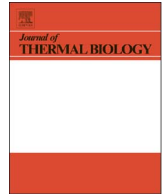




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Thermal biology in two syntopic lizards, *Phymaturus extrilidus* and *Liolaemus parvus*, in the Puna region of Argentina

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ABSTRACT

Body temperature is the most important ecophysiological variable affecting reptiles' life history. Moreover, thermoregulation in ectotherms implies a struggle to reach preferred temperatures in natural conditions due to the influence of biotic and abiotic factors. Our objective was to evaluate and compare the thermal biology of two syntopic species, *Phymaturus extrilidus* and *Liolaemus parvus*, in the Puna region of San Juan, Argentina. We determined body temperature (T_b), micro-environmental temperatures (T_a and T_s) and operative temperatures (T_e) in the field. In the laboratory, we measured preferred temperatures (T_{pref}) and calculated the index of thermoregulatory efficiency (E). Neither body temperatures in the field nor preferred temperatures varied between seasons and sexes. Body temperatures were lower than preferred temperatures for both species. Nevertheless, regardless of the low thermal offer available in habitat, both species did achieve body temperatures higher than operative temperatures during activity. Thermoregulatory effectiveness was moderate in *P. extrilidus* ($E=0.65$), while *L. parvus* presented greater thermoregulatory efficiency ($E=0.78$). We conclude that under the rigorous climate conditions of the Puna, *Phymaturus extrilidus* and *Liolaemus parvus* are able to actively and efficiently thermoregulate, maintaining body temperatures close to the preferred and higher than those of its habitat. Differences in thermal characteristics between *Phymaturus extrilidus* and *Liolaemus parvus* are a consequence of differential limitations imposed on each species by the environment and of forces inherent to their life histories.

1. Introduction

Body temperature is the most important ecophysiological variable affecting the life histories of reptiles as it directly influences locomotion (Angilletta et al., 2002; Christian and Tracy, 1981; Huey and Kingsolver, 1989; Van Damme et al., 1989), patterns of activity, selection of microhabitats (Smith and Ballinger, 2001; Willms et al., 2011), reproduction (Boretto and Ibarquengoytia, 2009; Ibarquengoytia, 2008), foraging rates, growth and metabolism (Angilletta et al., 2002; Espinoza and Tracy, 2000; Huey, 1982; Sears, 2005; Zug et al., 2001). Moreover, thermoregulation in ectotherms implies a struggle to reach optimal temperatures (Adolph and Porter, 1993; Bauwens, 1999; Vitt and Caldwell, 2009) in natural conditions due to the influence of biotic and abiotic factors (Heatwole, 1976; Huey, 1974). These factors include intraspecific and interspecific interactions, availability of microhabitats and daily and seasonal

variations in habitat temperature, among others (Belluire et al., 1996; Huey and Slatkin, 1976; Smith and Ballinger, 1994; Stevenson, 1985).

A habitat's thermal quality is one of the main environmental factors that changes with elevation and latitude (Ibarquengoytia et al., 2008). Species living in high altitudes, such as those in the Puna region, have problems maintaining body temperatures near the optimum range during periods of activity (Carothers, 1998; Veblen et al., 2007). This is due to the fact that the climate in these regions is characterized by extreme seasonal variations, overall lower air temperatures, and large daily temperature fluctuations (Hertz, 1977, 1980; Huey and Webster, 1975; Spellerberg, 1972). However, though lizards in cold environments do depend on the temperatures of their environment, they have developed behavioral and physiological mechanisms which allow them to both settle and remain in habitats with climatic challenges (Christian, 1998; Pearson, 1954; Pearson and Bradford, 1976). Such

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mechanisms may be shared with species that coexist in the same habitat as a reflection of the adverse climate conditions found at high altitudes (Vitt and Caldwell, 2009).

On the other hand, the complexity of the topographic structure in altitudinal environments results in marked thermal, spatial and temporal heterogeneity (Sears et al., 2011). This heterogeneity allows for an expansion of opportunities of activity and a regulation of the costs of behavioral thermoregulation in lizards, in addition to the fact that there are models that predict greater accuracy in thermoregulation when thermal resources are dispersed throughout space (Sears et al., 2016).

The genera *Phymaturus* and *Liolaemus* (Liolaemidae) coexist along latitudinal gradients in the Andes mountain range of both Argentina and Chile (Díaz Gómez, 2009). Our work studies the thermal biology of two syntopic species, *Phymaturus extrilidus* and *Liolaemus parvus*, in the Puna region of San Juan, Argentina. *Phymaturus extrilidus* belongs to the subclade “*P. punae*,” endemic to the locality of Sierras de la Invernada at 3100 m asl (Lobo et al., 2012) while *L. parvus* belongs to the subclade “*L. petrophilus*,” a group having a wide range of distribution in the Central Andes of Argentina between 2700 and 3500 m asl (Quinteros et al., 2008). These species, subject to environmentally harsh with unpredictable climate conditions and marked seasonal variations of prolonged winters and short summers, coexist using similar microhabitats for thermoregulation, foraging and shelter. *Phymaturus extrilidus* is viviparous, typically saxicolous, found on different types of rocks and crevices. As with *L. parvus*, also viviparous, it can be observed making general use of rocky promontories and bare soil, under bushes and vegas, showing similar patterns of daily activity (*pers. obs.*). However, *P. extrilidus* and *L. parvus* are different in their morphological and ecological aspects. *Phymaturus extrilidus* is robust (snout-vent length 98.5 mm) with a flattened dorsoventrally and has an herbivorous diet (Lobo et al., 2012), while *L. parvus* is thin (snout-vent length 65.1 mm) and has a generalist diet (Pérez, *pers.com.*).

Many authors have studied thermal characteristics of *Phymaturus* and *Liolaemus* (Carothers et al., 1997, 1998; Cruz et al., 2009; Gutiérrez et al., 2010; Ibarguengoytía and Cussac, 2002; Ibarguengoytía et al., 2008, 2010; Kubisch et al., 2015; Labra and Bozinovic, 2002; Marquet et al., 1989; Medina et al., 2009, 2011, 2012; Moreno Azócar et al., 2013, 2015; Rodríguez Serrano et al., 2009; Vidal et al., 2010; Villavicencio et al., 2007; among others), however, for *P. extrilidus* specifically, it has only been reported that it is a heliothermic species (Lobo et al., 2012) and for *L. parvus*, only some thermal aspects of populations in the Andes have been evaluated (Acosta et al., 2006; Laspiur et al., unpublished data). On the other hand, though thermal characteristics of sympatric species have been evaluated (Hertz, 1992; Hertz et al., 1993; Dias and Rocha, 2004; Lara Resendiz et al., 2014; Rocha and Vrcibradic, 1996; Sartorius et al., 2002), in Argentina, descriptive and comparative studies of thermoregulatory characteristics of syntopic species are uncommon (Corbalán et al., 2013; Ibarguengoytía, 2005; Laspiur et al., unpublished data; Valdecantos et al., 2013). As such, this syntopic study of *P. extrilidus* and *L. parvus* provides important new information on understudied populations living in rigorous environments.

Syntopic species may or may not separate themselves in time or space and this phenomenon is integrated into the resource model determining temperature regulation (Dunham et al., 1989; Roughgarden et al., 1981; Tracy and Christian, 1986). The segregation of one or both aspects leads to differences in thermoregulatory characteristics (Vitt and Caldwell, 2009; Zug et al., 2001). In addition, factors intrinsic to life history such as body size, sex, reproductive condition and diet impose varying restrictions on species' thermoregulation (Magnusson, 1993). It has been suggested that at the genus level many biological characteristics are conserved between species, principally for *Phymaturus* (Cruz et al., 2009; Debandi et al., 2012; Scolaro et al., 2008). Therefore, phylogenetic history may influence

thermoregulation of lizards, and species belonging to genera with different evolutionary pathways tend to differ with respect to mean body temperature during activity, even under the same environmental conditions (Bogert, 1949). Nevertheless, thermal characteristics (e.g. active body temperature, preferred temperature and critical maximum and minimum temperatures, among others) present different degrees of flexibility as a result of historical and ecological influences (Clusella Trullas and Chown, 2014). We hypothesize that despite the highly restrictive conditions and variables to which *P. extrilidus* and *L. parvus* are exposed in the Puna region, these species present different thermoregulatory characteristics and strategies, corresponding to each one's life history (morphological and ecological differences) and the influence of phylogenetic inertia.

