Functional Ecology

British Ecological Society

Functional Ecology 2013 doi: 10.1111/1365-2435.12106

The body temperature of active amphibians along a tropical elevation gradient: patterns of mean and variance and inference from environmental data

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Summary

1. Tropical montane amphibians have been the focus of recent and crucial conservation efforts. These initiatives require understanding on how elevation influences amphibian body temperature beyond the simplistic assumption of a monotonical decrease with elevation. This study addresses patterns and potential for inference in this context.

2. As elevation increases, mean body temperature (BT) of tropical montane amphibians decreases linearly, but intrapopulation variation (VAR) in BT increases exponentially. These relationships are influenced by biome structure, but display both local nuances and species-specific remarks.

3. Substrate temperature (ST) and BT hold a close relationship across elevation. The noise around this relationship is lowest in mid-elevation cloud forests and maximum in the paramo, a biome above the tree line.

4. The relationships between BT and ST, and between elevation and either BT or VAR, are valuable to infer general patterns of thermal ecology for amphibians and to highlight species-specific exceptional cases.

5. The BT of montane tropical amphibians can be estimated from temperature data collected at a scale compatible with the size and microhabitat of individual frogs. Estimates from elevation are valid as general trends that can be enhanced if natural history is taken into account. Worldclim data allow for rough inference only and have limited predictive power.

6. A framework is proposed to study how the BT and VAR of amphibians change with elevation. This framework encompasses information on biome structure and natural history.

Key-words: Andes, Amphibian, Anuran, Elevation, Body Temperature, Thermal Ecology, Tropical

Introduction

The impact of body temperature (BT) on amphibians is evident at various scales and levels of organization. Temperature affects physiological function and influence the behavioural and ecological performance of individuals (Navas, Gomes & Carvalho 2008). Thermal effects can also generate population patterns (Gibbs & Breisch 2001; Carroll *et al*. 2009), become significant when analysing the distribution of species (Girardello *et al*. 2010) and possibly impact susceptibility to fungal pathogens (Rohr & Raffel 2010). These pervading effects have generated interest on how and why climate change affects this taxon. Under generally accepted scenarios for ectothermic animals, temperatures approaching physiological limits elicit stress responses and cause decreased survival or reproductive breakdown (Somero 2011), particularly in thermally specialized species (Ghalambor *et al*. 2006). This general view is likely to apply to amphibians; indeed, climate change favouring exposure to high temperatures may affect species to different extents depending on the thermal tolerances of individuals (Duarte *et al*. 2012). Conversely, tolerance to

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freezing may determine the altitudinal threshold for species (Carvajalino, Bonilla & Navas 2011). However, thermal effects may be far more complex. For example, exposure to chronic high, yet noncritical temperature, stress amphibians (Narayan, Cockrem & Hero 2012), shifts in body temperature influence the effects of chemical stressors (Rohr, Sesterhenn & Stieha 2011) and enhanced thermal variance influences larval growth and developmental rates (Niehaus *et al.* 2012). In addition, the thermal landscape (understood as spatial and temporal variation in operative temperatures) matters because individual amphibians have variable preferred body temperatures (Bicego-Nahas *et al.* 2000; Bicego-Nahas, Gargaglioni & Branco 2001; Navas, Gomes & Carvalho 2008) and may select warmer spots when infected by pathogens (Myhre, Cabanac & Myhre 1977; Sherman *et al.* 1991).

The multifactorial influence of temperature on amphibian biology prompts for reliable body temperature data. Accurate information on amphibian BT seems valuable in contexts as diverse as distribution of species (Munguia *et al.* 2012), resilience of populations to climate change (Lowe 2012), susceptibility to disease (Lips *et al.* 2008; Muths, Pilliod & Livo 2008), the relevance of thermal environment in the concept of niche conservationism (Kozak & Wiens 2010) and the parameterization of models (e.g. Kolbe, Kearney & Shine 2010). These research scenarios gain relevance in tropical mountains because they are global hot spots of species richness (e.g. Orme *et al.* 2005) and exhibit high endemism (Lynch & Suárez-Mayorga 2002), conspicuous population declines (Catenazzi *et al.* 2011); and apparent susceptibility to climate change and extreme temperature events (Garcia, Albornoz & La Marca 2005), particularly in the Andes region (Lawler, Shafer & Blaustein 2010). Additionally, it is essential to understand the role of climate and elevation regarding amphibian susceptibility to chytridiomycosis in tropical mountain systems (Lips *et al.* 2008). Given these many relevant contexts, the simple assumption that BT decreases with elevation seems far behind the state of art of biological research. Information on mean temperature, thermal variation and thermal landscape seems indispensable. Current research would be greatly favoured by detailed information about general trends in amphibian BT along tropical mountain systems. In addition, the need of practical proxies for amphibian BT prompts for investigating the quality of inference using current techniques and climatic databases.

