

PHYSIOLOGICAL RESPONSES TO AMBIENT TEMPERATURE MANIPULATION BY THREE SPECIES OF BATS FROM ANDEAN CLOUD FORESTS

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In this paper we test the hypothesis that bats of the Andean highlands show distinctive metabolic responses compared with bats from lowland forests. We compared existing literature with new information on 3 bat species having the following food habits: a nectarivore (*Anoura latidens*), a frugivore (*Sturnira erythromos*), and an insectivore (*Tadarida brasiliensis*). Basal metabolic rate, as determined by oxygen consumption, thermal conductance, and body temperature were measured at ambient temperatures of 10–38°C. Some distinctive metabolic responses of these bat species, although varying with respect to food guild, allow us to separate them from counterpart species that are typically found in lowland forests. *A. latidens* is characterized by higher basal metabolic rate; however, thermal conductance and lower critical temperature values do not show an adaptation to cool environments, as expected. *S. erythromos* also increases its basal metabolic rate, but it maintains thermal conductance as expected, which implies a very important displacement of thermoneutral zone to lower temperatures. At temperatures below lower critical temperature, in addition to an endothermic response, *S. erythromos* sometimes expresses a hypothermic response or facultative torpor, independent of sex and body mass. *T. brasiliensis* has a lower basal metabolic rate and thermal conductance and also has its thermoneutral zone range displaced toward lower temperatures. Likewise, this species enters obligate torpor when ambient temperatures are below 22°C.

Key words: Andes, *Anoura latidens*, bats, cloud forests, metabolic rate, *Sturnira erythromos*, *Tadarida brasiliensis*, thermoregulation, Venezuela

In the bat communities of Andean cloud forests, frugivores represent the most species-rich guild, in contrast with lowland rain forest bat communities, where insectivores are the dominant guild (Fleming 1986; Graham 1983; Patterson et al. 1996; Soriano 2000; Soriano et al. 1999). Apparently, insectivores of tropical origin have a limit to their vertical distribution that prevents them from accessing Andean cloud

forests, and only some Vespertilionidae of Nearctic origin reach these forests, along with a few representatives of the Molossidae (Soriano 2000; Soriano et al. 1999).

Variations in metabolism observed in bats are mainly related to body mass and feeding habits: bats with insectivorous or hematophagous diets have low rates of metabolism; bats with combined diets (frugivore–carnivore) have low-to-intermediate rates of metabolism; frugivores have high rates of metabolism; and metabolic rates for

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nectarivores are very high. Associated with basal metabolic rate is the capacity to regulate body temperature; therefore, within the same feeding habit, large bats regulate their temperature better than small ones. Similarly, for bats of a given body mass, insectivores maintain lower body temperatures and are more dependent on environmental temperature variations than frugivores (Bonaccorso and McNab 1997; McNab 1969, 1970, 1982a, 1983, 1984, 1986, 1989).

At altitudes between 2,000 and 3,000 m in the tropical Andes, the mean temperature is 7–10°C lower than in the lowlands (Sarmiento 1986). By virtue of their lower temperatures, high mountain environments demand higher energetic expenditures for endotherms to maintain a constant body temperature. Therefore, for endotherms, the low temperatures of montane environments may impose important physiological constraints on the possession of an adequate energetic balance. Such constraints seem to occur in members of the Emballonuridae, Mormoopidae, Thyropteridae, Furipteridae, and Natalidae families, which never or rarely are found at elevations above 1,000 m (Graham 1983; Patterson et al. 1996; Soriano 2000; Soriano et al. 1999).

Successful adaptation to cold environments presupposes modifications of physiological responses characterizing high mountain species. Among such adaptive modifications, are one or several of the following physiological features: increase of basal metabolic rate, displacement of thermoneutrality zone to a lower temperature range, decrease of thermal conductance by compensatory increase of insulation, and daily facultative or obligatory torpor.

The purpose of this paper is to examine adaptive responses of 3 bat species with different food habits; responses, which the species use to solve problems of survival and energy balance in neotropical high mountains. Thus, we will take into account theoretical aspects of metabolism and temperature regulation to characterize physio-

logical features that distinguish some species that are capable of living in such environments.

MATERIALS AND METHODS

The species chosen for this study inhabit the Andean cloud forest (>2,000 m elevation) and belong to each of the 3 different dietary types found in this ecological unit. Thus, we worked with *Anoura latidens*, a nectar–polinivorous species with a wide elevational range (50–2,240 m) but found most frequently in montane localities (Handley 1984); *Sturnira erythromos*, a frugivorous bat that occurs in montane environments with a narrow elevation range in Venezuela (1,000–2,500 m—Handley 1976); and *Tadarida brasiliensis*, an insectivorous bat with a wide distribution range, which includes subtropical regions of North and South America and the tropical Andes (Wilkins 1989). In South America, *T. brasiliensis* seems to be absent in the Amazonian basin, and although it seems to prefer the mountain region in the Neotropics (up to 2,107 m—Handley 1976), this species may be found at low elevations (Koopman 1982; Wilkins 1989).

