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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards

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Abstract The importance of the thermal environment for ectotherms and its relationship with thermal physiology and ecology is widely recognized. Several models have been proposed to explain the evolution of the thermal biology of ectotherms, but experimental studies have provided mixed support. Lizards from the *Liolaemus goetschi* group can be found along a wide latitudinal range across Argentina. The group is monophyletic and widely distributed, and therefore provides excellent opportunities to study the evolution of thermal biology. We studied thermal variables of 13 species of the *L. goetschi* group, in order to answer three questions. First, are aspects of the thermal biology of the *L. goetschi* group modelled by the environment or are they evolutionarily conservative? Second, have thermal characteristics of these animals co-evolved? And third, how do the patterns of co-evolution observed within the *L. goetschi* group compare to those in a taxonomically wider selection of species of *Liolaemus*? We collected data on 13 focal species and used species information of *Liolaemus* lizards available in the literature and additional data obtained by the authors. We tackled these questions using both conventional and phylogenetically based analyses. Our results show that lizards from the *L. goetschi* group and the genus *Liolaemus* in general vary in critical thermal minimum in relation to mean air temperature, and particularly the *L. goetschi* group shows that air temperature is associated with critical thermal range, as well as with body temperature. Although the effect of phylogeny cannot be ignored, our results indicate that these thermal biology aspects are modelled by cold environments of Patagonia, while other aspects (preferred body temperature and critical thermal maximum) are more conservative. We found evidence of co-evolutionary patterns between critical thermal minimum and preferred body temperature at both phylogenetic scales (the *L. goetschi* group and the extended sample of 68 *Liolaemus* species).

Keywords Thermoregulation · Phylogenetic scaling · Co-evolution · Comparative analysis · *Liolaemus goetschi* group · Iguania

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Introduction

It is widely recognized that the physiological performance of ectotherms strongly depends on their ability to attain

near-optimal body temperatures (Huey 1982; Huey and Bennett 1987; Bauwens et al. 1999; Cruz et al. 2009; Anderson et al. 2011). This ability is influenced by many aspects of the biophysical environment, including spatial distribution of operative environmental temperatures in the habitat (Beaupre 1995), competition (Labra 1995) and predation risks (Huey 1982). Ectotherms living at high latitudes face low temperatures, high thermal amplitudes, and short activity seasons (Addo-Bediako et al. 2000; Klok and Chown 2003; Cruz et al. 2005).They are expected to survive such a harsh environment by two alternative means. First, they may show adaptation of physiological traits by exhibiting wider tolerance ranges (Hertz 1981; Hertz et al. 1983; Van Damme et al. 1989; Christian and Weavers 1996; Addo-Bediako et al. 2000; Janion et al. 2009; Clusella-Trullas et al. 2011; Schuler et al. 2011; Sunday et al. 2011). Second, they may compensate for unfavourable conditions by changes in behavioural thermoregulation, but this compensation may result in increased energy and time costs, as well as increased predation risks (Huey and Slatkin 1976; Lelièvre et al. 2011).

Despite the fact that phylogenetically closely related species are expected to show similar responses to resembling environments, several studies show that adaptations remain unclear. For example, one or several specific thermal variables (physiological and behavioural) of ectotherms may co-evolve in response to the environmental variation while others may remain unaffected due to constraints, such as trade-offs or genetic correlation (Huey and Bennett 1987; Garland et al. 1991; Kohlsdorf and Navas 2006; Rodríguez-Serrano et al. 2009; Cruz et al. 2009; Bonino et al. 2011). Alternative outcomes observed among these studies may be related to present day responses to the environment, different evolutionary trajectories, methodological flaws, or the magnitude of phylogenetic scaling (Garland et al. 1991; Gvoždík and Van Damme 2008).

Thermal biology is a key factor in the evolution of lizards, particularly after it was recognized that ectotherms may behaviourally regulate body temperature (Cowles and Bogert 1944). Body temperature may be affected by body size, ecological habits or systematic position (Bogert 1949). To determine whether these traits are adaptive or phylogenetically constrained, it is necessary to elucidate how thermal biology is affected by the environment in a phylogenetic framework.

