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Thermal biology of *Liolaemus* lizards from the high Andes: Being efficient despite adversity

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ABSTRACT

We studied the efficiency of thermoregulation in four high elevation *Liolaemus* species in the Andes of Salta, Argentina; *Liolaemus irregularis*, *Liolaemus multicolor*, *Liolaemus albiceps* and *Liolaemus yanalcu*. One of the species, *L. irregularis*, shows a broad distribution being in allopatry in some localities and in sympatry with *L. albiceps*, *L. multicolor* and *L. yanalcu* at different sites. Together with this variation in assemblages, the degree of phylogenetic relatedness is different with *L. irregularis* being most closely related to *L. albiceps* than to the other two species (*L. multicolor* and *L. yanalcu*). We measured body (T_b), microenvironmental (T_a, T_s), and operative temperatures (T_e) in the field, and preferred body temperature (T_{pref}) in laboratory for each one of the species of assemblages. Three out of the four species showed a high thermoregulatory efficiency except for *L. yanalcu*, a moderate thermoregulator. The species studied here show high T_b in the field compared to most of the recorded *Liolaemus* species. However, the T_{pref} values were similar to other *Liolaemus* species. No evidence of thermal niche segregation between species in sympatry was observed. Our results suggest that the species studied here, despite living at high elevation and harsh climatic conditions are able to behaviorally or physiologically thermoregulate to achieve T_bs close to their T_{pref}, probably because of low predation risk and perhaps low levels of competition.

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1. Introduction

One important aspect for ectotherms is their thermoregulatory efficiency, particularly in variable climates where temperature is a key factor. Temperature has a great impact on ectotherms affecting, physiological, behavioral and life history traits such as, reproductive timing (Zug et al., 2001; Labra and Bozinovic, 2002), reproductive mode (Shine, 2004), growth rate, survivorship (Huey, 1982), locomotion (Hertz et al., 1983; Angilleta et al., 2002) and diet (Espinoza et al., 2004). Additionally, the global increase in temperature has been suggested as a potential threat for lizards at a global scale (Sinervo el al., 2010). Incorporating thermal data from different types of environments may consequently help to disentangle the importance of thermal trends and their effects at local and global scales for lizard faunas. Geographic distribution gradients of elevation and latitude may result in different availability of thermal resources (Van Damme et al., 1987) and consequently affect thermal characteristics of lizards from different habitats (Andrews, 1998) at inter and intraspecific levels (Avery, 1976; Andrews, 1998; Huey et al., 2003).

Field and laboratory studies show that the accuracy of temperature regulation can be influenced by competition and predation (Huey, 1982). For example, interspecific competition in *Anolis* lizards show that the ranges of body temperature can vary, being broader in allopatric species than those of species sympatric with other *Anolis* species (Lister, 1976). On the other hand, a narrowly fixed body temperature due to a narrow thermoregulation may be maladaptive for a species, particularly if heat sources or microhabitats are rare or scattered thus imposing limitations on thermoregulation (Sears, 2005).

Since different species have different ranges it is likely that they may have different thermal requirements, where species with wider geographic ranges are expected to show a wider tolerance and conversely species with narrow distributions expected to be thermal specialists (Huey and Kingsolver, 1989; Addo-Bediako et al., 2000; Cruz et al., 2005). Therefore, different species may have a different susceptibility to global warming (Sinervo et al., 2010), depending on aspects such as distributional range, region where the species occurs, its physiology, among others. Additionally, in case of sympatric species, the degree of relatedness (phylogenetically or morphologically) may affect their interactions for limiting resources (Losos, 2000). Thus, a species with a wide

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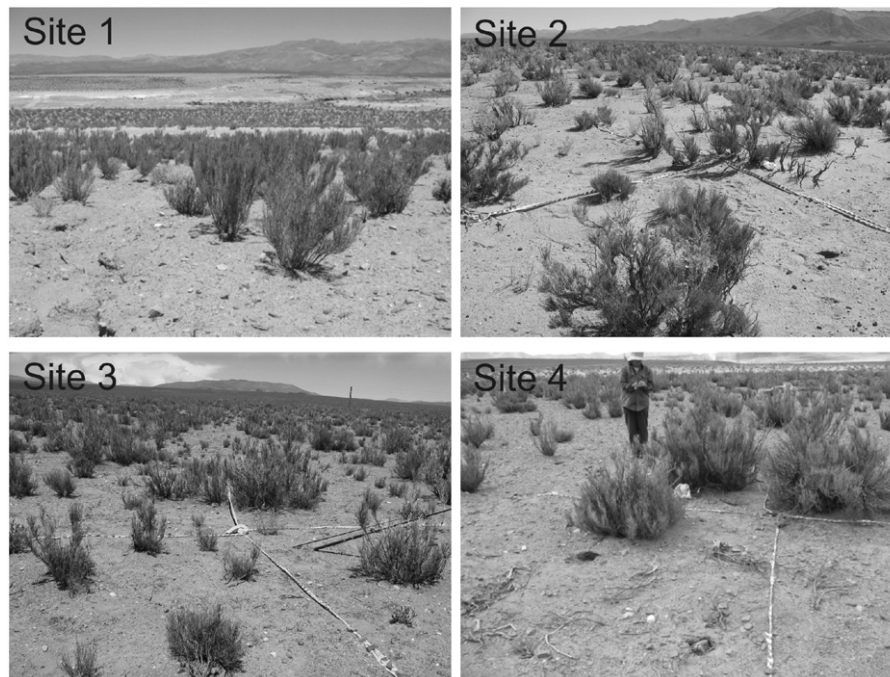
Fig. 1. Photographs of each one of the study sites (1–4). Notice the homogeneity of the environment.

geographic range contacting several congeneric species will have different interaction intensities with each sympatric species. The outcome of these interactions may be related to factors such as phylogenetic distance, aggressiveness, body size, among others.