The study was carried out with 1 individual (female) of *A. latidens*, 10 individuals of *S. erythromos* (4 males and 6 females), and 5 individuals of *T. brasiliensis* (4 males and 1 female), all captured in a cloud forest in Valle Grande, 8 km NE of the city of Mérida, at 2,400 m elevation. All the bats examined were adults, and the females did not show signs of reproductive activity (pregnancy or lactation). Individuals of *T. brasiliensis* were captured with mist nets near their shelter when they returned after nocturnal activities, between 0500 and 0630 h. They were brought to the laboratory for experiments and hand fed for 4 days with the feeding formula of Wilson (1988). Bats of *S. erythromos* and *A. latidens* were mist-netted between 1900 and 2300 h, isolated in cloth bags, and fed commercial baby food (fruit). In the laboratory, each bat was taxonomically identified and the following characteristics were recorded: sex, body mass, relative age, and reproductive condition. Bats were placed in metal cages (Wahman, Baltimore, Maryland), 22.5 by 17.5 by 38 cm, with plastic mesh walls and roof to allow bats to attach more easily. They were maintained in a temperature controlled room at 21°C. All experiments were started at least 4 h after the last food ingested

by the bats, to guarantee their postabsorptive condition.

For each species, metabolic rate ($\dot{V}O_2$), body temperature, and thermal conductance were measured. Although temperature intervals were not the same for each species, the experiments were done at ambient temperatures between 10 and 38°C. Measurements were taken in an open-flow respirometer using the following protocol: The bat was placed in an hermetic metabolic chamber of 450 ml with mesh plastic walls and roof to allow it to rest in a normal position. A sufficient quantity of lead bullets was put at the bottom of the chamber to permit submersion in a thermally controlled bath. Ambient temperatures inside the metabolic chamber were measured by thermocouples connected to a HH23 Microprocessor Digital Thermometer (Omega, Stamford, Connecticut). Air was pumped from the room through the chamber, maintaining an air flow of 70–80 ml/min, measured by a Matheson 601 rotameter (Secaucus, New Jersey). To ensure adequate mixing of air in the chamber, incoming and outgoing air tubes were placed at different levels. Outgoing air flowed through a column of indicating silica gel to dehydrate it, through another column of indicating soda lime that absorbed CO_2 , and finally through another column of indicating silica gel that absorbed the water produced in the preceding reaction. The O_2 in this water-free and CO_2 -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), and the signal from the sensor was transferred to a Cole Parmer (Chicago, Illinois) 8373-30 pen recorder. Before and after each experiment, baseline values for fraction of O_2 were obtained, passing air through the circuit without connecting the metabolic chamber. After 1.5 h and after O_2 consumption reached a minimum level at least once, the bat was taken from the chamber, body temperature was measured with a rapid-read thermometer, and body mass was measured. Rate of metabolism, as determined by rate of oxygen consumption, was calculated and expressed as a mass-specific rate with the equation of Depocas and Hart (1957):

$$\dot{V}O_2 = \frac{(F_1O_2 - F_2O_2)V_2}{(1 - F_1O_2)m}$$

where F_1O_2 represents the O_2 fraction in outgoing air obtained before and after connecting the chamber to the circuit, F_2O_2 is minimal O_2 fraction recorded while the chamber is connected to the circuit, V_2 is air flow in milliliters per hour, and m is body mass in grams.

Dry thermal conductance was calculated with the equation of McNab (1980):

$$C' = \frac{\dot{V}O_2}{(T_b - T_a)}$$

using corresponding values for rate of oxygen consumption ($\dot{V}O_2$), body temperature (T_b), and ambient temperature (T_a). All results were corrected to standard values of pressure and temperature. Linear regressions were used to test the effect of ambient temperature on physiological parameters measured. Values of basal metabolic rate (BMR), and thermal conductance (C') were compared with those expected, using allometric standard equations for mammals: $BMR = 3.45m^{-0.287}$ (McNab 1988—BMR in ml O_2 g^{-1} h^{-1} and m in grams); $C' = 1.02m^{-0.5}$ (Herreid and Kessel 1967— C' in ml O_2 g^{-1} h^{-1} $^{\circ}C^{-1}$). Statistical significance was accepted at $P \leq 0.05$. Mean values are presented as $\pm 1 SE$ (with n , number of measurements).

The lowest temperature at which a bat maintained its basal metabolic rate (lower critical temperature) was determined by finding the intersection between regression lines with best fit to data, calculated by minimal squares method for values inside and below the zone of thermal neutrality (Nickerson et al. 1989). In the case of *A. latidens*, the method of Nickerson et al. (1989) was not feasible because this species showed different conductances in and below thermal neutrality; consequently, we define lower critical temperature as the minimal value of ambient temperature in which the range of basal metabolic rate was independent of ambient temperature. An approximation to upper critical temperature was obtained as the inflection point in metabolic rate as ambient temperature increased. Differences in metabolic rate as well as in thermal conductance between normothermic and hypothermic bats were tested using 1-way analysis of variance. Analysis of covariance (ANCOVA) was used to test the impact of various factors on basal rate of different species of tropical bats for which data were available from the literature. Thus, \log_{10} of basal metabolic rate

