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ECOSYSTEMS

Thermal niches and activity periods in syntopic *Phymaturus* and *Liolaemus* lizards from the Andes, Argentina

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Abstract: Explanations for differences in thermal biology within and between species of lizards employ concepts of phylogenetic inertia and plasticity. We compared the thermal biology of three liolaemid species in the Andean highlands in Argentina: two allopatric congeners (*Phymaturus williamsi* and *P. aguanegra*) each in syntopy with *Liolaemus parvus*. We predicted intra and inter-generic differences in ecophysiological traits and periods of activity at both sites, ecotypic differences between the (labile) *Liolaemus* populations, but predicted no interspecific differences between the (putatively conservative) *Phymaturus*. We determined the operative temperatures (T_e), field body temperatures (T_b), preferred temperatures (T_{pref}), effectiveness of thermoregulation (E), and activity periods. As expected, *P. williamsi* differed from *L. parvus* in T_b, T_{pref}, and activity periods, likely as result of niche segregation. Contrary to predictions, the *Phymaturus* populations exhibited differentiation in T_b and T_{pref}, while *L. parvus* populations differed in T_{pref} and E. Accordingly, *Phymaturus* species tend to be effective thermoregulators whereas *L. parvus* populations behave as good thermoregulators or thermoconformers depending on thermal conditions in fluctuating habitats. *Phymaturus* may be less evolutionarily conservative than previously suggested. The suite of co-evolving traits affecting thermal ecology may not be collectively conservative nor labile but rather a continuum between both evolutionary paths.

Key words: *Phymaturus*, *Liolaemus*, thermal niche, activity periods, Andes, Argentina.

INTRODUCTION

Body temperatures (T_b) in non-avian reptiles influence physiological and behavioral processes, and consequently may have a profound impact on survival and fitness (Avery 1982, Huey 1982). Since T_b is also directly influenced by varying environmental temperatures (Angilletta 2009), many lizards reduce variation in their T_b through behavioral adjustments (Gvoždík 2012). In this sense, lizards have evolved a variety of mechanisms to control T_b (Cowles & Bogert 1944, Nelson et al. 1984, Stevenson 1985, Avery 1978) resulting in differences in the effectiveness of thermoregulation among species and populations (Hertz et al. 1993).

The achievement and maintenance of T_b within a range or near thermal optima that allows activity and enhances physiological performance depends on both the availability of suitable microhabitats and the effectiveness of thermoregulation (E, *sensu* Hertz et al. 1993, Beaupre 1995, Huey et al. 2003). However, the opportunity to bask at suitable temperatures will also depend on the risks and costs of thermoregulation, such as a high vulnerability to predation and the allocation of time for basking to the detriment of time for feeding and social activity (Adolph 1990, Blouin-Demers & Weatherhead 2001a, Gvoždík 2002). Maintenance of high T_b during the activity period and the overt usage of basking are common in diurnal lizards, but even more remarkable in those inhabiting climates with a wide diurnal fluctuation of ambient temperatures and a marked seasonality such as those present along the Andes range (Veblen et al. 2007). Under such an energetically challenging scenario, lizards that experience thermal extremes are expected to exhibit variation in their ability to thermoregulate (Veloso et al. 2007). Some authors pointed out that thermal physiology in closely-related taxa may be relatively similar as a result of a co-evolutionary process despite their subsequent ecological divergence even in allopatry (Hertz et al. 1983, Angilletta et al. 2002). However, differences in the effectiveness of thermoregulation in syntopic species subjected to similar thermal regimes would suggest different physiological requirements or resource use (Smith & French 2017).

Thermal preferences may differ among sex or age groups in each population (Ortega et al. 2016), because resource partitioning would occur according to a hierarchic system in which males would have access to better resources than females or juveniles (*e.g.*, suitable microhabitats for basking; *sensu* Vidal et al. 2010, Gómez Ales et al. 2017). In addition, since the males are larger than females in many species (Stamps 1983), it is possible that males achieved a higher accuracy and effectiveness of thermoregulation (Sagonas et al. 2013). Larger size and body mass affects the rate of heat exchange in the individual-environment interaction (Tracy 1982). Although, a more reliable individual-environment interaction indicator could be the body condition (scaled mass index, M_i, *sensu* Peig & Green 2009), which is an estimate of an individual's fitness (Green 2001). Hence, the variation of body condition can be directly influenced by local factors (*e.g.*, intraspecific competition, resource partitioning and predation pressure) with pronounced effects on several natural history traits including the thermal preferences (Siliceo-Cantero & García 2014).

Lizard thermal physiology can be evolutionarily conservative such that closely related taxa are expected to show similar thermal biological responses even when living in distinct habitats (Bogert 1949, Huey 1982, Díaz de la Vega-Pérez et al. 2013). This is, for example, the case for the parthenogenetic *Aspidoscelis cozumela* that inhabits a wide range of environmental conditions, including areas where the parental species *A. angusticeps* and *A. deppii* are absent, yet all three species exhibit similar thermal preferences (Díaz de la Vega-Pérez et al. 2013). Moreover, thermal conservatism in thermal tolerances has been reported for North American *Sceloporus* species across a wide elevational range (Buckley et al. 2015). However, studies of tropical *Anolis* argue that some taxa have readily adapted to differences in their environments showing interspecific differences in T_b, T_{pref} and T_{max} and such ecotypic differences have been observed even in closely related species (Huey 1982, Hertz et al. 1983). Nevertheless, in sibling species inhabiting contrasting habitats, the mismatches between the thermal environments and thermal optimum may lead to less activity, less energy acquisition and a sub-optimal energy budget and a consequent fitness decrease betraying slow adaptation to changes in the environments (Logan et al. 2012, 2015).

Liolaemidae is one the most diverse families of lizards, comprising more than 300 species distributed in three genera, *Ctenoblepharys* (1 sp.), *Phymaturus* (54 spp.) and *Liolaemus* (> 285 spp.), inhabiting a broad variety of environments in southern South America (Etheridge 1995, Abdala & Quinteros 2014, Troncoso-Palacios et al. 2018, Esquerré et al. 2019, Abdala et al. 2021, Lobo et al. 2022). This family is an appealing model to test hypotheses on the evolution of interspecific and ecotypic differences in thermoregulatory effectiveness. At present, the thermal biology studies in Liolaemidae point out that *Phymaturus* is conservative in its thermal traits (Cruz et al. 2009, Gómez Ales et al. 2017, Duran et al. 2018) while observations of the genus *Liolaemus* supports the labile hypothesis as they exhibit greater flexibility that may vary according to lineage specialization or habitat characteristics (Rodríguez-Serrano et al. 2009, Bonino et al. 2011, Medina et al. 2012, Moreno-Azócar et al. 2013). Indeed, *Phymaturus* lizards are more selective in their habitat use, being strictly herbivorous and viviparous, and occur only on rocky promontories in mountain habitat (Cei 1986, Habit & Ortiz 1994, Espinoza et al. 2004, Laspiur 2010, Castro et al. 2013, Boretto et al. 2014, 2018). Due to these features and restrictive discontinuous distribution, all *Phymaturus* species are considered “vulnerable” in the Argentinean Red List (Abdala et al. 2012). In contrast, the genus *Liolaemus*, exhibits a substantial variation in natural history traits such as diet, habitat, and reproductive mode (oviparous and viviparous), and has developed a broad range of adaptive responses to different thermal environments (Cei 1986, Scolaro 2005, Medina et al. 2011). Species of *Phymaturus* and *Liolaemus* often occur in syntopy on latitudinal gradients along the Andean mountain range in Argentina and Chile (Díaz-Gómez 2009) offering an opportunity to study different strategies for thermoregulation under similar environmental conditions (Rodríguez-Serrano et al. 2009, Vitt & Caldwell 2014). Lizards competing in syntopy tend to select distinctive thermal microhabitats (*sensu* Hertz et al. 1993, Scheers & Van Damme 2002) as a result of niche segregation and it is presumed that syntopic species will experience different thermal qualities of the environment (Magnusson et al. 1979, Paterson & Blouin-Demers 2016).