With over 220 recognized species, *Liolaemus* constitutes the world's second most specious lizard genus (Lobo et al. 2010; Breitman et al. 2011). Interestingly, this group of lizards shows a wide distribution range, diverse dietary habits and reproductive modes, while other traits are less variable (e.g. metabolic rate). This mixture of variable and conservative traits makes this genus very interesting. Additionally, some studies show constraints in morphology and physiology (Schulte et al. 2004; Pincheira-Donoso et al. 2008; Tulli et al. 2009, 2012; Ibargüengoytía et al. 2010; Cruz et al. 2011), whereas other studies suggest that Liolaemini lizards show adaptive responses in thermal and other morphological traits (Labra et al. 2009; Medina et al. 2009; Rodríguez-Serrano et al. 2009; Vanhooydonck et al. 2010; Tulli et al. 2011; Bonino et al. 2011). These discrepancies among studies on similar features are probably due to dissimilar methodologies applied or a different phylogenetic approach. Among *Liolaemus* species, entire monophyletic groups inhabit almost identical types of habitats; as found in the *L. lineomaculatus* series (Breitman et al. 2011; Bonino et al. 2011) and the *L. goetschi* group (Abdala 2007; this study). The latter group is found in open steppe, sandy areas, characterised by big, mainly spiny shrubs (mainly *Chuquiraga*, *Larrea*, *Lycium*, *Monttea*, *Suaeda*) that lizards use as refuges. The use of areas that are ecologically similar provides a good opportunity to test evolutionary responses to other environmental factors that do change across the areas which this group inhabits.

Here, we study the thermal biology and relationship to environmental temperatures of 13 out of 15 recognized species of lizards belonging to the *Liolaemus goetschi* group (Abdala 2007; Avila et al. 2010). These are medium- to large-sized lizards within *Liolaemus* (snout–vent length 55–110 mm). Most species within this group inhabit the Argentinean Monte and Patagonian steppe habitats, along a wide latitudinal range of approximately 2,300 km (28–48°S; Abdala 2007). The phylogenetic relationships of this group were previously studied by Abdala (2007), and here we provide a new analysis based on molecular data. Both phylogenetic arrangements will serve to test the effect of phylogeny and will be used for phylogenetically based analyses. We are also interested on testing the static and the labile hypotheses of lizard thermal physiology (Hertz et al. 1983; Andrews et al. 1999; Rodríguez-Serrano et al. 2009) in this group of lizards, in order to address to what extent thermal biology is constrained or adaptive. By doing this, we aim to answer the following questions: (1) is the thermal biology of the *L. goetschi* group (tolerance ranges, preferred temperatures, field body temperature) modelled by the environment or is it evolutionarily conservative; (2) have the thermal physiological and behavioural characteristics of these animals, such as thermal tolerance limits and preferred body temperatures, co-evolved; and (3) how the patterns of (co-)evolution observed within the *L. goetschi* group differ from those in a taxonomically wider selection of species of *Liolaemus*. For this last question, we used two hierarchical scales, i.e. within the *L. goetschi* group (13 species) and within the *Liolaemus* clade (68 species) under two different phylogenetic approaches. Additionally, we quantified the amount of phylogenetic signal (Blomberg et al. 2003) present in the studied variables. If the thermal biology of the species is

labile and modelled by the environment, we predict significant product–moment relationships between thermal biology and environmental variables. We also expect to find evidence for co-evolution of thermal tolerance limits and thermal preferences. Finally, we expect to find different evolutionary patterns denoting that the *L. goetschi* radiation evolved recently compared to those of the entire *Liolaemus* genus.

