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## Contrasting Thermal Strategies of Montane Neotropical Bats at High Elevations

I. Garin<sup>1\*</sup>, G. Chaverri<sup>2</sup>, L. Jimenez<sup>1</sup>, C. Castillo-Salazar<sup>3</sup>, J. Aihartza<sup>1</sup><sup>1</sup>Zoology and Animal Cell Biology, University of The Basque Country UPV/EHU, Sarriena z/g, 48940 Leioa, The Basque Country<sup>2</sup>Recinto de Golfito, Universidad de Costa Rica, Golfito, Costa Rica,<sup>3</sup>Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica

\*inazio.garin@ehu.eus

## Abstract

In the Neotropics, captive vespertilionid bats substantially reduce their metabolic rate at low ambient temperatures, similar to their temperate counterparts, whereas the ability of phyllostomids to lower metabolic rate seems to be more limited, even in mountain species. Nevertheless, field data on the thermal behaviour of syntopic individuals from these two families is lacking. Consequently, we aimed to test whether torpor was more common and deeper in vesper bats compared to leaf-nosed bats by studying skin temperature (Tsk) variation in individuals experiencing the same environmental conditions at a mountain area. Bats experienced ambient temperatures below 15°C. Average Tsk was 10°C in *Myotis oxyotus gardneri* (Vespertilionidae) during the day, while *Sturnira burtonlimi* (Phyllostomidae) regulated diurnal Tsk above 30°C. Constant food availability may explain why diurnal *Sturnira burtonlimi* pay the high energetic cost required to remain normothermic and to defend a wide Ta–Tsk gap but further studies are needed to elucidate additional strategies that may be employed by these bats to reduce the energetic demands of normothermy. Our study shows that the contrasting thermal strategies and torpor use adopted by vespertilionid insectivores and phyllostomid frugivores in captive settings also occur in free-ranging conditions, thus providing a basis to develop further studies with predictions more accurately rooted in field data.

## Graphical abstract

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Keywords: Phyllostomidae, Vespertilionidae, thermal behaviour, torpor, skin temperature

## Introduction

Tropical regions are often regarded as sites with mild weather, yet mountains located in the tropics are characterized by relatively harsh conditions such as high levels of solar radiation, low ambient temperatures (Ta), more abrupt meteorological changes, and lower productivity than lower elevations (Fahey et al., 2016; Rapp and

Silman, 2012; Still et al., 1999). Since the defense of normothermic body temperatures can compromise an individual's energy budget in such environments (McGuire and Boyle, 2013), endothermic organisms may adopt several non-mutually exclusive strategies to thrive in high elevations. These strategies may include altitudinal migrations, thereby taking advantage of reduced levels of competition or predation at high altitudes during peaks in resource abundance and retreating to the lowlands to reduce the costs of living in cold environments year-round (Boyle, 2017). Complementarily, endotherms may also balance their energy budgets through facultative heterothermy (Geiser, 2004).

In the Neotropics, three bat families commonly occur at high elevations: phyllostomids, molossids and vespertilionids (e.g., Flores-Saldaña, 2008; Martins et al., 2015; Patterson et al., 1996; Soriano, 2000; Tuttle, 1970; Vargas et al., 2008). These families appear to differ in their ability to reduce metabolic rate (MR) in response to adverse environmental conditions, such as low food availability or cold weather (reviewed by Stawski et al. 2014). Temperate vespertilionids use torpor, where MR is commonly reduced by over 95% from normothermic values (reviewed by Speakman and Thomas, 2003). Machado and Soriano (2007) showed that captive neotropical highland vespertilionids lowered MR by as much as 80% at low  $T_a$  ( $<20^\circ\text{C}$ ), assuming the bats entered shallow or deep torpor depending on the weather, food supply or reproductive state, in a manner similar to their temperate counterparts. Machado and Soriano (2007) argued that the relative abundance and diversity of vespertilionid bats at high elevations in the Neotropics is due to this ability. Neotropical insectivores from families such as Mormoopidae, Natalidae or Emballonuridae that are confined to lowlands either remain normothermic when  $T_a$  falls below the thermoneutral zone (Bonaccorso et al., 1992; Genoud et al., 1990; Genoud and Bonaccorso, 1986) or retain high minimum body temperatures ( $T_b$ ) when torpid, with only a slight depression in metabolic rate (Genoud et al., 1990). If they enter hypothermia ( $T_b <15\text{-}20^\circ\text{C}$ ), many are not able to arouse and die (Bonaccorso et al., 1992; Studier and Wilson, 1970).

