



The body temperature of active desert anurans from hyper-arid environment of South America: The reliability of WorldClim for predicted body temperatures in anurans

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ABSTRACT

The temperature of anuran activity from arid regions have been poorly studied. In recent years, the emphasis was placed on predicting the impacts of global warming on the fauna of ectotherms in general. Many times future impacts are predicted based on global thermal information (macroscale) but not on an individual scale. We used literature data about body temperature in anurans that inhabit the desert region of the Northwest of Argentina to analyze the role of the elevation, eco-region and substrate temperature on the individual scale. Also, we evaluated the predictive capacity that global environmental variables obtained from WorldClim for this region, and compared them with those of local scale. Our results showed that the activity body temperature of the toads in the arid region of western Argentina strongly influenced by elevation and the substrate temperature on the individual scale. We observed that data of the global scale (WorldClim) can predict the body temperature of the studied amphibians, but with a deviation, not less than 8 °C. According to our results, it is evident that to making reliable predictions of how global warming impacts on amphibians in the region, the environmental temperature data need to be recorded at the local scale (operative temperatures).

1. Introduction

The body temperature in ectothermic animals plays a major role in physiological and behavioural functions (Angilletta, 2009). Patterns such as seasonal and daily activity, locomotor performance, digestion rate, growth rate, oxygen consumption, gas exchange, reproduction are affected by body temperature (Lillywhite et al., 1973; Huey and Stevenson, 1979; Choi et al., 2000; Witters and Sievert, 2001; Marvin, 2003; Viscor et al., 2003; Navas et al., 2008; Valetti and Martino, 2012).

Amphibians generally rely on the environment to regulate body temperature (Hutchison and Dupré, 1992). Nocturnal amphibians maintain body temperature mostly by conduction and convection and their body temperatures tend to be lower than diurnal amphibians (Pough et al., 2001). The wet skin of amphibians increases the rate of evaporative water loss and is one of the main causes of heat loss (Spight, 1967; Johnson, 1971; Tracy, 1976; Sinsch, 1989; Shoemaker et al., 1992). The body temperature of amphibians is influenced by

changes in environmental temperature, thus limiting the spatial and temporal distribution of these organisms (Zug et al., 2001). The variation of body temperature with the altitude is well known, populations of high elevations are active at low body temperatures (Navas, 2002) and have the risk of freezing damage at temperatures below 4 °C (Costanzo et al., 1993; Costanzo and Lee, 1994). On the other hand, the global anthropogenic change, like the use of the pesticides, have impact over the thermal physiology of amphibians (Katzenberger et al., 2014; Quiroga et al., 2019), while the global warming is causing an increase in the global temperature at an accelerated rate, generating an increase in minimum winter temperatures (Stott, 2003; Corn, 2005; Webb et al., 2008), and increasing extreme weather events (Barnett et al., 2005; Milly et al., 2005) with recognized ecological implications (Ummenhofer and Meehl, 2017). Many organisms (terrestrial and aquatic) have shifted their geographic distributions in response to global warming (Root et al., 2003; Parmesan, 2006). High environmental temperatures have direct effects on the behaviour and physiology of amphibians (Rome et al., 2002). The thermal landscape

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where amphibians develop has a strong influence on body temperature (Navas, 1997).

The changes in the environmental temperatures in the desert at both macro and micro scale are abrupt (Whitford, 2002). These variations in environment temperatures depend mainly on cloud cover, wind speed, vegetation cover, boundary layer, relative humidity, among others (Warner, 2004). These factors influence the convection, and conduction of operative temperatures at the micro-scale (Gates, 1980). Also, thermal landscapes show a temporal change with the seasons where the dry season is more thermally homogeneous compared to the wet season (Sanabria et al., 2011, 2012b).

So far, the greatest effort is made to know the thermal ecophysiology of amphibians species from equatorial regions or the northern hemisphere. There are limited data of body temperature of free-living anurans in desert regions of South America, and there is a deficiency in records of micro-climatic temperatures (Navas et al., 2008). Our aim to evaluate the means and variations of the body temperature (Tb) of different species and population of desert anurans along the ecoregions, altitudinal and intra- and interpopulation variations. Also, we evaluate the means and variations of the body temperature (Tb) of different species and population of desert anurans along the ecoregions, altitudinal, intra- and interpopulation variations. In the same line, we analyze to what extent the data changes by the elevation, Tb and substrate temperature (Ts) can be integrated to highlight the specific deviations of the thermal ecology of the studied species/populations. We expect that Tb of desert amphibians will change with elevation and have a strong association with Ts. A second objective is to identify and discuss the changes of the Tb through ecoregions in the arid region of western Argentina. Finally, it is intended to evaluate the scope and limitations of large-scale environmental data, comparing environmental data collected at the micro-scale (individuals) and WorldClim data to infer the body temperature of amphibian's activity in the desert. We expected that microclimatic data at a scale compatible with individuals will be better predictors of variations in activity temperature and that WorldClim temperatures will be related, but weaker. To achieve our objectives, we rely on the analysis of a database that includes the Ts and Tb of 8 species and 29 populations of desert anurans from the central-west of Argentina.