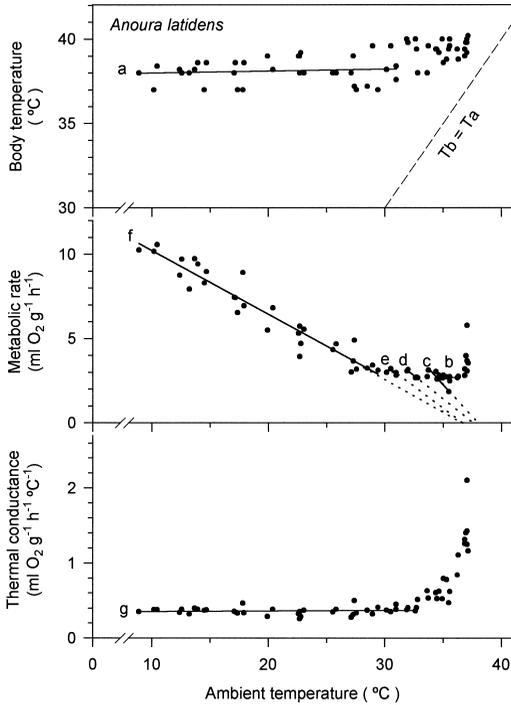


FIG. 1.—Relationship among body temperature (T_b), rate of metabolism ($\dot{V}O_2$), thermal conductance (C'), and ambient temperature (T_a) in *Anoura latidens* (1 individual). Abbreviations: a, regression of body temperature below thermoneutral zone; b, average metabolic rate in thermoneutral zone; c, regression of metabolic rate below lower critical temperature; d and e, metabolic rates whose slopes show intermediate thermal conductances; f, metabolic rate with the minimal thermal conductance; g, minimal thermal conductance. Dotted line: body temperature (T_b) equal to ambient temperature (T_a).

= $f(\log_{10}$ body mass, maximal elevation range, and diet).

RESULTS

Anoura latidens.—For this nectarivorous species, we captured only 1 adult female that was not pregnant or lactating and whose body mass (13.6 g) was in the range of the species (Linares 1998). The response of this individual to environmental temperatures was that of a typical endotherm (Fig. 1). It did not become torpid but maintained a relatively high and constant body temper-

ature ($38.12 \pm 0.12^\circ\text{C}$; $n = 35$), which was independent of environmental temperature below 31°C (line a, Fig. 1; $P = 0.54$).

Thermoneutrality was between lower critical temperature, 34.7°C , and upper critical temperature, 36.2°C . In this interval, the rate of oxygen consumption was independent of ambient temperature ($P = 0.28$; $n = 7$; line b, Fig. 1), with an average basal metabolic rate of $2.71 \pm 0.045 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n = 7$), which is 166% the expected value for a mammal with body mass of 13.5 g. Above upper critical temperature, the rate of metabolism increased steeply. Below lower critical temperature (about 34.7°C), 4 conductances can be defined: 1 that describes lower critical temperature (line c, Fig. 1, with a slope of -0.77), 1 that describes minimal thermal conductance (line f, Fig. 1), and 2 that are intermediate (lines d and e, Fig. 1, with slopes of -0.53 and -0.66 , respectively). The rate of metabolism for minimal conductance increases linearly and inversely with ambient temperature (line f, Fig. 1). This relation may be represented by the equation $\dot{V}O_2 = 14.01 - 0.38T_a$ ($r^2 = 0.93$; $P = 0.0001$; $n = 32$). Theoretically, this regression line intercepts the ambient temperature axis at body temperature value. Our results show this interception point at 36.7°C , with 95% confidence interval covering the range of body temperatures recorded during our experiments.

Below the thermoneutral zone, thermal conductance (line g, Fig. 1) did not vary with ambient temperature, and the slope of the regression line did not show significant differences from zero ($P = 0.49$). Minimal average of thermal conductance, $C' = 0.36 \pm 0.007 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($n = 39$), represents 128% of the expected value for a mammal with body mass of 13.5 g.

Sturnira erythromos.—Two contrasting types of response to low ambient temperatures are recognized in this frugivorous species, which were independent of sex and body mass. Whereas in some cases, bats were capable of maintaining high and con-