The ability of phyllostomids to employ torpor is widely accepted, even at relatively high  $T_a$  (Geiser and Stawski, 2011), although during torpor events they reduce body temperature by only a few degrees below the lower critical temperature of the

thermoneutral zone (Audet and Thomas, 1997; Soriano et al., 2002). Even the limited ability to reduce MR by phyllostomids can result in substantial energy savings. For example, the frugivorous *Sturnira lilium* and *Carollia perspicillata* save between 10% and 30% of daily energy expenditure by reducing  $T_b$  by only 6-13°C at  $T_a$  21°C (Audet and Thomas, 1997). Depressed  $T_b$  in these species seems to occur in response to food deprivation, as well-fed individuals remain normothermic at a  $T_b$  of 21°C (Audet and Thomas, 1997). Similarly, torpor in Australian blossom-bats (Pteropodidae), which also exhibit a limited ability to reduce MR (Stawski et al., 2014), is more pronounced when the seasonal supply of nectar is low (Geiser, 2006). It is unclear, however, whether phyllostomids will respond similarly in harsh mountain environments. In a montane region of Brazil, the mostly frugivorous *S. lilium* prefer to leave foraging areas, allegedly for warmer altitude belts, during the colder months of the year (average  $T_a$  12°C with occasional temperatures <0°C) even if food supply does not decline (Mello et al., 2008). This suggests that given the chance, phyllostomids may favour migration over residency in metabolically demanding environments.

Based on long-term capture records at Monteverde, Costa Rica, substantial seasonal changes in the abundance of *S. ludovici*—now renamed as *S. burtonlimi* in Panamá and Costa Rica (Chaverri et al., 2016; Velazco and Patterson, 2014)—, *Dermanura toltecus*, and *Hylonycteris underwoodi* have been reported, indicating altitudinal migration (Timm and LaVal, 2000). The interaction between the energy expenditure and the decrease in  $T_a$  from the lower critical temperature may also determine the decision to seek milder altitudes or remain facing the costs of normothermy. In captivity, *Sturnira erythromos*, a frugivorous phyllostomid that inhabits the high elevation belt of the Andean mountains (>1,800 m a.s.l.), shows a thermoneutral zone shifted toward temperatures as low as 25°C and facultatively displays hypothermy below that critical threshold (Soriano et al., 2002). Such adaptations might allow the species to cope efficiently with both average and extreme diurnal  $T_a$ . Thus, phyllostomids inhabiting mountains are expected to show both behavioural (migration, roosting) and physiological adaptations to reduce the energy expenditures imposed by cold environments.

The purpose of our study was to assess the thermoregulatory strategies employed

by the most abundant bats at high elevations in Neotropical regions, namely phyllostomids and vespertilionids. We predicted that the metabolic response to the low  $T_a$  encountered during daytime at high elevation (above 2,000 m) would differ between members of the two bat families, torpor being more common and deeper in vesper bats. Specifically, we tested whether (1) *Sturnira burtonlimi*, a phyllostomid whose distribution is restricted to mountains employs torpor at the very demanding conditions of high altitudes; (2) the *in situ* thermoregulatory response of a Neotropical highland vespertilionid bat such as *Myotis oxyotus* resembles its temperate counterparts; and (3) there is convergence in the thermoregulatory response between these two species.

### Materials and Methods

Our research occurred in La Amistad International Park (PILA), one of the largest protected areas in Central America. PILA comprises 400,929 ha shared between Costa Rica and Panama. This park encompasses highly diverse ecosystems due to a combination of variable elevations (range 80-3,550 m above sea level -asl-), diversity of soils, differing weather patterns on the Caribbean and Pacific slopes, and unique topographic elements (Soto Solis, 2010). At least 11 different vegetation types are known from the park, including tropical moist forests at ca. <500 m asl to subalpine rain paramo at >3300 m asl (Soto Solis, 2010).

The area known as Valle del Silencio, Costa Rica, is located on the Caribbean slope at 2,500 m asl. where the sole human-made structure in the Valley is a wooden hut we used as a field station (WGS84; Latitude 9.111°, Longitude -82.961°). The canopy vegetation is dominated by oaks (*Quercus* spp.), whereas the understory is dominated by bamboo (*Chusquea* spp.).