High elevation environments are thermally challenging, mostly because adequate thermal microhabitats may be scarce. The high elevation Puna habitat of Argentina (above 3500 masl) is a very simple type of habitat with few bushes and bare soil dominating the landscape (Fig. 1), air temperature varies between day and night in a dramatic fashion with hot days (above 30 °C) and nights with temperatures below zero (Cabrera, 1994).

In the Puna habitats several *Liolaemus* species occur. This genus includes more than 230 species (Lobo et al., 2010) that may be found in wet temperate or cold forests to extremely dry deserts, and from sea level to 5100 m above sea level (Cei, 1986; 1993; Aparicio and Ocampo; 2010), showing a great variability of habitat use and presumably a variable ecology. Studies on *Liolaemus* lizards showed both, intra and interspecific differences in daily activity patterns and the type of substrates used (Marquet et al., 1989; Carothers et al., 1997, 1998; Verrastro and Bujes, 1998; Labra et al.; 2001). Additionally, several species differ in their body temperatures in relation to climatic conditions (Halloy and Laurent, 1987; Rocha, 1991, 1995a, b; Labra, 1998; Labra et al., 2001; Ibargüengoytía and Cussac, 2002; Fernández et al., 2011). In the case of *Liolaemus*, reproductive mode is apparently related to elevation, where viviparity is predominant at high elevations (Schulte et al., 2000). Thermal tolerance may be also related to either high elevation or latitude (Cruz et al., 2005). At least one species (*L. lutzae*) was suggested to be threatened by an increase in temperature as a consequence of global warming (Sinervo et al., 2010). Thus, thermal characteristics of the environment may lead to different responses and consequences. Thermal biology of *Liolaemus* species, is labile across their geographic distribution (Rodríguez-Serrano et al., 2009; Moreno Azócar et al., 2012) and thermal tolerances vary in direct relation to the thermal variability of the environments they inhabit (Cruz et al., 2005). However, other studies found that members of the family Liolaemidae show little or no relationship between

thermal biology or resting metabolic rates when compared to the environment they inhabit (Cruz et al., 2009, 2011). Given these divergent results for different species, a mixture of adaptive and non-adaptive responses (Labra et al., 2009; Bonino et al., 2011, Moreno Azócar et al., 2012) may be expected.

The thermal biology of high elevation *Liolaemus* species has been seldom studied (but see Halloy and Laurent, 1987; Labra et al., 2001; Cruz et al., 2005). Here we study the thermoregulatory ability and thermal interactions of four species of *Liolaemus* living at high elevation in the Puna of Northwestern Argentina's Salta province; *Liolaemus irregularis*, *Liolaemus multicolor*, *Liolaemus albiceps* and *Liolaemus yanalcu*. The distribution of these species is of particular interest because *L. irregularis* shows a broad distribution being in allopatry in some localities. Yet this species shares its environment with *L. albiceps*, *L. multicolor* and *L. yanalcu* at different sites. Moreover, the degree of phylogenetic relatedness is different among these species, with *L. irregularis* and *L. albiceps* being sister species (Abdala, 2007) and *L. irrgularis* being phylogenetically closer to *L. multicolor* than it is to *L. yanalcu* (Lobo et al., 2010).

Here, we examine and compare the thermal biology in allopatry and sympatry of *L. irregularis* and its interactions with congeneric species with different degrees of phylogenetic relatedness. The main questions we want to answer are: (a) are these species inhabiting the high elevations of the Puna habitat efficient thermoregulators? (b) does the thermal biology reflect the phylogenetic relatedness of species? and (c) is there a relationship between thermal plasticity and distributional ranges in the Puna *Liolaemus* lizards? Additionally, we discuss our results relative to data available for other members of the genus.

2. Materials and methods

2.1. Study area and materials

The species studied here inhabit and are typical of the Puna habitat, which is a high elevation desert located in Northwestern

Argentina, Northern Chile and Southwestern Bolivia, it ranges from 3400 to 4000 m above sea level, the climate is cold and dry with a temperatures reaching 30 °C or more (Cabrera, 1994). There is also a high solar radiation, shortage of water and intense cold at night (reaching -17.2 °C in winter and -4.4 °C in summer, NASA website—http://power.larc.nasa.gov/cgi-bin/cgi wrap/solar). The dominant vegetation consists of shrubs of one half to one meter tall which grow scattered throughout the habitat (Fig. 1). The more common species of shrub are *Fabiana densa*, *Adesmia horrida*, *Baccharis incarum* and *Parastrephia quadrangularis* (Cabrera, 1976).

Field work was carried out at four sites in the Puna habitats nearby San Antonio de los Cobres city in Salta, province, Argentina. *L. irregularis* was present at the four sites, as follows; site I (24°15′18.1″ S, 66°21′18.6″ W; 3824 masl) where *L. irregularis* ($n=46$) is present in allopatry; site II (24°00′86.2″ S, 66°14′26.8″ W; 3478 masl), *L. irregularis* ($n=52$) is sympatric with *L. multicolor* ($n=28$); site III (24°13′28.5″ S, 66°15′73.5″ W; 3886 masl), *L. irregularis* ($n=22$) is sympatric with *L. yanalcu* ($n=12$), and site IV (24°16′39.8″ S, 66°13′20″ W; 3816 masl), where *L. irregularis* ($n=39$) and *L. albiceps* ($n=35$) are sympatric. During February 2009, lizards were captured by noose or by hand. Due to the drop in activity between 1300 and 1500 h (Labra et al., 2001; Villavicencio et al., 2001) lizards were not captured between these hours.

