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Journal of Thermal Biology

journal homepage: [www.elsevier.com/locate/jtherbio](http://www.elsevier.com/locate/jtherbio)

## Thermal biology of genus *Liolaemus*: A phylogenetic approach reveals advantages of the genus to survive climate change

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### ARTICLE INFO

#### Article history:

Received 16 September 2011

Accepted 12 June 2012

Available online 1 July 2012

#### Keywords:

Squamata  
Temperature  
Viviparity  
Phylogeny  
*Liolaemus*

### ABSTRACT

The trends of body temperatures in the field ( $T_b$ ) and preferred body temperatures in the laboratory ( $T_{pref}$ ) of the genus *Liolaemus* relative to reproductive mode, air temperature ( $T_{air}$ ), precipitation, latitude, and elevation were studied using phylogenetic comparative analysis. Results were discussed in the framework of the evolution of thermal physiology and vulnerability to global climate change. Reproductive mode affects  $T_b$  but not  $T_{pref}$ . Whereas  $T_b$  and  $T_{pref}$  showed a significant association with  $T_{air}$ , there was no relationship with latitude or elevation.

In most liolaemids,  $T_{pref}$  is significantly higher than  $T_{air}$  and  $T_b$  pointing to a primitive condition of  $T_{pref}$ , probably related to earlier Miocene environments. Phylogenetic trends in the evolution of liolaemid thermal physiology provide a physiological explanation for the lowest rates of observed contemporary climate-forced extinctions and those forecasted under climate warming scenarios up to 2080. Liolaemids have a much higher  $T_{pref}$  than is expected for their environments, especially for viviparous members of the genus, in contrast to other viviparous taxa in the sister family the Phrynosomatidae, which have evolved much lower  $T_b$  (and  $T_{pref}$ ) and currently experience a much higher rate of climate-forced extinction.

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### 1. Introduction

Reptiles depend on temperature for growth and reproduction, hence the selection of favorable thermal environments may have a direct influence on fitness (Angilletta, 2009). But, the influence of the environment on a lizard's body temperature can be compensated by thermoregulatory adjustments (Cowles and Bogert, 1944; Angilletta, 2009; Medina et al., 2009) and individuals are often capable of maintaining a relative constant body temperature through behavioral flexibility (compensation) even in temporally variable environments. Therefore, if environmental change is of long duration relative to the generation time of a species, lizards can accommodate local variation or elevation in ambient temperature through a combination of adaptive evolution, behavioral and/or physiological plasticity (Niewiarowski,

2001). However, during extreme or unpredictable changes in ambient temperature and/or precipitation, physiological plasticity in either  $T_b$  or earlier reproduction may be the only avenue for adaptation to altered thermal environments (Sinervo et al., 2010; Clusella-Trullas et al., 2011).

In circumstances when environmental changes occur rapidly, not even the behavioral adjustments can avoid the deleterious consequences of overheating. Consequently, in severe temperatures, lizards will respond by reducing the duration of activity, which may negatively influence reproductive success even resulting in reproductive failure (Sinervo et al., 2011). The reduction in activity limits food acquisition, courtship, as well as constrains embryonic development. Previous studies showed that the restriction in activity time due to global warming currently occurs in several lizard populations around the world. Moreover, viviparous species with average field body temperatures close to upper set point (75th percentile of  $T_b$ 's preferred in the laboratory; sensu Huey, 1982 and Hertz et al., 1993), living at low altitude and in tropical environments are especially vulnerable to

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rising temperatures (Sinervo et al., 2010). The model of Sinervo et al. (2010) is largely based on patterns of  $T_b$  derived from lizards in the family Phrynosomatidae. The geographic distribution of these species is contained largely in temperate, subtropical, and tropical habitats in the northern hemisphere. Data on the thermal biology of lizards from South America in relation to environmental factors and reproductive mode are scant, which precludes generating accurate predictions of their extinction risk given current global warming changes at southern latitudes.

The genus *Liolaemus* is represented by more than 220 recognized species (Breitman et al., 2011) that can be found in a variety of environments. The geographical distribution extends from the extremely arid Atacama Desert to the temperate *Nothofagus* rainforest (9°–53°S; Donoso-Barros, 1966; Cei, 1986, 1993; Etheridge and De Queiroz, 1988; Lobo, 2001), and from sea level in Coastal Argentina and Brazil, up to 5000 m asl in the Andes (Duellman, 1979; Cei, 1993; Scolaro, 2005, 2006), which makes this the most broadly distributed genus in the world. The ecologically versatile liolaemids show intra and interspecific differences in field body temperatures, thermoregulatory behavior, and in the daily activity patterns associated with climatic conditions (Fuentes and Jaksic, 1979; Jaksic and Schwenk, 1983; Martori et al., 2002; Marquet et al., 1989; Carothers et al., 1998; Labra, 1998). The high species richness and diversity of thermal conditions experienced by *Liolaemus* makes this genus well suited for studying the evolution of thermal physiology.