During our study (25 January to 6 February 2015), sunset occurred at 17:35, with twilight ending ~18:00.  $T_a$  ranged from 7-15°C with maxima around noon and minima 5 hours after sunset (own data). Rain was frequent, both during the day and at night, and relative humidity ranged from 68% to 96%.

We placed mist nets along the main trail at Valle del Silencio and El Jardín. We used a combination of polyester and ultra-thin monofilament nets of 16 and 20 mm mesh size (Ecotone, Poland). Monofilament nets were monitored constantly as bats quickly

chewed their way out. Nets varied from 3 to 12 m long and 2.5 m high, and linear distance covered by the nets ranged between 47 and 109 m nightly. Nets were opened from 17:30 to 23:00 h. Captured bats were stored immediately under our clothing to keep them warm. For each individual, we recorded forearm length, sex, and reproductive condition, and took small (3 mm diameter) wing-tissue samples (Worthington-Wilmer and Barratt, 1996). Species were identified *in situ* based on general morphology and biometric measurements (Timm et al., 1999; Velazco and Patterson, 2014). Sampling within La Amistad National Park was approved by the Costa Rican government (Ministerio de Ambiente y Energía permit numbers R-033-2013-OTCONAGEBIO and R-057-2015-OT-CONAGEBIO).

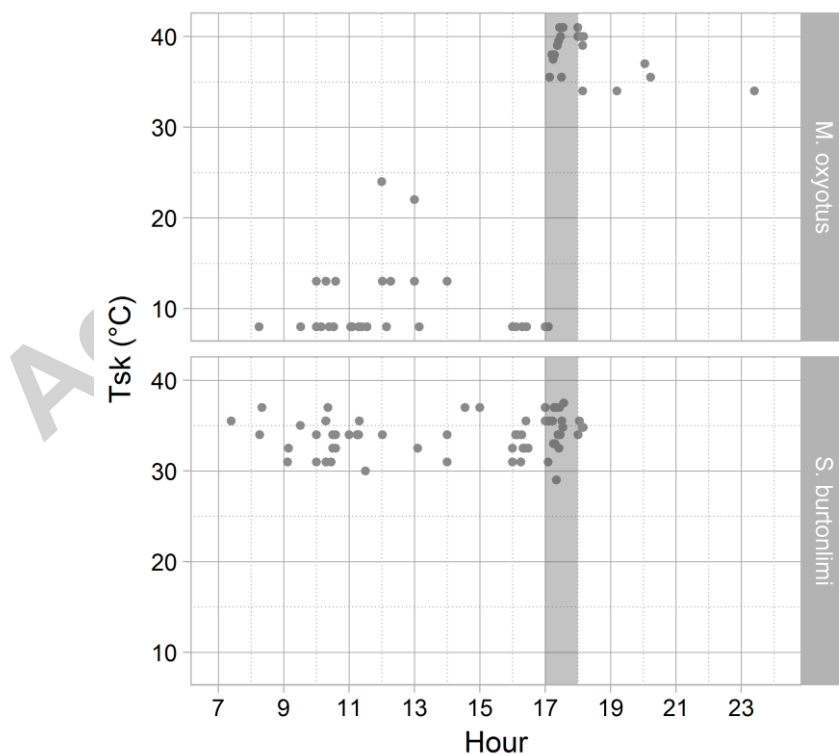
We affixed temperature sensitive (0.4 g) radio-transmitters (PIP31, Biotrack Ltd, UK) to five *Myotis oxyotus gardneri* (6.5–7.7 g), and six *Sturnira burtonlimi* (18.1–22.9 g). The tags represented 5–7% of the body mass of the small bats (*Myotis oxyotus*). We calibrated the radio-tags to confirm the relationship between pulse rate per minute (ppm) and temperature provided by the tag manufacturer was accurate. Radio-transmitters were glued between the shoulder blades after clipping the fur on that region so that the temperature sensor was in direct contact with the skin.

Bats were tracked on foot using radio-receivers (1000-XRS, Wildlife Materials, Carbondale, USA; and FT-290RII, A. Wagener Telemetrieanlagen, Köln, Germany) with three-element Yaggi antennas. During daylight, and beginning the day after tagging, as many bats as possible were tracked to locate roosts and measure the bat's skin temperature (Tsk). Geographic coordinates of roost locations were taken by GPS (Oregon 450, Garmin Ltd, Southampton, UK). Following Barclay et al. (2001), we ensured that variation among individual animals and transmitters was accounted for and thus, whenever possible, we recorded transmitter pulse rates also during nocturnal activity to compare with diurnal rate and assess changes in skin temperatures (Tsk). However, the short nature of our study precluded substantive tracking at night. We only considered for analysis tracking events that were at least one hour apart, except shortly before and during emergence (17:00 to 18:00 h) when only minutes separated tracking events to allow us to get an accurate assessment of putative Tsk changes.