2.2. Field data recording

We measured lizard body temperatures on sunny days and under similar climatic conditions (mean daily temperatures 23 °C) at the four sites. Body temperature was measured within 20 s after capture, and lizards were painted with noticeable colors on their back to avoid repeating measurements of body temperature for the same individuals. Body temperature (T_b) was recorded with an ultrafine thermocouple connected to a digital thermometer (Omega 871 Digital Thermometer, Type K TC, NiCr-NiAl, Stamford, CT, USA). We also recorded soil and air temperature on the site and moment of capture. Soil temperature (T_s) was measured by inserting the thermocouple 0.01 m within the substrate and air temperature (T_a) was measured at 0.05 m of height while projecting a shadow over the thermocouple tip, preventing wind gusts and direct sun light to reach the probe. We also recorded sun exposition (full sun, filtered sun by vegetation or full shade). Finally, we measured snout-vent length (SVL in mm), determined sex and other diagnostic characters (see Lobo and Laurent, 1995; Martínez Oliver and Lobo, 2002; Valdecantos and Lobo, 2007; Valdecantos et al., 2007) to identify the species under consideration (mostly because *L. irregularis* and *L. albiceps* are very similar in external appearance).

Operative temperatures (T_e, sensu Bakken, 1992), the product among the interactions of morphology and physical environment influencing T_b of an ectotherm, was registered in accordance to the activity hours, that is from 9:00 to 13:00 and from 15:00 to 18:30 h. For doing this we used six copper models distributed in three different microhabitats in each one of the four sites (Row and Blouin-Demers, 2006). Copper models were painted to imitate the lizard dorsum, and constituted of copper tubes 0.009×0.0013 m; models were previously calibrated with lizard carcasses ($r^2=0.967$, d.f.=119; $P < 0.001$) and live lizards ($r^2=0.937$; d.f.=57; $P < 0.001$). Then, models were deployed on each one of the three possible microhabitats in the Puna habitat (on bare soil exposed to full sun, under the filtered shade projected by the scarce bushes in the area and inside the center of bushes where shade is permanent). Under these circumstances the data models were set as follows; two models under 100% exposed to sun, two models under total shade and the remaining

two models under filtered sun. The copper models were connected to external HOBO data loggers (ONSET, Outdoor/Industrial, H08-008-04, # 325829, USA) and temperatures were recorded every 15 min, each data logger collected at least 282 data per site ($N=2091$).

2.3. Laboratory experiments

We obtained preferred body temperature (T_{pref}) from lizards collected in each study site as follows: site I ten *L. irregularis*, from site II twelve *L. irregularis* and twelve *L. multicolor*; five *L. irregularis* and three *L. yanalcu* from site III and finally, ten *L. irregularis* and ten *L. albiceps* belonging to site IV. These lizards were collected 100 m apart from the collection sites where T_b was obtained during a special field trip for this purpose (end of February 2009). One week later lizards arrived in the lab at San Carlos de Bariloche (41°09′ S, 71°18′ W). There lizards were fed with live crickets and flower buds ad libitum and water was sprayed two times a day. For this purpose lizards were placed individually in terraria permitting them reach their preferred temperature. Next they were fed with four size six crickets and three flower buds. Once crickets or flower buds were eaten lizards were removed and new lizards were introduced for this purpose. We set two thermal gradients in glass terraria (1.2 m $\times$ 0.6 m $\times$ 0.4 m) with a 0.03 m layer of sand on the bottom to avoid overheating. The thermal gradient terraria were divided in five lanes 0.12 m each separated by opaque walls. The thermal gradient obtained was from 46 to 19 °C (Cruz et al., 2009) produced by 150 W IR Light bulbs on one end of the terraria, a second 100 W incandescent bulb suspended 0.4 m from the heated end and 0.15 m higher and room temperature varied between 18 and 19 °C. Body temperature was recorded with an ultrafine thermocouple inserted 1 mm into the cloaca of the lizard, the thermocouple being connected to a digital thermometer (Omega 871 A Digital Thermometer, Type K TC, NiCr-NiAl, Stamford, CT, USA). Measurements were taken every hour from 9:00 to 18:00 h during 3 consecutive days. After body temperature was measured, lizards were always released in the center of the lane of the thermal gradient. Water was sprayed twice a day and lizards were not fed the day before T_{pref} trials to guarantee that all specimens were in the same condition (Cruz et al., 2009).

We obtained T_{pref} interquartile range set point per species following Hertz et al. (1993) by keeping the 50% of the data obtained in the T_{pref} trials in light of previous neurophysiological studies that show that ectotherms thermoregulate between this interquartile set point around a single T_b (Barber and Crawford, 1977). To estimate effectiveness of thermoregulation (E) in the field, we calculated the db (the deviations between T_b and T_{pref}) and de (the deviation between T_e and T_{pref}) indexes for each species and population for which we gathered field data after Hertz et al. (1993). By comparing both indexes, it is possible to assess to what extent the lizards thermoregulate by using the equation $E=1-(db/de)$. For example, when E is close to 1 it is considered as effective thermoregulation, if a species or population shows an E close to 0 it is considered as thermoconformer, finally E close to 0.5 is considered as moderate thermoregulation (Hertz et al., 1993; Bauwens et al.,1996; Medina et al., 2009).

2.4. Statistical analysis

We tested normality and homogeneity of variance assumptions with Shapiro–Wilks and Snedecor tests. When these assumptions were reached we used t-test, one-way ANOVAs and repeated measurements ANOVAs for comparisons. In the case the distributions failed to meet the aforementioned assumptions we ran Mann Whitney U and Kruskal Wallis tests. We ran

post hoc tests; LSD Fisher tests for parametric statistics and Dunn's test for non-parametric. We performed a Multiple Regression Analysis with a backward elimination model using T_b as dependent variable and T_s and T_a as independent variables. For all purposes we used the INFOSTAT package (Di Rienzo et al., 2010).