The best way to obtain data on amphibian BT is to measure it directly from individuals, for example using telemetric devices (Oromi, Sanuy & Sinsch 2010; Sinsch & Leskovar 2011), but this is not practical in many contexts. Inferring amphibian BT is also possible using temperature measured at scales compatible with individuals, for example substrate temperatures (ST) or temperature records obtained from data loggers fit to individual-scale models (Navas & Araujo 2000). However, even this approach may also be unfeasible in various contexts, for example when considering large ecological gradients or in global analyses. Therefore, it is important to discuss how climatic data at scales greater than individuals apply to problems focusing on climate at individual scale (Graae *et al.* 2012). An alternative is inference from climatic data obtained from field stations and climatic databases such as Worldclim (http://www.worldclim.org). However these data, given their nature, cannot directly account for microhabitat selection or patterns of activity, two determinant elements of anuran body temperature (Navas 1996a). In this case, the inference of body temperature from climatic stations or databases entails calibration or modelling and tests against empirical data. In addition, local nuances may be particularly relevant in tropical mountain systems. Although the BT of tropical amphibians decreases with elevation (Feder & Lynch 1982; Navas 2002), the impact of transitions across biomes on BT may be crucial given the notorious climatic changes that occur along tropical elevations (Sarmiento 1986; Bader, Rietkerk & Bregt 2007).

A first purpose of this study is to analyse the patterns of mean and variance of BT and ST across tropical elevation gradients, taking into account basic ecological information. On the same lines, we scrutinize the extent to which data on elevation, BT and ST can be integrated to highlight species-specific departures from main trends of thermal ecology. A second goal is to identify and discuss the impact of biome changes across elevation on the BT of tropical amphibians. We expect a change in BT with elevation following a lapse rate decrease in environmental temperature. However, biome structure must also matter because, in contrast to forested environments, the paramos (biome above the tree line in the tropical Andes) display notorious microclimatic extremes and daily shifts in environmental temperature (Azócar & Monasterio 1979; Bader, Rietkerk & Bregt 2007). A final aim is to evaluate the potential scope and limits of (i) elevation, (ii) environmental data collected at scales compatible with individuals and (iii) Worldclim data to infer the BT of amphibians across tropical elevations. When direct measurements are not possible, we expect temperature collected at scales compatible with individuals to offer the best BT estimates, and supposed a broad but loose relationship between Worldclim data and BT data. To attain the above goals, we rely on the analysis of a database comprising substrate and body temperature for 21 tropical anuran species (some including more than one population) located between 90 and 3550 m.

Materials and methods

GENERAL APPROACH

Using both published literature and novel measurements, we built a database on the BT of anuran species along a tropical elevation gradient comprising Panamá, Andes of the central Colombia (Cordillera Oriental) and Sierra Nevada de Santa Marta (Colombia). Then, we analysed the relationship between BT and environmental temperature and the strength of this relationship along elevation and across biomes. We also explored the relationship between body temperature and elevation, paying special attention to deviations from main trends. Next, we obtained Worldclim data using the coordinates of collection sites and analysed the relationship between BT data and Worldclim data. In all previous contexts, we incorporated information about biome domain, understanding that a given biome encompasses multiple vegetation physiognomies. Accordingly, we identified three dominant biomes in our sample: low-elevation tropical dry forest, mountain forest (cloud forest) and paramos. We also included basic information on natural history considering parameters that would be applicable even to poorly known species, such as habitat type and patterns of activity, two parameters that heavily influence activity temperature in high-elevation frogs (Navas 1996a). We considered the simplest possible category of habitat, splitting species just as mainly terrestrial (hereafter 'terrestrial') or mainly associated with bodies of water (hereafter referred to as 'aquatic'). An important caveat is that in our sample, 'aquatic' species are those associated to swampy shallow waters or to ponds, but we lack truly aquatic species such as lake-frogs in the genus *Telmatobious*, present only at Southern latitudes in the Andes. We also considered the time of day in which activity is maximal (assigning all species to either of the categories 'diurnal' or 'nocturnal').

BODY TEMPERATURE DATA SET

The data set includes body temperature reported in the literature (Navas 1996a) and new data. Literature data correspond to the body temperatures of some of the high-elevation species collected at the Chingaza Natural Park, all low-elevation species from Panama (Smithsonian Tropical Research Institute STRI at Gamboa, and the Nusagandi reserve) and some species of the mountain forest from Sierra Nevada de Santa Marta (see Table 1). Once an animal was detected, we measured its body temperature as described below and then measured substrate and air temperatures at the same spot the individual had just been collected. To pair temperature and elevation data, we assigned each species to one single altitude record, specifically the altitude at the site of collection or the average altitude when collection sites were different, yet geographically close (e.g. <60 m). The data set contains 21 species and generated 28 classes because two species were represented by populations at more than one elevation. Additionally, one species basks during the day but are mainly nocturnal callers (*Dendrosophus labialis*), so that day and night data were considered independently. For other species, we measured body temperature at the dominant time of day at which they were most active. Activity temperatures are particularly relevant from an ecological point of view, and the body temperature of inactive individuals is extremely difficult to assess in the field. Accordingly, this data set includes both nocturnal and diurnal species, but does not include the body temperature of sheltered, inactive individuals.