Skin temperature was described using mean and standard deviation. We fitted a generalized linear mixed model (GLMM) to data. Species and period of the day were included in the model as explanatory variables, as well as their interaction, in order to explain the observed variability of Tsk on the observed skin temperatures. Period of the day was originally classified into categories: day (from sunrise to 17:00h), emergence (between 17:00 and 18:00 h) and night (from 18:00 h, corresponding to sunset, to sunrise). Nevertheless, that explanatory variable had two levels, daytime (inactive period) and night (active period), as we were not interested in explaining the variability of Tsk during the arousal period. The GLMM included a variance structure allowing heteroscedasticity in the residuals of the variable species, and a random effect to deal with the lack of independence of observations coming from the same individuals (as affecting variability of the intercept). Data exploration, model simplification and model validation procedures were performed following Zuur et al. (2009) and Crawley (2013). We used *nlme* package (Pinheiro et al., 2017) in R (R Core Team, 2015).

## Results

Figure 1. Daylong Tsk (in °C) from three *Myotis oxyotus* and *Sturnira burtonlimi*. The grey area indicates the time interval between 17:00 and 18:00h, corresponding to sunset.



We tracked three *M. oxyotus* and three *S. burtonlimi*. *M. oxyotus* and *S. burtonlimi*

individuals were tracked for four to eight days (Table 1). Diurnal pulse rates (from sunrise to 17:00 h) were recorded at least once and at different times each day. In *M. oxyotus*, individual ranges of Tsk remained below 25°C during the day and declined to as low as 8°C in all individuals ( $mean=10.3^{\circ}C$ ,  $std=2.75$ ; Table 1). In contrast, all *S. burtonlimi* regulated diurnal Tsk above 30°C ( $mean=33.6^{\circ}C$ ,  $std=0.60$ ).

We were not able to locate the foraging areas of most individuals, thus the number of Tsk recordings was low after 18:00 h. The mean Tsk of *M. oxyotus* at night was 38.4°C ( $std=1.98$ ) while of *S. burtonlimi* was 34.8°C ( $std=0.19$ ); during emergence, these mean values were 38.9°C ( $std=1.21$ ) and 34.6°C ( $std=1.35$ ), respectively.

According to the best generalized linear mixed model fitted to the data the effect of the bat species on Tsk was statistically significant (ANOVA,  $F=251.8$ ,  $df=1,4$ ,  $p<0.001$ ) and that effect was also dependent on the period of the day (ANOVA,  $F=289.3$ ,  $df=1,78$ ,  $p<0.001$ ). The model estimated a significant mean difference in daytime Tsk between *S. burtonlimi* and *M. oxyotus* (23°C,  $SE=1.15$ ;  $t=20.09$ ,  $df=4$ ,  $p<0.001$ ), but according to the model no differences were expected between the mean Tsk of the two species at night ( $t=2.55$ ,  $df=4$ ,  $p=0.063$ ).

## Discussion

Our results provide evidence for different thermal strategies within a Neotropical montane bat community, and represent the first comparative data on thermal strategies and torpor use between syntopic free-ranging neotropical vespertilionids and phyllostomids. Estimated Tsk of *M. oxyotus* during daytime was 23°C lower than *S. burtonlimi*. This suggests a different thermoregulatory strategy between the two genera when facing the same  $T_a$  (<15°C), which were well below the estimated lower critical temperature of the two species (experimental data for *M. oxyotus*: 25°C, Machado and Soriano, 2007; expected data according to species similar to *S. burtonlimi*: 25–29°C, Soriano et al., 2002; Speakman and Thomas, 2003).

*S. burtonlimi* exhibited no decline or only a slight decrease (5–6°C) in Tsk during daytime, even at  $T_a$  that seldom rose above 15°C. They proved able to cope with  $T_a$  well below the minimum values found in the neotropical lowlands and to defend normothermy beyond the typical thermoneutral zone. This was unexpected, since meteorologically adverse conditions in mountainous regions have been proposed as a



context to explain the adaptive advantage of torpor in phyllostomids, particularly frugivorous bats (Almeida and Cruz-Neto, 2011; Audet and Thomas, 1997).