Herein, we describe aspects of thermal biology, activity periods, and effectiveness of thermoregulation within each of two pairs of syntopic *Phymaturus* and *Liolaemus* populations occurring in harsh environmental conditions in the highlands of the Andes, Argentina. We address three classical concepts on thermal biology and ecology. First, syntopic species exhibit niche segregation in thermal traits, manifest in their use of heat sources (thigmothermy and heliothermy), effectiveness of thermoregulation, and the timing of activity periods to reduce competitive interactions. Secondly, *Phymaturus aguanegra* and *P. williamsi* are more conservative than *Liolaemus parvus* populations in their thermal biology based on previous studies (Cruz et al. 2009, Rodríguez-Serrano et al. 2009, Bonino et al. 2011) and we predict that the T_b, T_{pref}, effectiveness of thermoregulation and thermoregulatory behaviour (thigmothermy and heliothermy) will differ between populations of *L. parvus* but not between *Phymaturus* species. Finally, we consider that the T_b and T_{pref} are explained by M_i and affects the accuracy (d_b) and the effectiveness of thermoregulation (E). Since these lizards could exhibit a degree of sexual size dimorphism biased toward larger males (Cabezas-Cartes et al. 2010, Castillo et al. 2011, Castro et al. 2011), and because body condition is a coefficient of the relative size of energy stores compared with structural body components (Peig & Green 2009), we expect that males and those showing a greater body condition may have higher T_b and T_{pref} and would be more accurate and effective thermoregulators. Because thermoregulation directly affects activity in lizards, this multi-species approach may allow greater understanding of the mechanisms involved in the resource partitioning in terms of temperature and activity in coexisting species. It will allow the exploration of the thermoregulatory strategies that lizards can adopt under different conditions in montane environments in the central Andes.

MATERIALS AND METHODS

Study areas, climate, and lizards

We compared thermoregulatory behaviour and effectiveness of thermoregulation among four populations: two allopatric species of *Phymaturus* at two sites, each syntopic with a local population of *Liolaemus parvus*. Specifically, we studied *Phymaturus aguanegra* at Paso Agua Negra (Iglesia Department; -30°23'S; -69°34'W, 3000 m asl) and *P. williamsi* at Quebrada Vallecito (Calingasta Department; -31°11'S -69°42'W, 3000 m asl), two microendemics separated by ~100 km (Lobo et al. 2013, Figure 1) and embedded in the highlands of San Juan Province, Argentina. Each *Phymaturus* species is syntopic with one of two separate populations of *L. parvus*, a species widely distributed from central-west La Rioja Province to northwest Mendoza Province (Quinteros et al. 2008). The three species are viviparous, but the *Phymaturus* are larger (snout-vent length: SVL ≤ 115 mm, Lobo et al. 2013) than *L. parvus* (SVL ≤ 74 mm, Quinteros et al. 2008).

These study areas belong to the Puna phytogeographic region characterized by xerophyllous plants such as the shrubs *Adesmia pinnifolia* and *Ephedra multiflora*, the cactus *Lobivia formosa*, and the dwarf shrub *Artemisia mendozana* (Cabrera & Willink 1973). The climate at both capture sites corresponds to cold arid

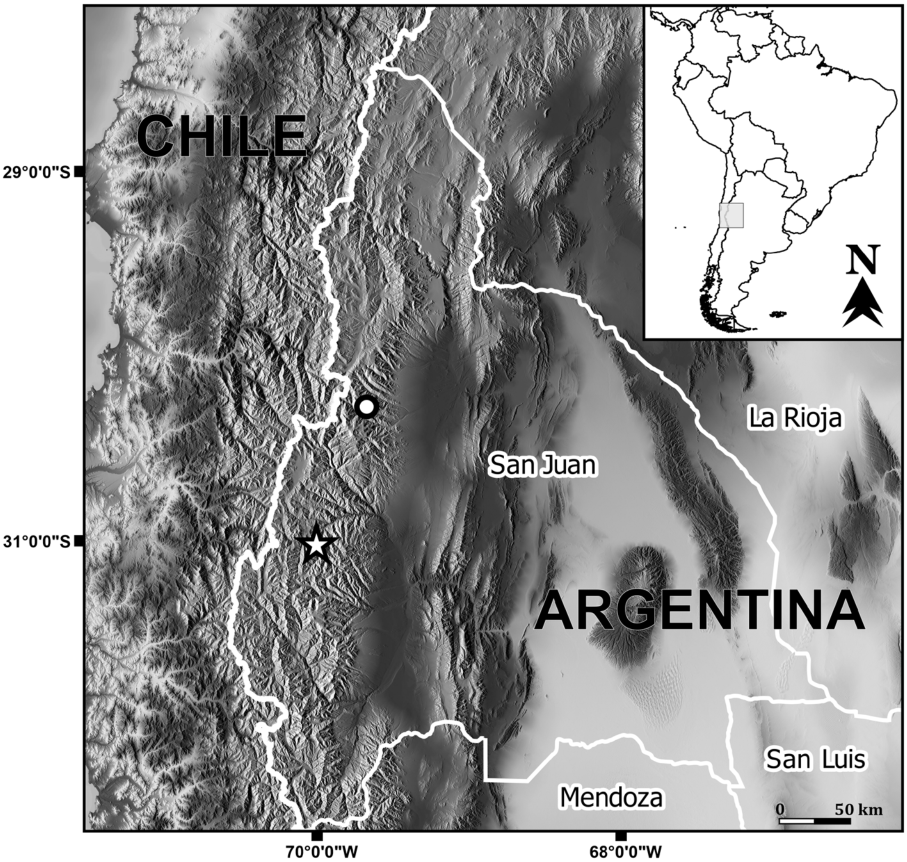

Figure 1. Capture sites of *Phymaturus aguanegra*, Paso Agua Negra, Iglesia Department (white dot) and *Phymaturus williamsi*, Quebrada Vallecito, Calingasta Department (white star), both species in syntopy with *Liolaemus parvus*, San Juan Province, west-central Argentina.

desert (BWk, Köeppen 1948, Peel et al. 2007) with rainfall ocurring mainly in winter, monthly mean temperatures < 18°C even in the warmest season, and prolonged snowfalls and mud slides in spring (Figure 2).

Lizards were captured during the activity season from late spring to early autumn of the southern hemisphere. All specimens were caught by hand or noose between 10:00 and 19:00 h, corresponding to the entire daily activity period of the three species (Laspiur 2010, Ausas 2011). *Phymaturus aguanegra* (N = 60; 25 males, 19 females, 16 juveniles) and *Liolaemus parvus* (N = 48; 24 males, 18 females, 6 juveniles) were captured at Paso Agua Negra during November 2005, December 2005, February 2006, April 2007 and March 2011. Meanwhile at Quebrada Vallecito, samples of *Phymaturus williamsi* (N = 84; 27 males, 40 females, 17 juveniles) and *Liolaemus parvus* (N = 87; 40 males, 37 females, 10 juveniles) were captured during October 2008, December 2008, and April 2009. Capturing and handling were conducted in accordance with international standards on animal welfare, being compliant with Argentinian regulations. All individuals were collected under permits Exp. N° 1300-4047 granted to JCA. After laboratory experiments, the captured specimens were euthanized using intraperitoneal injection of sodium pentobarbital Euthanyle ©, fixed in formalin (10%), preserved in ethanol (70%) and deposited into the herpetological collection housed in Centro Regional Universitario Bariloche (CRUB), Universidad Nacional del Comahue.

Field data

The following microenvironmental temperatures were recorded at the capture site for each individual lizard in order to determine the main heat source used: substratum temperature on rocks, bare soil or beneath dwarf shrubs (T_s, TES TP-K03 substrate probe), and air temperature 1 cm above the ground (T_a, TES TP-K02 gas probe). Each instrument was connected to a TES 1302 thermometer (TES ® Electrical Electronic Corp., Taipei, Taiwan, ± 0.01°C).

The operative temperatures (T_e, *sensu* Bakken 1992) were obtained using copper models set in the most heterogeneous and representative microhabitats used by the species in each field site. At Agua Negra,

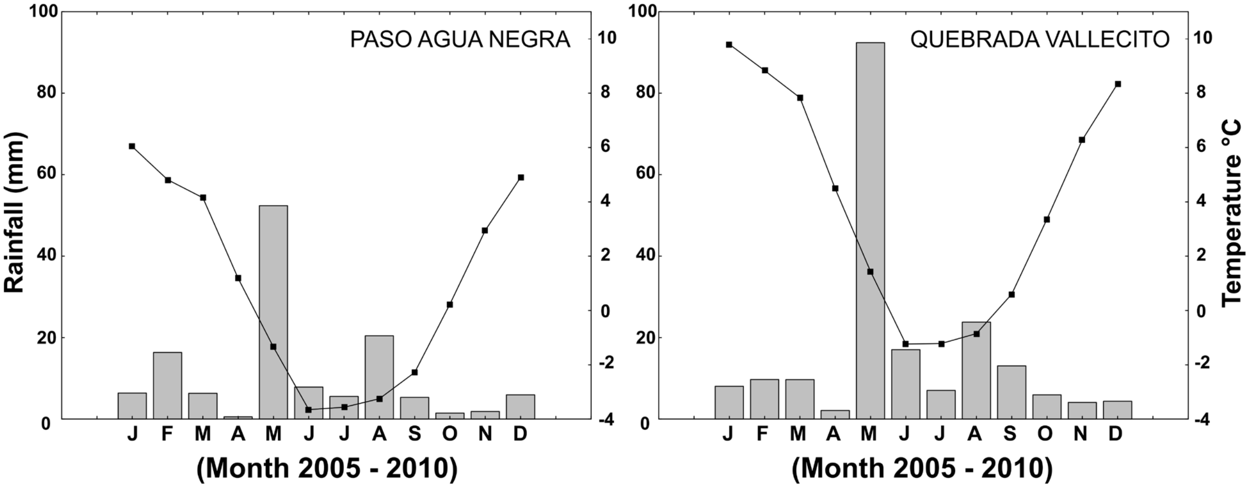

Figure 2. Monthly mean of rainfall (mm, gray bars) and temperatures (°C, polygons) at Paso Agua Negra and Quebrada Vallecito during the study (2005 – 2010). Greater rainfall during cooler winter months results in greater moisture availability. Climatic data provided by 3CN database (Centro de Investigaciones del Mar y Atmósfera).