3. Results

3.1. Relationship between body temperature and microenvironmental temperatures

Substrate and air temperatures (T_s and T_a, respectively) for *L. irregularis* varied among the four study sites (ANOVA T_s, $F_{(3, 149)}=3.09$, $P=0.029$; ANOVA T_a, $F_{(3, 149)}=12.12$, $P<0.0001$) and site II showed the higher values for both variables (LSD fisher $P<0.05$) (Table 1). When we compared sympatric species, we found significant differences between T_s of *L. irregularis* and *L. yanalcu* at site III (t-test, $t=2.19$, $P=0.037$; d.f.$=29$) and no significant differences at the other two sites (t-tests values $t<1.38$, $P>0.17$; d.f.$=78$, 69 for site 2 and site 4, respectively). In the case of T_a there were no significant differences among collection sites (t-test, values $t<1.69$, $P>0.096$; d.f.$=78$, 29, 69 from sites 2, 3 and 4, respectively). Substrate temperatures (T_s) were close to T_b in the allopatric *L. irregularis* site and when this species shared the habitat with *L. yanalcu* and *L. albiceps* (Table 1). Conversely, when *L. irregularis* was sympatric to *L. multicolor* T_s was higher than T_b for *L. irregularis* (t-test, $t_{54}=-2.4$, $P=0.02$). Particularly, *L. multicolor*, *L. albiceps*, and *L. yanalcu* showed similar values between T_b and T_s after repeated measurements ANOVA and post hoc tests (Table 1). Despite the similarity between T_s and

T_b, only allopatric *L. irregularis*, *L. irregularis* of site III and *L. albiceps* showed a significant correlation between T_b and T_s (Table 1). Air temperature was lower than T_b for all sites and species (Table 1). Multiple regression analysis showed low partial correlation values showing that T_b is barely explained by changes in microenvironmental variables (Table 2).

Body temperatures were similar in the four sites where *L. irregularis* was present (ANOVA, $F_{(3, 149)}=0.89$, $P=0.448$), showing that T_b is not affected by the presence of sympatric species. When analyzing sympatric species, we only found significant differences between species in site III (*L. irregularis* and *L. yanalcu*; t-test, $t_{29}=3.31$, $P=0.002$). In general, body temperature

Table 2
Multiple regression analysis with backward elimination. Body temperatures (T_b; °C), substrate temperature (T_s; °C) and air temperature (T_a; °C). Only shows the variables retained by the model. $T=$ t-test between variables; $r=$partial correlation. $P=$Significance <0.05 as * are indicated.

Multiple regression backward elimination	T_b vs. T_s	T_b vs. T_a	r
Site 1			
L. irregularis		$T=3.47, P=0.001$	0.23
Site 2			
L. irregularis			
L. multicolor		$T=2.14, P=0.04$	0.15
Site 3			
L. irregularis	$T=2.17, P=0.04$		0.19
L. yanalcu			
Site 4			
L. irregularis			
L. albiceps	$T=2.15, P=0.04$		0.12

Table 1
Mean $\pm$ standard deviation and ranges of body (T_b), substrate (T_s) and air temperature (T_a) values in celcius degrees (°C) for each species ($N=$sample size) from the four sites in our study. Repeated measurements ANOVA (parametric and non-parametric) was used for comparing T_b, T_s and T_a. F and χ^2 are parametric and non-parametric statistics, respectively; d.f.$=$degrees of freedom, $P=$significance value. Post hoc test (Holm-Sidac for parametric analysis and Tukey for non parametric) were performed, underlines show homogeneous groups $P>0.05$. Correlations between T_b vs T_s and T_b vs T_a are shown in the right columns ($r=$correlation coefficient, $P=$significance level). Significance <0.05 as * is indicated.

Especie	Variable	$F_{(df)}$ or $\chi^2_{(df)}$	P	Holm-Sidak or Tukey	r	P
Site 1						
L. irregularis N$=43$	$T_b=36.10\pm1.78$ (28.30–39.40)	$\chi^2_{(2,82)}=59.58$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=35.22\pm5.69$ (22.40–46.40)				0.44	0.003*
	$T_a=28.64\pm3.37$ (22.70–37.20)				0.48	0.001*
Sitio 2						
L. irregularis N$=52$	$T_b=36.59\pm1.37$ (33.10–39.30)	$\chi^2_{(2,98)}=32.0$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=39.20\pm7.73$ (21.40–57.50)				0.08	0.58
	$T_a=32.66\pm4.81$ (20.90–42.60)				0.05	0.74
L. multicolor N$=28$	$T_b=36.52\pm1.33$ (33.70–39.10)	$\chi^2_{(2,52)}=23.64$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=36.78\pm7.09$ (19.20–48.45)				0.33	0.09
	$T_a=30.91\pm3.64$ (21.10–37.70)				0.39	0.04*
Site 3						
L. irregularis N$=22$	$T_b=36.44\pm1.53$ (33.40–38.90)	$F_{(2,42)}=49.36$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=38.41\pm7.67$ (22.80–50.50)				0.44	0.04*
	$T_a=26.66\pm5.17$ (16.80–37.30)				0.43	0.05
L. yanalcu N$=9$	$T_b=34.16\pm2.21$ (31.00–36.80)	$F_{(2,16)}=3.47$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=30.63\pm11.70$ (15.20–47.80)				0.67	0.05
	$T_a=25.77\pm5.07$ (16.60–31.30)				0.14	0.72
Site 4						
L. irregularis N$=36$	$T_b=36.38\pm1.04$ (34.00–38.50)	$\chi^2_{(2,68)}=31.76$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=35.89\pm7.43$ (16.60–47.90)				0.14	0.42
	$T_a=29.06\pm4.58$ (21.00–39.00)				0.19	0.28
L. albiceps N$=35$	$T_b=36.17\pm1.92$ (29.40–39.50)	$\chi^2_{(2,66)}=50.03$	$<0.001^*$	$\underline{T_b}\ \underline{T_s}\ \underline{T_a}$		
	$T_s=36.83\pm6.77$ (20.50–51.20)				0.35	0.04*
	$T_a=28.71\pm3.96$ (17.50–37.50)				0.20	0.24

ranges of all species and sites were similar (Table 1) except for *L. yanalcu* which showed lower maximum temperatures (around 36 °C) than the rest of the species (around 38 °C).

