

**TEMPERATURE REGULATION IN TWO INSECTIVOROUS BATS (*MYOTIS KEAYSI*
AND *MYOTIS OXYOTUS*) FROM THE VENEZUELAN ANDES**

**REGULACIÓN TÉRMICA EN DOS MURCIÉLAGOS INSECTÍVOROS (*MYOTIS KEAYSI*
y *MYOTIS OXYOTUS*) DE LOS ANDES VENEZOLANOS**

Marjorie Machado¹ and Pascual J. Soriano²

¹*Universidad de Carabobo. Facultad Experimental de Ciencias y Tecnología.
Departamento de Biología. Address: Apartado 2005, Valencia, Venezuela.*

E-mail: mmachado3@uc.edu.ve

²*Universidad de Los Andes. Facultad de Ciencias. Departamento de Biología.
Address: Apartado 05, La Hechicera, Mérida 5101, Venezuela. E-mail: pascual@ula.ve*

ABSTRACT

We tested the hypotheses that thermoregulatory constraints are correlated with altitudinal segregation for Andean insectivorous bats, *Myotis keaysi* (body mass = 4.7-5.6 g) and *Myotis oxyotus* (body mass = 4.5-6.3 g) and also between these species and other lowland insectivorous non-vesperilionid bats. We measured body temperatures and oxygen consumption and calculated metabolic rates and thermal conductances at different ambient temperatures (2-35°C), employing open flow respirometry. Both species used torpor to save energy at temperatures below the lower critical temperatures of their thermoneutral zones. The basal metabolic rate of *Myotis keaysi* was 1.2 ± 0.02 ml O₂ g⁻¹ h⁻¹ with a narrow thermoneutral zone (29.2-33.4°C). Whereas the basal metabolic rate of *Myotis oxyotus* was lower at 0.92 ± 0.04 ml O₂ g⁻¹ h⁻¹ but with a wider thermoneutral zone (25.2-32.5°C) and a lower value of the lower critical temperature (25.2°C). Physiological features of both species were consistent with their elevation distribution. Both species exhibited differences in thermoregulatory strategies compared with lowland insectivorous bats.

Key words: Insectivorous bats, metabolic rate, thermoregulation, tropical Andes, Venezuela.

RESUMEN

En este trabajo se puso a prueba las hipótesis de que las restricciones termorregulatorias están correlacionadas con la diferenciación altitudinal de dos especies andinas de murciélagos insectívoros, *Myotis oxyotus* y *Myotis keaysi*, en los Andes venezolanos, así como también entre ellas y otras especies de murciélagos insectívoros de tierras bajas. Se midieron sus respectivas temperaturas corporales y consumo de oxígeno, a la vez que se calcularon sus tasas metabólicas y conductancias térmicas a diferentes temperaturas ambientales (2-35°C) empleando un respirómetro de flujo abierto. Ambas especies utilizaron el "torpor" como principal estrategia de ahorro energético cuando fueron expuestas a temperaturas ambientales por debajo de sus temperaturas críticas inferiores. *Myotis keaysi* mostró una tasa metabólica media de $1,2 \pm 0,02$ ml O₂ g⁻¹ h⁻¹ y una estrecha zona de termoneutralidad. Igualmente, la tasa metabólica basal de *Myotis oxyotus* fue de $0,92 \pm 0,04$ ml O₂ g⁻¹ h⁻¹ y mostró una zona termoneutral más extendida (7,3°C) así como un menor valor de temperatura crítica inferior (25,2°C). Los rasgos fisiológicos de ambas especies concuerdan con su distribución altitudinal y muestran fuertes contrastes en estrategias termorregulatorias con los murciélagos insectívoros de tierras bajas.

Palabras clave: Andes tropicales, murciélagos insectívoros, tasa metabólica, termorregulación, Venezuela.