four common microhabitats were used by *P. aguanegra* and *L. parvus* (basaltic rock, bare soil, shade beneath shrubs and exposed crevices): 16 models were used during sampling, 8 models for *Phymaturus* were localized in the 4 microhabitats simultaneously in two different zones of the field site (4 microhabitats x 2 replicates) and the other 8 models for *Liolaemus* using the same methodology (4 microhabitats x 2 replicates). At Quebrada Vallecito, we identified the six representative microhabitats used by *P. williamsi* (feldspathic rock, basaltic rock, shade beneath shrubs, bare soil, crevices, and at crevice opening with the model partially exposed), whereas *L. parvus* commonly used seven (basaltic rocks, leaf litter, shade beneath shrubs, mossy rock, bare soil, weathered small rock, and expose crevices): 39 models were used during sampling, 18 models for *Phymaturus* (6 microhabitats x 3 replicates) and 21 for *Liolaemus* (7 microhabitats x 3 replicates). The models were designed using simultaneous comparisons of the T_b of live *Phymaturus williamsi* and *L. parvus* with copper models of varying sizes and colours. During the comparisons, catheter probes TES TP-K01 (TES Electrical Electronic Corp., Taipei, Taiwan ± 0.01°C) were used simultaneously to register the temperatures of both the models and the lizards. The calibration experiments were conducted during three consecutive hours and we calculated the animal-model correlation for each type of model. The best-fit correlation was observed for a flat-black hollow copper cylinder with dimensions 90 mm length x 20 mm diameter x 10 mm thickness for *Phymaturus* (Spearman Rank correlation, T_b vs. model, R = 0.93, N = 122, P < 0.001) and 60 mm length x 10 mm diameter x 8 mm thickness for *Liolaemus* (Spearman Rank correlation, T_b vs. model, R = 0.99, N = 122, P < 0.0001). Measures of T_e were recorded during lizard activity from 10:00 to 19:00 h. Mean temperatures of each model were used to estimate the temperature that thermoconforming lizards would achieve at each field site (T_e).

Body temperatures (T_b, sensu Pough & Gans 1982) were taken only in active lizards using a catheter probe TES TP-K01 (1.62 mm diameter) introduced ca. 5 mm into the cloaca. Individuals were handled by the head to avoid heat transfer and temperature was recorded within 20 s of handling. Time of day at capture was also recorded. Snout-vent length (SVL, vernier caliper ± 0.02 mm) and body mass (BW, 10 – 50 g Pesola ® spring scale ± 0.5 g) were also registered.

Laboratory experiments

Experiments were performed 3 to 7 days after capture on a random subsample of lizards from each site: *P. aguanegra* (N = 44; 20 males, 14 females, 10 juveniles) and *L. parvus* (N = 41; 21 males, 17 females, 3 juveniles) from Agua Negra; *P. williamsi* (N = 34; 14 males, 18 females, 2 juveniles) and *L. parvus* (N = 30; 15 males, 15 females) from Quebrada Vallecito. Lizards were placed individually in open-top terraria (200 cm length, 15 cm width, 30 cm height) with a sand substrate and a thermal gradient produced by a length-wise row of four infrared lamps (250 W, 150 W, 150 W, 100 W). The heights of the lamps above the sand were adjusted to make a linear gradient from 69° to 15°C on the substrate for lizards to thermoregulate. White fluorescent lamps along the sides of each terrarium homogenized illumination. Body temperatures were taken using ultra-thin (1 mm) catheter thermocouples located approximately 5 mm inside the cloaca and taped at the base of the lizard's tail to prevent the thermocouple from being dislodged during the experiment. The temperature of each lizard was obtained every 10 min for 5 hr by connecting the thermocouple to a TES 1302 thermometer (TES ® Electrical Electronic Corp., Taipei, Taiwan, ± 0.01 °C) to avoid interference with their normal activities. The mean preferred body temperature (T_{pref}) and the inferior and superior set-point range temperatures (T_{set}, the interquartile range) were obtained for each lizard. In order to measure the accuracy of thermoregulation of these in their natural environment, the mean of the absolute values obtained from the deviations of $T_{b\text{-}i}$ from $T_{set\text{-}i}$ of each individual was calculated (individual deviation; $d_{b\text{-}i}$). The index of the average thermal quality of the habitat from the organism's mean (d_e) was calculated as the absolute values from the deviations of mean T_e for each population with respect to set-point range (T_{set}) of each population and species. The effectiveness of temperature regulation, E, was calculated as 1 - (mean d_b / mean d_e) for both populations at each site (Hertz et al. 1993). The values of E range from -1 to 1, and E-values near 0 represent thermoconformers, values near 0.5 moderate thermoregulators, and values near 1 effective thermoregulators. Negative values of E occur when lizards avoid thermally high-quality habitats with T_e within the range of T_{pref} (Christian & Weavers 1996, Blouin-Demers & Weatherhead 2001b, Gutiérrez et al. 2010).

Statistical analyses

For comparative purposes, mean, standard error, variance, and range of temperatures were indicated. The dependence between variables was analyzed by simple or multiple stepwise regression. An analysis of variance (one-way repeated measures ANOVA) was used to determine the main heat sources used by lizards comparing the T_b with the T_s and T_a. Paired *t*-tests or Wilcoxon Signed Rank tests were used to detect differences between T_b and T_{pref}. When ANOVA effects were significant ($P < 0.05$), multiple *post hoc* comparisons were performed using the Holm-Šídák method.

The periods of activity in this study were analysed using a 4 x 8 contingency table combining frequencies calculated for each population ($N = 4$), and for each activity period ($N = 8$, see Table IV). Pearson's Chi-square test (χ^2) was performed to evaluate the significance of differences between observed versus expected frequencies under assumptions of homogeneity of site use by lizards during the activity period (null hypothesis). *Post hoc* analyses were performed from the adjusted residuals to obtain z-scores for all cases. Subsequently, *P*-values were calculated from the transformation of Chi-square values derived from multiple tests (Beasley & Schumacker 1995, García Pérez & Nuñez Antón 2003). A Bonferroni Correction was applied by dividing the theoretical *P*-level of significance ($\alpha = 0.05$) by the number of multiple tests ($N = 32$). The adjusted α –level obtained for the whole model was $P < 0.001$.

Snout-vent length (SVL) and body mass (BW) were included in the scaled mass index of body condition in each individual (M_i, *sensu* Peig & Green 2009) to determine the scaled mass index of condition as an indicator of the health or quality assumed to be related to fitness. The scaled mass index was calculated as $(M_i) = M_i {}^{*} [SVL_o / SVL_i]$ ^ bSMA; where M_i and SVL_i are the BW and SVL of each individual, SVL_0 is the arithmetic mean SVL of each population, and bSMA is the standardized major axis slope from the regression of ln(BW) on ln(SVL) for each population (Peig & Green 2009). The scaling bSMA exponent was calculated directly using the software RMA v. 1.21 (Bohonak & van der Linde 2004). We then tested for the influence of M_i on thermal characteristics (T_b, T_{pref}, d_b and E) according to sex and age classes (males, females, and juveniles) in each population.

Variability in thermo-biological variables was described using descriptive statistics (mean ± standard deviation, minimum and maximum). Normality and variance homogeneity assumptions were tested using Kolmogorov-Smirnov's test and Levene's test, respectively. When normality or variance homogeneity assumptions were not met, non-parametric correlation, Mann–Whitney U-tests, and Kruskal-Wallis rank sum tests were used (Sokal & Rohlf 1969). Data were analyzed using Sigma Plot ® version 14.0 (Systat Software Inc., San José, CA), SPSS ® version 20.0 (IBM, SPSS Statistics for Windows, Armonk, NY), and figures were produced using Statistica ® version 10.0 (Statsoft Inc., Tulsa, OK).