Table 3
Percentage of body temperatures (T_b) and operative temperatures (T_e) falling within, and beyond the lower and upper set-points limits of preferred body temperatures (T_{pref}). Numbers between parentheses are number of observations.

	% T_b within T_{pref} set point	% T_b below T_{pref} set point	% T_b above T_{pref} set point	% T_e within T_{pref} set point	% T_e below T_{pref} set point	% T_e above T_{pref} set point
Site 1						
L. irregularis	39.53 (17)	37.21 (16)	23.26 (10)	3.15 (12)	87.75 (330)	11.10 (41)
Site 2						
L. irregularis	48.08 (25)	21.15 (11)	30.77 (16)	3.96 (11)	66.26 (188)	29.78 (85)
L. multicolor	39.29 (11)	3.57 (1)	53.57 (15)	4.92 (14)	63.39 (179)	31.69 (90)
Site 3						
L. irregularis	63.64 (14)	22.73 (5)	13.64 (3)	2.40 (7)	81.87 (232)	15.73 (44)
L. yanalcu	44.44 (4)	55.56 (5)	0.00 (0)	4.27 (12)	80.27 (232)	15.47 (38)
Site 4						
L. irregularis	47.22 (17)	2.78 (1)	50.00 (18)	9.33 (27)	74.13 (213)	16.53 (48)
L. albiceps	42.86 (15)	31.43 (11)	25.71 (9)	5.87 (17)	79.47 (229)	14.67 (42)

3.2. Preferred body temperature and operative temperature and their relationship to body temperature

After obtaining preferred body temperatures and their set point ranges, we observe that mean T_{pref} of *L. irregularis* was not different when compared across the four sites (Kruskal Wallis, $H=4.07$, $P=0.253$; Table 3). Mean T_{pref} of *L. multicolor* and *L. yanalcu* were lower than their sympatric *L. irregularis* individuals (Site II, t-test, $t_{20}=2.26$, $P=0.034$; Site III, Mann Whitney, $W=6.00$, $P=0.035$) and in site IV T_{pref} of both species (*L. irregularis* and *L. albiceps*) show similar values (Mann Whitney, $W=121.00$, $P=0.226$). Interestingly, no differences were observed when comparing the upper set point value among sympatric species (all t-tests values $t<1.79$, $P>0.089$) or *L. irregularis* from the four different sites (Kruskal Wallis, $H=5.63$, $P=0.131$). We observed however, significant differences when analyzed the lower set point limit, for example *L. irregularis* from site IV showed a significantly lower set point limit than the *L. irregularis* at the remaining sites (Kruskal Wallis, $H=8.42$, $P=0.038$, Dunn's test $P<0.05$). Finally, we observed significant differences between the lower set point limit corresponding to sympatric species, at sites II and III, respectively where *L. irregularis* showed a higher set point temperature (Site II $t_{13}=2.41$, $P=0.032$; Site III $t_6=2.52$, $P=0.045$), but at site IV this species showed the lowest set point ($W_{10}=135.00$, $P=0.023$).

Overall mean T_b was higher than mean operative temperatures (T_e) and the range of T_b values were narrower than the ranges of T_e (Figs. 2 and 3). On the other hand, mean T_b fell within the set point limits of T_{pref} obtained for each species and site, except for
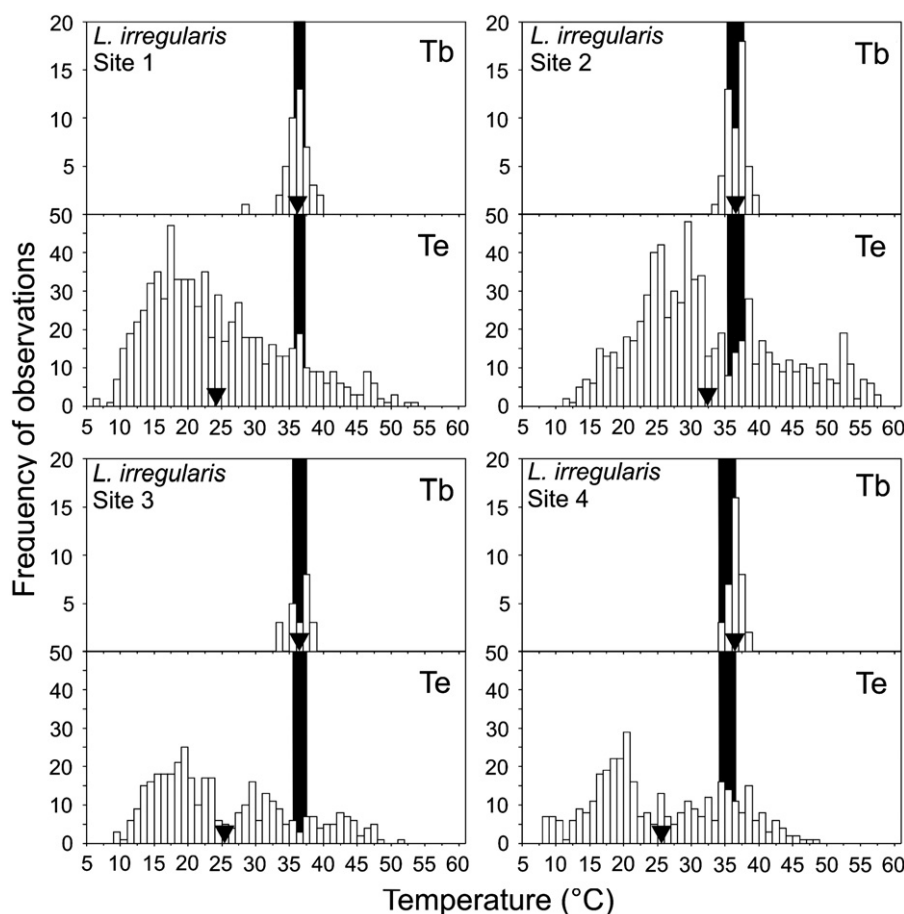

Fig. 2. Frequency of body temperatures (T_b; bars, upper panels) and operative temperatures (T_e; bars, lower panels) of *L. irregularis* from the four sites studied. The arrow head indicate the mean of T_b and T_e and black bars indicate 50% values between lower and upper set-points ranges of preferred body temperature.