STUDY SITES AND SPECIES

Table 1 presents a complete list of species and collection sites. Additional details on collection sites by *CAN* (author initials in italics) in Colombia, at Parque Nacional Chingaza (PNC, Piedras Gordas and Buitrago areas), and Panama, at Smithsonian Tropical Research Institute STRI at Gamboa and the Nusagandi Reserve, have been published elsewhere (Navas 1996a). *JMC* collected data in the same areas at PNC (*Pristimantis bogotensis*; *P. elegans* and *P. nervicus*), and in the area known as La Cascada in the Colombian department of Magdalena, 11°10′2·0″ N, 74°10′ 45·5″, 1560 m (*P. insignitus*; *P. megalops* and *P. sanctaemartae*). *LPS* collected data in three field sites in the Sierra Nevada de Santa Marta, Magdalena, Colombia, as follows: Puerto Mosquito, 11° 10′ 26″ N, y 74° 10′ 37″ W, 50 m (*Engystomops pustulosus*); La Victoria, 11° 07′ 37″ N, 74° 04′ 42″ W, 1150 m (*Colosthetus ruthveni* & *Ikakogui tayrona*); and San Lorenzo,11° 06‘ 29·7″ N, 74° 03′ 34·1″ W, 2200 m (*Geobatrachus walkeri* & *Ikakogui tayrona*). Some *Atelopus* data in the database were collected by *LARS* as part of a fully independent study on the thermal ecology of this genus in the high elevations of Sierra Nevada de Santa Marta, Colombia. Details on methods and localities are available elsewhere (Master's thesis directed by A. Amézquita, see Rueda 2010). Briefly, *LARS* collected at the same sites used by *JMC* (*Atelopus nahumae*) and *LPS* (*A. laetissimus*) in the Sierra Nevada de Santa Marta, and in the area known as Lagunas de Sevilla 10°54′03″ N, y 73°55′04″ W, 3500 masl (*A. carrikeri*).

MEASURES OF BODY TEMPERATURE

We estimated body temperature from skin temperature, which is the only possibility to obtain comparable and accurate measures given the different typical sizes of the species involved. Individuals from the species included in this study weighed typically less than 20 g, and some weighed less than 1 g. In very small species, cloacal readings are impracticable before manipulation affects results (Navas & Araujo 2000) and temperature gradients across the body are likely inconsequential. We detected animals by visual or hearing inspection within the study areas and measured body temperature to the nearest 0·1 °C. The body temperature data collected by *CAN* were obtained as described in the original paper (Navas 1996b). Briefly, body temperatures were measured by applying a temperature probe (Barnardt 115 thermistor, probe type J) at the proximal part of the left rear limb of individuals, disregarding any datum not recorded within 20 s of capture. Other authors used infrared thermometers applied to the dorsum of individuals at distances granting a maximum reading diameter of 1 cm, as follows: LPS Infrared thermometer IR201 Extech 6:1; *JMC*, thermocouple type K (7DX, Thurlby-Thandar); *LARS*, Infrared thermometer Oakton InfraPro D: S = 12:1. After a successful body temperature reading, we measured substrate and air temperature at the site of capture using the same equipment described above (*CAN* and *JMC*), a Schultheis rapid reading thermometer (*LPS*) and a Thermo-Hygro digital thermometer (*LARS*). Devices were independently calibrated against mercury thermometers and showed reliable temperature readings within the range of temperatures measured.

ANALYSIS OF VARIANCE IN BT ALONG ELEVATION GRADIENTS

We analysed the relationship between elevation/biome and ST, including both mean temperature and thermal variability. Then, we examined how these changes affect the BT of amphibians along the elevation/biome gradient, including patterns of intrapopulational variation in the activity temperature of frogs and relationship between BT and ST within populations. We also scrutinized the residual BT of a given species/population in the context of the interspecific/populational regression of mean BT for against elevation. We integrated these analyses to evaluate whether or not the thermal ecology of given species/populations adjusted to dominant trends.

A NOTE ON PHYLOGENETIC RELATIONSHIPS

We acknowledge that phylogenetic analyses became standard for interspecific comparative studies; however, it is not currently possible to apply such methods to this data set. To the extent of our knowledge, about half the species in this study do not have DNA sequences available (*Atelopus carrikeri, Atelopus laetissimus, Atelopus lozanoi, Atelopus nahumae, Colosthetus ruthveni, Diasporus*

Table 1. Summary data for the species considered in this paper. The first data group (body temperature, presented in °C) shows basic body temperature data, including number of individuals (*N*), minimum temperature recorded for active individuals (Mi), maximum temperature recorded for active individuals (Mx) and mean (Mean) and variance (Var) in body temperature during activity. The second data group (BT vs. ST) shows the correlation coefficient '*r*' of body temperature (BT) as a function of substrate temperature (ST). The column NH indicates basic ecology and patterns of activity as follows: TD, terrestrial diurnal; TN, terrestrial nocturnal; AD, aquatic diurnal; AN, aquatic nocturnal. The collection altitude, in metres, appears under the title 'Collect. altitude'. Site refers to the places described in the methods where species were collected, that is, Sierra Nevada de Santa Marta (SNSM), Chingaza Natural Park (CHIN) and localities in Panama (PANA, see text for details). Species letter codes as in Fig. 1