RESULTS

Effects of body condition (M_i) on thermal traits and thermoregulation indices

Thermal traits and thermoregulation were unrelated to body condition: body temperature (T_b), accuracy (d_b) and effectiveness of thermoregulation (E_i) were not significantly correlated with (M_i) in any of the four populations (Table I). The only exception was that T_{pref} increased with M_i in *L. parvus* from Paso Agua Negra (Table I).

Comparison of T_b and T_{pref} among males, females and juveniles within species and populations

Paso Agua Negra

T_b did not differ among males, females, and juveniles in either population (Kruskal-Wallis, $H_{P.\ aguanegra\ (2;\ 60)} = 3.167$, $P > 0.2$; $H_{L.\ parvus\ (2;\ 48)} = 4.486$, $P > 0.1$, Table II). Similarly, T_{pref} means were not different among those groups in both populations (ANOVA, $F_{P.\ aguanegra\ (2;\ 44)} = 2.338$, $P > 0.1$; Kruskal-Wallis, $H_{L.\ parvus\ (2;\ 41)} = 4.116$, $P > 0.1$, Table II).

Table I. Results of linear regressions of scaled mass index of body condition (M_i) with body temperature (T_b), preferred temperatures (T_{pref}), absolute values obtained from the individual deviation of T_b from T_{set} (d_b) and individual effectiveness of thermoregulation (E_i) of *Phymaturus aguanegra* and *Liolaemus parvus* at Paso Agua Negra, and *P. williamsi* and *L. parvus* at Quebrada Vallecito. Significant relationships are indicated in bold.

Species	Temperature	F (*N*)	t	P
P. aguanegra	T_b	0.091 (40)	0.303	0.76
	T_{pref}	3.073 (40)	-1.753	0.08
	d_b	0.755 (40)	-0.869	0.39
	E_i	0.284 (40)	0.553	0.59
L. parvus	T_b	0.119 (12)	0.345	0.73
	T_{pref}	4.974 (12)	2.230	**< 0.05**
	d_b	0.097 (12)	0.312	0.76
	E_i	0.001 (12)	-0.004	0.99
P. williamsi	T_b	3.501 (33)	-1.871	0.07
	T_{pref}	2.341 (33)	-1.530	0.13
	d_b	2.245 (33)	1.498	0.14
	E_i	2.449 (33)	-1.565	0.12
L. parvus	T_b	0.362 (28)	-0.602	0.55
	T_{pref}	1.262 (28)	1.123	0.27
	d_b	0.035 (28)	0.188	0.85
	E_i	0.772 (28)	-0.879	0.388

Table II. Mean ± SD of body mass (BM, g), snout-vent length (SVL, mm), scaled mass index of body condition (M_i), body temperatures (T_b, °C), preferred body temperatures (T_{pref}, °C), absolute values obtained from the individual deviation of T_b from T_{set} (d_b), index of the average thermal quality of habitats (d_e), and index of effectiveness of thermoregulation (E) between sexes and juveniles in each studied species/populations. The sample sizes *N* and range (between parentheses) are also indicated.

	Class	BM	SVL	M_i	T_b	T_{pref}	d_b	d_e	E
P. aguanegra (Paso Agua Negra)	Males	28.27 ± 6.83 (12.0 – 35.5) *N* = 20	95.15 ± 5.87 (82.7 – 104.5) *N* = 25	22.80 ± 4.04 (14.4 – 30.8) *N* = 20	30.22 ± 4.21 (14.9 – 35.3) *N* = 25	37.03 ± 1.32 (34.4 – 38.9) *N* = 20	4.73	10.98	0.56
	Females	22.53 ± 5.93 (11.0 – 30.5) *N* = 13	93.06 ± 9.41 (70.9 – 105.0) *N* = 19	20.70 ± 4.10 (14.2 – 26.7) *N* = 13	27.00 ± 6.56 (13.2 – 34.0) *N* = 19	37.81 ± 1.03 (35.8 – 39.4) *N* = 14	7.97	11.51	0.30
	Juveniles	10.77 ± 6.42 (2.5 – 20.9) *N* = 8	69.37 ± 11.13 (52.7 – 89.1) *N* = 11	22.72 ± 3.58 (18.8 – 27.7) *N* = 7	29.64 ± 4.70 (22.0 – 35.6) *N* = 16	37.67 ± 1.28 (34.7 – 39.7) *N* = 10	8.12	11.45	0.29
	Overall	23.03 ± 9.15 (2.5 – 35.5) *N* = 41	89.27 ± 13.02 (52.7 – 105.0) *N* = 55	22.14 ± 4.02 (14.2 – 30.8) *N* = 40	29.05 ± 5.29 (13.2 – 35.6) *N* = 60	37.43 ± 1.26 (34.4 – 39.7) *N* = 44	6.53	11.26	0.41
L. parvus (Paso Agua Negra)	Males	6.30 ± 1.29 (3.5 – 8.2) *N* = 23	65.42 ± 4.99 (55.0 – 69.0) *N* = 7	5.76 ± 0.47 (5.1 – 6.4) *N* = 7	33.26 ± 1.74 (29.4 – 36.0) *N* = 24	36.72 ± 1.32 (33.3 – 38.3) *N* = 21	2.59	8.93	0.70
	Females	5.44 ± 1.54 (3.5 – 9.7) *N* = 17	59.16 ± 4.07 (54.0 – 66.0) *N* = 6	5.90 ± 0.43 (5.3 – 6.3) *N* = 4	31.15 ± 3.47 (23.2 – 35.6) *N* = 18	37.32 ± 0.84 (35.0 – 38.5) *N* = 17	5.29	10.27	0.48
	Juveniles	2.72 ± 1.86 (0.7 – 5.0) *N* = 5	–	–	32.25 ± 3.40 (28.0 – 35.5) *N* = 6	35.91 ± 1.24 (35.0 – 37.3) *N* = 3	1.25	4.93	0.74
	Overall	5.58 ± 1.79 (0.7 – 9.7) *N* = 45	62.28 ± 5.34 (54.0 – 69.0) *N* = 14	5.75 ± 0.49 (4.8 – 6.4) *N* = 12	32.19 ± 2.86 (23.2 – 36.0) *N* = 48	36.91 ± 1.18 (33.3 – 38.5) *N* = 41	3.61	9.19	0.60
P. williamsi (Q. Vallecito)	Males	35.80 ± 3.96 (27.0 – 42.0) *N* = 15	101.40 ± 9.32 (71.0 – 123.0) *N* = 19	33.31 ± 3.05 (29.3 – 39.1) *N* = 14	29.35 ± 5.38 (15.8 – 37.3) *N* = 27	35.90 ± 1.66 (32.8 – 39.0) *N* = 15	4.91	8.86	0.44
	Females	34.88 ± 3.55 (28.0 – 39.8) *N* = 17	101.77 ± 7.47 (76.0 – 115.0) *N* = 36	32.88 ± 4.23 (25.4 – 40.9) *N* = 17	31.21 ± 4.35 (20.1 – 38.0) *N* = 40	36.50 ± 1.63 (32.2 – 38.8) *N* = 17	5.08	9.12	0.44
	Juveniles	12.42 ± 1.52 (11.3 – 13.5) *N* = 2	67.72 ± 10.74 (54.0 – 92.0) *N* = 14	23.88 ± 8.03 (18.2 – 29.5) *N* = 2	33.11 ± 5.91 (14.6 – 40.0) *N* = 17	36.30 ± 1.11 (35.5 – 7.1) *N* = 2	–	–	–
	Overall	33.99 ± 6.56 (11.3 – 42.0) *N* = 34	95.26 ± 16.22 (54.0 –123.0) *N* = 73	32.52 ± 4.44 (18.2 – 40.9) *N* = 34	31.00 ± 5.15 (14.6 – 40.0) *N* = 84	36.23 ± 1.60 (32.2 – 39.0) *N* = 34	4.47	9.06	0.50
L. parvus (Q. Vallecito)	Males	7.05 ± 1.26 (4.5 – 9.9) *N* = 15	64.50 ± 2.42 (60.0 – 69.0) *N* = 15	7.08 ± 1.04 (4.5 – 8.2) *N* = 14	33.34 ± 3.59 (24.5 – 39.4) *N* = 40	35.08 ± 1.53 (32.2 – 37.7) *N* = 15	2.42	2.31	-0.04
	Females	6.70 ± 1.87 (4.8 – 10.5) *N* = 15	65.91 ± 4.05 (60.0 – 74.0) *N* = 23	6.20 ± 1.56 (3.2 – 8.8) *N* = 14	32.45 ± 3.75 (25.8 – 41.1) *N* = 37	34.69 ± 1.68 (31.6 – 37.7) *N* = 15	3.85	2.82	-0.36
	Juveniles	–	51.87 ± 7.01 (37.0 – 59) *N* = 8	–	34.84 ± 3.72 (27.1 – 40.1) *N* = 10	–	–	–	–
	Overall	6.88 ± 1.57 (4.5 – 10.5) *N* = 30	63.24 ± 6.25 (37.0 – 74.0) *N* = 54	6.64 ± 1.37 (3.2 – 8.8) *N* = 28	33.14 ± 3.70 (24.5 – 41.1) *N* = 87	34.89 ± 1.59 (31.6 – 37.7) *N* = 30	3.13	2.57	-0.22