Materials and methods

Characterization of the environment

Two variables were used to characterize the thermal environment where individuals from each species were collected. We calculated average air temperatures (T_{air}), and thermal amplitude ($Range_{air}$). The latter was estimated as the average of the differences between maximum air temperature and minimum air temperature. These variables provide estimates of the thermal characteristics and variability of the environment. Both thermal variables were calculated for the period of activity, from September to April, over a 27-year period (1983–2010), and were based on daily average data freely available at the NASA website (http://power.larc.nasa.gov/cgi-bin/cgiwrap/solar/agro.cgi).

Characterization of thermal biology of the species

Field work was carried out in February and December 2009. A total of 259 adult lizards belonging to 13 species were caught by noose or hand at 13 different locations (Fig. 1). We obtained field body temperatures (T_b) from a subset of 125 lizards by using a K-type thermocouple (Extech 421502; Extech Instruments, Waltham, MA, USA) within 20 s of capture. Only T_bs from active lizards, caught between 1100 and 1900 hours were retained for further analysis. We calculated operative temperatures (T_e) from the data obtained from six i-Button data loggers (Maxim DS1921G Thermochron®; iButton, Sunnyvale, CA, USA) placed in the different microhabitats available (two in full sun, two in filtered sun in the proximity of the shrubs and two in full shadow near the main trunk of the shrubs) at each collection site. T_e was registered every 12 min during the capture time for at least 3 h at every site and measurements were used to calculate the effectiveness of thermoregulation (after Hertz et al. 1993), under the assumption that all the microhabitats are equally available for lizards (Row and Blouin-Demers 2006). This method was applied after calibrating data-loggers with lizard carcasses of the studied species in a pilot experiment, finding similar results as Vitt and Sartorius (1999). Captured lizards were transported to the laboratory in cloth bags, without mixing specimens of different species. All captures were authorised by the corresponding Provincial Fauna Offices or by National Parks (see "Acknowledgments"). After finishing all trials, individuals were euthanised and used for other studies.

In the laboratory, lizards were kept in cloth bags separated by species with no more than five specimens per bag. Water was provided twice a day, and every 2 days lizards were released into a terrarium, and fed. Air temperature was 20 °C, and all the experiments were performed within 10 days after lizards were captured. Animals that showed signals of stress were not used in the experiments.

To measure critical thermal minimum (CT_{min}), lizards were placed into plastic containers with ventilated lids and moved into a freezer (−9 °C). Body temperatures decreased at a rate of ~1 °C/min. We monitored body temperature using a K-type thermocouple attached to one of the lizard's flanks by Micropore® surgery tape, with the tip covered by five extra layers of the same tape to isolate the thermocouple from the environmental temperature. We previously tested for differences between cloacal temperature and temperature obtained as described above, and we found no significant differences between both methods (65 individuals from 8 species; *t* test and Mann–Whitney rank sum test, P value >0.05 in all cases; see Online resource 1). Therefore, temperature obtained from the flanks was preferred to the cloacal measurements, because it is less stressful for the lizards. After a lizard's body temperature reached 15 °C, we checked the lizard's response every 30 s. CT_{min} was estimated as the temperature at which lizards lost their righting response (Adolph 1990).

Preferred body temperatures (T_{pref}) were measured in a glass terrarium (1.2 m long, 0.6 m wide), divided into five lanes (0.12 m wide) by four opaque glasses, to prevent visual interactions. Lizards were placed individually in each lane, two 150 W IR bulbs were suspended 0.4 m above the lanes at one end, and an incandescent light bulb 100 W was placed at the same height, 35 cm from the IR bulbs. A thin sand cover layer (0.03 m) was used to provide traction. Room temperature ranged from 19 to 21 °C. Substrate temperatures at the extremes of each lane were approximately 48 and 19 °C (±1 °C). Body temperatures were taken every 40 min from 0940 to 1800 hours on 2 consecutive days (a minimum of 25 measurements per individual). One day before and during T_{pref} trials lizards were not fed, in order to standardise conditions across all individuals (Cruz et al. 2009). Water was sprayed over the specimens twice daily (at 0900 and 1830 hours). Every time the body temperature was recorded, lizards were released near the middle of the track. The mean of the preferred body temperatures from each individual was used to calculate T_{pref} for each species. In these analyses, sexes were also pooled after no significant differences were observed (nested ANOVA, model: sex by species:

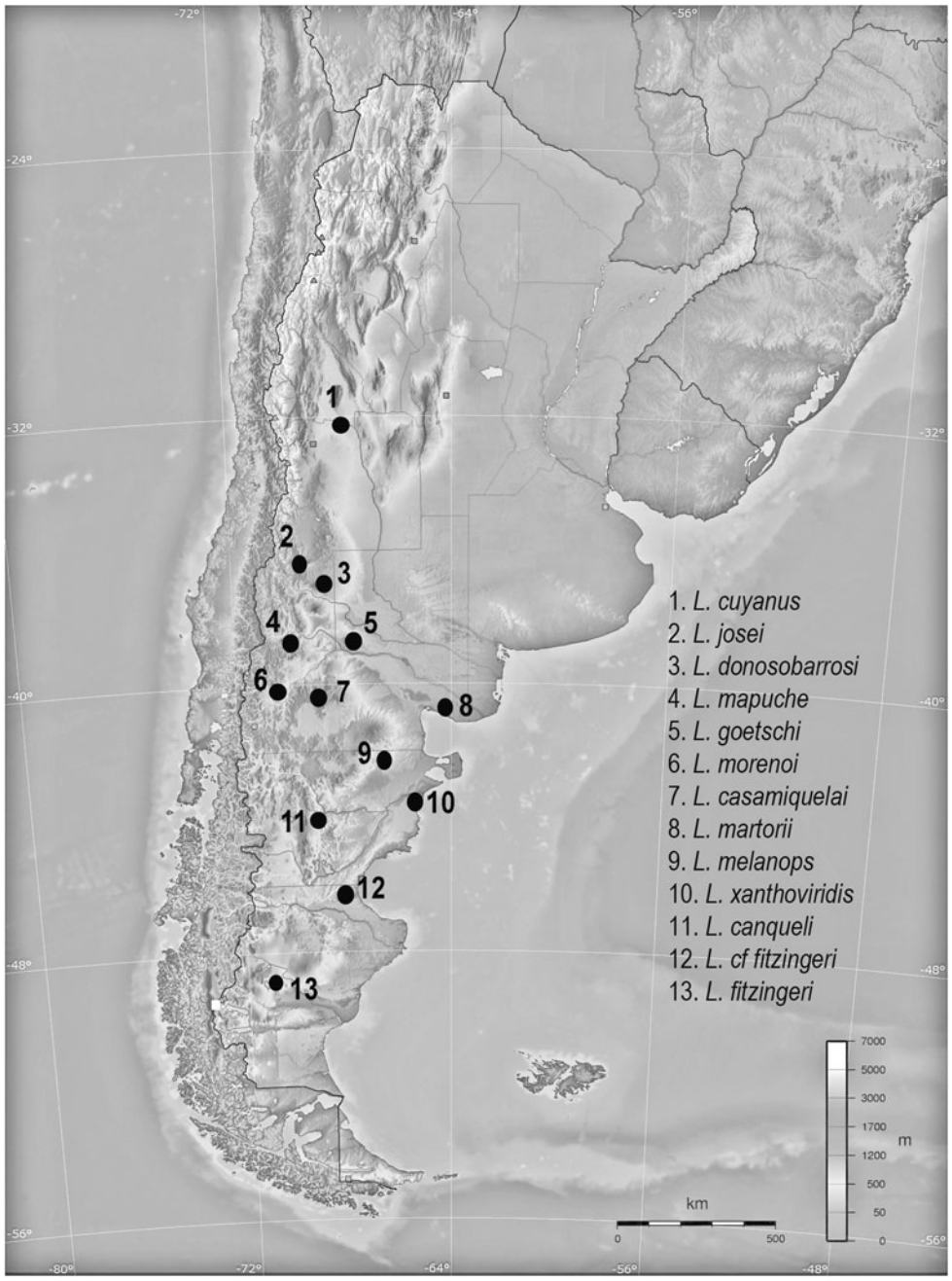

Fig. 1 Collection sites of the studied species

$F_{1,117} = 1.137$, $P = 0.337$; sex: $F_{1,117} = 0.555$, $P = 0.458$).