¹*Corresponding author*

INTRODUCTION

The mouse-eared bats (*Myotis*) are the most taxonomically diverse genus of bat, including 97 species. *Myotis* is absent only in Polar Regions and on some oceanic islands (Wilson & Reeder 1993, Nowak 1994). Although the majority of the representatives of this genus are temperate, 14 species occur in the Neotropics (LaVal 1973). However, some of these species still face conditions which could be considered 'temperate' because they live at high elevations (2000-3000 m asl) in the tropical Andes. The mean temperatures to which they are exposed are 7-10°C lower than those recorded in the lowlands (Sarmiento 1986). Therefore, for small endotherms, the low temperatures of these Andean environments may impose important physiological constraints, which could be correlated with certain adaptive features such as changes in their thermal conductance, thermoneutral zone, and use of torpor, which could allow them to inhabit these environments.

Myotis oxyotus (Peters, 1866) and *M. keaysi* (J. Allen, 1914) are the largest, most furred, species of *Myotis* and the only ones generally restricted to montane localities (> 1000 m asl) at the north of the Orinoco River in Venezuela (Handley 1976, Linares 1998). *Myotis oxyotus* (Montane myotis; body mass = 4.5-6.3 g) and *M. keaysi* (Hairy-legged myotis; body mass = 4.7-5.6 g) are morphologically similar in terms of body size, density and pelage colour, as well as shape of wing, sharing the same foraging strategy, consisting of slow, short and maneuverable flights (Norber & Rayner 1987, Linares 1998, Canals *et al.* 2001). Both species are considered to be mountain dwellers because captures of *M. oxyotus* have been restricted to elevations between 1500 and 3150 m, and captures of *M. keaysi* are restricted to 1100-2400 m (LaVal 1973). We used museum specimens housed in the Colección de Vertebrados de la Universidad de Los Andes (CVULA) Mérida-Venezuela, and we found that 87% and 98.6% respectively of the capture locations ($n = 54$) for *M. oxyotus* and ($n = 70$) for *M. keaysi* were above and below 2000 m, respectively; suggesting that, for the Venezuelan Andes these two species are altitudinally segregated (Soriano *et al.* 1999).

Such altitudinal segregation could be due to these animals having evolved physiological features allowing them to occupy different altitudinal belts, avoiding competition. However, adaptation by one

species to a specific belt could limit its ability to inhabit other elevations being the result an altitudinal segregation (Soriano *et al.* 2002).

There are a number of physiological characteristics that could allow tropical mountane insectivorous bats to cope with low temperatures: (1) displacement of the thermoneutral zone towards lower temperature values coupled with an increase in insulation (i.e. reduced thermal conductance); (2) an increase of the basal metabolic rate and displacement of the thermoneutral zone toward lower temperature values, leaving thermal conductance constant; (3) increased basal metabolic rate (BMR) and thermal conductance, maintaining the same thermoneutral zone; and (4) the use of hypothermia and/or torpor (Studier & O'Farrell 1976, Wang & Wolowyt 1988, Geiser 1993, Song & Geiser 1997, Soriano 2000, Speakman & Thomas 2003, Geiser 2003, Turbill *et al.* 2003, Geiser 2004a, Geiser 2004b, Geiser *et al.* 2004).

The purpose of our study was to examine adaptive physiological responses of these two species of montane insectivorous bats in order to explain their different altitudinal ranges, and compare their physiological responses respect to other tropical insectivorous bats from lowlands.

MATERIALS AND METHODS

Between August and September 2004, we measured 12 *M. keaysi* specimens (2 males and 10 females) from Cueva del Pirata, 600 m south-east of La Azulita (71°26'20''W; 08°42'57''N) Mérida State (1000 m asl), located in a montane semi-caducifolious forest *sensu* Ataroff & Sarmiento (2003). Additionally, on November and December 2004 and separated about 40 km from Cueva del Pirata, we captured 12 *M. oxyotus* (8 males and 4 females) at La Mucuy 10 km north-east of the city of Mérida (71°02'00''W; 08°38'10''N) caught at 2200 m in a montane cloud forest *sensu* Ataroff & Sarmiento (2003).