2. Material and methods

2.1. General approach

We built a database on the body temperature for anuran species in the desert environment from central-western of Argentina. Then, we analyzed the relationship between Tb and environmental temperature and the strength of this relationship across ecoregions proposed by Pol et al. (2005). We explored the relationship between Tb and elevation. Also, we obtained WorldClim data using the coordinates of collection sites and analyzed the relationship between Tb data and WorldClim data following to Navas et al. (2013). We analyzed the data concerning the different ecoregions; we incorporated information about ecoregions domain, understanding that a given biome encompasses multiple vegetation physiognomies. Accordingly, we identified four dominant ecoregions in our sample: Monte de Sierras y Bolsones (MSB), Monte de Llanuras y Mesetas (MLLM), Alto Andina (AA) and Chaco Árido (CHA) (Pol et al., 2005).

2.2. Study sites and species

The arid region of central-western Argentina is characterized by four arid ecoregions: AA, MSB, MLLM, and CHA.

The AA ecoregion (Fig. 1A), has poor vegetation, dominated by *Adesmia*, and *Azorella*, in the upper floors. This ecoregion is present above 2000 m of elevation. The temperature is relatively low, with an average maximum of 10 °C in summer and an average minimum of

– 15 °C in winter. Precipitation is concentrated in summer as rain, and in winter as snow (Reboratti, 2005). On the other hand, the Monte ecoregion divided into two, according to the feature of the land. The Monte ecoregions have an average of the annual rainfall of 80 mm, concentrated in the summer. In this environment, the dry season can last nine months (Lopez de Casenave, 2001). The maximum average summer temperatures can reach 25.7 °C, and the average winter temperature of 10.4 °C (Pol et al., 2005). The MSB (Fig. 1B) and the MLLM (Fig. 1C) are the driest ecoregions of South America. Xeric vegetation has representatives for the genus *Bulnesia*, *Prosopis*, *Larrea*, *Acacia*. Chaco Árido ecoregion (Fig. 1C) is dominated by vegetation as *Schinopsis*, *Acacia*, *Prosopis*, *Suaeda*, *Zizyphus* and *Cercidium* (Torrella and Adámoli, 2005). In this region rainfall is concentrated in summer as well, and reach an annual average of 300 mm, temperatures are high with an average maximum temperature of 25.3 °C and minimum 12.1 °C (Cabrera, 1976).

The studied species account for over 60% of the total diversity of amphibians in the region. The conservation status of all species is not threatened (Vaira et al., 2012). We studied 29 populations, along the four ecoregions mentioned above. *Rhinella spinulosa* (Andean toad) (Fig. 2A; 6 populations: Rs7 to Rs12), is a typical habitant of high lands and has prolonged activity period along the year. Males do not call during reproduction, have high salt tolerance, and supercoiling physiology (Ceí, 1980; Sanabria et al., 2011; Rodríguez et al., 2019). *Rhinella arenarum* (Fig. 2B; 6 population: Ra1 to Ra6) is widely distributed in Argentina, a walker and medium-size toad (SVL: 10–15 cm), with reproducing in the spring and generalist feeding behaviour (Ceí, 1980; Sanabria et al., 2007b; Quiroga et al., 2019).

Chacophrys pierotii (Figs. 2C and 1 population: Chp29) is a small toad (SVL: ~5 cm) recently found in the central-west of Argentina, an aggressive species, typically eat others anurans, and reproduce during summer rains (Bueno Villafañe et al., 2017; Schalk et al., 2014; Sanabria et al., 2012c). *Odontophrynus barrioi* (Fig. 2D, populations: Ob27 and Ob28) is a small toad (SVL: ~7 cm), a typical inhabitant of desert regions with generalist feeding behaviour (Ceí, 1980). *Pleurodema nebulosum* (Figs. 2E and 5 population: Pn16 to Pn20) and *Pleurodema tucumanum* (Figs. 2F and 6 populations: Pt21 to Pt26) are small species (SVL: ~5 cm), specialized living in the desert, their main distribution is in the central-west of Argentina, the reproduction takes place after summer rains (Ferraro and Casagrande, 2009; Faivovich et al., 2012).

Leptodactylus latrans (Fig. 2G, populations: Ll14 and Ll15) is a medium-size frog (SVL: ~10 cm) with a wide distribution in Argentina, generalist in alimentation and reproducing in the summer (Ceí, 1980). *Leptodactylus bufonius* (Figs. 2H and 1 population: Lb13) is a medium-size frog (SVL: ~6 cm) and build specialized foam nest (Philibosian et al., 1974).

Because we worked with a limited number of species, our data are not suitable for phylogenetic analysis (Blomberg et al., 2003). Therefore, we did not perform any phylogenetic signal analysis in our study. On the other hand, because species within the same genera are more related to each other than to any other species in the study, we incorporated phylogenetic considerations in topology-based data analysis (Fig. 3) retrieved from Pyron and Wiens (2011).