Lastly, we measured panting temperature (T_{pant}) as the upper limit of the tolerance range. We used T_{pant} instead of critical thermal maximum (CT_{max}). Panting behaviour is a typical response of lizards when body temperature is close to the critical maximum limit, and consists of a full opening of the mouth to increase the evaporative surface. T_{pant} is considered a reliable indicator of the upper thermal maximum (Carothers et al. 1997; Kohlsdorf and Navas 2006) and can be measured without risk of over-heating the animal. To determine T_{pant}, lizards were placed into a 5 l bucket with a 0.05-m sand layer on the bottom. An incandescent 100 W light bulb was placed 0.4 m above the sand surface. Body temperatures increased at a rate of 1 °C/min. An ultra-fine K-type thermocouple was attached to one of the lizard flanks as described above. Body temperature was monitored every 15 s, and T_{pant} was registered at the moment the lizard opened its mouth completely. Mean CT_{min} and T_{pant} were calculated for every species as the average of all the measurements (one per individual). Males and females were pooled together after confirming that there were no

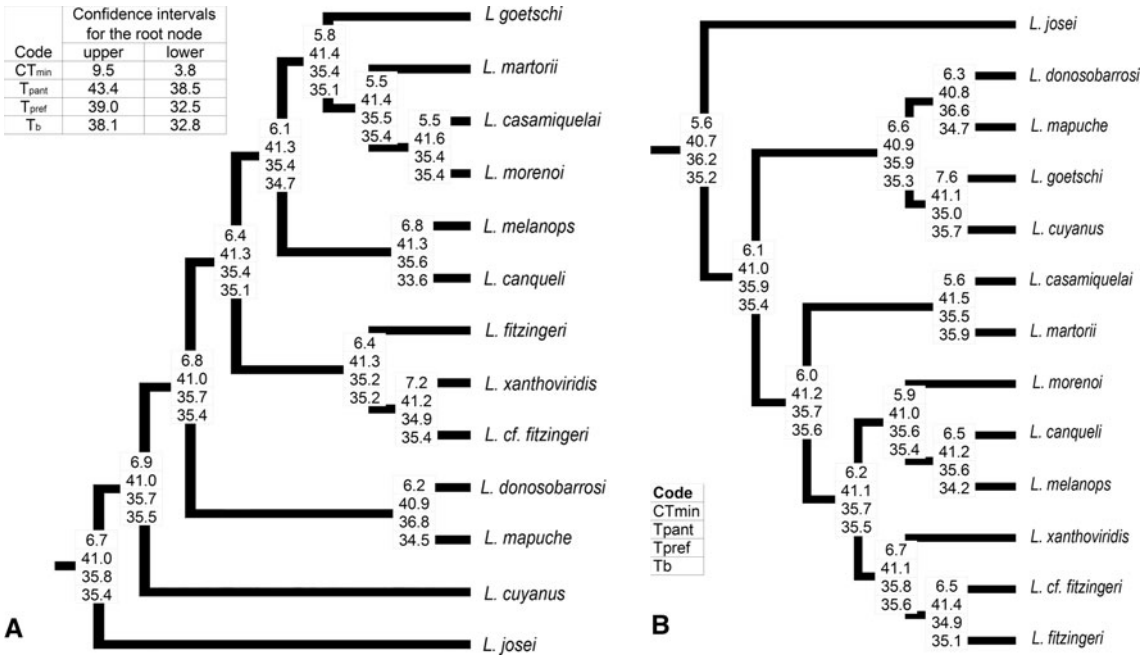

Fig. 2 Ancestral character state reconstruction for the *Liolaemus goetschi* group. Reconstructed values of critical minimum (CT_{min}), panting (T_{pant}), preferred (T_{pref}), and field body (T_b) temperatures are shown for every node. **a** Maximum likelihood tree using molecular data. **b** Total evidence tree

significant differences between sexes (nested ANOVA, model: sex by species: CT_{min}: $F_{1,151} = 0.930$, $P = 0.519$; sex: $F_{1,151} = 0.881$, $P = 0.349$; T_{pant}: $F_{1,100} = 1.130$, $P = 0.345$; sex: $F_{1,100} = 0.164$, $P = 0.686$). We estimated thermal tolerance range (CT_{range} = panting temperature − critical thermal minimum).