Previous studies in the genus suggest an evolutionarily flexible thermal physiology (Espinoza et al., 2004; Rodríguez-Serrano et al., 2009). The genus has high species diversity in the Andes, which suggests that behavioral compensation of thermal ecology allowed *Liolaemus* to colonize extreme altitudes (Hellmich, 1952; Carothers et al., 1998). These adjustments include a positive correlation between preferred body temperature in the laboratory and air temperature based on an analysis of seven species of *Liolaemus* (Labra, 1998). Other comparative studies using traditional statistical analysis, as well as phylogenetic approaches, showed that mean body temperature ( $T_b$ ) varies with ecological gradients of air temperature (Rodríguez-Serrano et al., 2009). However,  $T_b$  also depends on field opportunity for thermoregulation (Hertz et al., 1993), and ecological constraints may lead to lower  $T_b$  in *Liolaemus* from colder settings, even if thermal physiology (e.g.,  $T_{pref}$ ) is conserved within the genus (Medina et al., 2009; Ibarra-Goytia et al., 2010). In general, delimiting the ecological and life history factors that influence body temperature is complicated by the observation that there is a significant phylogenetic signal for  $T_b$  (Garland et al., 2005; Clusella-Trullas et al., 2011).

The main objective of this study was to review the current data of  $T_b$  and  $T_{pref}$  in the genus *Liolaemus* and using a phylogenetically informed approach determine their relationship to air temperature, latitude, elevation, precipitation and reproductive mode to better understand the adaptive landscape. The results of this study are discussed in the context of extinction risk given the recent findings by Sinervo et al. (2010) for *Liolaemus*. A second goal was to use the data on thermal biology of the genus to infer extinction risk of the group, relative to results reported on Phrynosomatid lizards.

## 2. Materials and methods

### 2.1. $T_b$ and $T_{pref}$ of the genus *Liolaemus*

Field body temperature of 70 species and preferred body temperature of 23 species of the genus *Liolaemus* were obtained from the literature and were coupled with data of mean air

temperatures ( $T_{air}$ ) and precipitation using the data sources from National Climatic Data Center (NCDC, in Asheville, USA) available at <http://worldclimate.com>. Data for latitude, elevation and longitude were obtained from the literature for each species and/or population. These coordinates were used in the worldclimate website to obtain the mean air temperature and precipitation (monthly) of each locality from September to May (historical data from 1961 to 1991), which coincides with the activity period of lizards. Mean data of  $T_b$  and  $T_{pref}$  of males and females during activity periods were obtained for each species (Appendix 1). If the species presented data of  $T_b$  or  $T_{pref}$  for more than one population the weighted mean ( $x_w = \sum wx / \sum w$ ) for each species was used for the analyses, and if the same  $T_b$  or  $T_{pref}$  was given for a range of latitudes and elevations, the highest location was selected. If latitude or elevation were not given for particular sites, these data were geo-referenced using Google Earth Plus. From these data we constructed a character matrix with  $T_b$ ,  $T_{pref}$ ,  $T_{air}$ , elevation, latitude, precipitation, and reproductive mode of the species of the genus *Liolaemus* (Appendix 1).

### 2.2. Statistical analysis

We used the statistical programs Sigma Stat 3.5 ®, SPSS 11.0 ®, Sigma Plot 10.0 ®, R 2.14.2 (R Development Core Team, 2011) and Mesquite 2.75 for phylogenetic analyses. A paired *t*-test was used to analyze differences between  $T_b$  and  $T_{pref}$  mean values of each species. The assumptions of normality and homogeneity of variance for parametric procedures were checked using Kolmogorov-Smirnov and Levene's tests, respectively (Sokal and Rohlf, 1969). Because the variables  $T_b$ ,  $T_{pref}$ ,  $T_{air}$ , elevation, latitude and precipitation did not conform to a normal distribution, we used log 10 transformations to ensure the variables met the assumptions of the parametric statistics, which also reduced skew and homogenized variances (Zar, 2009). We also conducted standard regression diagnostics to determine whether the data exhibited multicollinearity considering variance inflation factors (VIF). We found no evidence of multicollinearity, being all VIF values below the threshold VIF value 10 indicative of multicollinearity (Montgomery and Peck, 1992). In addition we presented the correlations among the variables (Appendix 2A) and the VIF values from the regression of  $T_b$  and  $T_{pref}$  with latitude, elevation,  $T_{air}$  and precipitation (Appendix 2B). We employed a backward elimination of variables to arrive at the most parsimonious model and the Akaike's Information Criterion was used for selecting the best model (Burnham and Anderson, 2002; Anderson, 2008).

### 2.3. Phylogenetic hypothesis

We derived a phylogenetic tree for the *Liolaemus* species included in our study, based on molecular phylogenetic hypotheses proposed by Schulte et al. (2000, 2004) and, a molecular dataset presented in Espinoza et al. (2004).

### 2.4. Phylogenetic signal

Prior to conducting our statistical analyses we determined whether the traits exhibited phylogenetic signal, i.e., the consistency in trait values with the phylogeny; the variables that presented low or absent phylogenetic signal were deleted from the analyses to avoid mistake to infer patterns of character evolution when absent (Blomberg et al., 2003). We estimated values for Pagel's  $\lambda$  (Pagel, 1999; Freckleton et al., 2002), which is a statistic commonly used to calculate phylogenetic signal. We used the package phytools (Revell, 2011) to generate values of  $\lambda$  conducted in the R statistical environment (R Core Development Team, 2011).

### 2.5. Phylogenetic comparative analyses

We employed the method of phylogenetic generalized least squares to determine the dependence of  $T_b$  and  $T_{pref}$  with latitude, elevation,  $T_{air}$ , and precipitation (Martins and Hansen, 1997; Garland and Ives, 2000). Because we did not have branch length information, all branches were arbitrarily set to a branch length of 1. Phylogenetic generalized least squares incorporates phylogenetic information into the error structure of generalized linear models by specifying the expected variance and covariances among related species using an explicit model of evolution. Thus, PGLS controls for the non-independence that is inherent in the analysis of species that are related phylogenetically. We implemented PGLS analyses using the package caper (Orme et al., 2010) in R.