2.3. Estimation of active body temperature (Tb)

The data set includes Tb reported in the literature (Sanabria et al., 2003a,b; 2007a, 2011; 2012a,b; 2013a,b; 2015) and new data from 29 populations of desert anurans. The species included in this analysis are *R. arenarum*, *R. spinulosa*, *L. latrans*, *L. bufonius*, *P. nebulosum*, *P. tucumanum*, *O. barrioi* and *C. pierotii*.

2.4. Measures of active body temperature

Body temperature (Tb) of free-ranging toads has measured at the

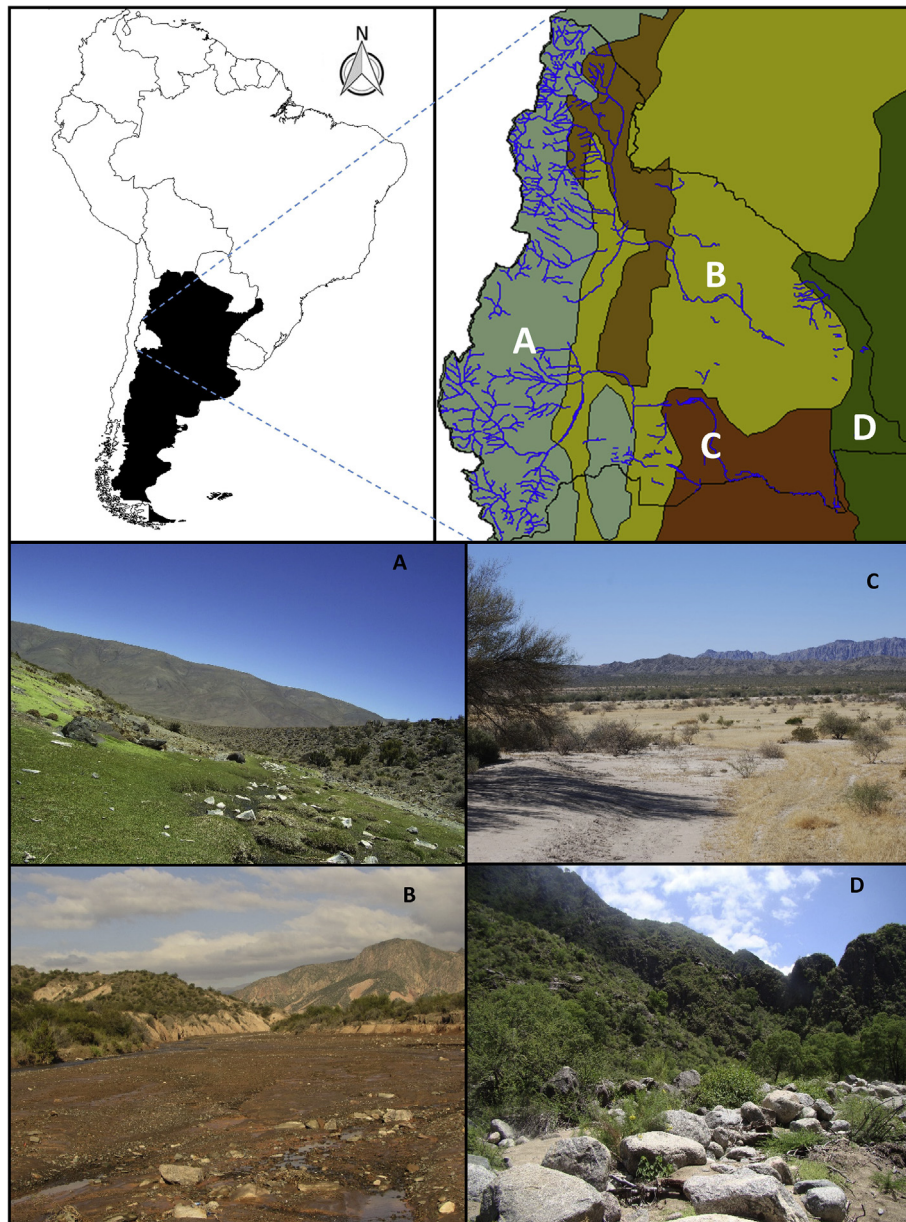


Fig. 1. The arid region of central-western of Argentina is characterized by four arid ecoregions: Alto Andina (A), Monte de Sierras and Bolsones (B), Monte de Llanuras and Mesetas (C), and Chaco Árido (D).

time of capture (catheter probes TES TP-K01) with a digital thermometer TES 1312 (TES Electrical Electronic Corp., Taipei, Taiwan, ± 0.1 °C). Toads were gripped by a forelimb to minimize heat exchange during manipulations, and a thermocouple was inserted 1 cm into the cloaca. At the same site of capture, we also recorded the microenvironment temperature and the substrate temperature (T_s) (TES TP-K03 substrate probe). We also measured the snout-vent length of toads (SVL) to the nearest 0.1 mm using a digital caliper. In this study, we didn't use inactive animals. We calculated the coefficient of variation (CV) in the percentage of T_b at different levels (populations/ecoregions) following the mathematical equation: $\%CV = (SD/\text{mean } T_b) \times 100$ where the SD = Standard deviation; mean = mean of T_b .

