tidemann 1993). This result is similar to male long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*, which employ shorter bouts during early winter to find mates (Turbill and Geiser 2008). Similar to the male *V. vulturnus* in our study, male *Nyctophilus* species also show prolonged bouts of torpor lasting several days during winter. As observed in many other studies TBD in *V. vulturnus* increased with decreasing T_a and T_{skin} over the T_a range torpid animals thermoconform (Twente and Twente 1965; French 1982; Stawski et al. 2009; Geiser 2021), likely to maximize energy savings to deal with the corresponding decrease in insect activity at lower T_a.

Bat activity was correlated with insect activity, with bats hibernating during periods of lower insect activity and expressing brief torpor bouts when insect activity was high. Therefore, it appears that the bats use a physiological approach to deal with reduced and variable insect activity during winter. Bats also were more willing to leave their roots on warmer days, again probably due to a higher abundance of food. Similar observations have also been made in *Scotophilus* sp., which increased torpor use to save energy while insect abundance was low during unfavorable environmental conditions (Jacobs et al. 2007). Richards (1989) also reported that insectivorous, echolocating bats respond to low prey availability by reducing foraging. As invertebrate activity is typically higher within the first hour of sunset, they use this time for brief foraging (Turbill 2008). Thus, our study supports previous studies within the reserve, which reported a positive relationship between increasing invertebrate abundance, an increase in T_a, and bat activity around dusk (Turbill and Geiser 2008).

Thermal physiology is also known to be affected by roost choice (Turbill et al. 2020). Bats in our study preferred large live trees ($N = 11$, 73.3%) perhaps because they retain heat for longer, due to heat stored by fluids within live tree stems (Paclík and Weidinger 2007; Coombs et al. 2010). It is also likely that these larger trees provide a more stable microclimate (Clement and Castleberry 2013), which could promote use of multiday torpor (Stawski and Currie 2016). Therefore, it seems that *V. vulturnus* select *Eucalyptus* trees as roosts based on the

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Table 1.—The top five models for torpor bout duration (Log_{10}(TBD)) and minimum skin temperature (MinimumT_{skin}) of free-ranging male *Vespadelus vulturnus* during winter (July–August 2017). The best-fit model for each variable is indicated in bold.

Variable	Model	AICc	Delta
Log_{10}(TBD)	**minimumT_a + maximumT_a + meanT_{skin} + bm + minimumT_a × insectmass**	138.6	0.0
	minimumT_a + maximumT_a + meanT_{skin} + bm + minimumT_a × Log_{10}(insectcount)	145.9	7.3
	minimumT_a + maximumT_a + meanT_{skin} + bm + minimumT_a × Log_{10}(insectcount) + minimumT_a × insectmass	150.9	5.0
	minimumT_a + maximumT_a + meanT_{skin} + insectmass + bm + minimumT_a × Log_{10}(insectcount) + minimumT_a × insectmass	150.9	0.0
	minimumT_a + meanT_a + maximumT_a + minimumT_{skin} + meanT_{skin} + Log_{10}(insectcount) + insectmass + bm + minimumT_a × Log_{10}(insectcount) + minimumT_a × insectmass	160.9	10.0
MinimumT_{skin}	**minimumT_a + Log_{10}(insectcount) + minimumT_a × Log_{10}(insectcount)**	294.8	0
	minimumT_a + maximumT_a + Log_{10}(insectcount) + minimumT_a × Log_{10}(insectcount)	299.7	4.9
	minimumT_a + meanT_a + maximumT_a + Log_{10}(insectcount) + minimumT_a × Log_{10}(insectcount)	302.3	2.6
	minimumT_a + meanT_a + maximumT_a + Log_{10}(insectcount) + insectmass + minimumT_a × Log_{10}(insectcount) + minimumT_a × insectmass	306.9	4.6
	minimumT_a + meanT_a + maximumT_a + Log_{10}(insectcount) + insectmass + bm + minimumT_a × Log_{10}(insectcount) + minimumT_a × insectmass	307.8	0.9