Finally, to estimate effectiveness of thermoregulation (E) in the field, we calculated the d_b (the deviations between T_b and T_{pref}) and d_e (the deviation between T_e and T_{pref}) indexes of those species for which we gathered field data after Hertz et al. (1993). By comparing both indexes, it is possible to assess to what extent the lizards thermoregulate.

Thermal biology data for *Liolaemus* species

Based on the available literature and data collected by us, we gathered information on the thermal biology (CT_{min}, CT_{max}, T_{pant}, CT_{range}, T_b and T_{pref}) of 68 species of *Liolaemus* (the *L. goetschi* group species included). In case of multiple datasets for a single species, we calculated the mean of every variable to use as a species value. For every species, we obtained T_{air} and $Range_{air}$ of the collection localities from the NASA database.

Phylogeny

For the two hierarchical scales analyzed here, we used two different sets of trees. One is based on Abdala (2007) in which molecular and morphological data were combined in a total evidence analysis (TEV) using maximum parsimony (Fig. 2b for *L. goetschi* species and Fig. 3 for the 64 *Liolaemus* species). For this tree, we set branch lengths equal to one. The second set of trees was reconstructed using DNA sequences spanning the mtDNA gene regions ND1 to COI sequenced and aligned using the molecular protocols and alignment structure described in Schulte et al. (2000). Aligned DNA sequence datasets for species sampled here are available in TreeBASE (Study Accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S13386). Phylogenetic trees were estimated using a priori partitioned mixed model maximum likelihood (ML) analysis with two taxa sampling schemes: (1) 13 species representing only the *L. goetschi* group; (2) 68 *Liolaemus* species (that includes the 13 species of the *L. goetschi* group) representing all phylogenetic diversity within the genus for which thermo-ecological data were also sampled (Figs. 2a, 3a, respectively). For each analysis, model testing was performed in MEGA 5.05 (Tamura et al. 2011). All models with the highest likelihood value for model testing were GTR + Γ + I, and the default model in RAxML 7.2.8 on XSEDE (Stamatakis et al. 2008) on the CIPRES Science Gateway (Miller et al. 2010) is GTR + Γ (Tavaré 1986). Due to this limitation, GTR + Γ was used for all analyses with model parameter values estimated from the data. For partitioned analyses, we assumed a priori partitions based on codon position with three partitions (codon positions 1, 2, 3) for all three protein-coding genes (ND1, ND2, COI)