		Body temperature					BT vs. ST				
Family	Species	N	Mi	Mx	Mean	Var	*r*	NH	Collect. altitude	Site	Source
Bufonidae	*Atelopus carriker* (A)	86	7·2	15·6	9·9	4·13	0·88*	TD	3500	SNSM	Rueda (2010)
	Atelopus carriker (B)	40	5·6	9·6	7·1	1·22	0·90*	TN	3500	SNSM	Rueda (2010)
	Atelopus laetissimus (A)	6	12·6	16·2	14·5	1·90	0·77*	TD	2100	SNSM	Rueda (2010)
	Atelopus laetissimus (B)	55	11·8	15·4	13·9	0·47	0·96*	TN	2100	SNSM	Rueda (2010)
	Atelopus lozanoi	27	7·7	16·2	11·4	4·96	0·76*	TD	3500	CHIN	Navas (1996a)
	Atelopus nahumae (A)	198	14·6	21·9	17·5	1·27	0·94*	TD	1560	SNSM	Rueda (2010)
	Atelopus nahumae (B)	32	14	16·8	15·9	0·54	0·98*	TN	1560	SNSM	Rueda (2010)
	Atelopus varius	20	23·5	25·4	24·2	0·23	0·16	TD	350	PANA	Navas (1996b)
Centrolenidae	*Ikakogi tayrona*	6	18	19·7	19	0·58	0·99*	TN	1100	SNSM	This study
Dendrobatidae	*Colosthetus ruthveni*	30	16	29	26·7	6·19	0·80*	AD	980	SNSM	This study
	Hyloxalus subpunctatus	69	7·2	19·9	13·4	5·94	0·75*	AD	3500	CHIN	This study, Navas (1996a)
	Silverstoneia flotator	17	24·3	27·9	26·6	1·16	0·78*	TD	90	PANA	Navas (1996b)
Eleutherodactylidae	*Diasporus diastema*	15	23·3	25·6	24·3	0·63	0·60*	TN	90	PANA	Navas (1996b)
Hylidae	*Dendropsophus ebraccatus*	16	23·4	27·1	24·8	1·25	0·83*	AN	90	PANA	Navas (1996b)
	Dendropsophus labialis (A)	9	14·2	19·7	15·8	2·92	0·15	AD	2900	CHIN	This study, Navas (1996a)
	Dendropsophus labialis (B)	12	9·5	14·8	12·2	2·32	0·35	AN	2900	CHIN	This study, Navas (1996a)
	Dendropsophus labialis (C)	27	12·1	17·1	14·7	3·55	0·44	AD	3500	CHIN	This study, Navas (1996a)
	Dendropsophus labialis (D)	19	9·3	11·9	10·9	0·43	0·60*	AN	3500	CHIN	This study, Navas (1996a)
	Dendropsophus microcephalus	16	24·1	28·5	25·8	2·19	0·80*	AN	90	PANA	Navas (1996b)
Strobomantidae	*Geobatrachus walkeri* (A)	10	16	18	17·1	0·54	0·67*	TD	2300	SNSM	This study
	Geobatrachus walkeri (B)	11	15	17	15·8	0·56	0·65*	TD	2432	SNSM	This study
	Pristimantis bogotensis	75	−0·05	15	8·2	9·93	0·78*	TN	3550	CHIN	This study, Navas (1996a)
	Pristimantis elegans	37	−4·3	11·1	7·4	9·12	0·98*	TN	3550	CHIN	This study
	Pristimantis insignitus	98	13·3	19·6	15·7	1·12	0·99*	TN	1560	SNSM	This study
	Pristimantis megalops	89	13·6	18·9	15·8	0·65	0·99*	TN	1560	SNSM	This study

(continued)

Table 1 (continued)

		Body temperature					BT vs. ST		Collect.		
Family	Species	N	Mi	Mx	Mean	Var	*r*	NH	altitude	Site	Source
	Pristimantis nervicus	17	−1·05	15·5	7·2	17·69	0·98*	TN	3550	CHIN	This study, Carvajalino, Bonilla & Navas (2011)
	Pristimantis sanctaemartae	85	13·5	18·9	15·8	1·08	0·99*	TN	1560	SNSM	This study
Leiuperidae	*Engystomops pustulosus*	31	23	29	25·3	2·09	−0·03	TN	73	SNSM	This study

*Significant at $P < 0{\cdot}05$.

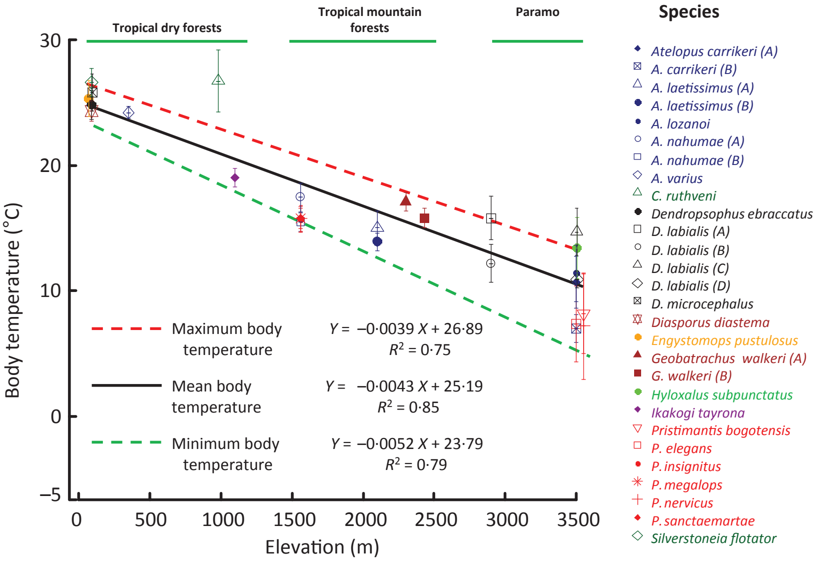

Fig. 1. Body temperature of tropical amphibians as a function of elevation. Symbols identify species/population and display mean and SD. Species with ample diel patterns of activity are coded as A (diurnal) or B (nocturnal). The species *D. labialis* was entered with populations at 2900 m and 3500 m (for the latter, C diurnal, and D nocturnal).