For these reasons, our objective was to evaluate and compare the thermal biology of the syntopic species *Phymaturus extrilidus* and *Liolaemus parvus*, so as to increase knowledge of the life history characteristics of this group of Puna lizards. Our specific objectives were (1) to evaluate the thermal relationships between field body temperature and micro-environmental temperatures (2) to determine the range of preferred temperatures or set-point range and (3) to determine the accuracy of field body temperature in relation to set-point range and thermoregulatory efficiency, evaluating the existence of sexual and seasonal variations.

2. Materials and methods

2.1. Study area and materials

Phymaturus extrilidus (N=60) and *Liolaemus parvus* (N=35) were captured by noosing and by hand during the fall and spring of 2014 at the “Don Carmelo” Reserve between 3146 m and 3184 m asl. This area is located in the Sierra La Invernada in the western part of Ullum department (30° 56.99' S, 69° 04.83' W; 3166 m asl), in the foothills of the Andes mountains in the province of San Juan, Argentina. Here we find the desert Puna, between 2700 and 3400 m asl (Roig Juñent et al., 2003). Its climate is cold and dry, with an average annual temperature lower than 8 °C, and is characterized by significant daily temperature fluctuations (night temperatures below zero and higher than 30 °C during the day) and seasonal temperature fluctuations, with frozen precipitation from June to October (Cabrera, 1994; Roig Juñent et al., 2003; Martínez Carretero, 1995; Roig and Martínez Carretero, 1998). Captures were authorized by the Secretaría de Medio Ambiente, Dirección de Conservación y Áreas Protegidas of the province of San Juan.

2.2. Field data recordings

Body temperature (T_b) was measured within the range of activity from 10 h to 19 h, using thermocouples (TES TP-K01; 1.62 mm diameter) by inserting the probe 0.5 cm into the cloaca. Individuals were handled by the head and measurements were taken within 10 s of capture so as to avoid heat transfer to the animal. A field body temperature record was taken per individual. At each capture site, we recorded micro-environmental temperatures in order to determine heat sources utilized by the lizards, measuring substrate temperature (T_s) with a substrate thermocouple (TES TP-K03) and air temperature (T_a) with an air thermocouple (TES TP-K02) connected to a digital thermometer TES © 1303 (TES Electronic Corp., Taipei, Taiwan, ± 0.01 °C). For each lizard captured, we recorded: sex, snout-vent length (SVL), body mass (BM), time and type of microhabitat (bare soil, over and under rocks, crevices, over and under bushes). The lizards that were not transferred to the laboratory to obtain the preferred temperatures were marked to avoid recapture.

The number of gestating females was limited, so they were included in the analysis along with non-gestating females. We could not make comparisons between gestating females and males and non-gestating females.

Table 1

Temperatures (°C): field body (T_b), micro-environmental: air (T_a) and substrate (T_s), preferred (T_{pref}) and set-point ranges (T_{set}) for *Phymaturus extrilidus* and *Liolaemus parvus* by overall population, season and sex. Mean \pm SD and sample size (N) are indicated.

| Species | Class | T_b | T_a | T_s | T_{pref} | T_{set} lower limit | T_{set} upper limit | N | |
|------------------------------|-------------------------|------------------|------------------|------------------|------------------|-----------------------|-----------------------|------------------|----|
| <i>Phymaturus extrilidus</i> | Overall | 32.32 \pm 3.13 | 19.5 \pm 4.79 | 30.4 \pm 5.3 | 35.74 \pm 1.8 | 34.92 \pm 2.03 | 36.78 \pm 1.65 | 60 | |
| | Males | 32.56 \pm 3.36 | 19.53 \pm 5.1 | 30.59 \pm 5.63 | 35.86 \pm 1.43 | 34.95 \pm 1.86 | 36.95 \pm 1.14 | 33 | |
| | Females | 32.01 \pm 2.85 | 18.68 \pm 4.43 | 30.16 \pm 4.96 | 35.6 \pm 2.18 | 34.88 \pm 2.27 | 36.59 \pm 2.13 | 27 | |
| | Fall | 32.86 \pm 3.09 | 22.13 \pm 3.41 | 31.91 \pm 5.41 | 35.72 \pm 1.4 | 34.91 \pm 1.86 | 36.76 \pm 1.08 | 34 | |
| | Males | 33.41 \pm 3.04 | 22.7 \pm 3.59 | 32.57 \pm 5.3 | 35.33 \pm 1.48 | 34.46 \pm 2.13 | 36.49 \pm 1.06 | 19 | |
| | Females | 32.16 \pm 3.1 | 21.4 \pm 3.14 | 31.06 \pm 5.62 | 36.21 \pm 1.15 | 35.48 \pm 1.31 | 37.1 \pm 1.04 | 15 | |
| | Spring | 31.6 \pm 3.09 | 15.25 \pm 3.31 | 28.42 \pm 4.53 | 35.77 \pm 2.25 | 34.92 \pm 2.28 | 36.82 \pm 2.22 | 26 | |
| | Males | 31.41 \pm 3.53 | 15.23 \pm 3.41 | 27.91 \pm 5.07 | 36.58 \pm 1.03 | 35.61 \pm 1.19 | 37.57 \pm 0.96 | 14 | |
| | Females | 31.82 \pm 2.62 | 15.28 \pm 3.34 | 29.02 \pm 3.93 | 34.84 \pm 2.91 | 34.13 \pm 2.98 | 35.94 \pm 2.92 | 12 | |
| | <i>Liolaemus parvus</i> | Overall | 33.74 \pm 2.46 | 22.54 \pm 4.61 | 34.54 \pm 5.5 | 36.66 \pm 1.34 | 36.03 \pm 1.6 | 37.7 \pm 1.26 | 36 |
| | | Males | 33.86 \pm 2.85 | 22.14 \pm 5.51 | 34.23 \pm 6.69 | 36.98 \pm 1.19 | 36.43 \pm 1.38 | 38.09 \pm 1.17 | 18 |
| | | Females | 33.61 \pm 2.09 | 22.95 \pm 3.61 | 34.84 \pm 4.14 | 36.35 \pm 1.42 | 35.64 \pm 1.74 | 37.33 \pm 1.27 | 18 |
| Fall | | 34.02 \pm 2.81 | 23.89 \pm 4 | 35.45 \pm 5.64 | 36.81 \pm 0.86 | 36.19 \pm 1.17 | 37.73 \pm 0.66 | 20 | |
| Males | | 33.72 \pm 3.57 | 23.78 \pm 4.71 | 36.53 \pm 7.11 | 37.14 \pm 0.63 | 36.64 \pm 0.67 | 37.92 \pm 0.63 | 10 | |
| Females | | 34.32 \pm 1.92 | 24 \pm 3.41 | 34.37 \pm 3.75 | 36.53 \pm 0.97 | 35.78 \pm 1.4 | 37.57 \pm 0.67 | 10 | |
| Spring | | 33.38 \pm 1.98 | 20.86 \pm 4.88 | 33.4 \pm 5.26 | 36.48 \pm 1.75 | 35.83 \pm 2.03 | 37.65 \pm 1.76 | 16 | |
| Males | | 34.04 \pm 1.78 | 20.08 \pm 6.05 | 31.36 \pm 5.18 | 36.81 \pm 1.66 | 36.2 \pm 1.94 | 38.28 \pm 1.62 | 8 | |
| Females | | 32.72 \pm 2.07 | 21.67 \pm 3.62 | 35.44 \pm 4.79 | 36.13 \pm 1.89 | 35.47 \pm 2.17 | 37.03 \pm 1.77 | 8 | |