We compared the slopes of  $T_b$  (or  $T_{pref}$ ) and climate variables between oviparous and viviparous modes of reproduction using comparative phylogenetic generalized least squares (PGLS) which compares the slope of the relationship between viviparous and oviparous taxa.

## 3. Results

### 3.1. Phylogenetic signal relationship of $T_b$ and $T_{pref}$ with latitude, elevation, air temperature and precipitation

All variables, latitude, elevation and air temperature showed a significant phylogenetic signal, except precipitation (these results are presents in Table 1). A multiple regression using phylogenetic generalized least squares (PGLS) found that neither latitude nor elevation predicted variation in  $T_b$  or  $T_{pref}$  (Table 2A and B, respectively). However, the best supported PGLS model found a significant effect of  $T_{air}$  on  $T_b$  and  $T_{pref}$ .

### 3.2. Differences of $T_b$ or $T_{pref}$ between oviparous and viviparous modes of reproduction

We also compared  $T_b$  and  $T_{pref}$  between species that varied in mode of reproduction. Mean  $T_b$  of oviparous species ( $34.01 \pm 0.38$  °C) were significantly higher than  $T_b$  of viviparous species ( $31.7 \pm 0.55$  °C) in both, conventional (ANOVA,  $F_{1, 72} = 12.3$ ,  $P = 0.001$ ) and phylogenetic analyses (PGLS:  $F_{2, 35} = 5.513$ ,  $P = 0.008$ , Fig. 1A). Similarly, oviparous species had a higher  $T_{pref}$  than viviparous species (ANOVA,  $F_{1, 37} = 6.42$ ,  $P = 0.02$ ; Mean  $T_{pref}$  oviparous =  $35.6 \pm 0.43$  °C and Mean  $T_{pref}$  viviparous =  $34.13 \pm 0.37$  °C), but this difference was not significant after accounting for phylogeny (PGLS:  $F_{2, 35} = 2.952$ ,  $P = 0.0654$ , Fig. 1B). The fit did not change when including latitude, elevation, or  $T_{air}$  into the model.

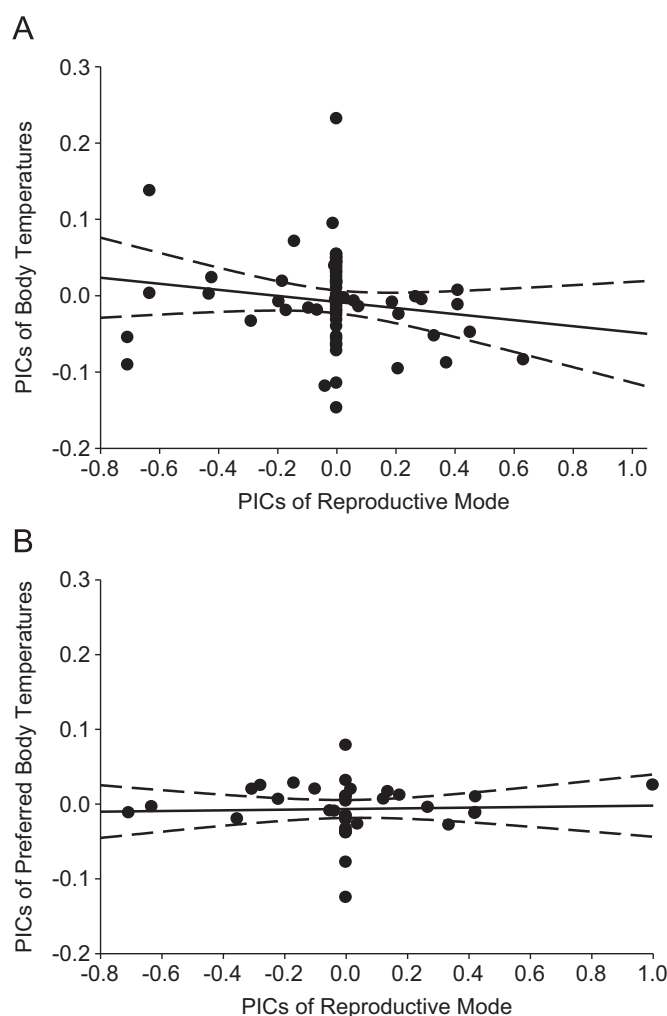
**Table 1**  
Phylogenetic signals of three environmental variables and three temperature variables.

Trait	$\lambda$	
	Estimate	P-value
Elevation	0.54	0.03
Latitude	0.68	0.001
Precipitation	0.17	0.303
$T_{air}$	0.74	0.02
$T_b$	0.76	0.001
$T_{pref}$	0.59	0.04

$P < 0.05$  is significant.

**Table 2**  
Results from a multiple regression based on a phylogenetic generalized least squares analysis. A. Results for Body Temperature ( $T_b$ ); B. results for Preferred Temperature ( $T_{pref}$ ).