We only studied adult individuals and females which did not exhibit signs of reproductive activity (pregnancy or lactation). Both species were captured in mist nets set between 19h00 and 20h00 outside roost sites. Bats were kept individually in cloth bags, transported to the laboratory and hand fed mealworms larvae (*Tenebrio molitor*) and water at a thermally controlled room (22°C) for 1-2 wk (Kunz & Kurta 1988, Wilson 1988). To calibrate the experiment durations, we left the trial

running all day (08h00-18h00) and determined that 6 h was sufficient to attain the lowest oxygen consumption values. In all experiences, when we obtained several lower values, we took the single lowest value. Therefore, all our trials had a minimum duration of 6 h. We began all measurements at 08h00, at least 8 h after bats fed, to ensure individuals were post-absorptives. Animals captured for this study were humanely treated, according to ASM guidelines.

We carried out four experiments daily (two simultaneously) with four different individuals (two at the same ambient temperature), thus we obtained one measurement from each bat every day. The animals used in the second pair of trials were introduced into a chamber at the given temperature, 2 h before it was connected to the oxygen analyzer. Each individual was trialed a total of 4-6 times, avoiding to repeat the treatment to the same individual at a given ambient temperature. We used the bats in all experimental conditions such as ambient temperature, metabolic chamber and analyzer channel.

For each species, we measured the metabolic rates (VO_2), and body temperatures (T_b), and calculated the thermal conductances (C'). The ambient temperature intervals over which metabolism values were measured were the same for both species (between 2 and 35°C). We took the measurements in an open-flow respirometer using the following protocol: we placed the bat in a 450-ml airtight chamber, with mesh plastic walls and a roof allowing the animal to rest in a normal position. We submerged the chamber in a thermally controlled bath. We recorded T_a inside the chamber using thermocouples connected to a HH23 Microprocessor Digital Thermometer (Omega, Stamford, Connecticut). Air was pumped from the ventilated room through the chamber, maintaining an air flow of 95-110 ml min⁻¹, measured by a Matheson 601 rotameter (Secaucus, New Jersey).

We obtained the flow values of rotameter from a calibration curve furnished by the manufacturer. To ensure adequate mixing of air in the chamber, incoming and outgoing air were injected and taken from different levels. Outgoing air flowed through a column of indicating silica gel to dehydrate it, then through a column of indicating soda lime which absorbed CO₂, and finally through another column of indicating silica gel which absorbed the water produced in the preceding

reaction.

The O₂ in this water-free and CO₂-free air was measured by an oxygen sensor which contained a porcelain galvanic cell connected to an Applied Electrochemistry Oxygen Analyzer S3A-II (Ametek, Pittsburgh, Pennsylvania, USA), and the signal from the sensor was transferred to a data acquisition system (built by the Scientific Instrumentation Laboratory of the University of the Andes, Mérida, Venezuela) and connected to a personal computer. Before and after each experiment, we calibrated the oxygen analyzer, obtaining the baseline by passing air through the circuit without connecting the metabolic chamber.

Once the experiment was concluded we measured body temperature using a thermocouple connected to the HH23 Microprocessor Digital Thermometer, and body mass using an analytical balance (Sartorius, Göttingen, Germany) to the nearest 0.1 g. Metabolism, as determined by rate of oxygen consumption, was calculated and expressed as a mass-specific rate using the equation of Depocas & Hart (1957):

$$VO_2 = \frac{(F_1O_2 - F_2O_2)V_2}{(1 - F_1O_2)m}$$

where F_1O_2 represents the O₂ fraction of excurrent air obtained before and after connecting the chamber to the circuit, F_2O_2 is the minimal O₂ fraction recorded while the chamber was connected to the circuit, V_2 is the air flux in ml h⁻¹, and m is the body mass in g.