2.3. Determination of operative temperatures

Operative temperatures (T_e , *sensu* Hertz et al., 1993) represent the null distribution of potential body temperatures expected in non-thermoregulating animals, integrating biotic and abiotic factors that influence T_b . They were measured using 20 biophysical models of polyvinyl chloride (PVC) placed in the different microhabitats that *P. extrilidus* and *L. parvus* utilize: basalt rocks, feldspar rocks, under rocks, crevices, over and under bushes and bare soil. Models were connected to dataloggers (HOBO © ProV2) and micro-environmental temperatures were recorded every 5 min within the range of activity from 10 h to 19 h. The T_e of the study site was obtained from averaging each 5 min log using the total models. The biophysical models of T_e (*sensu* Bakken, 1992) were calibrated using simultaneous comparisons of the body temperatures (T_b) of *P. extrilidus* and *L. parvus* and PVC models corresponding to the approximate size of each species. Heating (± 40 °C) and cooling (± 10 °C) tests were performed in laboratory by means of an artificial heat and cold source. We carried out calibration experiments for 2 consecutive hours (one hour for warm-up and one for cool-down) and used P-K01 catheters to record the temperatures simultaneously of the models and the body temperatures of the lizards. The best-fitting model was the PVC model measuring 95×20 mm for *P. extrilidus* and 75×15 mm for *L. parvus* (Spearman Rank correlation T_b vs Model, $R = 0.98$ $N = 65$, $P < 0.0001$).

2.4. Laboratory experiments

Thermoregulation experiments were carried out 3–4 days after capture. Lizards were placed individually in 150×45×80 cm terrariums. In the top part of the terrarium, we created a temperature gradient by using a series of infrared lamps of varying wattage arranged at different heights so as to generate a linear temperature gradient (17–65 °C), in which the majority of temperatures naturally experienced in the field are included. Experiments were performed during the activity range from 10 h to 18 h and we recorded body temperature every 5 min for 3 h. To do this, we connected each specimen by way of the cloaca to ultrafine thermocouples (1 mm) held in place with adhesive tape and connected to a TC-08 USB, thus acquiring 8 channels of data (OMEGA®). This methodology prevents having to handle the lizard each time cloaca temperature is taken.

For each individual, we obtained the mean value of preferred temperatures (T_{pref}), the interquartile range of selected temperatures (middle 50% of distribution) and its limits defined as lower set-point

(25% quartile) and upper set-point (75% quartile). We chose these variables taking into account the neurophysiological bases for the idea that ectotherms regulate their temperatures within an interquartile or set-point (Barber and Crawford, 1977; Firth and Turner, 1982).

2.5. Effectiveness of thermoregulation

To estimate thermoregulatory efficiency (E) in the field, we calculated average deviations between T_b and T_{pref} (index of individual deviation = db) and indices of habitat thermal quality de (deviation between T_e and T_{pref}) for each individual and for each species. Using the means of db and de , we calculated thermoregulatory efficiency with the equation proposed by Hertz et al. (1993) $E = 1 - (db/de)$. Values of E approaching 1 represent precise or effective thermoregulation, while those equal to or approaching 0 indicate passive or moderate thermoregulation (Hertz et al., 1993). Negative values of E are attributed to individuals which avoid thermally stable microhabitats for various reasons, such as the presence of predators or lack of foraging opportunities in thermally optimal microclimates (Crowder and Magnusson, 1983; Hertz et al., 1993; Huey and Slatkin, 1976).

2.6. Statistical analyses

Data were analyzed using descriptive statistics: means, medians, variances and standard deviations. We compared means using *t*-test and ANOVA and evaluated dependency among variables using correlation and regression analysis. We analyzed normality and homogeneity of variance assumptions using the Kolmogorov-Smirnov and Shapiro Wilk tests, respectively. In cases where data failed to meet normality requirements, we used nonparametric statistics, running Mann-Whitney *U*-tests and Kruskal-Wallis tests (Sokal and Rohlf, 1969). Sigma Stat 3.5® and Statistica version 7.0 (Statsoft Inc., Tulsa, OK) were used to complete these statistical analyses.

3. Results

3.1. Micro-environmental and body temperatures

Results for T_b and micro-environmental temperatures T_a and T_s by sex, season and overall population are shown in Table 1.

Phymaturus extrilidus was mainly captured while sunning on basalt rocks and as such had a body temperature (T_b) significantly higher than air (T_a) and substrate (T_s) temperatures (ANOVA, F_2 ; 58