2.5. WorldClim variables

To analyzed the power that WorldClim has to predict the T_b of activity of desert amphibians 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 ($\sim 1 \text{ km}^2$) data grids. We preprocessed the information using DIVA-GIS. We used seven variables extracted the WorldClim database to evaluate the capacity of prediction of active body temperature: mean temperature of the last 50 years, maximum temperature of the hottest, minimum temperature of the coldest month, mean temperature of the wettest quarter (4 month period), mean temperature of the driest quarter, mean temperature of the warmest quarter and mean temperature of the coldest month.

2.6. Data analysis

We show all thermal variables using descriptive statistics (mean $\pm$ variance) of the populations/species studied and summarized in Table 1. We conducted regressions to evaluate the relationship between the active body temperature of amphibians (T_b) and the

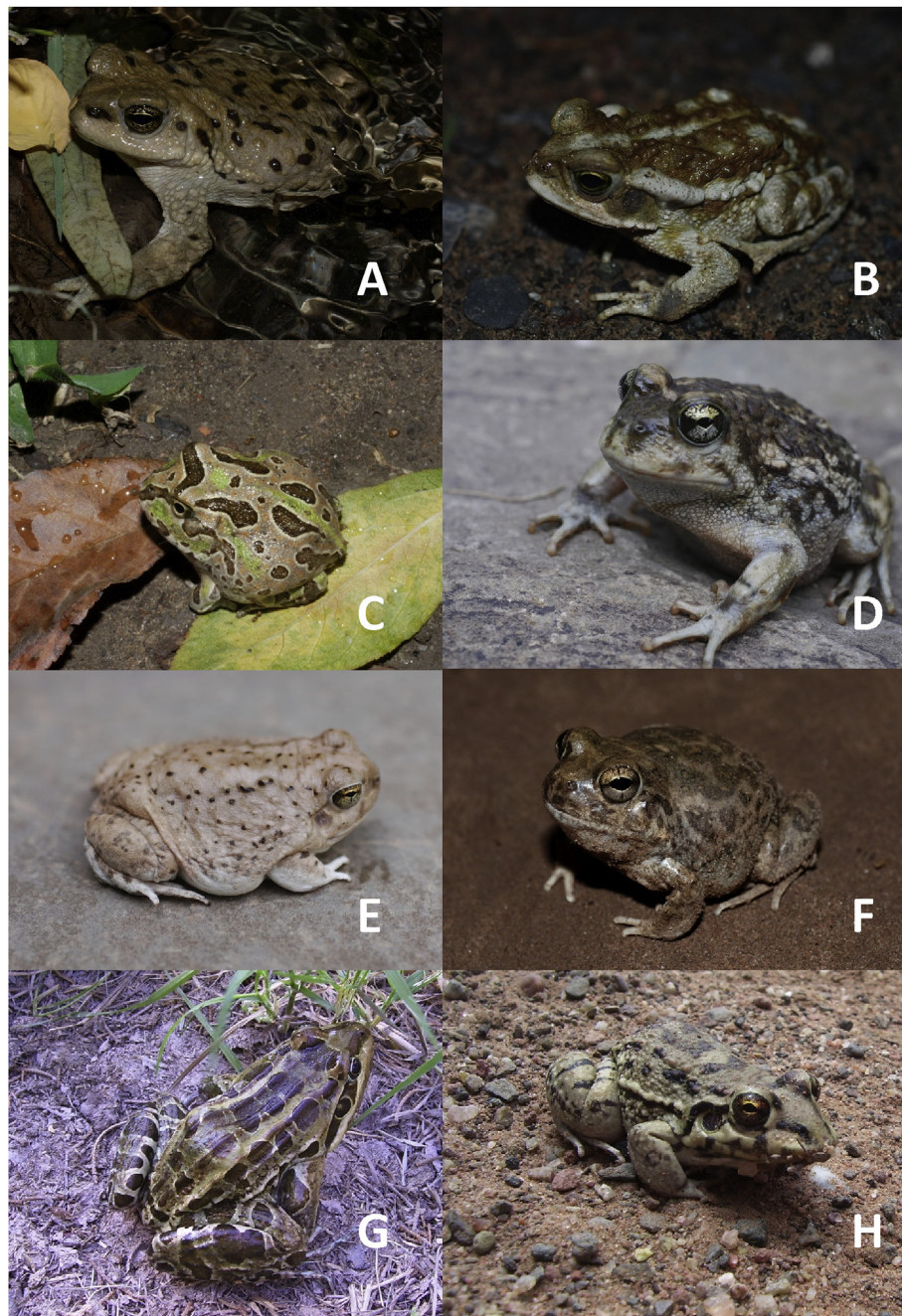


Fig. 2. Study species of the desert region from Western of Argentina. A) *Rhinella spinulosa*, B) *Rhinella arenarum*, C) *Chacophrys pierotii*, D) *Odontophrynus barrioi*, E) *Pleurodema nebulosum*, F) *Pleurodema tucumanum*, G) *Leptodactylus latrans*, H) *Leptodactylus bufonius*.

environmental temperature and altitude of the different biomes. We used generalized linear models to construct a multiple regression to evaluate the effect of global climatic variables obtained from WorldClim for each of the sampled locations of each studied population of anurans from Monte desert. In this multiple regression (stepwise), we included seven WorldClim variables and the substrate temperature obtained at the micro-scale, in this way, we intended to compare the predictive capacity of global and micro environmental variables. We did not exclude variables from our multiple correlation model because the partial correlations were resolved below 0.7 and following the criterion proposed by Zar (2009).