Quebrada Vallecito

T_b values of *P. williamsi* were significantly higher in juveniles than in males (Kruskal-Wallis, $H_{(2; 84)} = 8.445$, $P < 0.01$; Dunn's test, $Q_{\text{juveniles-males}} = 2.892$, $P < 0.05$; $Q_{\text{juveniles-females}} = 2.111$, $P > 0.05$; $Q_{\text{males-females}} = 1.141$, $P > 0.05$, Table II), whereas mean T_bs of *L. parvus* were not different among males, females and juveniles (ANOVA, $F_{(2; 87)} = 1.773$, $P < 0.17$, Table II). Meanwhile, T_{pref} means were not different among males, females and juveniles in *P. williamsi* (ANOVA, $F_{(2; 34)} = 0.500$, $P > 0.5$, Table II) or between females and males in *L. parvus* (Student's *t*-Test, $t_{(1; 30)} = -0.654$, $P > 0.5$, Table II). Juveniles were not analyzed in *L. parvus*.

Determination of the main heat sources for thermoregulation

Paso Agua Negra

Phymaturus aguanegra and *L. parvus* were found basking with T_b and T_s higher than T_a, while T_b and T_s were not different (Table III). T_bs of *P. aguanegra* increased only with T_ss (Stepwise Regression, $F_{\text{Tb-Ts (57)}} = 27.79$, $P < 0.001$; $F_{\text{Tb-Ta (57)}} = 0.148$, $P > 0.70$), while in *L. parvus,* T_bs did not depend on T_ss or T_as (Stepwise Regression, $F_{\text{Tb-Ts (41)}} = 6.83$, $P > 0.40$; $F_{\text{Tb-Ta (41)}} = 3.48$, $P > 0.06$). In both species, T_bs follows the fluctuation of T_ss throughout the day, whereas T_as and T_es were lower than T_bs (Figure 3a and 3b).

Quebrada Vallecito

In *Phymaturus williamsi* and *L. parvus,* the T_b values were significantly higher than the T_s and T_a values (Table III). The T_bs of *P. williamsi*

Table III. Intraspecific comparisons among field body (T_b, °C), substrate (T_s, °C) and air (T_a, °C) temperatures of *Phymaturus aguanegra*, *P. williamsi* and *Liolaemus parvus* populations. Shown are means ± SD. The One-way Repeated Measures ANOVA and the Holm-Šídák t-Test (only for significant differences in the main factors) are also indicated. Asterisks indicate statistical significance ($P < 0.05$).

Paso Agua Negra			
P. aguanegra		T_s	T_a
	T_b = 29.05 ± 5.29	t = 0.154	t = 8.57*
	T_s = 29.14 ± 7.24	-	t = 8.73*
	T_a = 23.65 ± 5.17	-	-
	ANOVA, $F_{2,59} = 49.92$, $P < 0.001$		
L. parvus		T_s	T_a
	T_b = 32.34 ± 2.84	t = 0.78	t = 6.76*
	T_s = 32.92 ± 7.11	-	t = 7.46*
	T_a = 26.92 ± 4.31	-	-
	ANOVA, $F_{2,46} = 34.25$, $P < 0.001$		
Quebrada Vallecito			
P. williamsi		T_s	T_a
	T_b = 31.00 ± 5.15	t = 2.18*	t =14.58*
	T_s = 29.86 ± 6.76	-	t = 12.39*
	T_a = 23.41 ± 4.82	-	-
	ANOVA, $F_{2,83} = 123.75$, $P < 0.001$		
L. parvus		T_s	T_a
	T_b = 33.14 ± 4.46	t = 2.90*	t = 17.90*
	T_s = 31.78 ± 6.14	-	t = 14.99*
	T_a = 24.76 ± 5.24	-	-
	ANOVA, $F_{(2, 86)} = 184.66$, $P < 0.001$		

increased only with T_ss (Stepwise Regression, $F_{Tb\text{-}Ts\,(81)} = 47.47$, $P < 0.001$; $F_{Tb\text{-}Ta,\,(81)} = 0.622$, $P > 0.434$). Also, the T_bs and T_ss were similar through the activity period, and were higher than T_a and T_e (Figure 3c). The T_bs of *L. parvus* increased with both T_ss and T_as (Stepwise Regression, $F_{Tb\text{-}Ts\,(84)} = 37.65$, $P < 0.001$; $F_{Tb\text{-}Ta\,(84)} = 7.339$, $P < 0.006$). T_bs followed the substrate temperature (T_ss) through the day, and it was higher than T_a, but T_e was higher than T_b during the warmer hours 13:00 – 15:00 h, coinciding with the highest frequency of lizard activity (Figure 3d).

Preferred body temperatures and effectiveness of thermoregulation

Paso Agua Negra

The T_{pref} values in *P. aguanegra* and in *L. parvus* were higher than T_b (Wilcoxon signed-rank test, *P. aguanegra*: W = 988, z = 5.76, $P < 0.001$, $N = 44$; *L. parvus*: W = 859, z = 5.56, $P < 0.001$, $N = 41$; Table II).

In *P. aguanegra* the lower and upper T_{set} limits were 36.22°C ± 1.90 and 38.96°C ± 1.00, respectively (Figure 4a). Most of the T_bs ($N = 40$, 91%) were lower than the minimum $T_{set.}$, and 9%