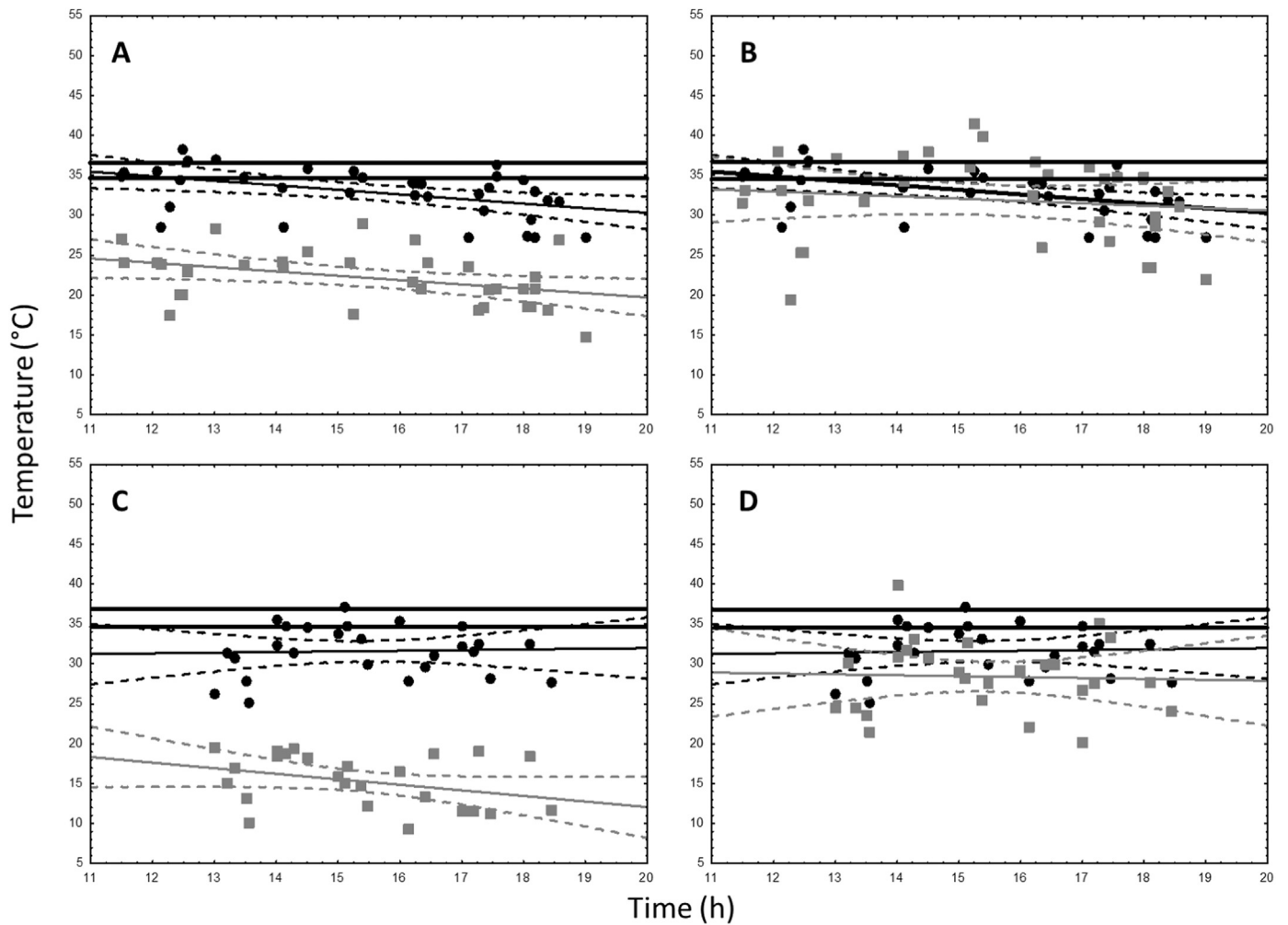


Fig. 1. Relationships between body temperature (T_b ; black circles) and micro-environmental temperatures (gray squares): air (T_a , panels A and C) and substrate (T_s , panels B and D) vs. time of activity (h) of *Phymaturus extrilidus* population. Fall (top panels, A and B); Spring (lower panels, C and D). Solid black lines indicate the lower and upper mean set-points of the selected temperature (T_{set}). Dashed lines indicate confidence interval $\alpha=95\%$.

=149.61, $P < 0.001$; Holm-Šidák test, $T_{Tb-Ta} = 16.01$; $T_{Ta-Ts} = 13.67$; $T_{Tb-Ts} = 2.33$, $P < 0.05$; Table 1). *Liolaemus parvus* was mainly captured on rocky promontories and its T_b was similar to T_s at capture sites, though T_b and T_s were significantly greater than T_a (ANOVA, $F_{2,34} = 84.38$, $P < 0.05$; Holm-Šidák test, $T_{Tb-Ta} = 10.84$; $T_{Ta-Ts} = 11.61$, $P < 0.05$; $T_{Tb-Ts} = 0.77$, $P > 0.05$; Table 1).

In the fall, the T_b of *P. extrilidus* and *L. parvus* do not depend on T_a and T_s (Stepwise regression, *P. extrilidus* $F_{Tb-Ta, 2; 32} = 3.09$, $F_{Tb-Ts, 2; 32} = 4.06$; *L. parvus* $F_{Tb-Ta, 2; 18} = 0.07$, $F_{Tb-Ts, 2; 18} = 0.71$, $P > 0.05$; Figs. 1A-B and 2A-B, respectively). However, in the spring the T_b of *P. extrilidus* does depend significantly on T_a and T_s (Stepwise regression, $F_{Tb-Ta, 2; 24} = 5.45$, $F_{Tb-Ts, 2; 24} = 8.35$, $P < 0.01$; Fig. 1C-D), while for *L. parvus* there is no relation between T_b and micro-environmental temperatures (Stepwise regression, $F_{Tb-Ta, 2; 14} = 0.03$, $F_{Tb-Ts, 2; 14} = 0.04$, $P > 0.05$; Fig. 2C-D).

The T_a and T_s of *P. extrilidus* varied between seasons (Mann-Whitney U -test, $U_{Ta} = 69.50$, $U_{Ts} = 264.50$, $P < 0.001$), being higher in the fall (Table 1). For *L. parvus*, there were no significant differences in T_a and T_s between seasons (t -test, $t_{Ta} = 2.29$, $t_{Ts} = 1.82$, $P > 0.05$; Table 1).

The T_a and T_s at *P. extrilidus* and *L. parvus* capture sites do not vary significantly during times of activity (ANOVA, *P. extrilidus* fall: $F_{Ta, 2; 32} = 0.56$, $F_{Ts, 2; 32} = 0.63$; spring: $F_{Ta, 2; 24} = 3.17$, $F_{Ts, 2; 24} = 0.03$; *L. parvus* fall: $F_{Ta, 2; 18} = 0.72$, $F_{Ts, 2; 18} = 1.26$; spring: $F_{Ta, 2; 14} = 0.73$; $F_{Ts, 2; 14} = 0.61$; $P > 0.05$).

3.2. Relationship between body temperature (T_b and T_{pref}) and snout-vent length, body mass and sex

Phymaturus extrilidus and *Liolaemus parvus* snout-vent length and body mass did not differ between sexes (t -test, *P. extrilidus*: $t_{SVL, 58} = -0.32$, $t_{BM, 58} = -0.34$, $P > 0.05$; *L. parvus*: $t_{SVL, 34} = 1.73$, $t_{BM, 34} = 0.34$, $P > 0.05$; Table 2). The T_b and T_{pref} did not show significant associations with SVL for both *P. extrilidus* and *L. parvus* (Regression, *P. extrilidus*: $F_{Tb-SVL, 2; 58} = 3.22$, $F_{Tpref-SVL, 2; 58} = 0.677$, $P > 0.05$; *L. parvus*: $F_{Tb-SVL, 2; 34} = 0.104$, $F_{Tb-SVL, 2; 33} = 0.129$, $P > 0.05$); however, *P. extrilidus* and *L. parvus* body mass was negatively associated with T_b (Regression, *P. extrilidus* $Tb-BM, 2; 58 = 5.31$, *L. parvus* $Tb-BM, 2; 34 = 2.38$, $P < 0.05$), though not with T_{pref} (Regression, *P. extrilidus* $Tpref-BM, 2; 24 = 0.68$, *L. parvus* $Tpref-BM, 2; 15 = 1.06$, $P > 0.05$).

In the fall, there were no differences in T_b and T_{pref} among *P. extrilidus* and *L. parvus* males and females (t -test, *P. extrilidus*: $t_{Tb} = -0.23$, $t_{Tpref} = 1.94$, $P > 0.05$; *L. parvus*: $t_{Tb} = -0.71$, $t_{Tpref} = 1.64$, $P > 0.05$; Table 1); nor was there significant difference between the sexes in the spring (t -test, *P. extrilidus*: $t_{Tb} = -0.72$, $t_{Tpref} = 1.72$, $P > 0.05$; *L. parvus*: $t_{Tb} = 1.35$, $t_{Tpref} = 0.76$, $P > 0.05$; Table 1).

3.3. Seasonal variation of T_b and T_{pref}

The T_b of *P. extrilidus* and *L. parvus* did not vary between the seasons of fall and spring (Mann-Whitney U -test, $U_{P. extrilidus} = 139$; $U_{L. parvus} = 122$, $P > 0.05$; Table 1). Likewise, the T_{pref} of both species