Dry thermal conductance was calculated using McNab's (1980) equation:

$$C' = \frac{VO_2}{(T_b - T_a)}$$

and the relevant values of VO_2 , T_b , and T_a . All results were corrected to standard values of pressure and temperature. We used a sigmoid function to describe the effect of T_a on the metabolic rate, because it showed the better fit. The values of BMR, and C' were compared with those expected, using allometric standard equations for bats: BMR = 2.97 m^{-0.256} (Speakman & Thomas 2003); BMR in ml O₂ g⁻¹ h⁻¹ and m in g; $C' = 1.54 m^{-0.54}$

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(Bradley & Deavers 1980; C' in $\text{ml O}_2 \text{g}^{-1} \text{h}^{-1} \text{°C}^{-1}$). Statistical significance was accepted at $P=0.05$. Mean values are presented ± 1 SE (with n = number of measurements).

For neither bat species, could we use the method of Nickerson *et al.* (1989) because of the narrowness of the thermal neutral zone. Therefore, we determined the lowest ambient temperature at which the bat maintained basal metabolic rates (lower-critical temperature, T_{lc}), as the temperature values at which VO_2 values began to be temperature dependent. Excluding a point at a time, until have the slope value was zero ($P > 0.05$ and $r^2 = 0.001$). Using the same procedure, we obtained an approximation to upper critical temperature (T_{uc}) as the inflection point in metabolic rates as T_a increased.

To test for differences between sexes, we employed Wilcoxon's non-parametric test, because in both species, one of sexes was represented by few individuals. We used an analysis of covariance (ANCOVA) to test the impact of different factors on BMR for different species of insectivorous bat from literature available data. Thus, \log_{10} of BMR = $f(\log_{10}$ body mass and elevation).

RESULTS

Myotis keaysi

This species did not maintain its body temperature, below a lower critical temperature of about 29.2°C (Figure 1). This relation may be represented by the equation:

$$T_b = 0.615 + 1.066 T_a$$

$$(r^2 = 0.965; P < 0.001; n = 52)$$

Below T_{lc} all individuals used torpor (line a, Figure 1). We adjusted the relation between metabolic rate and T_a in the whole considered interval using a logistic sigmoid function, which showed the better fit, and it is represented by the equation:

$$\text{VO}_2 = 0.215 + 0.99 / (1 + \exp(-T_a - 28.7) / 0.533))^{0.154}$$

$$(r^2 = 0.89; P < 0.0001; n = 61)$$

This equation showed an increment of metabolic rate with the ambient temperature. The thermoneutral zone (TNZ) ranged from $T_{lc} = 29.2 \text{°C}$ ($P = 0.917$, $r^2 = 0.001$) to $T_{uc} = 33.4 \text{°C}$

(line b, Figure 1) with BMR being $1.2 \pm 0.02 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$ ($n = 12$). This was independent of T_a and represents 61% of the expected value for a bat with an average body mass of $5.0 \pm 0.18 \text{ g}$. The lowest metabolic rate was obtained below 20°C (line c, Figure 1), corresponding to a torpor metabolic rate (TMR) of $0.25 \pm 0.02 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$ ($n = 26$). There were no significant differences between males and females for BMR ($P = 0.273$, $n = 12$) or TMR ($P = 0.855$, $n = 26$). C' was independent of T_a when $T_a < 15 \text{°C}$ (line d, Figure 1) with an average value of $0.18 \pm 0.03 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1} \text{°C}^{-1}$ ($n = 13$), which corresponds for torpid animals only.

Myotis oxyotus

In our experiences, individuals of this species did not maintain a constant T_b (line a, Figure 2). This relationship was represented by the equation

$$T_b = 0.705 + 1.071 T_a$$

$$(r^2 = 0.919; P < 0.001; n = 30)$$

All individuals entered torpor at T_a below $T_{lc} = 25.2 \text{°C}$ (line b, Figure 2). We adjusted this relation to a logistic sigmoid function represented by the equation