Effect	Estimate	S.E.	t-value	P
A. Response variable: $\log_{10} T_b$ ( $N=73$ )				
Intercept	2.08	0.63	3.27	0.003
( $\log_{10}$ ) Latitude	0.12	0.09	1.25	0.22
( $\log_{10}$ ) Elevation (m)	0.01	0.02	0.16	0.87
( $\log_{10}$ ) $T_{air}$	0.34	0.13	2.68	0.01
B. Response variable: $\log_{10} T_{pref}$ ( $N=40$ )				
Intercept	2.77	0.37	7.59	0.0001
( $\log_{10}$ ) Latitude	0.02	0.04	0.55	0.58
( $\log_{10}$ ) Elevation (m)	0.01	0.01	0.16	0.87
( $\log_{10}$ ) $T_{air}$	0.16	0.07	2.17	0.04
( $\log_{10}$ ) $T_b$	0.66	0.09	0.66	0.51



**Fig. 1.** Phylogenetic independent contrasts of body temperatures versus reproductive mode (Panel A), and phylogenetic independent contrasts of preferred body temperatures versus reproductive mode (Panel B) in the genus *Liolaemus*. Linear regressions (solid lines) and 95% confidence intervals (dashed lines) are indicated.

### 3.3. Differences between $T_b$ and $T_{pref}$

The conventional analysis showed that  $T_{pref}$  was significantly higher than  $T_b$  (Pair  $t$ -test,  $t_{40} = -6.2$ ,  $P = 0.0001$ ; Mean  $T_{pref} = 34.6 \pm 0.24$  °C, Mean  $T_b = 32.07 \pm 0.46$  °C).

**Table A1**Georeference data, climatic data,  $T_b$ ,  $T_{pref}$ , and reproductive mode for species/populations included in the study.