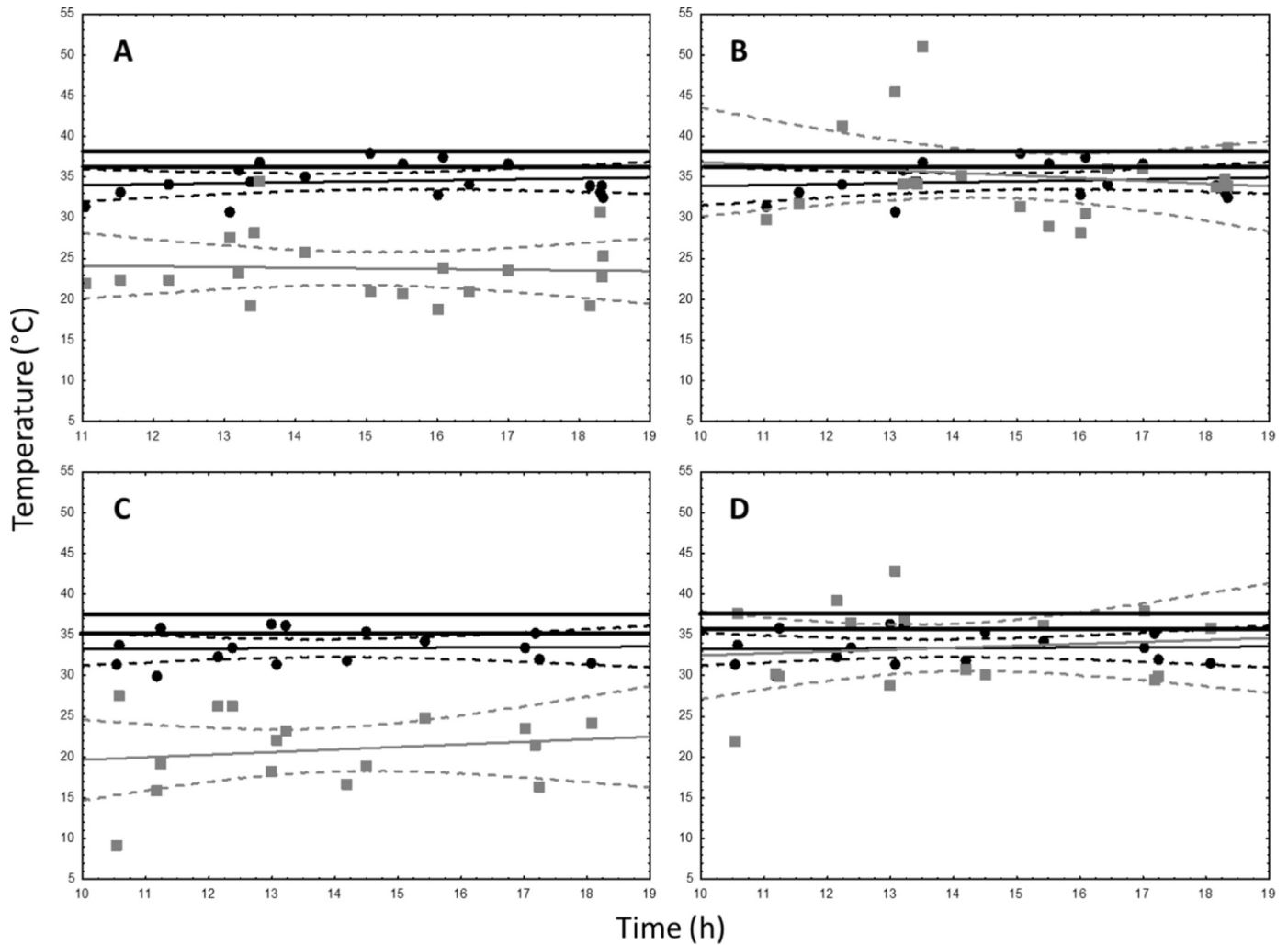


Fig. 2. Relationships between body temperature (T_b ; black circles) and micro-environmental temperatures (gray squares): air (T_{as} , panels A and C) and substrate (T_{sub} , panels B and D) vs. time of activity (h) of *Liolaemus parvus* population. Fall (upper panels, A and B); Spring (lower panels, C and D). Solid black lines indicate the lower and upper mean set-points of the selected temperature (T_{set}). Dashed lines indicate confidence interval $\alpha=95\%$.

Table 2

Snout-vent length (SVL) and body mass (BM) of the population of *Phymaturus extrilidus* and *Liolaemus parvus* for overall and sex. Mean \pm SD and sample size (N) are indicated.

| Species | Class | SVL \pm SD (mm) | BM \pm SD (g) | N |
|------------------------------|----------------|-------------------|------------------|----|
| <i>Phymaturus extrilidus</i> | Overall | 94.06 \pm 5.4 | 29.71 \pm 6.03 | 60 |
| | Males | 94.27 \pm 5.11 | 29.95 \pm 5.03 | 33 |
| | Females | 93.81 \pm 5.91 | 29.41 \pm 7.16 | 27 |
| <i>Liolaemus parvus</i> | Overall | 58.83 \pm 5.33 | 4.83 \pm 1.74 | 36 |
| | Males | 59.83 \pm 5.24 | 4.93 \pm 1.32 | 18 |
| | Females | 56.83 \pm 5.13 | 4.73 \pm 2.11 | 18 |

did not demonstrate seasonal variation (t -test, $t_{P. extrilidus} = -0.11$, $t_{L. parvus} = 0.74$, $P > 0.05$; Table 1).

3.4. Operative temperatures (T_e)

Mean (\pm SD) operative temperatures for *Phymaturus extrilidus* and *Liolaemus parvus*, by season, time range and microhabitat are shown in Table 3.

The operative temperature for large models (*Phymaturus*) and small models (*Liolaemus*) were not significantly different (t -test, $t = -0.379$, $P > 0.7$), and as such the following analyses were carried

out integrating the data from both models. There were significant differences in T_e between fall and spring (Mann-Whitney U -test, $U = 68$, $P < 0.005$), with higher temperatures occurring in the fall.

During periods of activity, T_e varied significantly (Kruskal-Wallis, $H_8; 273 = 84.07$, $P < 0.001$; Table 3; Fig. 3), with a range of 9.53–41.34 °C, with the highest temperatures being recorded from 13 to 17 h. There were also significant differences between T_e of different substrates (Kruskal Wallis, $H_8; 35 = 18.49$, $P < 0.01$), with the highest T_e in bare soil as compared to under rock and crevices (Table 3). As such, habitat structure demonstrates a high degree of thermal heterogeneity.

For both *Phymaturus extrilidus* and *Liolaemus parvus*, T_e was significantly lower than field T_b s (Mann-Whitney U -test, $U_{P. extrilidus} = 117$, $U_{L. parvus} = 31$, $P < 0.001$).

3.5. Preferred body temperatures, individual deviation values (db), index of mean habitat thermal quality (de) and thermoregulation effectiveness (E)

Mean (\pm SD) preferred temperatures (T_{pref}) and upper and lower set-points (T_{set}) for *Phymaturus extrilidus* and *Liolaemus parvus*, by sex, season and overall population are shown in Table 1.

The T_{pref} of *Phymaturus extrilidus* and *Liolaemus parvus* was significantly greater than T_b measured in the field (Wilcoxon test, $T_{P. extrilidus} 2; 58 = 160$; $T_{L. parvus} 2; 33 = 31.5$, $P < 0.001$). For *Phymaturus extrilidus*, 73.33% of T_b was below the lower T_{set} quartile,

Table 3
Operative temperature (T_e) for biophysical models overall, large (*Phymaturus*) and small (*Liolaemus*), seasons, time range and type of microhabitat. Mean ($\bar{x} \pm SD$) and significant differences (P) are indicated.

| | Class | $\bar{x} \pm DS$ | P |
|---------------------------------|----------------------|------------------------|------------------|
| Models | Overall | 24.55 \pm 5.41 | > 0.05 |
| | <i>Phymaturus</i> | 24.2 \pm 5.73 | |
| | <i>Liolaemus</i> | 24.9 \pm 5.23 | |
| Seasons | Fall | 27.17 \pm 3.47 | < 0.05 |
| | Spring | 21.79 \pm 5.80 | |
| Time Range (h) | 11–12 ^{ac} | 20.86 \pm 6.27 | < 0.05 |
| | 12–13 ^{ab} | 24.14 \pm 6.35 | |
| | 13–14 ^b | 28 \pm 6.98 | |
| | 14–15 ^b | 28.87 \pm 6.60 | |
| | 15–16 ^b | 28.55 \pm 6.42 | |
| | 16–17 ^b | 27.04 \pm 6.06 | |
| | 17–18 ^a | 22.28 \pm 5.58 | |
| | 18–19 ^c | 17.65 \pm 4.71 | |
| | Microhabitats | Bare soil ^a | 31.93 \pm 2.99 |
| Cracks ^b | | 20.88 \pm 5.3 | |
| Under rocks ^b | | 19.28 \pm 9.28 | |
| Basaltic rocks ^{ab} | | 25.05 \pm 3.93 | |
| Feldspathic rocks ^{ab} | | 24.06 \pm 4.29 | |
| Over bushes ^{ab} | | 24.45 \pm 3.67 | |
| Under bushes ^{ab} | | 25.24 \pm 2.35 | |

*Different letters (a- b- c) indicate significant differences.