Fig. 3. Frequency of body temperatures (T_b; bars, upper panels) and operative temperatures (T_e; bars, lower panels) of *L. multicolor*, *L. albiceps* and *L. yanalcu* from sympatric sites with *L. irregularis*. The arrow head indicate the mean of T_b and T_e and black bars indicate 50% values between lower and upper set-points ranges of preferred body temperature.
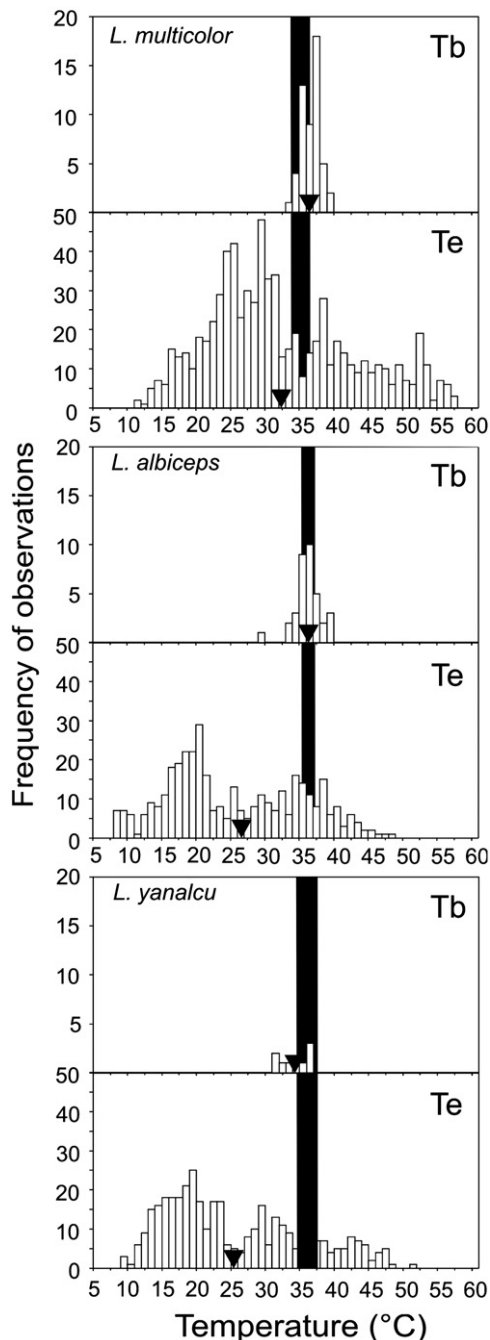
L. yanalcu (Figs. 2 and 3). Additionally, we observed that T_bs of *L. irregularis* from site IV and *L. multicolor* (site II) were significantly higher than their mean T_{pref}s (*L. irregularis* Site 4, $W = 152.50$, $P = 0.028$; *L. multicolor*, $t_{36} = 2.77$, $P = 0.009$), while the other species or sites showed no significant differences (t-test, values $t < 1.42$, $P > 0.056$).

When *L. irregularis* was in sympatry; 50% or more of T_bs data fell within the set point limits of T_{pref}. However, the allopatric *L. irregularis* population and the rest of species showed a lower percentage of T_bs data falling within the set point ranges. Interestingly, in overall no more than 10% of T_e fell within the set point limits (27 out of 288, Table 3) and more than 60% (179 out of 283)

Table 4
Percentage of lizards observed in each microhabitat patch taking into consideration sun exposure. Numbers between parentheses are sample sizes.

	% individuals full sunny patches	% individuals filtered sunny patches	% individuals full shade patches
Site 1			
L. irregularis (43)	67	33	–
Site 2			
L. irregularis (52)	54	42	4
L. multicolor (28)	50	43	7
Site 3			
L. irregularis (22)	77	23	–
L. yanalcu (9)	67	33	–
Site 4			
L. irregularis (36)	72	28	–
L. albiceps (35)	86	14	–

of T_e fell below lower set point limit (Table 4), showing that thermal environment was suboptimal.

3.3. Lizard thermoregulation

All species used mainly full and filtered sun patches at the four sites (Table 4) and showed T_bs close to their own T_{pref}s. Thus, they have low values of d_b index (Table 5). On the other hand, the mean d_es were high as most of the T_e observed fell out of the T_{pref} set point (Tables 3 and 5). Therefore, we obtained high temperature regulation effectiveness (E) values (between 0.88 and 0.97), indicating that these high elevation lizard species from all sites are careful and effective thermoregulators (Table 5).