3. Result

3.1. Thermal relationship

The activity Tb of the populations/species studied showed a negative relation with the increase of the elevation ($R^2 = 0.41$, $p < 0.0001$; Fig. 4). The Tb of the population/species of high elevation was less than those of population/species are at the lower altitude.

3.2. Influence of desert ecoregions

The study species showed a strong correlation between Tb and Ts in all ecoregions: MSB ($R^2 = 0.69$, $p < 0.00001$, $Tb = 0.802 + 0.8738 * Ts$; Fig. 5A), CHA ($R^2 = 0.95$, $p < 0.00001$, $Tb = 0.78 + 0.9584 * Ts$;

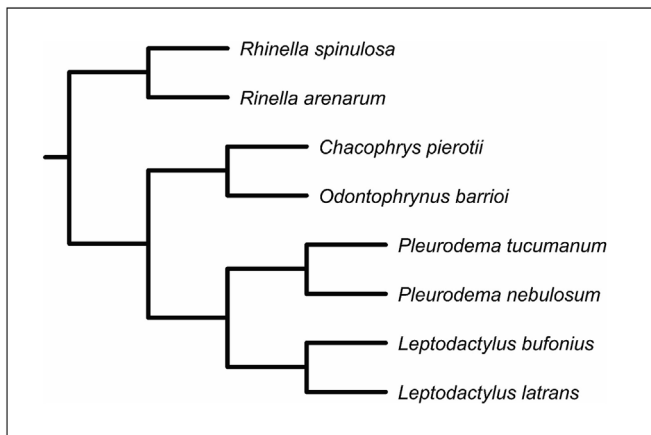


Fig. 3. Phylogenetic relationship of study species. Redraw from Pyron and Wiens (2011).

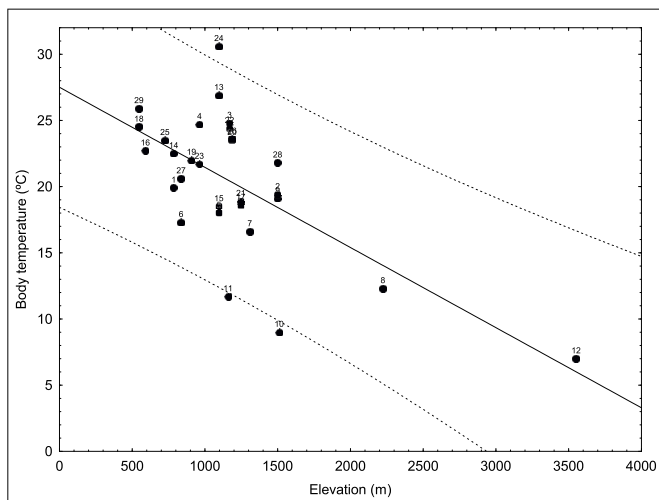


Fig. 4. Thermal variation of active body temperature versus elevation of the capture site of population/species from central Western of Argentina. The numbers indicate the population/species for more detail see Table 1.

Fig. 5B), AA ($R^2 = 0.98$, $p < 0.00001$, $T_b = 0.832 + 0.9198 * T_s$; Fig. 5C), and MLLM ($R^2 = 0.98$, $p < 0.00001$, $T_b = 5.1233 + 0.8011 * T_s$; Fig. 5D). Where 26 of the study populations showed an adjustment, greater than 60% and 12 population adjusted above 90% (Table 1). At this population scale, the relationship between T_b and T_s did not depend on the elevation (regression between intraspecific R^2 and elevation $p = 0.39$), or the macrohabitat where populations were found (no variation of coefficient of regression between the ecoregions ANOVA: $p > 0.42$).

On a larger scale (distributional type) the species/population showed a strong linear connection between T_b and T_s ($R^2 = 0.74$, $p < 0.00001$, $T_b = 0.3261 + 0.9117 * T_s$; Fig. 6).

At the ecoregion scale, and even though the ecoregions are not directly arranged by an altitudinal gradient, the elevation had the greatest influence on T_b (ANCOVA: $F(3, 1778) = 130.49$, $p < 0.00001$; Cov. LHC). T_b was lower in the highest elevated ecoregion (AA), with MLLM and CHA showed higher T_b activity. On the other hand, the %CV didn't show significant variation between ecoregions (ANOVA, $p > 0.86$), or populations (ANOVA, $p > 0.94$).

3.3. Inference of body temperature (T_b) from WorldClim

The climatic variables obtained from WorldClim for each species/population treated with multiple regression (stepwise) through a

generalized linear model, this approximation showed that the body temperature explained for the global climatic data ($R^2 = 0.98$ $F(9,19) = 157.7$, $p < 0.00001$; $EE = 0.73$). The regression model showed that the best predictor of the active T_b of desert anurans is the variable measured at the microscale (T_s) being highly significant ($p < 0.000001$). Regarding the global estimations, the one variable that can predict the T_b of activity was the maximal temperature of the hottest month ($p < 0.003$). We observed that the relationship between T_b of anurans and the T_s obtained at microscale has a linear relationship and with scarce deviation. On the other hand, the environmental temperature obtained from WorldClim that best explains the activity body temperature of the desert anurans has a logarithmic function with a wide deviation in certain values (Fig. 6).