diastema, Geobatrachus walkeri, Pristimantis bogotensis, Pristimantis insignitus, Pristimantis megalops, Pristimantis sanctaemartae), and some *Atelopus* cannot be collected due to access and permit restrictions. In preliminary tests restricted to the anuran families represented with 3 or more species, the variable 'Family', when analysed together with elevation, influenced BT ($F_{3,21} = 7{\cdot}14$, $P = 0{\cdot}002$). However, adding the two variables of natural history to the model reduced dramatically the impact of family ($F_{3,19} = 2{\cdot}015$, $P = 0{\cdot}146$). These analyses do not substitute formal phylogenetic analysis but, within the context of existing constraints, suggest that elevation and natural history influence BT more than shared ancestry. Consequently, through the paper, we have treated the data as putatively independent of phylogenetic position.

DATA FROM THE WORLDCLIM DATABASE

We downloaded representative climatic data for the past fifty years (~1950–2000) from Worldclim database (www.worldclim.org), obtaining measures from coordinates as close as possible to our sampling locations. We improved the accuracy of the data using the highest available resolution in this context, that is, standardized 30 arc-seconds (~1 km) data grids. We preprocessed the information using DIVA-GIS to construct an appropriate '.CLM' file from plain 30 × 30 degrees generic format files containing separate climatic variables in Geographic Zone No. 23 (Panamá, Colombia and the Caribbean). To do this, we followed standard procedures described in detail elsewhere (Scheldeman & van Zonneveld 2010). Various types of climatic and bioclimatic variables could be extracted from Worldclim data, allowing the comparison of models regarding the ability to predict amphibian BT based on Mean temperature of last 50 years, Maximum temperature of hottest month, Minimum temperature of coldest month, Mean temperature of the wetter quarter (4 month period), Mean temperature of the drier quarter, Mean temperature of the warmer quarter and Mean temperature of coldest month. All these variables produced relationships with BT that were similar in slope and comparable from the standpoint of the Akaike Information Criterion (AIC), with values ranging between 139·2 and 140·7. Therefore, we opted to use 'Mean temperature of last 50 years' as the variable for analysis, which would be referred onwards as Worldclim temperature (WCT).

Results

GENERAL PATTERNS OF THERMAL ECOLOGY

Table 1 presents a summary of the thermal ecology for each species/populations in this study. Elevation was a dominant driver of amphibian mean body temperature, so that species at higher elevation exhibited lower mean values. The pattern was explained by a simple linear relationship that encompassed 85% of the variance in mean BT ($F_{1,22} = 853{\cdot}48$, $P < 0{\cdot}001$), with lower fit for the maximum and minimum BT registered for each species/population (Fig. 1). Within most species studied, the BT and ST of individuals were closely related, so that the correlation coefficient of this relationship (r) was higher than 0·60 in all but five species, with values higher than 0·9 in 10 species and a mean of 0·73 (see Table 1). At this individual scale, the relationship between BT and ST was not dependent on elevation, patterns of activity or general habitat of the species (comparison of the correlation coefficient between BT and ST frog species from different biomes, patterns of activity and general habitat, ANOVA $P > 0{\cdot}12$ in all tests. Correlation between intraspecific r and elevation, $P = 0{\cdot}71$). The weakest correlations between BT and ST in the sample were for the only basking species in the sample, *D. labialis*, and for *Engystomops pustulosus*, the only species in which BT and ST were unrelated (see Table 1). At scales compatible with the distribution of species, BT and ST were also strongly related, approaching a linear trend (Fig. 2). The mean residual BT for frog species in each one of the three biomes studied drew near zero (ranges between −0·09 °C and 0·21 °C in an analysis considering all individuals tested).

INFLUENCE OF BIOME

Independent effects of biome and altitude are difficult to assess because the biomes considered were distributed along an altitudinal range. However, the variance of the BT distributions was higher for species in the paramo (above the tree line) than in any of the two forested biomes tested (variances: paramo = 12·4, dry forest = 6·0, montane forest = 2·9, Levene's test, $P = 0{\cdot}043$). Frogs from the montane humid forests had lower variation in BT around the regression line, particularly in the warmest mountain forests studied (see Fig. 2). Therefore, although the average residuals were close to zero and comparable for the groups of species representing each one of these three biomes, these residuals were about one order of magnitude lower in the group of species from montane humid forests. The dispersion of the BT of species around the regression curve varied between 5·7 °C and −7·4 °C, with considerable lower values in species from montane humid forests (Figure S1, Supporting information). Biome structure also affected the amplitude of the thermal landscape, measured as the difference between maximum and minimum ST at a given location. Effects were particularly high during daytime and did not follow a simple relationship with elevation (Fig. 3).