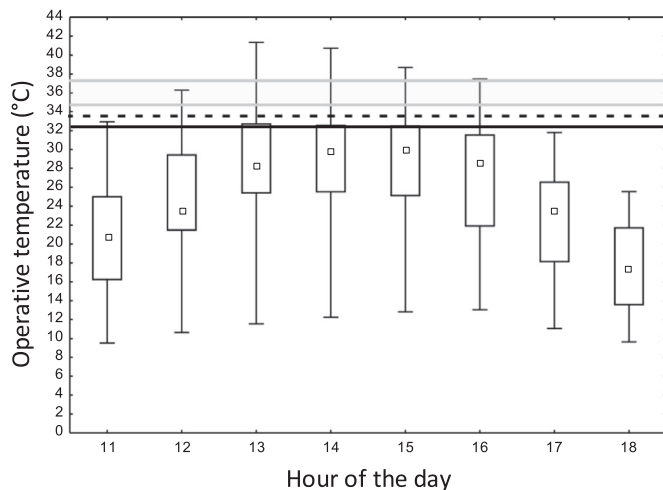


Fig. 3. Variation of operative temperatures (°C) during the hours of activity (h) of the lizards. Mean field body temperature of *P. extrilidus* (solid black line) and *L. parvus* (black dashed line) is indicated. The gray band includes the range of selected temperatures (T_{set}) of both species. It is observed that the thermal environment available for the lizards' thermoregulation is suboptimal during the period of activity.

8.34% was above the upper T_{set} quartile and 18.33% was within the set-point range (Fig. 4A). For *Liolaemus parvus*, 74.28% of T_b was below the lower T_{set} quartile, 2.86% was above the upper T_{set} quartile and 22.86% was within the set-point range (Fig. 4B). With respect to T_e for *P. extrilidus* and *L. parvus*, 100% of T_e was below the lower T_{set} quartile (Fig. 4).

Index values of individual deviation (db), thermal quality (de) and thermoregulatory effectiveness (E), calculated for *Phymaturus extrilidus* and *Liolaemus parvus* populations, and their sexual and seasonal variations are shown in Table 3.

Thermoregulatory effectiveness was moderate for the *P. extrilidus* population during both seasons, with an average value of $E=0.65$, and females had values similar to males ($E=0.62$ and $E=0.70$, respectively). For the *L. parvus* population, the effectiveness of thermoregulation was efficient during both seasons, with an average of $E=0.78$, and here

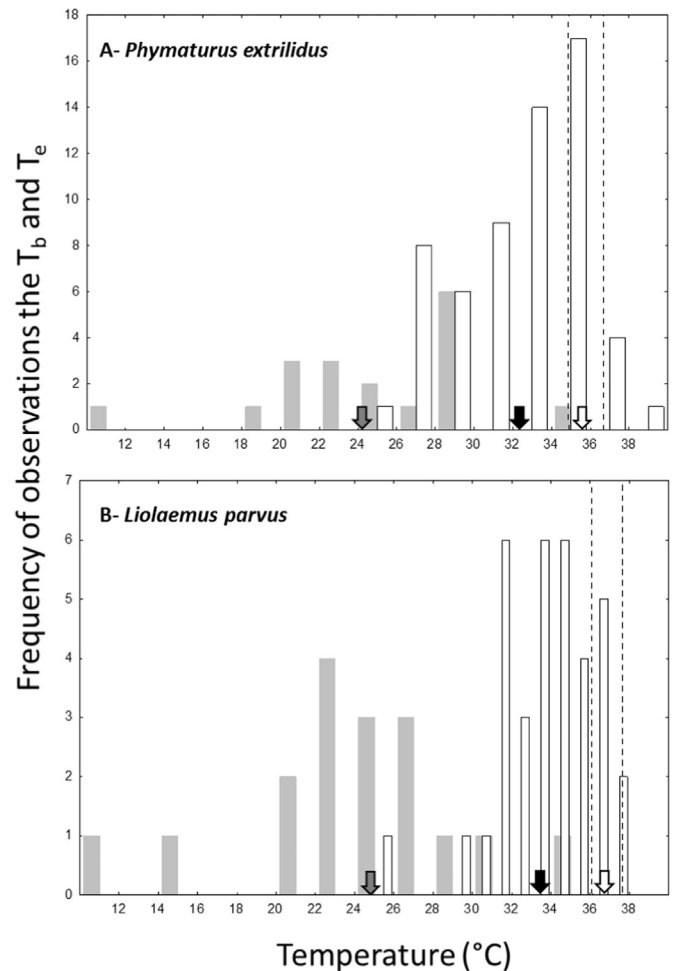


Fig. 4. Distribution of body temperatures (T_b , white bars) and operative temperature (T_e , gray bars) of *Phymaturus extrilidus* (panel A) and *Liolaemus parvus* (panel B) in the Sierras de la Invernada. The black arrow indicates the mean body temperature (T_b), the gray arrow indicates the mean operative temperature (T_e) and the white arrow indicates the mean of the preferred temperature (T_{pref}). The dashed lines indicate the lower and upper set-point range of selected temperature (T_{set}).

females also had values similar to males ($E=0.81$ and $E=0.78$, respectively).

3.6. Comparison between species

The micro-environmental temperatures T_a and T_s of *L. parvus* were greater than those of *P. extrilidus* (Mann-Whitney U -test, $U_{T_a} = 599$, $U_{T_s} = 627$, $P < 0.01$, Table 1).

T_b and T_{pref} of *L. parvus* were higher than the T_b and T_{pref} of *P. extrilidus* (ANOVA, $F_{T_b, 2; 94} = 5.38$, $P < 0.02$; Mann-Whitney U -test, $U_{T_{pref}} = 664$, $P < 0.03$; Table 1). Absolute differences between T_b and T_{set} (db) did not vary among the species (Mann-Whitney U -test, $U=922$, $P > 0.05$), though the de index was indeed significantly different (Mann-Whitney U -test, $U=641$, $P < 0.01$), which suggests that habitat thermal quality is better for *P. extrilidus*.

4. Discussion

Lizards belonging to the same genus tend to have similar T_b s regardless of their habitat, suggesting that thermal biology in lizards is phylogenetically conserved (Bogert, 1949; Clusella Trullas and Chown, 2014; Grigg and Buckley, 2013). Nevertheless, some thermoregulation studies at the genus level suggest that T_b s depend heavily on environmental temperatures (Labra et al., 2008). For the genus *Phymaturus*,

of wide altitudinal and latitudinal distribution, a relatively wide range of field T_b has been reported (22.5–32.3 °C). *Phymaturus extrilidus* had a T_b (32.32 °C) similar to that reported for *P. antofagastensis*, *P. punae* and *P. williamsi* from the “palluma” group (Cruz et al., 2009; Iburgüengoytia et al., 2008; Laspiur et al., unpublished data) and to *P. indistinctus*, *P. payuniaie*, *P. patagonicus* and *P. tenebrosus* from the “patagonicus” group (Corbalán et al., 2013; Cruz et al., 2009; Iburgüengoytia et al., 2008). Moreover, T_b is markedly higher than that found for *P. vociferator* and *P. dorsimaculatus* with similar altitudinal and latitudinal distribution (22.5 °C; Cruz et al., 2009; Labra and Vidal, 2003) and also higher than *P. zapalensis* at lower altitudes (26.4 °C; Cruz et al., 2009).