4. Discussion

Our results show that T_b s of the studied populations/species strongly influenced by the environmental abiotic variables and elevation. The thermoregulation of amphibians out of the water is challenging since their skin is permeable, which gives them little control of the evaporation, increasing rapidly the loss of caloric energy (Wygodna, 1988; Tracy et al., 2010; Köhler et al., 2011). In general, T_b of amphibians correlates strongly with the ambient temperature (Brattstrom, 1968; Tracy, 1976; Carey, 1978). Adjustments being between T_b and T_s as a classical approach used to determine the degree of thermoregulation that ectotherms possess (Huey and Slatkin, 1976). All the analyzed populations in the present study had nocturnal activity, and the T_b s was strongly associated with the T_s , being thigmothermy the most possible way exchanging caloric energy (Sanabria et al., 2003b). The thigmothermic behaviour is compatible with the absorption of water from the wet substrates, thus maintaining the water balance (Cree, 1989). This would not indicate that the study species are fully thermoconformers since it was observed in some species of bufonids that there is some degree of thermoregulation which may vary seasonally (Sanabria et al., 2011; Anderson De Oliveira et al., 2018). The correct prediction of the T_b of anurans is important because is normal temperature during the activity (Pough and Gans, 1982) and it's essential to make accurate predictions for the niche modelling (Navas et al., 2013). At the same time, T_b is the temperature that anurans select from an environmental thermal mosaic at a specific time when there are costs, such as predation (risk of mortality), drying out, and benefits such as high rates of digestion and growth, locomotor efficiency, among others (Huey and Slatkin, 1976; Huey, 1982; Angilletta, 2009). The populations that live at ecoregions at high altitude showed a lower T_b concerning their congeners that live at low altitude (Rueda et al., 2016). The mountain toad, *R. spinulosa*, lives at high elevations and it's typically nocturnal, being active at low body temperatures ($\sim 6^\circ\text{C}$). Amphibians that are active at temperatures near $\sim 4^\circ\text{C}$ generate physiological antifreeze responses (Costanzo et al., 1993; Costanzo and Lee, 1994). Probably the activity of this species has high energy costs due to the production of antifreeze metabolites (Ben, 2001; Rodriguez et al., 2019). On the other hand, the species/populations that live in warmer ecoregions (CHA, MLLM and MSB) showed a higher average from $T_b \sim 20\text{--}24^\circ\text{C}$, respectively. Similar relationships between elevation and T_b have been reported for salamanders, where the populations of high areas had a lower mean T_b than low-altitude populations (Feder and Lynch, 1982).

In the analysis of our data, we could not detect statistically significant differences between the CV for populations/ecoregions. We believe that the CV of the T_b are conserved between the ecoregions because the animals are nocturnal, and many of these species use the aquatic medium as a buffer of the temperature during night hours (Lillywhite, 1970). Navas et al. (2013) observed changes in the amplitude of T_s with an increase in elevation, and these variations in the environmental temperature modify the T_b of the animals. In our study, we observed that the changes in T_s during the activity period had