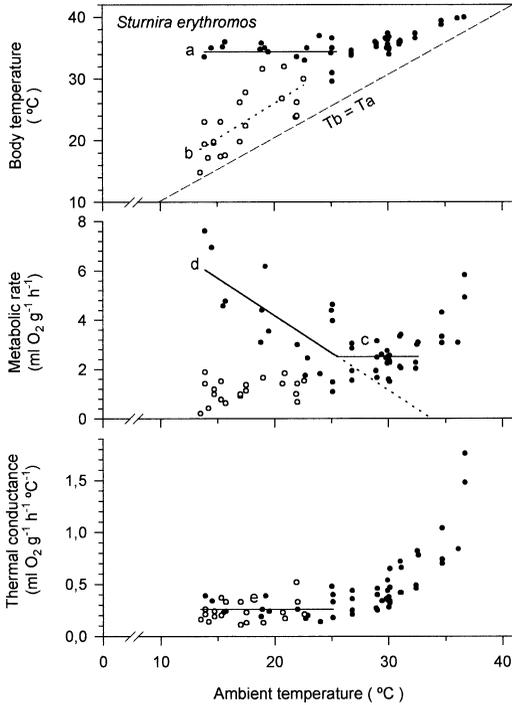


FIG. 2.—Relationship among body temperature (T_b), rate of metabolism ($\dot{V}O_2$), thermal conductance (C'), and ambient temperature (T_a) in *Sturnira erythromos* (10 individuals). Abbreviations: a, body temperature of normothermic bats below thermoneutral zone; b, body temperature of hypothermic bats below thermoneutral zone; c, average metabolic rate in thermoneutral zone; d, regression of metabolic rate below lower critical temperature; e, thermal conductance of normothermic and hypothermic bats below thermoneutral zone. Dotted line: body temperature (T_b) equal to ambient temperature (T_a). Solid circles represent normothermic individuals, and open circles represent hypothermic individuals.

stant body temperatures (normothermia), in other cases, body temperature was dependent on ambient temperatures (hypothermia). This last response may be considered facultative torpor.

Normothermic bats maintained an average body temperature of $34.40 \pm 0.45^\circ\text{C}$ ($n = 17$), independent of ambient temperatures, between 14 and 25.5°C (line a, Fig. 2). The slope of this regression (line a, Fig.

2) did not differ significantly from 0 ($P = 0.29$). When ambient temperatures were higher than 27°C , body temperature showed a linear increase with slope approximating 1. Below 25°C , hypothermic bats showed body temperature linearly dependent on ambient temperature (line b, Fig. 2). A regression line fitted to these values is represented by the equation $T_b = 3.15 + 1.14T_a$ ($r^2 = 0.53$; $P = 0.0003$; $n = 20$).

The thermoneutral zone (line c, Fig. 2) was between lower critical temperature, 25.5°C , and upper critical temperature, $31\text{--}32^\circ\text{C}$. In this interval, oxygen consumption was independent of ambient temperature ($P = 0.34$), with an average basal metabolic rate of $2.51 \pm 0.14 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n = 34$; line d, Fig. 2), which is 161% of the expected value for a mammal with body mass of 15.9 g. Below lower critical temperature, near 25°C , normothermic bats showed a linear increase of metabolic rate as ambient temperature declined (line d, Fig. 2). This relation is expressed by the equation $\dot{V}O_2 = 10.28 - 0.31T_a$ ($r^2 = 0.47$; $P = 0.004$; $n = 16$). The projection of the regression line for metabolic rate below lower critical temperature intercepts the horizontal axis at $T_a = 33.8^\circ\text{C}$, with 95% confidence limits covering the range of body temperatures recorded during these experiments. For hypothermic bats, metabolic rate at ambient temperatures below the thermoneutral zone was lower than for normothermic bats. Above the upper critical temperature, metabolic rate of all individuals increased, and their average body temperature was 39.5°C .

When ambient temperature was below lower critical temperature, normothermic and hypothermic bats did not show significant differences in thermal conductance ($F = 1.72$; $d.f. = 1, 35$; $P = 0.20$); consequently, the average for all (line e, Fig. 2) was $C' = 0.26 \pm 0.02 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($n = 37$). Thermal conductance was independent of ambient temperature, and the slope of the regression line did not differ significantly from 0 ($P = 0.89$). Average thermal conduc-

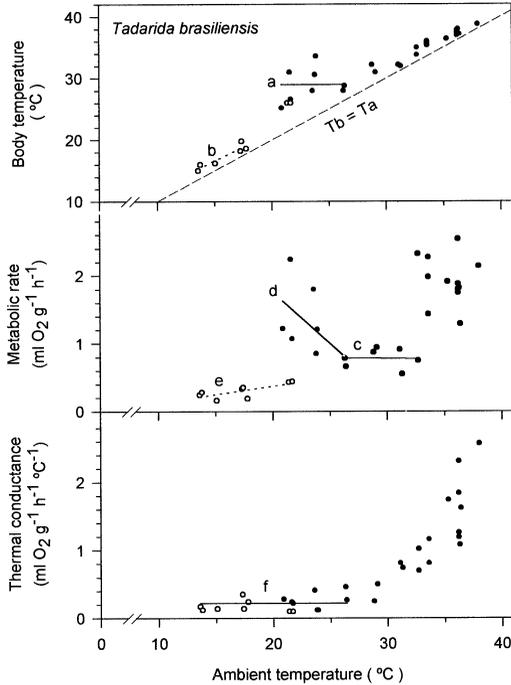


FIG. 3.—Relationship among body temperature (T_b), rate of metabolism ($\dot{V}O_2$), thermal conductance (C'), and ambient temperature (T_a) in *Tadarida brasiliensis* (5 individuals). Abbreviations: a, b, c, and d as in Fig. 2; e, regression of metabolic rate below lower critical temperature for hypothermic individuals; f, minimal thermal conductance below thermoneutral zone of normothermic and hypothermic bats. Solid circles represent normothermic individuals, and open circles represent hypothermic individuals. Dotted line: body temperature (T_b) equal to ambient temperature (T_a).

tance represents 104% of the expected value for a mammal with body mass of 15.9 g.