$$\text{VO}_2 = 0.358 + 0.56 / (1 + \exp(-T_a - 25.1) / 0.027))^{0.04}$$

$$(r^2 = 0.80; P < 0.0001; n = 45)$$

Similarly, this equation represents the increment of metabolic rate with the ambient temperature. TNZ values were between $T_{lc} = 25.2 \text{°C}$ ($P = 0.989$, $r^2 = 0.000$) and $T_{uc} = 32.5 \text{°C}$ (line b, Figure 2), and the average value of BMR was $0.92 \pm 0.04 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$ ($n = 15$), representing 46% of the expected value for a bat with the body mass of *M. oxyotus* ($4.85 \pm 0.16 \text{ g}$). We found significant differences in BMR between both species ($P = 0.0033$). TMR was reached when $T_a < 23.3 \text{°C}$, and the average value was $0.36 \pm 0.02 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$ ($n = 19$). There were no significant differences between males and females in BMR ($P = 0.787$, $n = 15$) or TMR ($P = 0.944$, $n = 27$). C' was independent of T_a when $T_a < 16.8 \text{°C}$ (line d, Figure 2), with an average value of $0.23 \pm 0.03 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1} \text{°C}^{-1}$ ($n = 17$), which corresponds for torpid animals only.

Our ANCOVA analysis using the available data (Table 1) for 15 tropical insectivorous bats

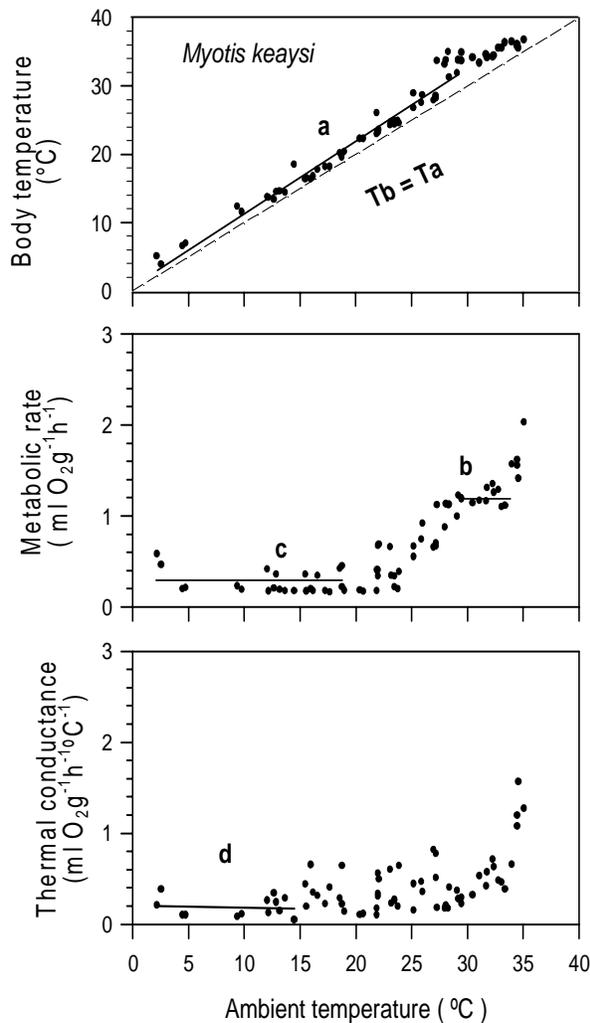


Figure 1. Relationship between body temperature (T_b), rate of metabolism (VO_2), thermal conductance (C'), and ambient temperature (T_a) in *Myotis keaysi* (12 individuals). Abbreviations: a, regression of body temperature below thermoneutral zone; b, average metabolic rate in thermoneutral zone (TNZ); c, torpor metabolic rate (TMR); d, minimal thermal conductance. Dashed line: body temperature (T_b) equal to ambient temperature (T_a).

(12 from lowlands and 3 from highlands) indicated that \log_{10} BMR was significantly related to \log_{10} (body mass) ($F = 57.9$; $df = 1$; $P < 0.05$) and elevation range ($F = 8.59$; $df = 1$; $P < 0.05$), which was represented by the equation $\log_{10}(\text{BMR}) = 0.295 + 0.745 \log_{10}(m) - 0.112 e_h$; where m = body mass and e_h = elevation for highland species.