Species	$T_b$	$T_{pref}$	Latitude	Elevation	$T_{air}$	Precipitation <sup>a</sup>	Reproductive mode	References
<i>Liolaemus alticolor</i>	29.1	34.5	18.25	4500	20	51.2	Viviparous	Marquet et al., 1989
<i>Liolaemus alticolor</i>	32.9	32.92	18.10	4350				Labra et al., 2009
<i>Liolaemus alticolor</i>	30.6		18.17	4350				Espinoza et al., 2004
<i>Liolaemus araucaniensis (altissimus)</i>	33.03		33.40	2850	18.1	8.78	Viviparous	Carothers et al., 1998
<i>Liolaemus austromendocinus</i>	35		38.77	723	20	58.74	Viviparous	Espinoza et al., 2004
<i>Liolaemus belli</i>	32.7	36	33.06	3200	17.7	9.14	Viviparous	Labra, 1998
<i>Liolaemus belli</i>	34.2	35.31	33.20	2300				Labra, 1998
<i>Liolaemus belli</i>		33.9	36.04	2100				Labra, 1998
<i>Liolaemus belli</i>	35.6		32.30	2530				Espinoza et al., 2004
<i>Liolaemus bibronii</i>	28.3	34.08	43.01	622	13.3	23	Oviparous	Medina et al., 2009
<i>Liolaemus bibronii</i>	27.7	34.14	46.37	263				Medina et al., 2009
<i>Liolaemus bibronii</i>	31.22	35.14	43.32	168				Labra et al., 2009
<i>Liolaemus bisignatus</i>	32.77	34.75	26.09	710	17.9	0.5	Oviparous	Labra et al., 2009
<i>Liolaemus bitaeniatus</i>	32.1		26.83	1860	17.9	0.5	Oviparous	Espinoza et al., 2004
<i>Liolaemus buergeri</i>	34.7		35.16	1968	16.3	9.4	Viviparous	Espinoza et al., 2004
<i>Liolaemus chaltin</i>	32.3		22.69	3360	21.05	45.24	Oviparous	Espinoza et al., 2004
<i>Liolaemus chiliensis</i>	34.1		33.49	1800	18.1	8.78	Oviparous	Carothers et al., 1998
<i>Liolaemus chiliensis</i>	36.55	35.16	33.55	890				Labra et al., 2009
<i>Liolaemus constanzae</i>	30.8	34.31	26.46	2400	17.9	0.5	Oviparous	Labra et al., 2001
<i>Liolaemus curis</i>	32.9		34.97	1700	16.3	9.4	Viviparous	Labra et al., 2009
<i>Liolaemus curis</i>		35.9	34.57	1768				Labra et al., 2009
<i>Liolaemus cyanogaster</i>	32.9	33.79	40.57	700	12.7	36.58	Viviparous	Labra et al., 2009
<i>Liolaemus dicktracyi</i>	35.9		28.91	2800	17.4	49.82	Viviparous	Espinoza et al., 2004
<i>Liolaemus elongatus</i>	33.2		41.10	700	11.7	36.58	Viviparous	Ibargüengoytía and Cussac, 2002
<i>Liolaemus elongatus</i>	29.8		41.60	800				Viviparous
<i>Liolaemus elongatus</i>	30.3	29.9	41.50	970				Ibargüengoytía, 2005
<i>Liolaemus fitzgeraldi</i>	33.05	35.68	32.50	2901	17.7	8.37	<sup>b</sup>	Labra et al., 2009
<i>Liolaemus fuscus</i>	33.7		33.58	50	18.1	8.78	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus fuscus</i>	35.6		33.58	1000				Fuentes and Jaksic, 1979
<i>Liolaemus fuscus</i>	36	35.3	33.35	890				Labra and Bozinovic, 2002
<i>Liolaemus fuscus</i>	34.61		33.49	1200				Carothers et al., 1998
<i>Liolaemus gracilis</i>		40.8	35.04	1380	16.9	23.27	Oviparous	Espinoza et al., 2004
<i>Liolaemus hellmichi</i>	29.06	33.69	23.32	100	18.3	0.11	<sup>b</sup>	Labra et al., 2009
<i>Liolaemus hermani</i>	34.97	35.25	34.57	1768	16.3	9.4	<sup>b</sup>	Labra et al., 2009
<i>Liolaemus istugensis</i>	28.2		19.42	4000	19.5	51.2	Viviparous	Marquet et al., 1989
<i>Liolaemus lemniscatus</i>	35.9		33.04	1000	18	8.78	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus lemniscatus</i>	33.9		33.04	50				Fuentes and Jaksic, 1979
<i>Liolaemus lemniscatus</i>	35.1	35.2	33.35	890				Labra and Bozinovic, 2002
<i>Liolaemus lemniscatus</i>	34.6		33.55	1200				Carothers et al., 1998
<i>Liolaemus lemniscatus</i>		35.8	33.27	600				Labra, 1998
<i>Liolaemus lemniscatus</i>		34.3	33.23	950				Labra, 1998
<i>Liolaemus lemniscatus</i>		35.5	33.32	500				Labra, 1998
<i>Liolaemus leopardinus</i>		34.24	33.22	2353	17.7	8.37	Viviparous	Labra et al., 2009
<i>Liolaemus leopardinus</i>	34.1		33.40	2850				Carothers et al., 1998
<i>Liolaemus lorenzmuelleri</i>	34.65	36.13	29.51	3206	15.9	2.57	Oviparous	Labra et al., 2009
<i>Liolaemus monticola</i>	35.4		33.40	1000	18	8.78	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus monticola</i>	36.7	36.8	33.35	890				Labra and Bozinovic, 2002
<i>Liolaemus monticola</i>	35.3		33.35	2200				Carothers et al., 1998
<i>Liolaemus nigromaculatus</i>	34.8		33.04	50	16.8	23.27	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus nigromaculatus</i>	34.08	35.12	29.34	336				Labra et al., 2009
<i>Liolaemus nigroroseus</i>	33.9	34.74	26.46	2400	17.9	0.5	Viviparous	Labra et al., 2001
<i>Liolaemus nigroviridis</i>	35.9		33.40	2000	18	9.52	Viviparous	Fuentes and Jaksic, 1979
<i>Liolaemus nigroviridis</i>	35.3	36.31	33.22	2353				Labra et al., 2009
<i>Liolaemus nigroviridis</i>	34.96		33.40	2675				Carothers et al., 1998
<i>Liolaemus nitidus</i>	35.4		33.58	100	18	8.78	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus nitidus</i>	34.9	36.2	33.21	1985				Labra, 1998
<i>Liolaemus nitidus</i>	35.5		33.40	2200				Carothers et al., 1998
<i>Liolaemus nitidus</i>		35	30.39	200				Labra, 1998
<i>Liolaemus nitidus</i>	35.43		33.35	890				Labra et al., 2009
<i>Liolaemus parvus</i>	32		33.22	3700	17.7	8.37	Viviparous	Acosta et al., 2006
<i>Liolaemus petrophilus</i>	34.4		41.46	1188	17.9	23	Viviparous	Espinoza et al., 2004
<i>Liolaemus petrophilus</i>		35.2	42.33	1150				Espinoza et al., 2004
<i>Liolaemus pictus argentinus</i>	33.2		41.10	700	11.7	36.58	Viviparous	Ibargüengoytía and Cussac, 2002
<i>Liolaemus pictus argentinus</i>	28.8	36.71	41.15	1700				Gutiérrez et al., 2010
<i>Liolaemus pictus argentinus</i>	32.6	36.6	41.07	700				Gutiérrez et al., 2010
<i>Liolaemus p. pictus</i>	31.8	33.8	35.36	1150	12.7	36.58	Viviparous	Labra, 1998
<i>Liolaemus p. pictus</i>		35.4	41.06	1000				Labra, 1998
<i>Liolaemus p. pictus</i>	32.04		40.57	700				Labra et al., 2009
<i>Liolaemus platei</i>	37.5		33.04	1000	17.7	8.37	Oviparous	Fuentes and Jaksic, 1979
<i>Liolaemus platei</i>	35.3		33.04	50				Fuentes and Jaksic, 1979
<i>Liolaemus platei</i>	33.82	34.5	27.03	200				Labra et al., 2009
<i>Liolaemus puna</i>	33.3		22.44	4358	21.1	0.11	Viviparous	Espinoza et al., 2004
<i>Liolaemus ramirezae</i>	32.2		26.67	1770	17.9	0.5	Oviparous	Espinoza et al., 2004
<i>Liolaemus robertmertensi</i>	36.6		27.83	690	17.9	0.5	Oviparous	Espinoza et al., 2004
<i>Liolaemus sanjuanensis</i>	30.1		31.22	2994	23.2	23.27	Oviparous	Acosta et al., 2006

Table A1 (continued)