With respect to the *Liolaemus parvus* population, T_b (33.74 °C) remained steady within the wide range of temperatures reported for *Liolaemus* (24.4–37.7 °C) from different geographical regions (Table 1 in Medina et al., 2012). Likewise, the T_b of this population was distinctly lower than that reported for other species of the “chiliensis” group such as *L. austromendocinus*, *L. chiliensis* and *L. dicktracyi* (Espinoza et al., 2004; Labra et al., 2009) and also lower than that observed for *Liolaemus* living in the Puna region (Valdecantos et al., 2013). However, it was greater than T_b s observed in Andean populations of *L. parvus* (Acosta et al., 2006; Laspiur et al., unpublished data) and in the sympatric species *L. rubali* (Villavicencio et al., 2006).

As such, differences in T_b observed among *Liolaemus* species which are related, interpopulational, sympatric and with analogous distributions are consistent with the labile explanation of the wide variation of T_b s for *Liolaemus*. This explanation affirms that T_b for the genus varies according to an ecological gradient of environmental temperatures (Bonino et al., 2011; Labra, 1998; Labra et al., 2009; Medina et al., 2012; Rodríguez Serrano et al., 2009). Likewise, for the genus *Phymaturus*, despite more conservative than *Liolaemus* (Cruz et al., 2009), T_b s may be affected by the altitudinal and longitudinal variation of the environmental conditions imposed throughout the range of distribution of the genus.

Differences in T_b among syntopic species may be due to little overlap in activity times and microhabitat use which therefore leads them to exhibit different thermal requirements for T_a and T_s (Corbalán and Debandi, 2013; Lara Reséndiz et al., 2014; Schoener, 1975). In this sense, *P. extrilidus* makes a differential use of heat sources during activity time, using convection radiation during the first hours of the day and later heating itself through conduction, sunning on the substrate which maintains relatively constant temperatures (Fig. 1). As such, it alternates between heliothermic and thigmothermic thermoregulation strategies, akin to *P. vociferator* and *P. williamsi* (Vidal et al., 2010; Laspiur et al., unpublished data). *Liolaemus parvus* begins to be active when thermal resources are high and is able to maintain its T_b constant notwithstanding micro-environmental variation (Fig. 2) by employing opportunistic and general strategies, alternating between different heat sources. Lack of selective heliothermic or thigmothermic behavior has also been observed for *L. multicolor*, *L. yanalcu* (Valdecantos et al., 2013) and *L. pictus* (Iburgüengoytia and Cussac, 2002). In addition, we find that T_a and T_s at capture sites are greater for *L. parvus* than for *P. extrilidus*, indicating that they exhibit different thermal requirements and therefore exploit thermal offers differently (thermal resources, e.g. T_a and T_s).

On the other hand, characteristics such as the size, shape and body mass of an individual may play an important role in thermoregulation (Christian, 1998; Du et al., 2000; Stevenson, 1985). For *P. extrilidus* and *L. parvus*, we did not find an association between SVL and body temperatures, as with other species of *Phymaturus* and *Liolaemus* (Carothers et al., 1997; Iburgüengoytia et al., 2008; Labra et al., 2008; Pincheira Donoso et al., 2008). However, body temperature varied according to body mass, with lower temperature in individuals with greater weight. For *P. extrilidus*, we found lower body temperatures than *L. parvus*, which could be associated with notable differences in size and body mass among these species (Table 2).

Differences in thermoregulation strategies and thermal resources segregation, due to the heterogeneity of microclimates that may explode in the Puna region, could explain the differences in T_b between *P. extrilidus* and *L. parvus*. This differs from observations made by Iburgüengoytia (2005) who found no differences in T_b s for the sympatric species *P. tenebrosus* and *L. elongatus* in Patagonia; likewise, *P. roigorum* and *P. payuniaie* in syntopy and *L. irregularis* sympatric with *L. multicolor*, *L. yanalcu* and *L. albiceps* present similar T_b s (Corbalán et al., 2013; Valdecantos et al., 2013). Barbault (1991) purports that differences in thermal ecology between syntopic lizard species contribute to coexistence instead of resulting from it. We therefore agree with the thermal niche segregation hypothesis (Pianka and Huey, 1978) supported by differences in thermal requirements; that together with trophic niche segregation, the herbivorous *P. extrilidus* (Blanco et al., unpublished data) and omnivorous *L. parvus* (Pérez et al., pers. com.) could favor the syntopic coexistence of these species.

Body temperature may be affected by sexual conditions (Beuchat, 1988; Braña, 1993; Iburgüengoytia and Cussac, 2002; Labra and Bozinovic, 2002; Shine, 1980; Woolrich Piña et al., 2015). Differences in T_b between sexes could be due to differing microhabitat use (Dias and Rocha, 2004; Smith et al., 1993) and behavioral changes in thermoregulation during gestation (Shine, 1980, 2004). In viviparous lizards such as the genus *Phymaturus* and *L. parvus*, gestating females are able to regulate embryonic development through thermoregulation and compensate for the short seasons (Shine, 1985) characteristic of the Puna region. In the viviparous species *Sceloporus jarrovi*, gestating females regulate temperature more accurately and T_{pref} drop, as temperatures selected by males and non-gestating females are detrimental for embryonic development (Mathies and Andrews, 1997). In this context, we find no differences between T_b and T_{pref} for *P. extrilidus* and *L. parvus* males and females, both in fall and spring. Nevertheless, in the fall we observed that *P. extrilidus* females are less efficient thermoregulators than males. On the contrary, *L. parvus* males were less efficient thermoregulators than females (Table 4), despite there being no differences between T_b and T_{pref} . In some viviparous lizards such as *Eulamprus tympanum*, gestating females are able to thermoregulate more efficiently (Robert et al., 2006), thus diminishing the risks to embryonic development that daily and seasonal environmental temperature variations impose. In our work, the number of gestating females captured was limited and we were therefore unable to analyze the potential effects that reproductive

Table 4

Index individual deviation (*db*), thermal quality (*de*) and index of thermoregulatory efficiency (*E*) of *Phymaturus extrilidus* and *Liolaemus parvus* for the population for overall, season and sex. Mean \pm SD and sample size (*N*) are indicated.

| Species | Class | <i>db</i> | <i>de</i> | <i>E</i> | <i>N</i> | |
|------------------------------|-------------------------|----------------|-----------|----------|----------|----|
| <i>Phymaturus extrilidus</i> | Overall | 3.33 | 9.64 | 0.65 | 60 | |
| | Males | 3.09 | 10.38 | 0.70 | 33 | |
| | Females | 3.65 | 9.66 | 0.62 | 27 | |
| | Fall | 2.80 | 7.19 | 0.61 | 34 | |
| | Males | 2.16 | 6.74 | 0.67 | 19 | |
| | Females | 3.60 | 7.76 | 0.53 | 15 | |
| | Spring | 4.02 | 12.84 | 0.68 | 26 | |
| | Males | 4.27 | 13.52 | 0.68 | 14 | |
| | Females | 3.73 | 12.04 | 0.69 | 12 | |
| | <i>Liolaemus parvus</i> | Overall | 2.53 | 11.76 | 0.78 | 35 |
| | | Males | 2.82 | 12.79 | 0.78 | 17 |
| | | Females | 2.17 | 11.81 | 0.81 | 18 |
| Fall | | 2.29 | 9.57 | 0.76 | 19 | |
| Males | | 3.06 | 10.02 | 0.69 | 9 | |
| Females | | 1.59 | 9.16 | 0.82 | 10 | |
| Spring | | 2.81 | 14.36 | 0.80 | 16 | |
| Males | | 3.07 | 13.86 | 0.77 | 8 | |
| Females | | 3.08 | 13.98 | 0.77 | 8 | |

conditions have on temperatures and thermal efficiency. On the other hand, there were no differences in BM, SVL and microhabitat use between *Phymaturus extrilidus* and *Liolaemus parvus* males and females (*pers. obs.*), factors that could explain the observed similarities.