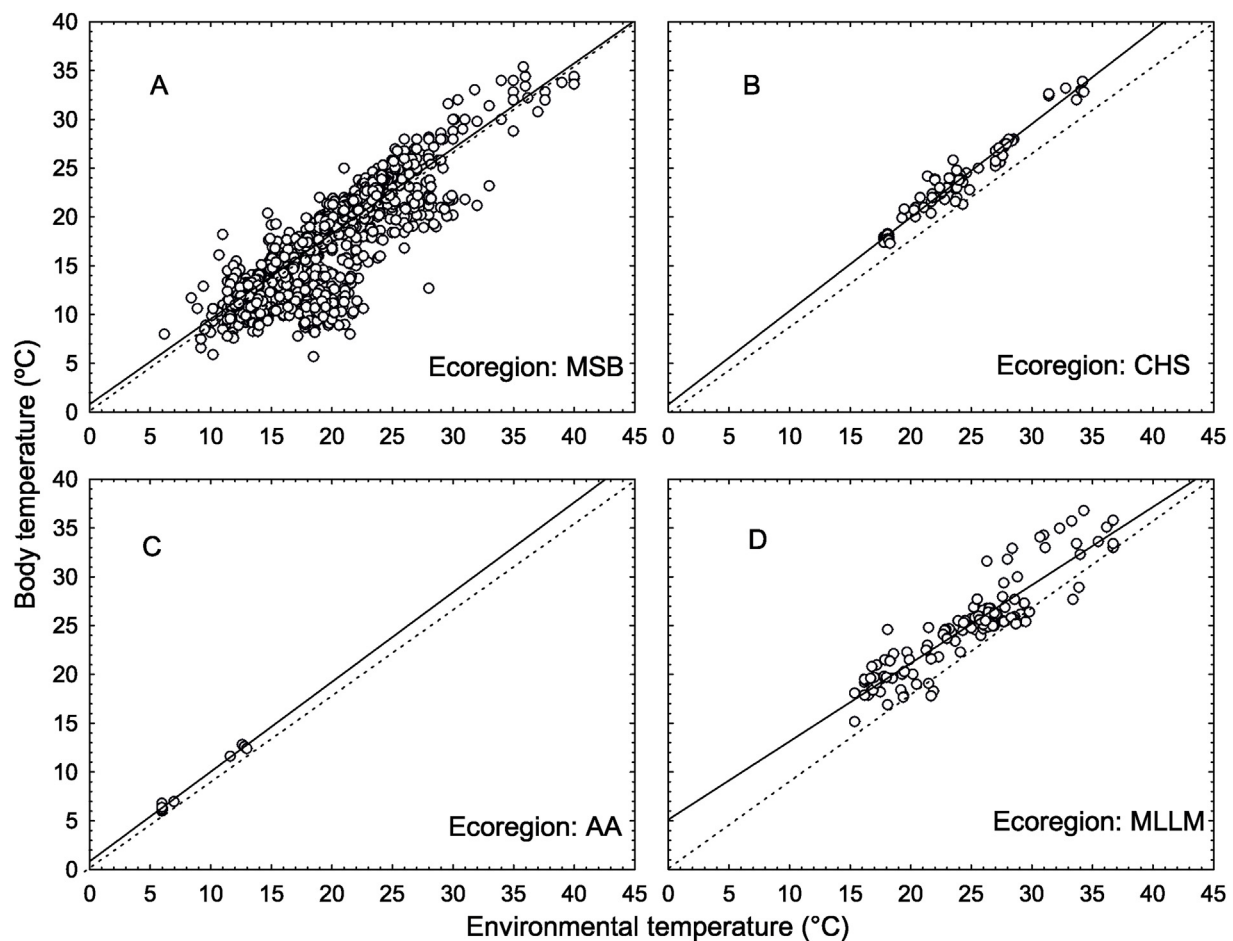


Fig. 5. The relation between active body temperature and substrate temperature in different ecoregions from central western of Argentina. MSB = Monte de Sierras y Bolsones, CHA = Chaco Árido, AA = Alto andina, MLLM = Monte de llanuras y mesetas.

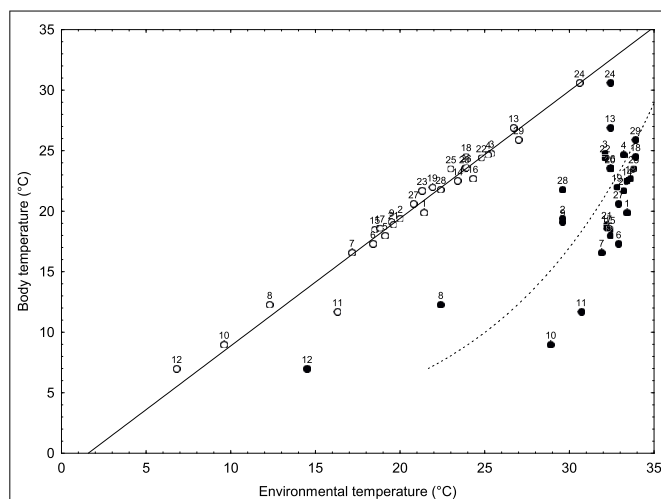


Fig. 6. The relation between active body temperature of the study population of anurans and microclimatic temperatures (substrate temperatures, empty dot) and mean environment temperature of the last 50 years (WorldClim database, black dot). The numbers indicate the population/species, for more detail, see Table 1.

greater variation at low altitude. The lack of thermal variability in high mountain environments is probably because thermal environments are more homogeneous during night hours (Warner, 2004). We included linear prediction models that allow us to predict Tb of the anurans in

different arid ecoregions of western Argentina, which must be validated to use in other environments. Regarding the models of 21 anuran species in an altitudinal gradient in Colombia obtained by Navas et al. (2013), the variation of Tb is strongly associated with Ts. Global data can predict the Tb values of the study populations/species. Only the maximal temperature of the hottest month could predict Tb out of the seven WorldClim variables. Hence, we could not obtain predicted values with a deviation of less than $\sim 8^\circ\text{C}$. Besides, we observed that the distribution of the data is not linear, which further widens the error in the prediction.

The data obtained from WorldClim are poor determinants of the environment where toads live, and it is advisable to make these predictions from microclimatic data.

It is important to take into account the scale at which the studies developed, as it is crucial to achieving a good interpretation of the data, for more accurate and realistic predictions (Suggitt et al., 2011; Graae et al., 2012; Navas et al., 2013; Bovo et al., 2018). Similar observations have been reported in insects (Pincebourde and Casas, 2015; Rebaudo et al., 2016), where global climatic data models fail to predict activity temperatures. Global climate data are not adequate predicting micro-scale temperatures and the daily variation dissolved in the general averages. Therefore, they are not able to predict the temperature of animals that are specialists and live in thermal buffering habitats, or that have certain hours of activity (eg. nocturnal).