Tadarida brasiliensis.—This strictly insectivorous species also exhibited normothermic and hypothermic responses, both independent of sex and body mass. In experiments carried out between 21 and 26°C, bats were normothermic, maintaining an average body temperature of $28.97 \pm 0.94^\circ\text{C}$ ($n = 8$), which was independent of ambient temperatures; the slope of these values was not significantly different from 0 ($P = 0.57$; line a, Fig. 3). In experiments carried out at temperatures below 17.8°C,

body temperatures were linearly dependent on ambient temperature and 1–2°C above it. The regression line (line b, Fig. 3) indicates $T_b = 2.99 + 0.90T_a$ ($r^2 = 0.87$; $P = 0.006$; $n = 6$). The thermoneutral zone (line c, Fig. 3) is defined as values of ambient temperature between 26.3 and 32.7°C (lower and upper critical temperatures, respectively). In this range, the oxygen consumption was independent of ambient temperature ($P = 0.95$) and shows an average basal metabolic rate of $0.78 \pm 0.05 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n = 7$), which is 45% the expected value for a mammal with body mass of 11.0 g. Above maximum critical temperature, the rate of metabolism increased sharply, and the average body temperature was 35.2°C.

Within the values 26.3 and 22°C, in normothermic bats, the metabolic rate increased linearly as ambient temperature declined (line d, Fig. 3). This relation is represented by the equation $\dot{V}O_2 = 4.81 - 0.15T_a$ ($r^2 = 0.34$; $P = 0.13$; $n = 8$). This regression line intercepts the horizontal axis at ambient temperature of 31.6°C, and 95% confidence limits include the mean body temperature of $28.97 \pm 0.94^\circ\text{C}$.

All experiments carried out at temperatures below 22°C showed a hypothermic response, where values for metabolic rate were smaller than those observed in the thermoneutral zone, and they linearly decreased with ambient temperature (line e, Fig. 3). This regression line is defined by the equation $\dot{V}O_2 = -0.13 + 0.02T_a$ ($r^2 = 0.57$; $P = 0.03$; $n = 8$). When ambient temperatures were below the lower critical temperature of 26.3°C, thermal conductance of both normothermic and hypothermic bats did not differ significantly ($F = 3.25$; $d.f. = 1, 14$; $P = 0.09$; $n = 16$); average thermal conductance for all of them (line f, Fig. 3) is described by the equation $0.22 \pm 0.03 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($n = 16$). Thermal conductance was independent of ambient temperature at 13.6–26°C; consequently, the slope of regression line was not significantly different from 0 ($P = 0.44$). This average of minimal thermal conductance rep-

resents 68% of expected value for a mammal with body mass of 11.0 g.

DISCUSSION

Anoura latidens.—Absolute and mass-specific values of basal metabolic rate obtained for the montane nectarivorous bat *A. latidens* are among the highest known for glossophagine bats (Table 1). The high basal metabolic rate permits *A. latidens* to maintain constant body temperature. Such physiological response has been demonstrated previously for mammals with feeding habits based on carbohydrates (McNab 1986). All representatives of the genus *Anoura* inhabit mountain environments and use caves, caverns, and rocky shelters as diurnal refuges, where they roost in small groups (Lemke and Tamsitt 1979). Within diurnal refuges, they are exposed to ambient temperatures below their lower critical temperature (19°C—A. Ruiz, in litt.); consequently, high basal metabolic rate allows them to resist the temperature differential between their body and the environment (Arends et al. 1995).

The patterns seen in *A. latidens* tested are similar to those for *A. caudifera*, which is the only montane Neotropical species of Glossophaginae (reported up to 2,000 m elevation—Handley 1976) for which previous data are available (McNab 1969, 1982b). Thus, basal metabolic rate as a function of body mass places these montane species above the 95% confidence limits of the regression obtained for these parameters for lowland glossophagines. These 2 species also show thermal conductance values outside the 95% confidence intervals of regression obtained for thermal conductance as a function of body mass of lowland glossophagines. Nevertheless, they differ in that the value for *A. latidens* is located above that predicted by the relation of Herreid and Kessel (1967), whereas the value for *A. caudifera* is below it, as would be expected for a montane species. In addition, *A. caudifera* shows several morphological features that may increase insulation, such as

long and dense fur, reduced uropatagium, hairy feet and toes, and small ears (Handley 1984). Such features are in agreement with their lower-than-expected conductance value (Table 1). Although *A. latidens* shares with *A. caudifera* some of these features, further data for more individuals are required to fully characterize this species.