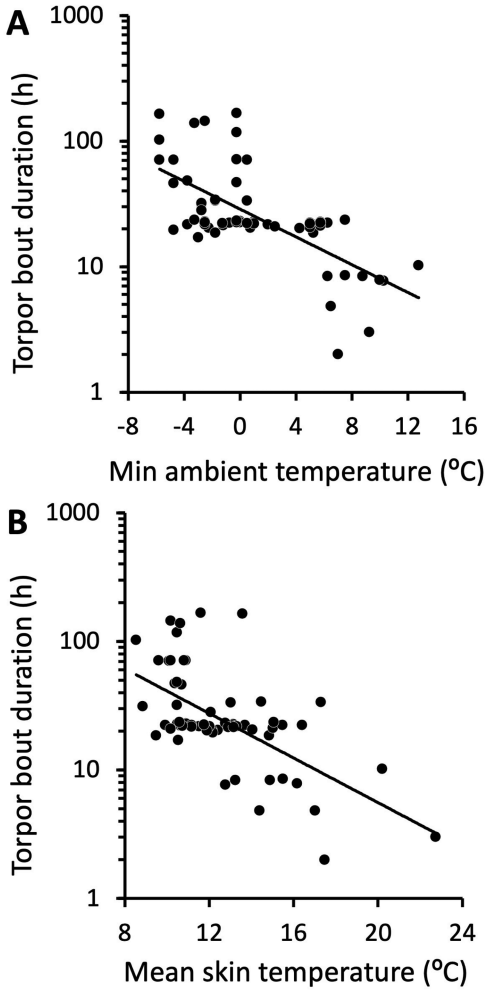


Fig. 5.—The relationship between torpor bout duration (TBD) of free-ranging *Vespadelus vulturnus* and (A) minimum ambient temperature (T_a) ($P < 0.001$, $R^2 = 0.46$, $\log_{10}$TBD = –0.055 * minimum T_a + 1.46) and (B) mean skin temperature (T_{skin}) during torpor ($P < 0.01$, $R^2 = 0.37$, $\log_{10}$TBD = –0.087 * mean T_{skin} + 2.48) in winter (July–August 2017).

tree's microclimate properties, and while some bats were seen leaving the roost high within the tree canopy, it appeared that bats emerged from a tree hollow. Further, there was no evidence for bats roosting under bark, in agreement with previous findings on *V. vulturnus* (Rueegger et al. 2018). This is in contrast to *Nyctophilus* spp. (~7–12 g), a species common at the study site, which have very different roosting needs and primarily roost under bark with occasional roosting in shallow tree cavities, which enable frequent passive rewarming to save energy (Turbill 2006b; Turbill et al. 2008). Unlike *Nyctophilus* that show little seasonal fattening and appear to rely on frequent foraging during low T_a for energy supply, *V. vulturnus* fatten substantially (Tidemann 1993; Geiser et al. 2019), which may explain their different preference of roosts. Further, large and tall trees with hollows with narrow openings can reduce the risk of predation, as low-positioned roosts may subject the bats to higher exposure to predators (Lumsden et al. 2002; Ruczynski and Bogdanowicz 2008).

Five of the six male bats exhibited low roost fidelity and frequently switched roost sites. This appears to be a common

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characteristic in many tree-roosting bat species and similar roost-switching frequencies have been recorded for *Nyctophilus* bats within Imbota (Turbill et al. 2020). Previous studies have confirmed that female *V. vulturnus* often roost in groups (Campbell et al. 2005), whereas there is no published information on the roosting preferences of males. Males of the closely related *V. pumilus* do appear to prefer to roost alone (Law and Anderson 2000), similar to the males in our study. Within Imbota, female *Nyctophilus* bats are also more likely to roost in insulated tree hollows and in groups in comparison to males (Turbill et al. 2020). Bats resided near open water, minimizing commuting distances between day roosts, proximity to water, and optimal foraging grounds (Campbell 2009; Webala et al. 2010; Burgar et al. 2015). However, the short distances found between roosts in the current study may reflect the small size of the reserve and the lack of suitable roosting trees in the surrounding agricultural landscape.

Our study revealed important implications for the management of *V. vulturnus*. The data suggest that areas of their known habitats should be protected within a minimum of 500-m radius from permanent water sources, and the retention of large *Eucalyptus* trees to ensure that *V. vulturnus* can effectively manage their daily energetic requirements throughout the year, and hence their long-term survival. It is possible that these needs vary between habitats and that populations of *V. vulturnus* show differing physiological and behavioral strategies, particularly in larger areas of protected woodlands. For an effective sustainable forest management strategy, investigation of physiology and behavior during all seasons is required to understand how environmental variables impact the survival of insectivorous bats and other animals. This is particularly important for tree-roosting species as the physical features of hollows can have an enormous impact on a species' survival during extreme environmental conditions, and energetically costly reproductive seasons (Ruczynski and Bogdanowicz 2008).

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