Increased MR at low  $T_a$  must have occurred to defend normothermy, or even shallow torpor, during the diurnal meteorological conditions experienced at 2,500 m in the park. Captive *Sturnira* spp. double their MR to maintain a constant  $T_b$  at ambient temperatures only 5-7°C below the lower critical temperature (Audet and Thomas, 1997; Soriano et al., 2002). Bats from the genus *Sturnira* feed variably on fruits produced by plants from families Solanaceae and Piperaceae (Sánchez et al., 2012; Silveira et al., 2011), although the former are preferred (Muyllaert et al., 2014). *Solanum* and *Piper* fruits are both rich in sugar (Castaman-Francener, 2006), and the digestive abilities of these bats seem to suit the high nutritional value of these items as staple foods (Saldaña-Vázquez and Schondube, 2013). Since body condition is thought to dictate thermoregulatory responses by phyllostomid bats (Audet and Thomas, 1997; Kelm and Von Helversen, 2007), we assume that the high energy input required to sustain a high resting  $T_b$  was possible given the high-energy content of preferred food items consumed by *S. burtonlimi*.

*Sturnira burtonlimi* exhibits some additional features that may help in reducing the high thermoregulatory cost of normothermy. It may have a high mass-specific basal metabolic rate (BMR) as in other *Sturnira* spp. (Almeida and Cruz-Neto, 2011; Soriano et al., 2002); and/or a low thermal conductance (Soriano et al., 2002) as the noticeably thick pelage suggests. These characteristics might allow the bats to expand their lower critical temperature beyond the limits of their lowland congeners (around 29°C in *S. lilium*, Speakman and Thomas, 2003) and approach the values observed in mountain *S. erythromos* (25°C, Soriano et al., 2002). Furthermore, *Sturnira bilobatum* is able to decrease heart rate for short periods during the day (O'Mara et al., 2017). If our study animals would have done so, they might also reduce considerably the energetic costs of defending normothermy (~10% of the BMR). We did not find evidence that thermogenic processes, either shivering or nonshivering, also acted to increase heat production at low  $T_a$  (Almeida and Cruz-Neto, 2011). Note that the major brown fat deposition in many small mammals is located between the shoulder blades (Smith and Horwitz, 1969), thus during cellular combustion of brown fat (non-shivering thermogenesis) the radiotags would have recorded a

sudden change in temperature.

*Myotis oxyotus* depressed Tsk substantially during the day, indicating they entered deep torpor; thus, they would have saved a substantial amount of energy on a daily basis (Speakman and Thomas, 2003), averaging 61% of the BMR in captive animals (Machado and Soriano, 2007). Geiser and Stawski (2011) showed that torpor at Ta around 10°C is an energetically economic strategy in vespertilionids, as the metabolic rate during torpor is well below BMR. Under harsh environmental circumstances insect prey acquisition is also uncertain, thus torpor pays a double reward. Recurrent increases in transmitter pulse rates after 17:00 h suggest that arousal from torpor was mainly active and not driven passively by exogenous heat sources.

Clearly, defense of euthermy at high Tb–Ta differentials may be prohibitive in the long term. Hence, one feasible option for a bat that allegedly roosts alone clinging from mosses (pers. obs.) and cannot benefit from huddling is to migrate and to seek an environment with a reduced Tb–Ta gradient, provided that food is available. Even though migration at a large geographic scale has been described as a solution to the energetic bottleneck of bats (Fleming and Eby, 2003), torpor and hibernation are commonly envisaged as the obvious (often the only) biological alternative to individuals facing food shortfalls (Speakman and Thomas, 2003). Mountains, however, offer high thermal diversities in short distances, not only due to the elevation gradient but also through differences in sunlight level and prevailing winds between slopes. Consequently, mountain phyllostomids facing adverse conditions might solve metabolic constraints by engaging in small-scale movements over their range.

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#### Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Precisely, bat capture and handling protocols were approved by the Institutional Animal Care and Use Committee of the University of Costa Rica (CICUA-04-14).

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**Highlights:**

- Diurnal thermal strategy was different between two mountain Neotropical bat species
- *Myotis oxyotus* kept a low diurnal skin temperature
- *Sturnira burtonlimi* defended high skin temperatures at low ambient temperatures
- Both bat species showed typical temperatures during the nocturnal flight