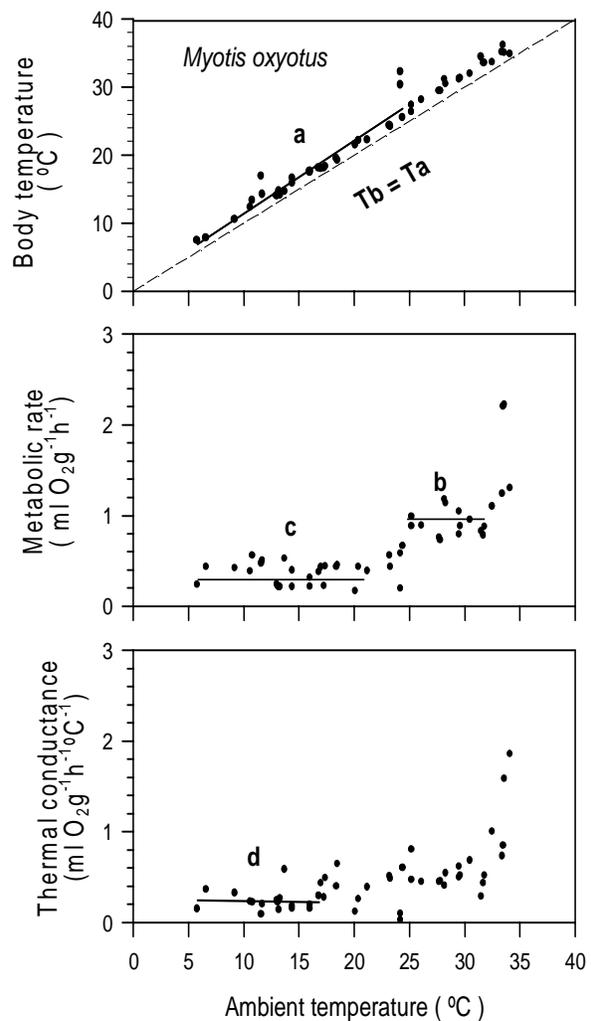


Figure 2. Relationship between body temperature (T_b), rate of metabolism (VO_2), thermal conductance (C'), and ambient temperature (T_a) in *Myotis oxyotus* (12 individuals). Abbreviations: a, regression of body temperature below thermoneutral zone; b, average metabolic rate in thermoneutral zone (TNZ); c, torpor metabolic rate (TMR); d, minimal thermal conductance. Dashed line: body temperature (T_b) equal to ambient temperature (T_a).

DISCUSSION

Our results indicate that both *M. keaysi* and *M. oxyotus* enter torpor when $T_a < T_{lc}$. This represents an important difference from the laboratory data obtained from some lowland tropical insectivorous non-vesperilionid bats, which are

Table 1. Energetic variables for insectivorous bat species from Tropical lowlands and Andean highlands. For basal metabolic rate predicted value is from Speakman & Thomas (2003).

Species	Source ^a	Habitat ^b	Body mass (g)	Basal metabolic rate		Torpor metabolic rate (ml O ₂ h ⁻¹)	Thermal conductance (ml O ₂ h ⁻¹ °C ⁻¹)	Lower critical temperature (°C)	Upper critical temperature (°C)
				(ml O ₂ h ⁻¹)	% Predicted				
Vespertilionidae									
<i>Myotis keaysi</i>	A	H	5.0	1.2	61	0.25	0.18 ^(c)	29.2	33.4
<i>Myotis oxyotus</i>	A	H	4.8	0.92	46	0.36	0.23 ^(c)	25.2	32.5
Molossidae									
<i>Tadarida brasiliensis</i>	H	H	11.0	0.78	48.4	-	0.22	26.3	32.7
<i>Molossus molossus</i>	F	L	16	1.25	85.6	-	-	-	-
<i>Eumops perotis</i>	E	L	56	0.71	67	-	-	31.0	-
Mormoopidae									
<i>Mormoops blainvilli</i>	G	L	8.9	0.97	57	-	-	-	-
<i>Mormoops megalophylla</i>	B	L	16.5	1.46	100.7	-	0.3	33.5	39.5
<i>Pteronotus davyi</i>	B	L	9.4	1.63	97.6	-	0.4	34.5	43.0
<i>Pteronotus parnellii</i>	B	L	19.2	1.6	115.1	-	0.26	34.0	40.5
<i>Pteronotus personatus</i>	B	L	14.0	1.64	108.6	-	0.3	34.0	38.5
<i>Pteronotus quadridens</i>	G	L	4.8	1.25	62.8	-	-	-	-
Emballonuridae									
<i>Peropteryx macrotis</i>	D	L	5.1	2.31	117.8	-	0.55	30.5	37.0
<i>Saccopteryx bilineata</i>	C	L	8.2	1.86	107.5	-	0.32	-	-
<i>Saccopteryx leptura</i>	C	L	4.2	2.26	110.2	-	-	-	-
Natalidae									
<i>Natalus tumidirostris</i>	D	L	5.4	1.54	79.8	-	0.41	28.0	35.5