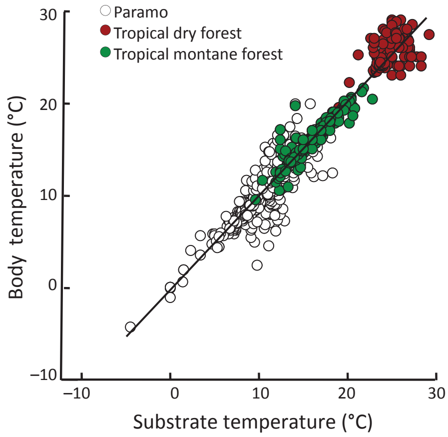

Fig. 2. Individual body temperature as a function of substrate temperature in tropical montane amphibians. Note the reduced variance around the curve in tropical montane forests, particularly at the warmest range of this biome.

INFERENCE OF BT FROM ELEVATION AND NATURAL HISTORY

In addition to the dominant impact of elevation, BT was also influenced by natural history variables (Habitat, terrestrial vs. aquatic: $F_{1,22} = 58{\cdot}47$, $P < 0{\cdot}001$; Pattern of activity, diurnal vs. nocturnal: $F_{1,22} = 70{\cdot}87$, $P < 0{\cdot}001$). Because both natural history variables influenced the relationship between altitude and BT, specific equations of BT as a function of altitude could be provided for each one of the four ecological types considered in this study (DA, diurnal aquatic; DT, diurnal terrestrial; NA, nocturnal aquatic; and NT, nocturnal terrestrial). The regression

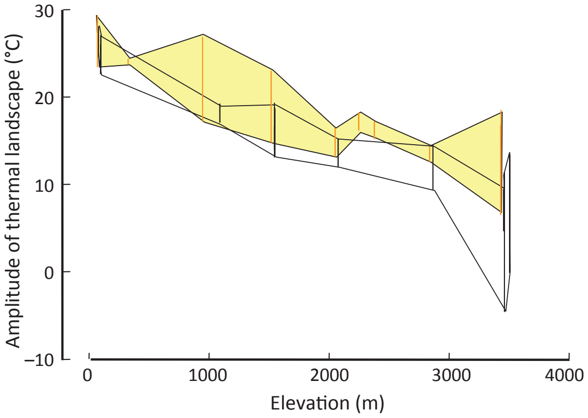

Fig. 3. Amplitude of thermal landscape at various elevations estimated as the maximum and minimum substrate temperature recorded at any elevation. Diurnal data are reported in yellow and are expected to be more consequential in terms of scope for thigmothermic behaviours. Nocturnal data are presented in white. The outer border of both polygons indicates the full thermal amplitude at a given elevation. The vertical lines within polygons indicate data-collection points.

lines for DT and NT species were parallel, but differed in about 8 °C. The other two groups, NA and DA, displayed very similar relationships between BT and altitude (Fig. 4). However, note that these equations are informative about trends in mean BT, but not about the variance in BT. As elevation increased, the BT of amphibian species became more variable, so that the coefficient of variation in BT for a given species related exponentially with altitude (Fig. 5).

INFERENCE OF BT FROM WCT

Because WCT is obtained at scales much greater than those compatible with individual frogs, different frog populations in this study were necessarily associated to the same WCT. Therefore, although Worldclim temperature was unequivocally related to BT (Fig. 6), the predictive power of this relationship was poor (Table S1, Supporting information). For example, locations generating a WCT of 20 °C were associated to mean BTs ranging between 15·8 and 26·7 °C. The overall dispersion around the regression line was high, with residuals ranging from about −4 to 7 °C. WCT temperatures underestimated severely the BT of frogs at low temperatures (<15 °C) and overestimated frog BT at high temperatures (>20 °C). Applying a regression equation enhanced inference, not by improving prediction power but by distributing error more homogeneously across the thermal range tested. Accordingly, the residuals of the regression of BT on WTC, and the absolute differences between BT and WCT for frogs at a given location displayed about the same range (11 °C) and comparable means (Regression residuals 0 °C vs. absolute differences −0·6 °C), but differed in variance (Regression residuals 7·3 °C, absolute differences 11·5 °C).

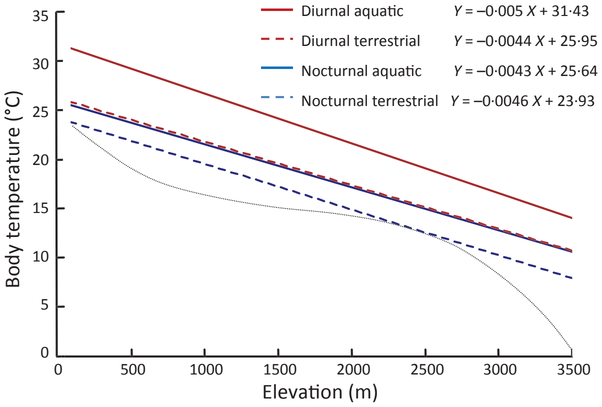

Fig. 4. Regression lines defining the decrease in body temperature as a function of altitude in tropical amphibians. Each line represents one of four ecological groups. The grey dot line is a cubical approximation (best fit) to the lowest BT recorded at any given elevation and signals freezing risk at elevations higher than 3500 m.