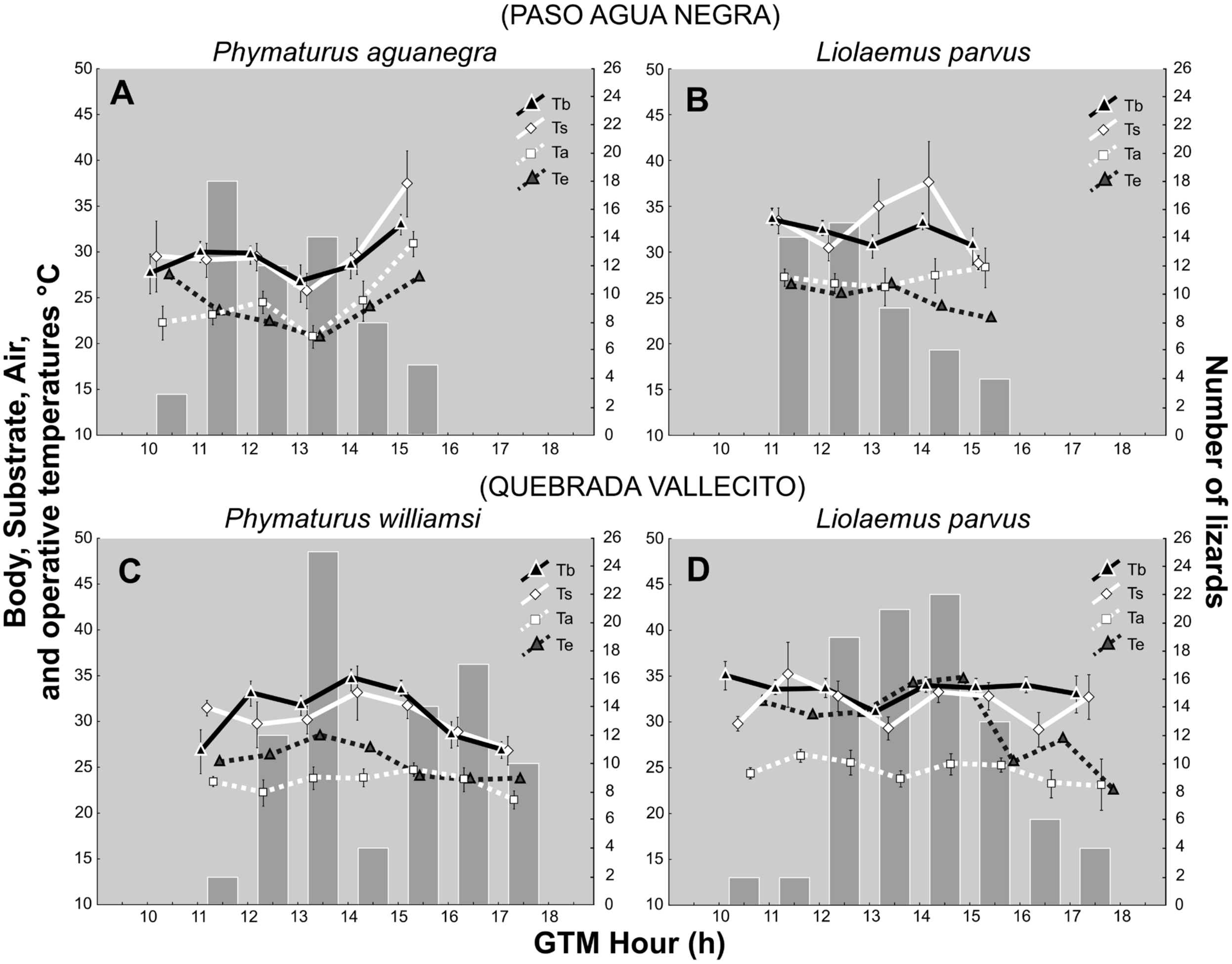

Figure 3. Variation during activity in mean body temperature (°C; T_b, black triangles with white foreground), micro-environmental temperatures: substrate (C°, T_s, white diamond), air (°C; T_a, white squares), and operative temperatures (°C; T_e grey triangles with black foreground) vs. time (h) of *Phymaturus aguanegra* (panel a) and *Liolaemus parvus* (panel b) at Paso Agua Negra, and *Phymaturus williamsi* (panel c) and *Liolaemus parvus* (panel d) at Quebrada Vallecito. Polygons connect the mean ± SE of the variables through the activity period. Grey bars are the mean number of active lizards per hour.

($N = 4$) were included within the T_{set}. Likewise, in *L. parvus* the lower and upper T_{set} limits were 35.71 ± 1.93°C and 38.46 ± 0.84°C, respectively (Figure 4b). Most of the T_bs ($N = 37$, 90%) were lower than the minimum $T_{set.}$, and 10% ($N = 4$) were included within the T_{set}.

The T_{set} values exceeded T_e in all *P. aguanegra* individuals and in all but one individual of *L. parvus* showed T_{set} lower than T_e. Males of *P. aguanegra* and juveniles of *L. parvus* exhibited the highest E-values compared with the other demographic classes in each population (Table II).

Quebrada Vallecito

The T_{pref} values of *P. williamsi* and *L. parvus* were higher than the T_bs (Paired *t*-test, *P. williamsi*: $t_{(33)} = -8.189$, $P < 0.001$; *L. parvus*: $t_{(29)} = -2.61$, $P < 0.01$; Table II). In *P. williamsi* lower and upper T_{set}s were 35.02 ± 1.71°C and 37.74 ± 1.68°C, respectively (Figure 4c). A majority ($N = 28$, 82%)

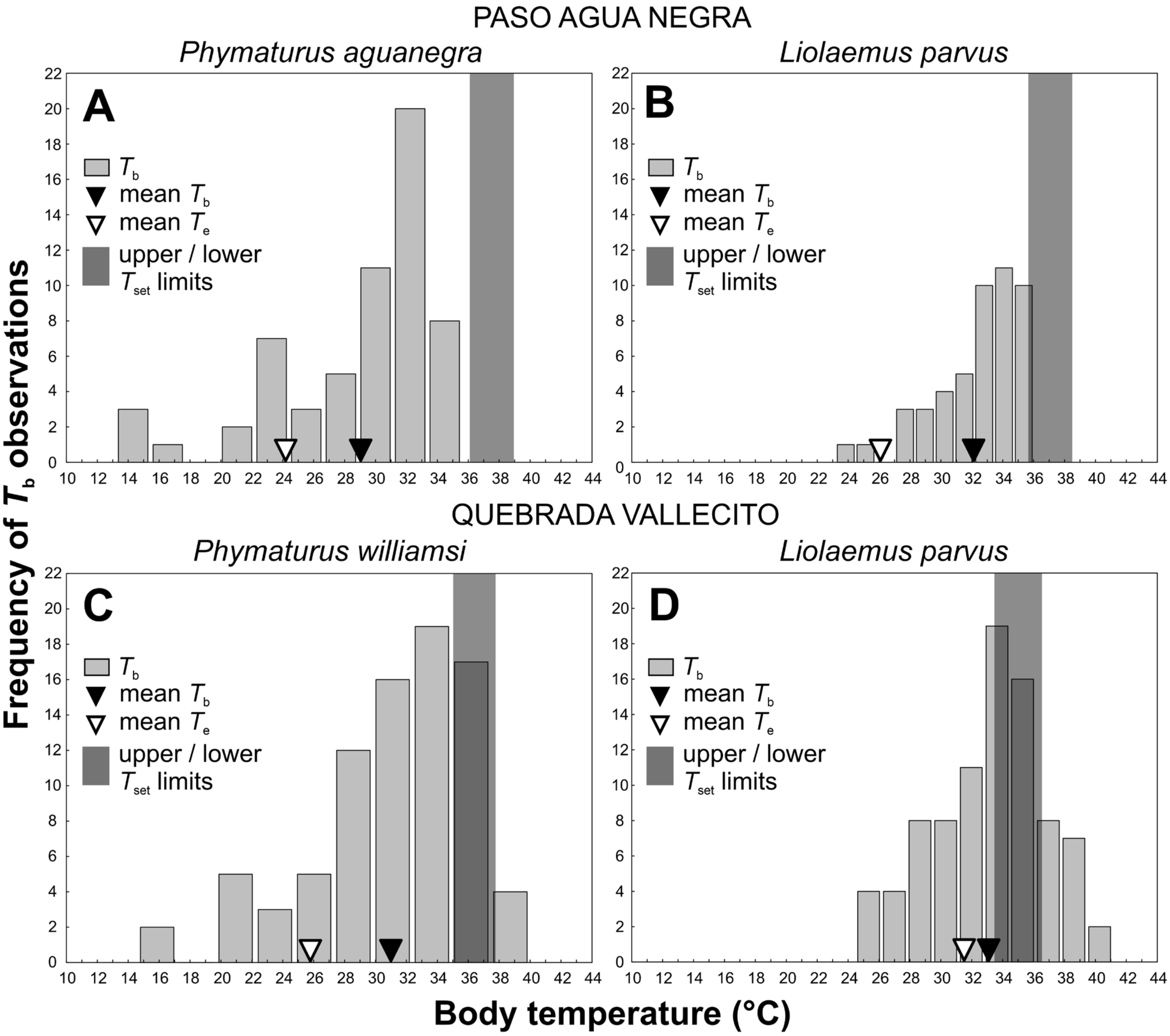

Figure 4. Distribution of body temperatures (T_b) at capture of *Phymaturus aguanegra* and *Liolaemus parvus* at Paso Agua Negra and *P. williamsi* and *L. parvus* at Quebrada Vallecito. The white arrows indicate median operative temperatures (T_e), black arrows indicate median T_b values and the dark shaded column indicates the lower and upper set-point ranges of selected temperatures (T_{set}).

of the T_bs were lower than the minimum T_{set}, 15% (*N* = 5) were included within T_{set}, and 3% (*N* = 1) were higher than the maximum T_{set}. In *L. parvus,* the lower and upper T_{set} were 33.47°C ± 1.79 and 36.65°C ± 1.46°C, respectively (Figure 4d). About half (*N* = 16, 53%) of the T_bs of *L. parvus* were lower than the minimum T_{set}, 17% (*N* = 6) of T_bs were included within the T_{set}, and 30% (*N* = 9) were higher than the maximum T_{set}.

The T_{set} of *P. williamsi* (100%) was higher than the T_e. In *L. parvus,* the 37% (*N* = 11) of the individuals, the minimum T_{set} was lower than T_e, the 7% (*N* = 2) the maximum T_{set} were lower than T_e (7%, *N* = 2), and the in remainder (56%, *N* = 17) the T_{set}s were higher than T_es.

Males and females of *P. williamsi* showed similar E-values, being both moderate thermoregulators, whereas in *L. parvus,* both the males and females exhibited negative E-values indicating there are non-thermal constraints or risks that prevent them from thermoregulating within their set-points of T_{pref} (Table II).

Comparison of T_b, and T_{pref} between sites for *Phymaturus* and *Liolaemus*

The T_b of *P. williamsi* was higher than that of *P. aguanegra* (Mann-Whitney U-test, $U_{Tb\ (1)} = 1923$, $P < 0.01$, $N_{P.\ aguanegra} = 60$, $N_{P.\ williamsi} = 84$). Conversely, the T_{pref} of *P. aguanegra* was higher than those in *P. williamsi* (Student *t*-test, $t_{Tpref\ (76)} = -3.69$, $P < 0.0001$, Table II).