^a Source of data: A, this study; B, Bonaccorso *et al.* (1992); C, Genoud & Bonaccorso (1986); D, Genoud *et al.* (1990); E, Leitner (1966); F, McNab (1969); G, Rodríguez-Durán (1995); H, Soriano *et al.* (2002). ^b Habitat: H, highlands; L, lowlands.

apparently not capable of doing this (Bonaccorso *et al.* 1992, Genoud & Bonaccorso 1986, Genoud *et al.* 1990, Genoud 1993, Rodriguez-Durán 1995).

Torpor is a strategy used to save energy, and this mechanism is likely more important in small bats which inhabit environments with high thermoregulatory costs, due to their high surface-volume ratio (McNab 1969, Speakman & Thomas 2003, Geiser & Körtner 2004). This acquires a remarkable importance for daily torpor, in which bouts usually last <12 h occur within a 24-h cycle (Geiser *et al.* 2004). In addition, representatives of tropical bat families such as Emballonuridae, Mormoopidae, Thyropteridae, Furipteridae and Natalidae, are never or rarely found above 1000 m asl (Nowak 1994). The capacity to enter torpor could be one of the possible factors that allow insectivorous bats, such as Molossidae and Vespertilionidae, to inhabit tropical highlands (Soriano 2000, Soriano *et al.* 2002). Therefore, temperate origin of South American vespertilionid bats could represent an advantage in terms of their adaptive features to face cool environments, occupying successfully those montane environments in which representatives of tropical families of insectivorous bats cannot reach because they are not capable of entering torpor.

The fact that the *Myotis* species studied here employed torpor whereas the bats from the tropical families previously studied did not, could be explained by their phylogenetic differences. However, in Neotropical lowlands there are vespertilionids that do not live above 1000 m. Therefore, this restriction in altitudinal distribution could indicate that these lowland vespertilionid bats have the same physiological limitation as representatives of those families. Further thermoregulatory information about lowland tropical vespertilionid bats is required to better support this statement.

Although we know that the patterns of torpor exhibited in the laboratory can vary from those under natural conditions (Geiser *et al.* 2000), the individuals with which we worked maintained or increased their body mass, during the experimentation period. Therefore, we do not believe that torpor was a laboratory artifact. Although our data of TMR show important differences (about 10-fold higher) with those available for vespertilionid bats from temperate environments (Speakman & Thomas 2003), comparisons must be done with tropical vespertilionids, because these animals only enter

daily torpor unlike temperate vespertilionids which can enter both seasonal and daily torpor. Therefore, these data could not be directly compared, and further information on TMR from Neotropical vespertilionids must be obtained.

It has been proposed that temperate insectivorous bats have a limited thermoregulatory capacity and they frequently use torpor as a consequence of their low body masses, low BMR and C' , or as a result of variation in resource availability (McNab 1969, 1982, Kurta & Kunz 1988). However, Bonaccorso *et al.* (1992) argued that torpor is not a direct consequence of small size and normal (or low) BMR; on the contrary, conditions that enhance torpor in small-sized bats also contribute to induce low BMR and low C' , as was established for certain vespertilionid bats (Willis *et al.* 2005).