With the exception of high conductance, our results are in agreement with predictions made about highland nectarivores, whose rich carbohydrate diet does not impose constraints on energy expenditure and which in turn permits a physiological response such as continuous endothermy. Nectarivores like *A. latidens* have sufficient energy reserves to allow them to maintain a high rate of metabolism. A similar strategy has been observed for *A. caudifera*, which remains normothermic at low ambient temperatures in laboratory experiments as well as in diurnal shelters (Arends et al. 1995; McNab 1969). From the foregoing argument, it can be expected that representatives of this guild show a low or null capacity to enter daily torpor (Arends et al. 1995). Nevertheless, it has been observed that *Glossophaga soricina* in Brazil, *Monophyllus redmani* in Puerto Rico, and the pteropid nectarivores *Syconycteris australis* and *Macroglossus minimus* from Papua, New Guinea all show both normothermy and torpor in response to low temperatures. Such behavior has been interpreted as an adaptive response to habitats with fluctuations in both temperature and food supply (Bonaccorso and McNab 1997; Coburn and Geiser 1998; Cruz-Neto and Abe 1997; Geiser and Coburn 1999; Rasweiler 1973; Rodríguez-Durán 1995).

Sturnira erythromos.—This frugivorous bat shows both the highest mass-specific basal metabolic rate among those known for lowlands and a high value among frugivore bats for minimal thermal conductance (Table 1). The basal metabolic rate of *S. erythromos* is above the 95% confidence limit for the regression obtained for the mass-specific basal metabolic rate of fru-

TABLE 1.—Energetic variables reported for bat species with different diets and from lowland and montane habitats. Actual values measured are compared with predicted values (as percentages of predicted). For basal metabolic rate, predicted value is from McNab (1988), and for thermal conductance, predicted value is from Herreid and Kessel (1967).

Species by dietary category	Source ^a	Body mass (g)	Basal metabolic rate		Thermal conductance		Body temperature (°C)	Lower critical temperature (°C)	Upper critical temperature (°C)	Habitat
			(ml O ₂ g ⁻¹ h ⁻¹)	% predicted	(ml O ₂ g ⁻¹ h ⁻¹ °C ⁻¹)	% predicted				
Nectarivores										
<i>A. latidens</i>	A	13.5	2.71	166	0.36	128	38.0	34.7	36.2	Montane
<i>A. caudifera</i>	F	12.0	3.05	181	0.28	95	36.0	27.0	35.0	Montane
<i>Leptonycteris curasoae</i>	B	24.0	1.42	103	0.24	115	35.3	30.5	37.0	Lowland
<i>Glossophaga longirostris</i>	B	13.5	1.96	121	0.30	112	37.5	31.5	36.0	Lowland
<i>G. soricina</i>	D	6.8	2.60	132	0.40	106	36.5	31.4	35.2	Lowland
<i>Choeronycteris godmani</i>	B	10.1	1.89	107	0.31	97	36.6	32.0	—	Lowland
<i>M. redmani</i>	G	8.7	1.28	69	0.58	175	—	—	—	Lowland
Frugivores										
<i>S. erythromos</i>	A	15.9	2.51	161	0.26	104	34.4	25.5	32.6	Montane
<i>S. litium</i>	F	22.0	1.79	127	0.19	89	36.4	28.1	37.1	Lowland
<i>Rhinophylla pumilio</i>	F	10.0	1.71	97	0.31	95	34.7	30.0	35.0	Lowland
<i>C. perspicillata</i>	F	15.0	2.11	134	0.27	104	36.4	28.2	37.7	Lowland
<i>Uroderma bilobatum</i>	F	16.0	1.64	106	0.25	101	35.1	28.0	35.6	Lowland
<i>Platyrrhinus lineatus</i>	F	22.0	1.47	104	0.19	85	36.4	28.0	—	Lowland
<i>Artibeus concolor</i>	F	20.0	1.67	115	0.21	93	35.3	28.0	—	Lowland
<i>A. jamaicensis</i>	F	45.0	1.25	109	0.14	95	36.4	25.0	35.8	Lowland
<i>A. lituratus</i>	F	70.0	1.21	111	0.11	95	37.3	25.0	37.7	Lowland
Insectivores										
<i>T. brasiliensis</i>	A	11.0	0.78	45	0.22	68	29.0	26.3	32.7	Lowland and Montane
<i>Mormoops megalophylla</i>	C	16.5	1.48	97	0.30	120	36.9	33.5	39.5	Lowland
<i>Pteronotus personatus</i>	C	14.0	1.64	102	0.30	115	37.5	34.0	38.5	Lowland
<i>P. parnellii</i>	C	19.2	1.60	110	0.26	111	36.4	34.0	40.5	Lowland
<i>P. davyi</i>	C	9.4	1.63	91	0.40	131	38.8	34.5	43.0	Lowland
<i>Pteropterus macrootis</i>	E	5.1	2.31	108	0.55	120	34.4	30.5	37.0	Lowland
<i>Natalus tumidirostris</i>	E	5.4	1.54	73	0.41	92	32.2	28.0	35.5	Lowland

^a Source of data: A, this study; B, Arends et al. (1995); C, Bonaccorso et al. (1992); D, Cruz-Neto and Abe (1997); E, Genoud et al. (1990); F, McNab (1969, 1982b); G, Rodriguez-Durán (1995).

givore bats from neotropical lowlands. Its thermal conductance value places it at the upper end of the expected range for a regression line of lowland frugivorous bats (Table 1). On the other hand, the range of thermoneutral zone is the smallest of the guild (Table 1), and *S. erythromos* also shows the lowest lower critical temperature in relation to size; this value is shared with other much larger species such as *Artibeus jamaicensis* and *A. lituratus* (Table 1).