Liolaemus parvus populations did not differ in T_b between Agua Negra and Quebrada Vallecito (Mann-Whitney U-test, $U_{(1)} = 1630.500$, $P > 0.11$, $N_{L.\ parvus\ \text{Agua Negra}} = 45$, $N_{L.\ parvus\ \text{Quebrada Vallecito}} = 87$), but T_{pref} values of *L. parvus* from Agua Negra were higher than those in *L. parvus* from Quebrada Vallecito (Student *t*-test, $t_{(69)} = -6.147$, $P < 0.0001$, Table II).

Periods of activity

Paso Agua Negra

Phymaturus aguanegra were active for about 6 hours (10:00 – 16:00 h), whereas *L. parvus* was active for about 5 hours (11:00 – 16:00 h). In both species, the observed frequencies were not different than expected on an hour-by-hour basis (Table IV). Both species show a unimodal pattern of activity, with the highest number of lizards active 11:00 to 14:00 (Figures 3a and 3b).

Quebrada Vallecito

Phymaturus williamsi was active during 7 hours (11:00 – 18:00 h), and the observed frequencies of individuals were lower than expected during the 13:00 – 14:00 h interval (Pearson Chi-Square test, $\chi^2_{(21)} = 13.06$, Multiple comparison, z = -3.61, $P < 0.0001$, Table IV). *P. williamsi* showed a bimodal pattern of activity with the most active individuals during late morning (12:00 – 14:00 h) and afternoon (15:00 – 18:00 h; Figure 3c). Likewise, *L. parvus* was active daily for 8 hours (10:00 – 18:00 h) and the observed frequencies were lower than expected during the 11:00 – 12:00 h interval (Pearson Chi-Square test, $\chi^2_{(31)} = 19.72$, Multiple comparison, z = -4.44, $P < 0.00001$, Table IV) but the population showed a unimodal pattern of activity (Figure 3d).

DISCUSSION

Phymaturus species are exposed to a broad range of climatic factors and thermal environments along the high cordilleras on both slopes of the southern Andes and eastward to the Patagonian steppe. The field body temperatures observed in *P. aguanegra* (mean = 29.05°C) and *P. williamsi* (mean = 31.00°C) varied according to the environmental conditions those populations experienced in their natural habitats, typical of the Puna biogeographic region (Fig. 2). The habitat of *P. aguanegra* is characterized by steep slopes with extensive debris aprons of

Table IV. Summary of Pearson's Chi-Square test. Frequencies of activity of lizards by hour are indicated as frequencies and percentage (%). *Post hoc* analysis are indicated by their adjusted z-scores (Adj. z-score) and probabilities (*P*). Bonferroni's correction (*P* > 0.001), and total sample sizes, and percentages are also indicated. Significant differences are in bold (*).

Hour of the day (h; GMT-3)		**Pearson Chi-Square test $_{(21)}$ = 70.73, *P* < 0.0001**				**Total**
		***Phymaturus aguanegra* (Agua Negra)**	***Phymaturus williamsi* (Qa. Vallecito)**	***Liolaemus parvus* (Agua Negra)**	***Liolaemus parvus* (Qa. Vallecito)**	
10:00 – 11:00	Frequency	3	0	0	2	5
	% within hour	60.0%	0.0%	0.0%	40.0%	100.0%
	Adj. z-score	2.11	-1.48	-1.03	0.43	
	P < 0.001	0.034	0.138	0.303	0.667	
11:00 – 12:00	Frequency	18	14	14	2	48
	% within hour	37.5%	29.2%	29.2%	4.2%	100.0%
	Adj. z-score	2.96	-0.16	2.41	-4.44	
	P < 0.001	0.003	0.872	0.015	**0.00001***	
12:00 – 13:00	Frequency	12	25	15	19	71
	% within hour	16.9%	35.2%	21.1%	26.8%	100.0%
	Adj. z-score	-1.09	1.09	1.01	-0.93	
	P < 0.001	0.275	0.275	0.312	0.352	
13:00 – 14:00	Frequency	14	4	9	21	48
	% within hour	29.2%	8.3%	18.8%	43.8%	100.0%
	Adj. z-score	1.42	-3.61	0.31	2.07	
	P < 0.001	0.155	**0.0001***	0.756	0.038	
14:00 – 15:00	Frequency	8	14	6	22	50
	% within hour	16.0%	28.0%	12.0%	44.0%	100.0%
	Adj. z-score	-1.05	-0.36	-1.08	2.16	
	P < 0.001	0.293	0.718	0.280	0.030	
15:00 – 16:00	Frequency	5	17	4	11	37
	% within hour	13.5%	45.9%	10.8%	29.7%	100.0%
	Adj. z-score	-1.27	2.26	-1.11	-0.20	
	P < 0.001	0.204	0.023	0.266	0.841	
16:00 – 17:00	Frequency	0	10	0	6	16
	% within hour	0.0%	62.5%	0.0%	37.5%	100.0%
	Adj. z-score	-2.16	2.91	-1.88	0.56	
	P < 0.001	0.030	0.003	0.060	0.575	
17:00 – 18:00	Frequency	0	0	0	4	4
	% within hour	0.0%	0.0%	0.0%	100.0%	100.0%
	Adj. z-score	-1.05	-1.32	-0.92	2.99	
	P < 0.001	0.293	0.186	0.357	0.002	
Total	Frequency	60	84	48	87	279
	%	21.5%	30.1%	17.2%	31.2%	100.0%

basaltic rocks with interspersed dwarf shrubs at the base. The habitat of *P. williamsi*, is different since rocky outcrops are distributed in a gentler open-gully landscape leading to differences in sun and wind exposure between both locations with remarkable consequences for the thermal heterogeneity (Paso Agua Negra, ΔT_e = 9.62 °C vs. Quebrada Vallecito, ΔT_e = 6.42 °C; Figures 2 and 4). Thus, lower T_b values in *P. aguanegra* than *P. williamsi* could have resulted from a greater thermal restriction ($d_{e\ P.\ aguanegra}$ = 11.26; $d_{e\ P.\ williamsi}$ = 9.06). The activity patterns observed in *Phymaturus* species also corroborates the difference in thermal restriction with shorter periods of activity in *P. aguanegra* and a longer, but bimodal pattern in *P. williamsi* (Table IV; Figure 3). In contrast, the T_b values of *L. parvus* from Paso Agua Negra (mean = 32.19 °C) and in Quebrada Vallecito (mean = 33.14 °C) did not show differences, and were similar to those reported in another *L. parvus* population from a high-altitude site in the Puna region (Gómez Ales et al. 2017). Indeed, the *L. parvus* activity period was shorter in Paso Agua Negra (5 h) than in the milder environment of Quebrada Vallecito (8 h).

In general, the variability in T_b may be adaptive phenotypic plasticity favoured by the use of multiple and changing microenvironments (Kingsolver & Buckley 2017, Huey et al. 2003). The microenvironments used by the populations of *P. aguanegra*, *P. williamsi* and *L. parvus* (from Paso Agua Negra) varied substantially according to differences in the type of substrate, exposure to radiation, wind or cloudiness (Laspiur 2010). The strong similarity and dependence of T_b on T_s in *P. aguanegra* suggests that they heat mainly by thigmothermy during most hours of activity while, in *P. williamsi* there is a significant relationship between T_b and T_s, but T_b is higher than T_s suggesting they use both heat sources, thigmothermy and heliothermy. These results support our observation of *Phymaturus* lizards flattening the ventral surface of their body to the rock, maximizing heat transfer while orienting their body dorsum perpendicularly to incident solar radiation, as reported for *P. palluma* (Vicenzi et al. 2019). In contrast, *L. parvus* from Paso Agua Negra were seen occupying exposed homogeneous microsites composed of small weathered rocks beneath dwarf shrubs and they showed an opportunistic thermoregulatory behaviour. *Liolaemus parvus* is heliothermic when T_s substantially exceeds the T_b, but turns to thigmothermy during the colder hours in the late afternoon (See Figure 3, Panel B). Moreover, the finding of higher T_bs in *L. parvus* from Agua Negra compared to *P. aguanegra* was probably caused by behavioral selection of warm microenvironments with markedly greater exposure to radiation and sheltering from winds than those selected by *P. aguanegra*. Conversely, in Quebrada Vallecito, T_bs of *L. parvus* and *P. williamsi* have shown a strong relationship with T_ss, and T_bs were higher than T_ss and T_as suggesting that both species alternate between thigmothermy and heliothermy for thermoregulation. Furthermore, it would be interesting to study whether there is competition for thermal micro-environments within the rocky outcrops they use for thermoregulation and, if so, that would explain the lower T_b found in *P. williamsi* compared to *L. parvus*. The bimodality in activity period likely represents temporal niche partitioning (Fig. 3c and 3d) and could be explained by territorial or temporal segregation of both species related to thermal restrictions. In this sense, *Liolaemus parvus* exhibited 8 hours of activity, being more active during the warmest hours when the micro-environmental and operative temperatures reach their maxima, and depicting a unimodal pattern activity (Figure 3d, Table IV). In contrast, *P. williamsi* was active earlier and for only 6 h with a significant decrease in activity during the warmest periods (14-15 h). This resulted in a bimodal pattern of activity, probably as a way to avoid exposure to high environmental temperatures (Figure 3c, Table IV) and to take advantage of warm microenvironments early in the morning before *L. parvus* starts activity. A similar bimodal daily activity pattern, with cessation of activity at ~15:00 h, also occurs in *P. vociferator* from Laguna del Laja, central Chile (Vidal et al. 2010). In contrast, *P. aguanegra* showed a unimodal pattern like that reported for other species in the *P. palluma* group: *P. palluma* (Vicenzi et al. 2019), *P. roigorum* (Corbalán & Debandi 2014), and for the northernmost species in the *P. patagonicus* group, *P. payuniae* (Corbalán & Debandi 2014). Thus, environmental temperature has a strong effect on the activity of lizards during the day, and pattern differences may reflect different restraints for thermoregulation between coexisting species. In Quebrada Vallecito, our results support the prediction that syntopic species exhibit differences in T_b, T_{pref}, and activity periods as a result of niche segregation.