Taking into account that in the tropical Andes the altitudinal thermal gradient is 0.6°C per 100 m (Sarmiento 1986), the relatively narrow TNZ (4.2°C) exhibited by *M. keaysi* (29.2 – 33.4°C; Table 1), could be only explained 700 m of 1300 m corresponding to the known altitudinal range for this species (1100-2400 m). Supposing that under natural conditions the individual response was the same, theoretically this means that between 1100-1800 m an individual could maintain a high body temperature without increasing its energetic expenditures, assuming the temperature in that altitudinal band was above the T_{lc} . We speculate that clustering (social thermoregulation) could improve the individual thermal balance (Audet & Fenton 1988, McNab 1974) and allow it to inhabit the rest of the range.

M. oxyotus individuals had a lower T_{lc} than *M. keaysi* (25.2°C; Table 1) and a broader thermoneutral zone (7.3°C (Table 1). If prey and roost are enough, a reduced T_{lc} should translate into a greater ability for establishing roosts at higher elevations with lower ambient temperatures, without minimal additional energy expenditure. Nevertheless, this ability to occupy higher elevations did not seem to prevent *M. oxyotus* for using lower montane environments. Although *M. oxyotus* was also capable of using clustering (pers. obs.) and selecting warmer roosts to maintain body temperature, our data of TNZ could indicate that this individual physiological response enabled it to inhabit most of its altitudinal interval (1216 of 1650 m). Thus, the metabolic patterns of a species could give it certain plasticity and

advantages for both initiation of colonies and resource exploitation.

Both species can use torpor, and have low BMR, C' and T_{lc} values. These features contrast with those of non-*Myotis* bats from Neotropical lowlands which do not enter torpor and have higher BMR and T_{lc} values (Table 1). Thus we suggest that both species of *Myotis* are suited to montane environments, although they inhabit different elevation ranges. However, the fact that these species show differences in their BMR could reflect adaptations to specific altitudinal intervals. Furthermore, laboratory data for *Tadarida brasiliensis* (Table 1), another insectivorous (Molossidae) bat from the Venezuelan Andes, showed that all assayed individuals entered into torpor at $T_a < 22^\circ\text{C}$ and their BMR was lower than *M. oxyotus*, instead having higher body mass; nevertheless, their TNZ was almost the same (Table 1; Soriano *et al.* 2002).

Finally, differences uncovered by our ANCOVA analysis based on BMR support the hypothesis that tropical insectivorous bats from highlands and lowlands have different physiological features (Soriano 2000, Soriano *et al.* 2002, this paper). These may include physiological and anatomical characteristics such as use of torpor, low BMR and T_{lc} , as well as dense and long fur, a hairy uropatagium and hind feet, and relatively high body mass, with respect all representatives of the genus in Venezuela, which can be understood as energy-conserving mechanisms necessary to survive in cold environments. On the other hand, all tropical insectivorous bats from lowlands studied to date, exhibit physiological and anatomical features, such as short-haired, naked uropatagium and legs, inability to enter torpor, and higher T_{lc} , which appear to be adaptive for warmer conditions. This argument seems to be supported by the species replacement that can be observed along an Andean altitudinal gradient (Graham 1983). Likewise, we could expect that one tropical species exhibits regional differences according local environmental characteristics, such as has been reported for some vespertilionid bats from temperate latitudes (Willis *et al.* 2005).

CONCLUSIONS

The available evidence at date suggests that the use of torpor, low BMR and T_{lc} typify the thermoregulatory behaviour of the Neotropical

insectivorous bats which occur in mountain environments (Soriano *et al.* 2002, and this paper). These strategies are not found in bats from Neotropical lowlands.

Although individual BMR values did not allow us to explain the altitudinal segregation between *M. keaysi* and *M. oxyotus*, T_{lc} values and TNZ range support the fact that *M. oxyotus* occurs at higher elevations and has a more extended elevations range than *M. keaysi*. Further complementary field and laboratory studies are required to elucidate the adaptive thermoregulatory pattern of other tropical insectivorous bat species.

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