It is necessary to know the life histories of the species to select the appropriate model for the operating temperatures (Guisan and Thuiller, 2005).

Based on the scale of the study, the environmental data should be

Table 1

Summary data of the species shown in this paper. The body temperature column includes the descriptive parameters for the active body temperature of study anurans (N = number, Tb = mean of population active body temperature, Var = variance, Min = minimum body temperature recorder during activity; Max = maximum body temperature recorded during activity). The coefficient of correlation between Tb versus Ts represented by r. Elevation of collected data expressed in meters. The anuran population ecoregion (EcoR): MSB = Monte de Sierras y Bolsones, MLLM = Monte de Llanuras y Mesetas, AA = Alto Andino; CHA = Chaco Seco (Pol et al., 2005). The information and code of different population see Materials and Methods. Asterisk (*) indicate the dates for the present study.

Familia	sp	Population	Body temperature						Elevation	EcoR	Source	
			N	Tb	Var.	Min	Max	r				
Bufonidae	<i>R. arenarum</i>	Ra(1)	532	19.9	4.4	10.3	35.4	0.88	800	MSB	Sanabria et al., 2003b	
		Ra(2)	13	19.4	2.7	16.0	22.2	0.99	1311	MSB	*	
		Ra(3)	11	24.8	1.0	23.0	25.7	0.79	1020	MSB	*	
		Ra(4)	23	24.7	2.2	20.4	32.0	0.58	943	CHS	*	
		Ra(5)	230	18.0	3.4	10.3	24.6	0.96	743	MSB	Sanabria et al., 2011	
		Ra(6)	26	17.3	1.6	13.3	20.7	0.85	1331	MSB	*	
	<i>R. spinulosa</i>	Rs(7)	22	16.6	2.1	11.9	19.7	0.87	1450	MSB	*	
		Rs(8)	3	12.3	0.6	11.6	12.8	0.95	1400	AA	*	
		Rs(9)	8	19.1	1.6	17.7	22.3	0.79	1311	MSB	*	
		Rs(10)	11	9.0	2.0	5.9	12.9	0.34	1517	MSB	*	
		Rs(11)	302	11.7	2.4	5.7	22.2	0.28	1248	MSB	Sanabria et al., 2015	
		Rs(12)	10	7.0	1.9	6.0	12.4	0.98	3635	AA	*	
Laptodactylidae	<i>L. bufonius</i>	Lb (13)	10	26.9	1.2	24.0	28.0	0.93	1000	CHS	*	
		Li(14)	38	22.5	4.3	14.2	34.0	0.90	800	MSB	Sanabria et al., 2003a	
	<i>L. latrans</i>	Li(15)	3	18.5	1.0	17.4	19.3	0.80	1300	MSB	*	
		<i>P. nebulosum</i>	Pn(16)	31	22.7	2.5	19.8	28.6	0.87	916	MSB	*
	Pn(17)		27	18.6	1.9	17.6	23.9	0.98	1534	CHS	*	
	Pn(18)		101	24.5	5.1	15.2	36.8	0.92	638	MLLM	Sanabria et al., 2006	
	Pn(19)		19	22	1.8	19.6	25.7	0.88	916	MSB	*	
	Pn(20)		8	23.5	0.6	22.8	24.3	0.49	1168	MSB	*	
	<i>P. tucumanum</i>		Pt(21)	11	18.9	1.8	17.3	21.8	0.95	1534	CHS	*
		Pt(22)	9	24.4	1.1	22.4	26.0	0.63	1020	MSB	*	
		Pt(23)	12	21.7	1.1	20.0	24.2	0.58	899	CHS	*	
		Pt(24)	8	30.6	4.3	23.1	33.9	0.97	1000	CHS	*	
		Pt(25)	8	23.5	0.8	22.0	24.8	0.39	839	CHS	*	
		Pt(26)	4	23.6	0.7	22.7	24.3	0.50	1168	MSB	*	
	Odontophrynidae	<i>O. barrioi</i>	Ob(27)	276	20.6	3.3	11.3	25.7	0.94	743	MSB	Sanabria et al., 2012b
			Ob(28)	7	21.8	1.0	20.8	23.5	0.49	1311	MSB	*
Ceratophryidae	<i>C. pierottii</i>	Chp (29)	30	25.9	0.7	24.7	27.7	0.30	638	MLLM	*	

obtained by direct measurement of the environmental temperature at the moment of capturing the specimens, or by means of null physical models placed in the study sites (Navas and Araujo, 2000; Bartelt and Peterson, 2005; Tracy et al., 2007). Many researchers are currently working on improving predictions on a global scale by incorporating microenvironmental data into their models (Guisan and Thuiller, 2005; Kearney and Porter, 2009; Kearney et al., 2014; Pincebourde and Casas, 2015; Rebaudo et al., 2016; Oyamaguchi et al., 2017). These efforts produce models with more realistic and reliable predictions. It is necessary for the future models to build microclimatic databases, especially for small ectothermic species (insects, amphibians and small lizards) because many of these species are thermosensitive to local environmental conditions.

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