4. Discussion

The *Liolaemus* species studied here inhabit high elevations (above 3600 masl). Interestingly, however, three out of the four studied species show body temperatures above 36 °C (*L. irregularis*, *L. multicolor* y *L. albiceps*), while *L. yanalcu* show moderate values of T_b (34.2 °C). The high T_bs registered here are among the higher body temperatures reported for the genus together with *L. fuscus*, *L. monticola* and *L. tenuis* (Labra and Bozinovic, 2002; Medina et al., 2012; Moreno Azócar et al., 2012). From recent studies (Medina et al., 2012; Moreno Azócar et al., 2012), we derive that only one sixth of the *Liolaemus* species show T_b higher than 36 °C, and among them eleven inhabit hot desert localities in Argentina (*L. scapularis*, *L. riojanus*, *L. salinicola*, *L. grosseorum*, *L. espinozai*, *L. olongasta*, *L. koslowskyi*, *L. darwinii*, *L. cuyanus* and *L. robertmertensi*), or equivalent laititudes in Chile (*L. tenuis*, *L. chiliensis* and *L. platei*). Only few species with high T_b occur in Patagonia (*L. xanthoviridis*, *L. rothi*, *L. martorii* and *L. melanops*). Interestingly, high elevation *Liolaemus* and *Sceloporus* species from temperate zones show higher T_bs than congeneric high elevation species at lower latitudes (Andrews, 1998, this study). However, it has to be considered that in the case of *Sceloporus* species of temperate zones, the elevation does not surpass 3000 masl, whereas elevations of tropical *Sceloporus* species (with low T_bs) are much higher (Andrews, 1998) and presumably lower air temperatures might be registered. Probably, high solar radiation levels in our study site may influence the observed high T_bs of

Table 5

Mean preferred body temperatures in laboratory (T_{pref}; °C ± standard deviation), lower and upper set-point limits of the preferred body temperature (°C) sensu Hertz et al. (1993); mean operative temperature (T_e; °C ± standard deviation), mean absolute deviations of T_b from T_{pref} (db), mean of index of the quality of habitat (de) and effectiveness of temperature regulation (E) all indices were calculated following Hertz et al. (1993). Numbers between parentheses are sample sizes.

| | T_{pref} | T_{pref} set point | | T_e | db | de | E |
		lower	upper				
Site 1							
L. irregularis	36.41 ± 1.27 (10)	35.72	37.21	24.16 ± 9.59 (380)	0.62 ± 1.24	13.06 ± 7.37	0.95
Site 2							
L. irregularis	36.16 ± 1.84 (12)	35.33	37.29	32.18 ± 10.52 (283)	1.09 ± 5.23	8.80 ± 5.65	0.88
L. multicolor	35.19 ± 0.54 (12)	33.96	36.56		0.51 ± 0.75	8.13 ± 5.58	0.94
Site 3							
L. irregularis	36.57 ± 0.21 (5)	35.59	37.61	25.33 ± 9.92 (283)	0.44 ± 0.73	12.18 ± 7.17	0.96
L. yanalcu	35.81 ± 0.75 (3)	34.59	37.56		1.16 ± 1.46	11.39 ± 6.95	0.90
Site 4							
L. irregularis	35.37 ± 0.56 (10)	34.07	36.57	25.60 ± 9.54 (288)	0.31 ± 0.49	10.23 ± 7.34	0.97
L. albiceps	36.19 ± 0.66 (10)	35.45	37.19		0.71 ± 1.19	11.19 ± 7.78	0.94

the *Liolaemus* lizards. Notably, other *Liolaemus* species living at the similar latitude range (23–25°S) but lower elevation (near 2000 masl) exhibit lower T_b than the species of the Puna (e.g. *L. ornatus, L. hellmichi, L. dorbignyi, L. bisignatus, L. quilmes, L. constanzae, L. nigroroseus* and *L. fabiani;* Marquet et al., 1989; Labra et al., 2001; Medina et al., 2012; Moreno Azócar et al., 2012). In addition, T_b partly also depends on field opportunities for thermoregulation (Hertz et al., 1993). For example, environmental constraints (e.g. air temperature) may lead to lower T_b, as observed by Marquet et al. (1989). Additionally, the decrease of T_b with increasing elevation in tropical latitudes was also noted in frogs that inhabit the Andes (Navas, 1997). Thus, it remains unclear why *Liolaemus* species from our study site show high T_bs, mostly when considering the documented thermal environment limitations for other ectothermic vertebrates that exhibit low temperatures at high elevations (Marquet et al., 1989; Navas, 1997; Andrews, 1998). Our results are similar to those found by Fox and Shipman (2003) in a comparative study of *Liolaemus* species from sites with different elevations in the Andes of central Chile. Contrary to the expectations, the high elevation sites studied by these authors offered suitable T_es during the months of activity of the lizards, and then it is not surprising to find examples in this genus that do not follow certain rules established in other groups.

Similarly, in the case of preferred body temperatures, the species studied here show similar T_{pref}s as other members of the genus for which data are available (Fuentes and Jaksic, 1979; Carothers et al., 1997; Labra, 1998; Labra et al., 2009; Moreno Azócar et al., 2012), showing that this thermal character may be ancestral for the genus. The set point ranges obtained in the laboratory for the *Liolaemus* species from the Puna are narrower than for species from Patagonia, such as *L. bibronii, L. magellanicus, L. sarmientoi* (Medina et al., 2009; Ibargüengoytía et al., 2010). It seems possible that, despite the fact that Patagonia and Puna habitats are both harsh cold environments, the difference in thermal cycles (on a daily basis in Puna and on a seasonal basis in Patagonia) may have an effect on the length of the activity of *Liolaemus* lizards (Medina et al., 2009) and probably show a different effect on minimum thermal limits which are lower in Patagonian *Liolaemus* species (Cruz et al., 2005; Moreno Azócar et al., 2012) and thus making the set point range of patagonian *Liolaemus* species broader than the congeneric species occurring in the Puna.