Seasonally, T_b did not vary in *P. extrilidus* and *L. parvus*, an interesting fact to note as the environmental temperature (T_e) did vary and was greater in the fall. Moreover, the lizards' T_b s remained above T_e in both seasons. As such, these lizards may be making changes in their thermoregulatory behavior in order to compensate for differences in thermal availability, for example spending more time sunning than foraging or changing body positioning throughout the day (Corbalán and Debandi, 2013). Likewise, in *P. extrilidus*, T_a and T_s were lower in the spring than in the fall. Seasonal air and substrate changes, together with variations in behavior and use of space, allow these lizards to maintain constant T_b as the seasons progress (Adolph, 1990; Adolph and Porter, 1993; Smith and Ballinger, 1994).

From an evolutionary perspective, T_{pref} correspond to fixed thermal adjustments carried out by populations or species in response to local pressures, in contrast to rapid changes (e.g. T_b) produced in response to daily and seasonal environmental variations (Ortega et al., 2014). In this sense, the T_{pref} of both species did not vary seasonally, indicating a possible absence of acclimatization mechanisms for preferred temperatures under changing environmental conditions (Angilletta, 2009; Wilson and Franklin, 2002).

The selected temperatures of *Phymaturus extrilidus* were found to be within the range of temperatures reported for the genus (31–36 °C; Iburgüengoytía, 2005; Cruz et al., 2009; Corbalán et al., 2013; Laspiur et al., unpublished data). This similarity is to be expected due to the conservative nature of the genus (Debandi et al., 2012) in relation to different ecological aspects, including reproduction, diet and thermal characteristics such as T_{pref} , supporting the idea that for *Phymaturus* many ecological attributes are subject to evolutionary limitations (Cruz et al., 2009). In the case of the genus *Liolaemus*, it has been found that selected temperatures, even with narrow temperature ranges, are related to environmental conditions such as local temperature and climate (Labra, 1998; Rodríguez Serrano et al., 2009; Stellatelli et al., 2013). On the other hand, some authors maintain that a strong phylogenetic effect exists on selected temperatures (Labra et al., 2009; Medina et al., 2012; Moreno Azócar et al., 2013). In this context, the T_{pref} found in the *Liolaemus parvus* population falls within the reported range for the genus (30–37 °C; Carothers et al., 1997, 1998; Gutiérrez et al., 2010; Labra, 1998; Marquet et al., 1989; Medina et al., 2009, 2011, 2012; Moreno Azócar et al., 2013; Iburgüengoytía et al., 2010; Valdecantos et al., 2013).

In a similar manner, the T_{pref} and set-point ranges for the *L. parvus* population in the Puna are similar to those found in Andean populations of *L. parvus*, in other *Liolaemus* from Puna regions and in phylogenetically related species (Espinoza et al., 2004; Laspiur et al., unpublished data; Valdecantos et al., 2013). This reinforces the static hypothesis, at least for the T_{pref} for the genus, though this is a topic still up for discussion (Labra et al., 2009; Medina et al., 2012; Moreno Azócar et al., 2013).

Average T_b was lower than T_{pref} for *Phymaturus extrilidus* and *Liolaemus parvus*, which has also been observed in other *Liolaemidos* such as *P. tenebrosus*, *P. roigorum*, *P. payunia* and *L. yanalcu* (Corbalán et al., 2013; Iburgüengoytía, 2005; Valdecantos et al., 2013) yet it differs from information reported for *Liolaemus* from the Puna where T_b are found within the T_{set} range (Valdecantos et al., 2013). These results indicate that *P. extrilidus* and *L. parvus*, due to the influence of biotic and abiotic factors, do not always reach the preferred temperatures. However, some optimal temperatures for performance may be found below the T_{pref} (Martin and Huey, 2008). For example, locomotor performance is optimal at temperatures below T_{pref} for *P. extrilidus* and *L. parvus* (Gómez Alés et al., unpublished data). On the other hand, despite the low thermal quality of the environment

(indicated by high values of the *de* index), they are capable of reaching higher T_b than T_e during times of activity (Fig. 3). Regarding thermoregulatory accuracy, both for *P. extrilidus* and *L. parvus*, the majority of recorded T_b were found to be below the lower set-point, though *L. parvus* showed slightly greater accuracy than *P. extrilidus* (*db*; Table 4).

According to the index of thermal effectiveness (Hertz et al., 1993), *P. extrilidus* ($E = 0.65$) behaves as a moderate thermoregulator; similar to that reported for *P. payunia* ($E = 0.64$; Corbalán et al., 2013). It is more efficient than *P. roigorum* in the Payunia region of Argentina ($E = 0.39$; Corbalán et al., 2013) and the Andean species *P. aguanegra* ($E = 0.5$) and *P. williamsi* ($E = 0.56$; Laspiur et al., unpublished data). *L. parvus* behaves as an efficient thermoregulator ($E = 0.78$); in a Andean population of *L. parvus* a similar value was observed ($E = 0.74$; Laspiur et al., unpublished data) and it is less efficient than four species of *Liolaemus* from the Puna ($E \sim 0.90$; Valdecantos et al., 2013). It was also markedly more efficient than *L. boulengeri* ($E = 0.5$ and 0.59) and *L. lineomaculatus* ($E = 0.41$ and 0.45) from the Argentine Patagonia region (Medina et al., 2011) and the more southern species *L. sarmientoi* ($E = 0.30$) and *L. magellanicus* ($E = -0.04$; Iburgüengoytía et al., 2010), despite the fact that these regions' unfavorable thermal conditions (elevated *de*) are similar to those of the Puna region. However, interannual variations and therefore variations in microclimatic conditions are likely to influence thermoregulatory efficiency and could explain the observed differences between the species mentioned.

Interestingly, we found that *Liolaemus parvus* thermoregulates more efficiently than *Phymaturus extrilidus*, in syntopic under the same thermal conditions. This may be due to interspecific differences in intrinsic factors such as body size and body mass, as well as differences in thermoregulatory behavior. Species of small size, such as *L. parvus*, heat up faster than large lizards, such as *P. extrilidus*, so they require less time spent basking. Although we did not evaluate basking behavior, *P. extrilidus* has been observed basking on rocky promontories for longer periods than *L. parvus* (*pers. obs.*). This implies a greater exposure of *P. extrilidus* to natural predators such as the birds *Geranoaetus polyosoma* (Pérez et al., 2013) and *Agriornis montanus* (Corbalán and Debandi, 2013; Videla, 1982; *pers. obs.*), and therefore a compromise between thermoregulation and evasion of predators. Moreover, *L. parvus* occupies a greater variety of microhabitats available for thermoregulation than *P. extrilidus*, restricted only to rocky areas. Therefore, *L. parvus* is likely to exhibit different strategies for thermoregulation. Thus, these factors underlying thermoregulation could explain a lower thermoregulatory efficiency for *P. extrilidus*.

We conclude that under the rigorous climate conditions of the Puna region between 3146 m and 3184 m asl and faced with daily and seasonal temperature fluctuations in their environment, *Phymaturus extrilidus* and *Liolaemus parvus* are able to thermoregulate actively and effectively, maintaining body temperatures near preferred temperatures and higher than environmental temperatures. The absence of seasonal and intrapopulation variation suggests that physiological or behavioral mechanisms that favor temperature adjustment could be implicated in temperature regulation or perhaps this is due to evolutionary restrictions in the lizards' thermal physiology. Likewise, differences in thermal characteristics between *P. extrilidus* and *L. parvus* exposed to the same environmental conditions of the Puna are the result of differential limitations imposed on each species by the environment, as well as of forces inherent to their life histories.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtherbio.2017.02.001>.

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