Discussion

As expected, the BT of amphibians decreases with elevation along a tropical high-elevation gradient. Although this trend is unambiguous, outliers are expected because at high elevations, topographically controlled microhabitats can generate small areas of high climatic stability (Scherrer & Körner 2010) and in mid-elevation tropical systems, local climates may diverge from main trends (Jones, Szyska & Kessler 2011). However, once main trends of BT with elevation are well-established for a geographical zone, species with outlying thermal ecology can be detected. For example, *Colosthetus ruthveni* displays BT higher than expected for its elevation, a pattern likely due to local climate. Daytime *D. labialis* bask (Valdivieso & Tamsitt

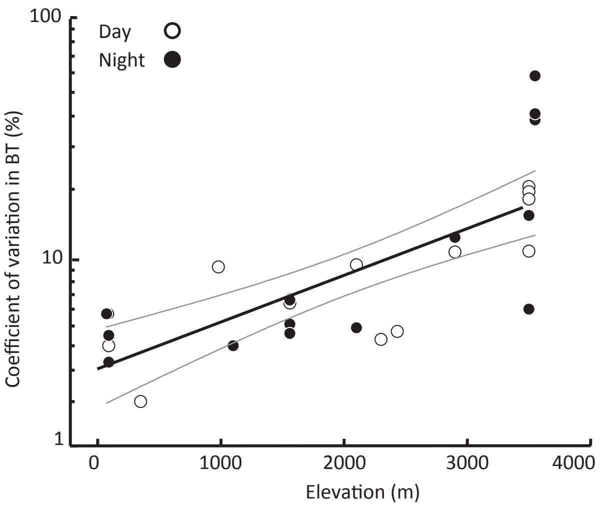

Fig. 5. Intraspecific coefficient of variation in the body temperature of tropical amphibians. In this plot, the coefficient of variation is presented as a function of elevation, although the pattern is also influenced by biome (see main text).

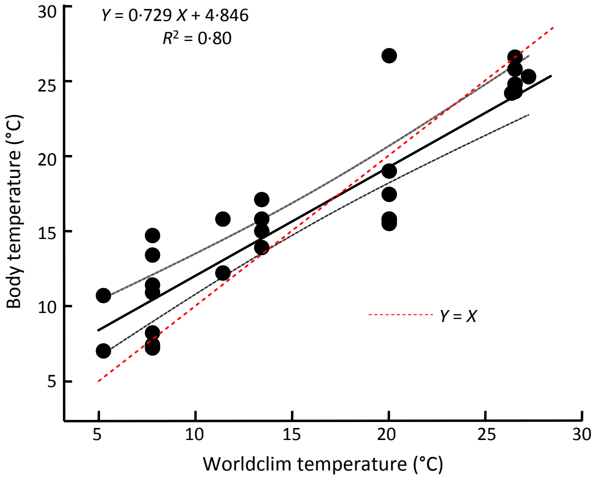

Fig. 6. Body temperature of tropical amphibians as a function of Worldclim temperature reported for their collection sites. The figure presents the equality line (red dot line), regression line and confidence intervals.

1974; Navas 1996a), and possibly due to this behaviour, they are moderate outliers for both the BT-vs.-elevation and the BT-vs.-ST curves. The species *E. pustulosus* exhibits BT that cannot be predicted from ST, perhaps due to physiological modulation of body temperature via water evaporation (Lillywhite 1970, 1971). These proposed traits of thermal biology are, at this point, speculations in need of confirmation. However, the main message is that combined analyses of elevation, BT and ST are a powerful tool to hypothesize on the thermal ecology of amphibian species and to identify unusual thermal characteristics that have value in conservation and risk assessment.

In comparison with cloud forests, paramos exhibit more pronounced daily variation in temperature, more extreme contrast between clear and cloudy days and diel changes surpassing seasonality effects (Bader, Rietkerk & Bregt 2007). Given the thermal stability of cloud forests (Bohlman, Matelson & Nadkarni 1995), frogs in this biome exhibit limited variance in BT, a tight relationship between BT and ST, have access to a narrow thermal landscape and are likely stenothermic. In deep contrast, frogs at elevations higher than the cloud forest (paramo) display remarkable daily variance in body temperature, have available wide thermal landscapes and have evolved an eurythermic thermal physiology (Navas 1996b). Consequently, tropical montane amphibians in geographically proximate areas that are dominated by different biomes experience contrasting thermal ecologies and are likely to differ in natural selection on thermal physiology. Huge contrasts may occur even at equivalent elevation in adjacent areas because the tree line may vary according to local ecological and geological factors (Bader & Ruijten 2008) and forests may grow as islands according to historical factors, local climate and terrain type (Coblentz & Keating 2008).