Previous studies indicate that activity body temperatures recorded in the field generally match preferred temperatures measured in the laboratory in diurnal lizards (Huey, 1982), except for some high altitude and high latitude populations at the onset

of the activity period (Hertz and Nevo, 1981; Vial, 1984; Hertz et al., 1988; Bauwens et al., 1990). However, several studies in *Liolaemus* lizards reveal that field body temperatures are between 0 °C and 2 °C lower than T_{pref} (Marquet et al., 1989; Labra et al., 2009; Medina et al., 2009; Gutiérrez et al., 2010; Ibargüengoytía et al., 2010; Medina et al., 2012; Moreno Azócar, 2012). Particularly, species that live at high elevations (above 3300 m) show lower T_b than T_{pref} (*L. alticolor, L. eleodori, L. jamesi, L. lorenzmuelleri, L. ornatus, L. walkeri*; data from Marquet et al., 1989; Medina et al., 2012, Moreno Azócar et al., 2012) and only *L. dorbignyi* (actually, *L. scrocchii* Abdala com. Pers.) shows a similar thermal behavior compared to the species studied here, indicating that thermoregulation is a difficult task at high elevations. It was suggested that this situation corresponds to a common and particular pattern in the genus (Ibargüengoytía et al., 2010). Our study and Labra et al. (2001) who studied *L. nigroroseus* and *L. fabiani* from the Atacama Desert (Chile) show that mean T_bs fall within the T_{pref} set-point ranges. Moreover, T_bs and T_{pref}s are not that different in our study. These findings question the presence of a particular thermal biology pattern in *Liolaemus* genus.

According to previous studies, *Lioalemus* lizards are excellent thermoregulators (Carothers et al., 1997, 1998), even at very high elevations (Pearson and Bradford, 1976). Species that bask more frequently than expected tend to be more efficient in their thermoregulation (Van Damme et al., 1987; Bauwens et al., 1996). However, it is more likely that thermoregulatory efficiency is the consequence of complex interactions rather than simple reasons (Rodríguez-Serrano et al., 2009). Despite the apparent limitations for thermoregulation offered by the Puna microhabitats and typical for high elevations (Hertz et al., 1993) the low structured habitats (few and small shrubs surrounded by bare soil) where *L. irregularis, L. multicolor, L. yanalcu* and *L. albiceps* occur, provide thermal microhabitats that may be used by all species. Our results indicate that the species studied here efficiently thermoregulate (behaviorally or physiologically) to achieve T_bs close to their T_{pref}. This may be beneficial when associated costs are low (Huey and Slatkin, 1976). Despite the fact that the Puna habitat does not offer a complex structure; it may be typified as a harsh environment. In addition, the available thermal environments at our study sites are constrained (T_e are generally lower than T_{pref}, Figs. 2 and 3). However, *Liolaemus* lizards in the Puna habitat are active at a body temperature close to their thermal preferenda. It is notable that T_e varies among different localities, but T_b is relatively constant among sites. Despite the different thermoregulation effectiveness values, it is clear that the four species studied here are within the range of effective thermoregulators. It is possible that these

lizards are choosing available particular thermal microhabitats to thermoregulate because predation risk is low at these high elevations in the Andes (Huey et al., 2003). Other features, like color, positioning towards the sun or physiology may be possible ways for these lizards to achieve T_b values close to their T_{pref}. However, we have no detailed data to support either of these possibilities.

Apparently *Liolaemus* lizards inhabiting the Puna habitat are less threatened than expected in light of being good thermoregulators. Recently Sinervo et al. (2010) suggested that thermoregulators are less susceptible to climate change than thermoconformers. The observed high thermoregulatory efficiency and the broad thermal tolerance that the species studied here achieve (Cruz et al., 2005) suggests that these lizards are less threatened than species inhabiting extremely hot places or forests (Sinervo et al., 2010). Yet, mechanistic approaches are needed to elucidate this problem more precisely (Gunderson and Leal, 2012). Thermoregulation is a complex process that must integrate sensing of temporal and spatial variation in the thermal environment with behavioral and physiological responses (Seebacher and Shine, 2004). Thus, we need additional information to understand the high efficiency in thermoregulation by these lizards of the Puna.

With regard to the interactions among species or between pairs of species in the Puna, our results do not support the thermal niche segregation hypothesis (Pianka and Huey, 1978) in *L. irregularis* and two sympatric species (*L. albiceps* and *L. multicolor*) which independently of the degree of phylogenetic relatedness or aggressiveness showed similar T_bs in sympatry. Among these three Puna species it is possible that they have been in sympatry for only a short time, despite the fact that the divergence time between members of the *L. irragularis* and *L. multicolor* clades is nearly 5.3 my (Fontanella et al., 2012) and the divergence time within the *Liolaemus darwinii* clade (where *L. irregularis* and *L. albiceps* belong to) is nearly 3.7 my (Fontanella et al., 2012). However, *L. albiceps* and *L. irregularis* diverged recently (Camargo et al., 2012). Another alternative is thermal niche tracking (Labra et al., 2009). Thus, time may have not been long enough to develop segregations, at least in these species. On the other hand, *L. yanalcu* showed lower T_b and T_s compared to the rest of the species studied here, indicating some degree of thermal niche differentiation in this species. Additionally, *L. yanalcu* belongs to the *L. chiliensis* group (Lobo et al., 2010) and shows similar T_b values to most of the members of this clade (Medina et al., 2009), indicating probable phylogenetic constraints.

Several questions arise from our results; Is the Puna habitat really thermally limiting?, how do these lizard species achieve such high thermoregulatory efficiency?, why do *Liolaemus* species inhabiting other low thermal quality environments such as Patagonia not develop the same thermoregulatory abilities (Medina et al., 2009; Ibargüengoytía et al., 2010)? *Liolaemus* species are more often distributed in dry desert habitats, among them the Patagonia and Puna. However, despite the fact that both habitats may be typified as climatically similar, thermal opportunities are probably quite different. For example, the daily availability of sun light and sufficient radiation may be an important factor; the same probably holds for the length of the favorable season which is different between the Puna and Patagonia (Ramírez-Pinilla, 1991; Espinoza Pers. comm.).

Although species at elevations higher than 3500 masl may be ecologically constrained in their ability to thermoregulate (Marquet et al., 1989), the range of T_b's is wide (from 27 to 36 $\pm$ 1 °C) and cannot be explained using simple arguments (Rodríguez-Serrano et al., 2009). In summary, as proposed by Labra et al. (2009) many species are conservative in some aspects

(e.g. T_{pref}), yet labile in others (e.g. T_b) allowing them to inhabit a wide range of environments.

Acknowledgments

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