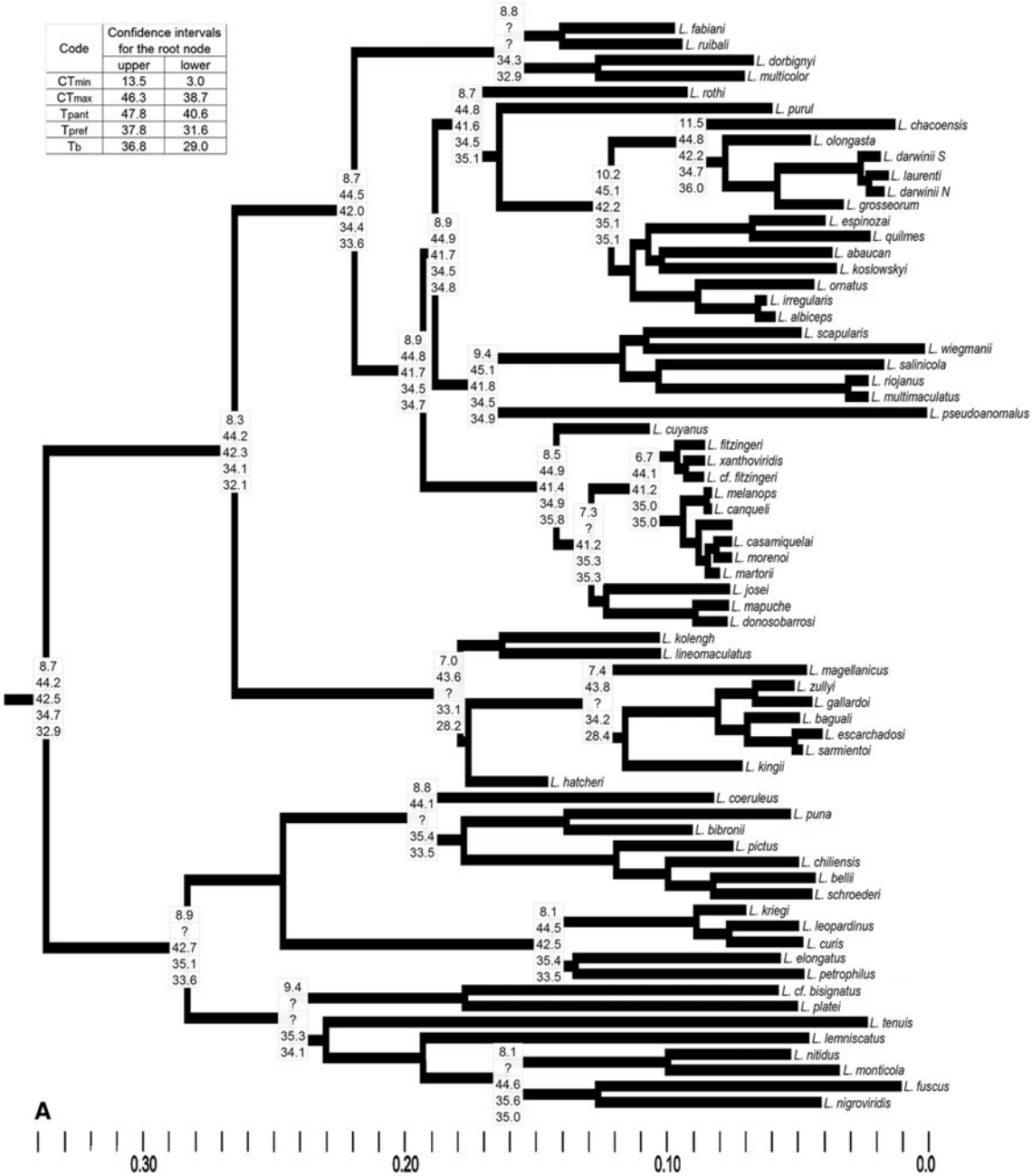

Fig. 3 Ancestral character state reconstruction for the *Liolaemus* species. Reconstructed values of critical minimum (CT_{min}), critical maximum (CT_{max}), panting (T_{pant}), preferred (T_{pref}) and field body temperatures (T_b) are shown in the nodes. **a** Maximum likelihood tree using molecular data. **b** Total evidence tree

combined and one partition for combined tRNA and non-coding positions for a total of four partitions. There are other possible partitioning schemes we could have assumed, but, given the results of Schulte and de Queiroz (2008) and studies cited within, partitioning by codon position most often explains the data better than other partitioning scheme using likelihood ratio tests or Bayes factor estimates.