Body temperature can also be affected by differences in activity patterns, use of microhabitats, and thermal preferences of males, females or juveniles (Bull et al. 1991, Butler et al. 2000, Lailvaux 2004, Ortega et al. 2016). Gender and reproductive condition can often cause differences in hierarchical social behaviour, physiology and ecology (Vitt and Cooper 1986, Irschick & Garland 2001, Lovern 2011, Sinervo & Miles 2011). In this sense, despite the differences in body size or mass existing among demographic groups (males, females and juveniles; Table II) the T_b or T_{pref} values were similar across groups as none showed a relationship with M_i in neither the *L. parvus* population nor in the *P. aguanegra* population. An exception was observed in *P. williamsi* from Quebrada Vallecito, where juveniles exhibited a higher mean T_b than adult males. Similarly, *L. parvus* juveniles at Agua Negra showed a higher E value than adults (Tables I and II). This could have been caused by smaller individuals with faster heating rates needing shorter exposures to maintain their temperature within the preferred range, while bigger body sizes resulted in higher thermal inertia. Hence, our results partially support our hypothesis that thermal traits would be different between juveniles and adults and affected by body condition. Probably, there are underlying and confounding factors such as thermal behaviour, predation pressure or competition that could also drive the thermal patterns within populations (Ortega et al. 2016).

Phymaturus aguanegra and *L. parvus* from Paso Agua Negra, and *P. williamsi* from Quebrada Vallecito are effective thermoregulators being able to maintain field body temperatures higher than $T_{e,}$ despite the marked daily and seasonal fluctuations in air temperature and precipitation present in the highlands of the Andes (Aguado 1983, Borsdorf & Stadel 2015). Both *Phymaturus* species showed similar indices of effective thermoregulation ($E_{P.\ aguanegra}$ = 0.41 and $E_{P.\ williamsi}$ = 0.50), behaving as moderate thermoregulators. *Liolaemus parvus* E-values differed between sites, behaving as moderate-to-good thermoregulators in Paso Agua Negra ($E_{L.\ parvus}$ = 0.60) but as a thermoconformer in Quebrada Vallecito ($E_{L.\ parvus}$ = - 0.22). This difference could be attributed to the fact that the *L. parvus* population in Quebrada Vallecito needed less active thermoregulation as result of inhabiting a “less heterogeneous habitat” (*sensu* Basson et al. 2017). In fact, a high proportion of T_b were similar to T_e during the warmer hours. *Liolaemus parvus* pays the cost of T_bs that often exceed their T_{set} in Quebrada Vallecito, resulting in a negative E-value. Despite having suitable microenvironments available for thermoregulation, lizards may not use them because of other factors, such as the presence of greater predation risk, or lack of prey (Christian & Weavers 1996, Gutiérrez et al. 2010, Sinervo et al. 2010).

The existing difference in T_{pref} but similarity in T_{b} between *L. parvus* populations resulted in the difference in the effectiveness of thermoregulation, being medium to high at Paso Agua Negra and low (thermoconformer) at Quebrada Vallecito. So, even though *L. parvus* displays plasticity in thermoregulatory behavior, switching between heliothermy and thigmothermy, its thermoregulation appears to be constrained as only 17% of the population have values within the T_{set}. Even the index of the average of quality of the habitat from an organism's perspective ($d_{\text{e}} = |T_{\text{e}} - T_{\text{set}}|$; *sensu* Hertz et al. 1993) is high ($d_{\text{e}} = 2.57$) in Quebrada Vallecito, there may be other restrictions, such as competition for microenvironments for thermoregulation with *P. williamsi*, that preclude them from effectively thermoregulating, resulting in low accuracy for thermoregulation ($d_{\text{b}} = 3.13$). However, *L. parvus* has the ability to tolerate harsh environmental conditions and to succeed in a wide geographic range in the Andes. The extent of the spatial distribution of *L. parvus* in the Andean and pre-Andean environments is a good indicator of the success of *Liolaemus* in comparison with the geographically restricted populations of *Phymaturus* (Quinteros et al. 2008, Díaz-Gómez 2009, Lobo et al. 2013).

Two contrasting views exist on thermal biology traits in lizards (Rodríguez Serrano et al. 2009). The first view holds that thermal biology traits are evolutionary conservative and they respond gradually to directional selection (Hertz & Huey 1981, Van Damme et al. 1990, Rodríguez-Serrano et al. 2009). The second view (labile view) asserts that thermal biology traits can rapidly adapt via directional selection to changing environmental pressures or changes within populations as experienced by some taxa (Huey & Kingsolver 1989, Van Damme et al. 1990, Rodríguez-Serrano et al. 2009, Sinervo et al. 2010). Our results indicate significant differences in T_{b} and T_{pref} between *P. aguanegra and P. williamsi*, and these species thermoregulate with high accuracy and effectiveness despite considerable site differences and low thermal qualities of their habitats in the Central Andes ($d_{\text{e } P.\ aguanegra} = 11.26$; $d_{\text{e } P.\ williamsi} = 9.06$). Thus, our results do not confirm the prediction of conservativism in *Phymaturus* contrasting with some previous studies (Cruz et al. 2009, Gómez Ales et al. 2017, Duran et al. 2018). On the other hand, the *L. parvus* populations studied here exhibited similar T_{b} values but differed in T_{pref} and E, suggesting that these lizards respond to short-term environmental temperature fluctuations. Hence, *L. parvus* exhibited lower variation in T_{b} but greater variation in T_{pref}, accuracy and effectiveness of thermoregulation and these results support an alternative to the *labile*-traits hypothesis (*sensu* Rodríguez-Serrano et al. 2009): some traits impacting thermal biology may be conserved within a population while others simultaneously show a combination of conservative and flexible-traits evolution (Bonino et al. 2011).

Phymaturus and *Liolaemus* occupy similar altitudinal ranges along the Andes mountains and therefore experience comparable environmental conditions and similar levels of availability of microhabitats. Nevertheless, differences in microhabitat selection among species may play a role in thermoregulation more so than gender, age or body condition. The Andean environments offer thermal opportunities for thermoregulation in which most lizards exhibit high thermoregulatory efficiency. High-elevation species suffer higher vulnerability in the face of a warming-climate scenario, and such vulnerability can be detected when T_{e} is closer to T_{pref} and particularly when species show T_b values greater than their T_{set} as observed for *L. parvus* from Quebrada Vallecito. Hence, future complementary studies on thermal tolerance and physiological plasticity are necessary to evaluate physiological thresholds to predict possible responses to climate change based on physiological models (Sinervo et al. 2018).

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Alejandro Laspiur designed the study, participated in the sampling and analysis of samples, data acquisition and curation, methodology, results analysis, wrote the original draft and final version of the manuscript, designed and constructed the figures, and contributed to funding acquisition. Marlin Medina and María Soledad Ausas designed the study, participated in the data acquisition, and wrote the original draft of the manuscript. Juan C. Acosta designed the study, participated in the sampling and data acquisition, methodology, and wrote the original draft of the manuscript. John D. Krenz participated in the methodology, figures construction, wrote the final version of the manuscript, and revised the grammar. Nora Ibargüengoytía designed the study, participated in the methodology, data acquisition, results analysis, wrote the original draft and final version of the manuscript, and contributed to funding acquisition. All authors discussed the results and commented on the manuscript.