The above considerations matter when discussing why amphibian regional diversity tends to be highest at intermediate elevations (Smith *et al.* 2007; Kozak & Wiens 2010), why diversification is highest on restricted regional areas, as reported for montane salamanders in Middle America (Garcia-Paris *et al.* 2000), or how to enhance distribution models (e.g. Forero-Medina, Joppa & Pimm 2011). In these contexts, a key unanswered question is whether amphibians adapted to a narrow thermal range adapt/adjust more easily to a different narrow thermal range or to a variable climate. Implications for conservation also exist. Thermal specialization is a key issue when hypothesizing about the impact of climate change on ectothermic vertebrates (Ghalambor *et al.* 2006; Huey *et al.* 2009), and under this scenario, forest frogs would be more prone to negative impacts. In terms of climate-related shifts in distribution, the concept of mountains as barriers, usually centred on temperature gradients (Janzen 1967; Ghalambor *et al.* 2006), could gain new insights for amphibians given the need to consider both mean temperature and thermal variance. Also, nowadays the transition from forested to open environments is heavily influenced by human activity (Bonilla-Moheno, Aide & Clark 2012) with shifts in the landscape that may generate drastic changes in the variance of BT of amphibians. Whether or not species are physiologically prepared for such enhanced thermal variability would affect resilience to deforestation. Note, for example, that *Batrachochytrium dendrobatidis* grows well (Piotrowski, Annis & Longcore 2004) and is particularly pathogenic (Andre, Parker & Briggs 2008) at temperatures compatible with those reported here for montane forest anurans in the tropics. Given that experimental thermal treatments compatible with behavioural fever ameliorate infection by *B. dendrobatidis* (Woodhams, Alford & Marantelli 2003; Chatfield & Richards-Zawacki 2011), the amplitude of the thermal landscape may be of great relevance, even as a factor in the evolution of the thermal physiology and immunology of amphibians. These considerations may lead to mechanisms explaining why deforestation can lower the risk of emerging disease in amphibians (Becker & Zamudio 2011).

Our study informs regarding methods to infer the BT of amphibians when direct measures are unavailable. Rough estimates of maximum, minimum and mean BT can be inferred from elevation data, and the quality of inference improves with information on whether species are diurnal or nocturnal, and aquatic or terrestrial. We provide equations that describe general trends (validation is advised before applying them to new systems) but that are inappropriate to infer on species-specific cases. In this context, gathering environmental temperature data at scales compatible with the size of individuals (e.g. Suggitt *et al.* 2011) may convey the best results, particularly if collected at spots finely attuned with the microhabitat preferences of target species. By extension, these findings support the use of casts (e.g. agar models and other) as a tool to obtain accurate estimates of BT (Navas & Araujo 2000; Seebacher & Alford 2002). Worldclim temperature (WCT) unequivocally relates to BT, but the relationship is loose, noisy and uninformative regarding VAR. In our study, the difference between real BT and WCT surpassed 7 °C, an error range that may lead to misrepresentative inference. Corrections are possible to distribute the error homogeneously across an environmental temperature range, but not to enhance the predictive power of this relationship. Our data corroborate that considerations about scale are essential when discussing the impact of climate change on the biota (Suggitt *et al.* 2011; Graae *et al.* 2012) and that raw WCT are extremely poor descriptors of microhabitat. However, efforts are being made to enhance microhabitat modelling based on a combination of both GIS data and local geo-climatic traits (Kearney & Porter 2009). The data presented here can offer opportunity for calibration of such models, in the specific context of thermal microenvironments.

In conclusion, the BT of tropical amphibians is influenced by natural history and ecology, including the biome occupied. In these taxa, the relationship between patterns of BT and elevation is complex and important nuances are evident only at scales compatible with individuals. These nuances, most likely relevant in the contexts of distribution, susceptibility to climate change and disease risk assessment, involve the absolute value and amplitude of thermal extremes as well as the composition of the thermal landscape. In this context, the dominating biome, and the specific habitat type within a biome, influence microclimate to the point of making likely that species at similar elevation and geographically close experience dramatically contrasting thermal regimes. Similarly, geographically distant species at similar habitats may experience comparable thermal regimes. These considerations must be taken into account when analysing the microclimate of amphibians along tropical elevations. The discussion here presented shall enhance analysis and inference and hopefully encourage much needed detailed studies in other tropical systems, particularly along elevation gradients.

Acknowledgements

This research received support from FAPESP, the state of São Paulo Science Foundation, processes 2008/57687-0 to *CAN* and from Fundación para la Promoción de la Investigación y la Tecnología, Banco de la República, Colombia, process 251. *JMC* and *LPS* were supported by a fellowship from the programmes (i) 'Jóvenes Investigadores e Innovadores Virginia Gutiérrez de Pineda' from COLCIENCIAS, Colombia, (ii) 'Programa De Movilidad en el Posgrado' from Red de Macrouniversidades Publicas de América Latina y El Caribe, Colombia, and (iii) CNPq, National Council for Scientific and Technological Development, PhD scholarship 142096/2012-1. Work permits for data specifically collected for this article were granted by CORPAMAG (No. 1997 de 2010) to *LPS* and Natural National Parks of Colombia (DTAO-CH-26 10/08 and DTAO 037-09) to *JMC*. *LARS* thanks Natural National Park of Colombia, Conservation International-Colombia and the Conservation Leadership Programme for financial and logistic support necessary for fieldwork and the indigenous of Sierra Nevada of Santa Marta who allowed research on their territories. *LARS* also thanks the community of the locality San Pedro de La Sierra for friendship and guidance in the study area.

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Received 2 November 2012; accepted 8 April 2013
Handling Editor: Raoul Van Damme

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Ability of Worldclim data (WCT) to predict actual body temperature (BT), using the variable 'Mean temperature last 50 years (MTL50). This table shows the Residual (R), Prediction limit (PL), and Range of Prediction Limits (RPL) of BT based on WCT'.

Fig. S1. Residuals of the regression of body temperature on substrate temperature for each species included in this study.