Species	T <sub>b</sub>	T <sub>pref</sub>	Latitude	Elevation	T <sub>air</sub>	Precipitation <sup>a</sup>	Reproductive mode	References
<i>Liolaemus schroederi</i>	35.3		33.40	2000	18	9.52	Viviparous	Fuentes and Jaksic, 1979
<i>Liolaemus schroederi</i>	31.6	34.6	35.36	1150				Labra, 1998
<i>Liolaemus schroederi</i>	33.4		33.40	2350				Carothers et al., 1998
<i>Liolaemus schroederi</i>		35.5	33.20	2300				Labra, 1998
<i>Liolaemus pseudolemniscatus</i>	34.29	34.6	29.34	336	15.9	2.57	Oviparous	Labra et al., 2009
<i>Liolaemus tenuis</i>	36.9	37.2	33.35	890	18	9.52	Oviparous	Labra and Bozinovic, 2002
<i>Liolaemus tenuis</i>	34.6		33.55	1500				Carothers et al., 1998
<i>Liolaemus umbrifer</i>	33.1		26.86	3381	17.9	121.5	<sup>b</sup>	Espinoza et al., 2004
<i>Liolaemus kriegii</i>		35.6	38.00	1420	20	13.18	Viviparous	Cruz et al., 2009
<i>Liolaemus poecilochromus</i>		34.2	25.30	3820	20.5	112.78	<sup>b</sup>	Cruz et al., 2009
<i>Liolaemus walkeri</i>	24	33.76	22.36	4250	21.1	0.11	Viviparous	Labra et al., 2009
<i>Liolaemus abaucan</i>	33.8		27.79	1684	25.1	49.82	Oviparous	Espinoza et al., 2004
<i>Liolaemus albiceps</i>	32.9		24.34	4004	20.5	112.78	Viviparous	Espinoza et al., 2004
<i>Liolaemus canqueli</i>		33.7	43.30	900	13.3	23	Oviparous	Cruz et al., 2009
<i>Liolaemus canqueli</i>	33.6		44.15	528				Espinoza et al., 2004
<i>Liolaemus cuyanus</i>	37.7		32.11	1530	23.2	23.27	Oviparous	Espinoza et al., 2004
<i>Liolaemus darwinii</i>	36.4		30.20	928	23.2	23.27	Oviparous	Espinoza et al., 2004
<i>Liolaemus dorbignyi</i>	33.6		24.42	4320	20.5	112.78	Viviparous	Espinoza et al., 2004
<i>Liolaemus dorbignyi</i>	29.4	31.01	22.36	4250				Labra et al., 2009
<i>Liolaemus duellmani</i>	36.4		36.35	2084	16.9	9.14	Viviparous	Espinoza et al., 2004
<i>Liolaemus eledori</i>	32.34	35.87	27.04	3670	17.9	0.5	<sup>b</sup>	Labra et al., 2009
<i>Liolaemus fabiani</i>	29.8	30.03	26.46	2400	17.9	0.5	Viviparous	Labra et al., 2001
<i>Liolaemus fabiani</i>	31.8	33.03	26.46	2300				Labra et al., 2001
<i>Liolaemus fabiani</i>		32.7	26.46	2300				Labra, 1998
<i>Liolaemus fitzingerii</i>	32.4		43.01	626	13.3	23	Oviparous	Medina Unpublish Data
<i>Liolaemus fitzingerii</i>	33.4		44.60	334				Espinoza et al., 2004
<i>Liolaemus grosseorum</i>	37.3		35.04	1380	16.9	23.27	Oviparous	Espinoza et al., 2004
<i>Liolaemus huacahuasicus</i>	32		30.11	4500	17.9	16.58	Viviparous	Halloy and Laurent, 1988
<i>Liolaemus huacahuasicus</i>	31.5		26.96	399				Espinoza et al., 2004
<i>Liolaemus irregularis</i>	35.5		24.04	3809	20.5	112.78	Viviparous	Espinoza et al., 2004
<i>Liolaemus jamesi</i>	30.36	32.94	18.10	4350	20	51.20	Viviparous	Labra et al., 2009
<i>Liolaemus jamesi</i>	29.1		19.42	4500				Marquet et al., 1989
<i>Liolaemus kingii</i>	27.9	36.6	43.01	622	16.3	23	Viviparous	Medina unpublish data
<i>Liolaemus kingii</i>	24.9		46.37	263				Medina unpublish data
<i>Liolaemus kingii</i>		34.8	34.20	500				Cruz et al., 2009
<i>Liolaemus kingii</i>	30.8		47.47	141				Espinoza et al., 2004
<i>Liolaemus koslowskyi</i>	34.8		28.49	1200	25.1	49.82	Oviparous	Martori et al., 2002
<i>Liolaemus koslowskyi</i>	36.2		28.53	1250				Espinoza et al., 2004
<i>Liolaemus laurenti</i>	35.9		28.27	1197	25.1	49.82	Oviparous	Espinoza et al., 2004
<i>Liolaemus lutzae</i>	33.9		22.92	119	21.1	0.11	Oviparous	Espinoza et al., 2004
<i>Liolaemus magellanicus</i>	27		53.24	76	12.6	21.24	Viviparous	Jaksic and Schwenk, 1983
<i>Liolaemus magellanicus</i>	23.5	31.79	50.28	980				Ibargüengoytía et al., 2010
<i>Liolaemus sarmientoi</i>	26.18	34.43	51.56	133	12.6	21.24	Viviparous	Ibargüengoytía et al., 2010
<i>Liolaemus melanops</i>	36.6		41.33	856	12.7	36.58	Oviparous	Espinoza et al., 2004
<i>Liolaemus multicolor</i>	31.6		22.72	3360	21.1	0.11	Viviparous	Espinoza et al., 2004
<i>Liolaemus occipitalis</i>	30.9		30.24	0	22.7	108.48	Oviparous	Bujes and Verrastro, 2006
<i>Liolaemus olongasta</i>	32.1		31.19	700	23.2	23.27	Oviparous	Cánovas et al., 2006
<i>Liolaemus ornatus</i>	32.41	35.32	19.15	3710	19.5	51.20	Viviparous	Labra et al., 2009
<i>Liolaemus ornatus</i>	30.7		19.42	4000				Marquet et al., 1989
<i>Liolaemus pseudoanomalous</i>	32		31.19	700	23.2	45.50	Oviparous	Villavicencio et al., 2007
<i>Liolaemus quilmes</i>	34.3		22.43	4311	21.1	0.11	Oviparous	Espinoza et al., 2004
<i>Liolaemus rothi</i>	36.6		41.67	1000	17.9	36.58	Oviparous	Espinoza et al., 2004
<i>Liolaemus ruiibali</i>	24.4		31.10	3000	23.2	23.27	Viviparous	Villavicencio et al., 2007
<i>Liolaemus salinicola</i>	36.7		32.12	1530	17.5	23.27	Oviparous	Espinoza et al., 2004
<i>Liolaemus scapularis</i>	36.2		26.07	1650	20.5	121.5	Oviparous	Espinoza et al., 2004
<i>Liolaemus signifer</i>	33		15.85	4300	14.5	76.55	Viviparous	Pearson and Bradford, 1976
<i>Liolaemus signifer</i>	34		15.85	4000				Pearson, 1954
<i>Liolaemus uspallatensis</i>	35.7		32.48	2370	17.7	8.37	Oviparous	Espinoza et al., 2004
<i>Liolaemus xanthoviridis</i>	33.9		43.41	194	17.9	36.58	Oviparous	Espinoza et al., 2004
<i>Liolaemus lineomaculatus</i>	26.2	34.5	43.01	626	13.3	23	Viviparous	Medina et al., 2011
<i>Liolaemus lineomaculatus</i>	26.1	32	46.37	263				Medina et al., 2011
<i>Liolaemus boulengeri</i>	28.9	33.8	43.01	626	13.3	23	Oviparous	Medina et al., 2011
<i>Liolaemus boulengeri</i>	27.8	32.9	46.37	263				Medina et al., 2011
<i>Liolaemus hermannunezi</i>		35.3	37.40	1450	20	45.87	<sup>b</sup>	Cruz et al., 2009
<i>Liolaemus vallecurensis</i>	31.5	35.91	29.51	3206	15.9	2.57	Oviparous	Labra et al., 2009