Anatomical features such as very dense fur, absence of an uropatagium, small ears, and densely haired feet and toes (de la Torre 1961) can partially compensate for the tendency for rapid heat loss caused by high temperature differentials between the bat and the ambient air. An additional feature is the dual response that *S. erythromos* shows to temperatures below the lower critical temperature, which we interpret as facultative torpor. We observed that individuals could respond as typical normotherms or as hypotherms (Fig. 2). As hypotherms, bats entered reversible torpor and decreased their body temperature (hypothermia). This physiological response allows them to reduce energetic expenditures. *S. lilium* can economize between 10% and 30% of its reserves under similar conditions via hypothermia (Audet and Thomas 1997).

Hypothermic response can be experimentally induced by low ambient temperatures and when food or water supply is inadequate (Calder 1994; Rasweiller 1973; Studier and Wilson 1970, 1979; Vogt and Lynch 1982). At least for *Carollia perspicillata* and *S. lilium*, it has been demonstrated that hypothermia is not a laboratory artifact but an adaptive strategy that allows adaptation to low ambient temperatures (Audet and Thomas 1997). The captive bats used in our experiments were under similar dietary and environmental conditions to those of Audet and Thomas (1997).

In natural conditions, energetic and nutritional balance is not always ideal because it may be restricted by strong rains, lunar conditions, or both (Morrison 1978a,

1978b), which limit time available for feeding. In montane climates, nocturnal temperatures impose an additional thermoregulatory cost. Facultative daily torpor could be an important means for allowing both frugivorous and insectivorous bats to face climatic limitations on feeding activities (Audet and Thomas 1997).

The genus *Sturnira* shows its highest taxonomic diversification in the tropical Andes, mainly above 1,000 m elevation, where many species in this genus are endemic (Koopman 1976, 1982). Some species of *Sturnira* are replaced by another along an altitudinal gradient. For example, *S. lilium*, which in the Andes occupies lowlands, piedmont, and medium elevations, is replaced by *S. erythromos* above about 1,800 m. It is probable that species of this genus use facultative daily torpor to maintain a favorable energetic balance, as has been suggested for the species of *Carollia* and *Artibeus* in the altitudinal range of 0–1,550 m (Cloutier and Thomas 1992).

Species of *Sturnira* show roost fidelity and mainly use hollow trees as day-shelters (Fenton et al. 2000; McNab 1969; Nowak 1994). In these roosts, heat losses are reduced by convection, which keeps daily temperatures constant and independent of external variations (Genoud and Bonaccorso 1986). Such circumstances permit bats that use protected roost microclimates to obtain a more favorable energetic savings than those that use less protected foliage roosts and must face larger thermal differentials (Soriano 2000).

Tadarida brasiliensis.—This insectivorous species shows the lowest basal metabolic rate and thermal conductance measured for any tropical bat (42% and 68%, respectively, of expected values for their body mass; Table 1). These values appear below the 95% confidence limit for regressions for lowland insectivorous bats, both for basal metabolic rate and for thermal conductance as a function of body mass. Likewise, *T. brasiliensis* shows the lowest values known for upper and lower critical

temperatures (Table 1). Although some of these features differ from those found for the nectarivores and frugivores examined in this study, they are in agreement with what can be expected for insectivorous bats.

Below the thermoneutral zone, *T. brasiliensis* shows a dual response; unlike *S. erythromos*, it became hypothermic in all the experiments performed at ambient temperatures lower than 22°C (Fig. 3). Below 22°C, *T. brasiliensis* enters obligate torpor (McNab 1969). This strategy allows *T. brasiliensis* to compensate for its limited thermoregulatory capacity and very low rate of metabolism (Geiser 1988). However, the response to low ambient temperatures seen in many species in exclusively lowland families (such as Mormoopidae, Natalidae, and Emballonuridae) is continued normothermia as long as energy reserves remain (Table 1). Although emballonurids sometimes are exceptions (Genoud and Bonaccorso 1986), the limited or null capacity of these lowland families to enter into torpor and their limited access to high caloric food prevent their adaptation to montane environments. Thus, primary ambient temperatures in their refuges are within their thermoneutral zone, as is the case of natalids and mormopids (Bonaccorso et al. 1992). In some cases, hypothermia is not a suitable strategy because it precludes quick flight from a predator, as with emballonurids (Genoud and Bonaccorso 1986; Genoud et al. 1990).

Tadarida brasiliensis lacks some of the morphologic adaptations that other insectivores (vespertilionids) of cloud forests show, such as dense fur, small ears, and densely haired uropatagium and hind feet. In this species, fat reserves often are an alternative means of insulation (Herreid 1963). In Jamaica, *T. brasiliensis* has been recorded with seasonally variable fat reserves (McNab 1976). It is likely that *T. brasiliensis* from cloud forests maintains notable fat reserves, which offer insulation. In addition, gregarious behavior, in combination with refuges exposed to solar heating

(such as tiled roofs—P. J. Soriano, in litt.), offers microclimates with ambient temperatures near the lower critical temperature, as has been hypothesized for *Macrotus californicus*, which uses caves or mines that are geothermally heated (Bell et al. 1986). In lowlands, *T. brasiliensis* is capable of tolerating high air temperatures in its shelters, which often exceed 40°C, by using heat-loss mechanisms (Henshaw 1960; Herreid 1967; Licht and Leitner 1967). This thermal plasticity allows this species to access both lowland and montane environments.

In temperate latitudes, the vespertilionid bat *Eptesicus fuscus* uses facultative daily torpor linked to environmental and reproductive conditions (Audet and Fenton 1988). However, the cost of this mechanism in pregnant females is prolonged gestation. Characteristics shown by *E. fuscus* possibly occur in tropical montane representatives of the Vespertilionidae, permitting this family to have a higher representation than Molossididae in tropical cloud forests.

Comparisons between species.—The ANCOVA analysis (Table 1) of data available for 21 tropical bat species and the 3 species in this study indicates that \log_{10} of basal metabolic rate is significantly correlated with \log_{10} of body mass ($P = 0.0035$, $r^2 = 0.40$) and with food habits ($P = 0.00002$). It is not significantly correlated with maximal elevation range ($P = 0.56$). Although elevation did not show an effect on \log_{10} of basal metabolic rate, when both elevation and food habits are taken into account, a statistically significant impact on \log_{10} of metabolic rate was obtained ($P = 0.0002$). This implies that elevation does not have the same effect as diet on metabolic responses of the various dietary groups examined. Our results seem to show that both the nectarivorous *A. latidens* and the frugivorous *S. erythromos* increase their basal metabolic rate as a response to elevation, whereas the insectivorous *T. brasiliensis* shows the opposite response, prob-

ably as a consequence of its poor energetic budget.

CONCLUSIONS

Although available information is yet very limited, there is evidence to support the hypothesis that thermoregulatory restrictions prevent some species of bats from inhabiting high mountain environments. This includes the tendency for metabolic rate, minimal thermal conductance, and lower critical temperature in some bat species in Andean cloud forests to vary with food habits. Qualitative and quantitative differences separate Andean mountain bats from those of lowland forests.

The nectarivorous bat, *A. latidens*, is endothermic and has a high basal metabolic rate; however, its high thermal conductance and lower critical temperature do not show an adaptation to cool environments as expected. Further data from additional individuals are necessary to characterize this species. The frugivore *S. erythromos* has a high basal metabolic rate and maintains thermal conductance as expected, which implies a very important displacement of thermoneutral zone to lower temperatures. At temperatures below the lower critical temperature, some bats express a hypothermic response or facultative torpor. One insectivore, *T. brasiliensis*, has very low basal metabolic rate and thermal conductance and a thermoneutral zone range displaced toward lower temperatures, and all the individuals enter obligate torpor at ambient temperatures $<22^{\circ}\text{C}$.

Each of the 3 species shows a different adaptive strategy to the cool environments of Andean cloud forests. These strategies are probably related to their feeding habits. Thus, it could be expected that nectarivorous bats show continuous endothermy as a consequence of their rich carbohydrate diet, whereas frugivores and insectivores use hypothermia and facultative or obligate torpor as a consequence of a medium- and low-caloric diet, respectively. This allows them

to conserve more of their precious energy stores on a daily basis.

RESUMEN

En este trabajo examinamos la hipótesis de que los murciélagos de las tierras altas de los Andes muestran respuestas metabólicas distintivas con relación a sus contrapartes de selvas de tierras bajas. Aportamos nueva información sobre tres especies de murciélagos con diferentes hábitos alimentarios: un nectarívoro (*Anoura latidens*), un frugívoro (*Sturnira erythromos*) y un insectívoro (*Tadarida brasiliensis*). Establecemos comparaciones con la información de la literatura para especies de tierras bajas. En cada especie medimos el consumo de oxígeno a temperaturas ambientales entre $10\text{--}38^{\circ}\text{C}$ y determinamos su tasa metabólica basal, conductancia térmica y temperatura corporal. Aunque parece que las respuestas son particulares de acuerdo al género, nos permiten separarlas de aquellas que ofrecen las especies típicas de tierras bajas. *A. latidens* se caracteriza por mostrar la mayor tasa metabólica basal; sin embargo los valores de conductancia térmica y temperatura crítica inferior no son fáciles de interpretar como adaptaciones a los ambientes fríos. *S. erythromos* también incrementa su tasa metabólica basal, pero mantiene su conductancia térmica de acuerdo a lo esperado para su masa corporal, lo cual implica un importante desplazamiento de la zona de termoneutralidad hacia valores de temperaturas más bajas. Por debajo de la temperatura crítica inferior, además de la respuesta endoterma, *S. erythromos* puede mostrar una respuesta hipotérmica o torpor facultativo, independiente del sexo y la masa corporal. *T. brasiliensis* tiene las menores tasa metabólica y conductancia térmica, a la vez que muestra un desplazamiento de su zona de termoneutralidad hacia temperaturas más frías. Igualmente, *T. brasiliensis* entra en torpor obligado a temperaturas ambientales inferiores a 22°C .

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