<sup>a</sup> From information available at <http://worldclimate.com>.

<sup>b</sup> Reproductive mode is unknown.

#### 4. Discussion

The analyses of inter-specific thermal and behavioral responses are relevant regarding the ability of liolaemid lizards to inhabit a broad spectrum of environments each with unique

challenges. The genus *Liolaemus* has done a large radiation and exploits habitats differing markedly in physiognomy, elevation, and therefore in exposure to climatic factors (Fuentes and Jaksic, 1979; Cei, 1986), showing varying thermoregulation behaviors (Pearson, 1954; Halloy and Laurent, 1988; Marquet et al., 1989;

Gutiérrez et al., 2010; Ibagüengoytía et al., 2010). However, the dependence of  $T_b$  in the liolaemids analyzed here with  $T_{air}$  and reproductive mode, point out that behavioral compensation does not account completely for the differences in the thermal environments, neither by the constraints imposed by the viviparous mode of reproduction such as the possibly increased difficulty to forage (Martori, 2005), predation vulnerability and parental care (Halloy and Halloy, 1997). Great variations in  $T_b$  within clades of 20 species of *Liolaemus* were also found by Labra et al. (2009) and Rodríguez-Serrano et al. (2009).

Thermoregulation or the selection of different micro-environments of *Liolaemus* (Medina et al., 2009; Gutiérrez et al., 2010; Ibagüengoytía et al., 2010) seem to be flexible enough to cope with the environmental constraints in most species, except in those that are in the extremely harsh austral-most environments, such as *L. magellanicus* and *L. sarmientoi* (Ibagüengoytía et al., 2010). Herein, we found that preferred body temperatures of *Liolaemus* although considered to be a conservative trait ( $T_{pref}=34-37\text{ }^\circ\text{C}$ ; Medina et al., 2009), varied with  $T_{air}$ , but cannot be predicted by  $T_b$ , elevation, latitude or reproductive mode.  $T_{pref}$  only approached values close to  $T_b$  in species from warm environments at lower latitudes or elevations (Marquet et al., 1989; Labra, 1998; Martori et al., 2002; Gutiérrez et al., 2010). But, preferred temperatures usually exceeded  $T_b$  ( $27-29\text{ }^\circ\text{C}$ ) by  $6\text{ }^\circ\text{C}$  or more, especially in species that inhabit higher elevations or latitudes (Marquet et al., 1989; Medina et al., 2009; Ibagüengoytía et al., 2010; Gutiérrez et al., 2010). These results, together with the absence of differences between oviparous and viviparous mode of reproduction, point out that  $T_{pref}$  reflects an ancestral condition, more than an adaptation to the present environment. Coincidentally, the fossil records at high latitude in Patagonia provide evidence for the occurrence of *Liolaemus* in the earlier Miocene (20.4–20 Myrs; Albino, 2008; Schulte and Moreno-Roark, 2009). This period consisted of warm and humid climate conditions with gallery forests, prior to the Andean uplift (Belloso, 2010). Under this scenario, the ancestral *Liolaemus* lizards would have attained high body temperatures from warm Miocene environment, close to current  $T_{pref}$  of the genus *Liolaemus* (Espinoza et al., 2004). In addition, results reported in Sinervo et al. (2010) SOM Fig. S8 indicate that behavioral thermoregulation in lizards has evolved 9 times across lizard families, with one evolutionary reversal to thermoconformers, which suggests that evolved changes in the largely thermoregulating *Liolaemus* are derived relative to a thermoconforming ancestor for all extant lizard families.

In the framework of recent studies of global climate change (Sinervo et al., 2010) the evolution of viviparity in *Sceloporus* species appears to elevate extinction risk because a higher evolved  $T_b$  may compromise embryonic development *in utero* (Beuchat, 1986), thus necessitating the evolution of a lower  $T_{pref}$ .

This context makes viviparous females intolerant of rising temperatures associated with climate warming and can even cause a cessation of reproduction during warm spell events (Sinervo et al., 2011). In addition to the low  $T_b$  elevating extinction risk, oviparous species that were previously limited by physiology at lower latitude and elevation (Brown, 1984) have also expanded into historically cooler habitat that is now warmer because of global warming (Massot et al., 2008) and these range expansions may have contributed directly to local extinction of montane, viviparous taxa, perhaps via competitive exclusion (Sinervo et al., 2010). Based on a recent analysis, *Liolaemid* lizards have a significantly lower extinction rate, due to climate warming, compared to *Sceloporus* lizards of Mexico, which are characterized by a high risk of extinction (Sinervo et al., 2010). The few extinctions recorded in *Liolaemid* lizards have been observed only in the northernmost species on the Brazilian Coast (*Liolaemus lutzae*) or in the lowest elevation populations of the Patagonian steppe (*Phymaturus tenebrosus*) suggesting a largely environmental cause to the extinctions (e.g., warm thermal range limits) that are driven by climate warming. In contrast, evidence for Phrynosomatids suggests extinctions are due to a combination of evolved adaptations that heighten extinction risk (both viviparity and low evolved  $T_{pref}$ ) as well as species competition, which all act in concert with climate warming.

In addition, our findings on the exceptionally low  $T_b$  of liolaemids in nature (relative to  $T_{pref}$ ), and thus by inference their low  $T_e$ s experienced during activity seasons, could provide a simple physiological explanation why liolaemids among the 12 other strictly heliothermic families on the planet (Sinervo et al., 2010, Table 1) currently exhibit among the lowest rates of observed climate-forced extinctions and forecasted extinctions under climate warming scenarios up to 2080. Only the Teiidae, with their exceptionally high average  $T_b$ , have a slightly lower contemporary extinction risk, but by 2050–2080 extinction risk of Teiids is projected to exceed those predicted for liolaemids (see Table 1, Sinervo et al., 2010). We suggest that the low  $T_e$  in the environments inhabited by lizards in the genus *Liolaemus*, the great difference between  $T_b$  and  $T_{pref}$ , together with the lower  $T_b$  in viviparous than in oviparous, may give this genus a safety margin to buffer climate change related extinctions compared to other lizard families of the world.

### Acknowledgments

We wish to express our gratitude to E. Forti and V. Forti for their help in the field and to Dr. Víctor Cussac for his insightful comments on the manuscript. This work was partially supported by Universidad Nacional del Comahue (04B129), CONICET

**Table 2A**

Correlations among the variables included in the analysis. Values in the lower triangle are based on tip (non-phylogenetic) data, whereas values on the upper triangle are based on phylogenetic independent contrasts. Values in bold are significant. Numbers in parentheses are either sample size or number of independent contrasts.

Traits	Latitude	Elevation	$T_{air}$	$T_b$	$T_{pref}$	Precipitation
Latitude	–	–0.29** (73)	–0.29** (73)	–0.11 (70)	–0.23 (35)	0.13 (73)
Elevation	–0.48*** (82)	–	0.01 (73)	0.15 (70)	0.29 (35)	–0.32** (73)
$T_{air}$	–0.57*** (83)	0.28** (82)	–	0.02 (70)	0.57*** (35)	0.02 (73)
$T_b$	–0.03 (79)	–0.03 (78)	0.18 (79)	–	0.33* (32)	–0.05 (70)
$T_{pref}$	–0.01 (45)	0.10 (45)	0.22 (45)	0.48** (41)	–	–0.01 (35)
Precipitation	0.25* (83)	0.07 (82)	–0.05 (83)	0.09 (79)	0.06 (45)	–

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

**Table 2B**

Variance Inflation Factor (VIF) values from the regressions of body temperature ( $T_b$ ) and preferred temperature ( $T_{pref}$ ) with environmental variables: latitude, elevation,  $T_{air}$  and precipitation.

Body temperature ( $T_b$ )		Preferred temperature ( $T_{pref}$ )
Variable	VIF	VIF
Latitude	3.0037	2.8405
Elevation (m)	1.5669	1.5475
$T_{air}$	3.0753	3.1180
Precipitation	1.3832	1.3436
$T_{pref}$	1.2262	–
$T_b$	–	1.1922

(PIP 100271) awarded to Nora R. Ibagüengoytía and NSF grant IOS-1022031 awarded to Barry Sinervo and Donald B. Miles.

## Appendix 1

See (Table A1).

## Appendix 2

See (Tables 2A and 2B).

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