Statistical analyses

As related species in comparative studies cannot be considered as independent data points, we calculated independent contrasts (IC, Felsenstein 1985) for all variables using the PDAP 1.15 module (Midford et al. 2003) in Mesquite 2.74 (Maddison and Maddison 2010). We used the two different topologies described above as the

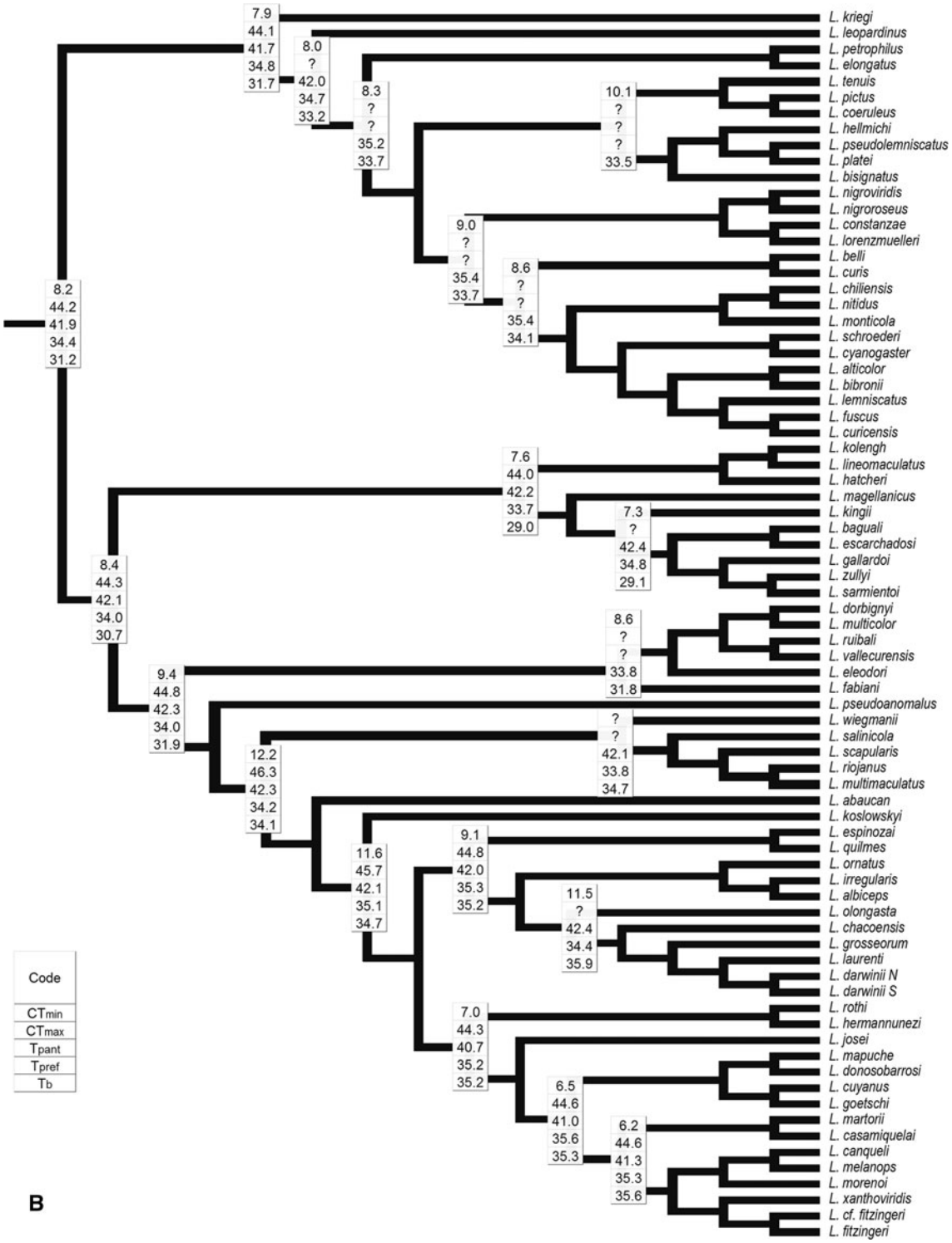

Fig. 3 continued

phylogenetic framework for these analyses. Three datasets were therefore used in our analyses: the raw data, the IC of the TEV tree, and the IC of the ML tree.

To examine if the environment models the thermal biology of the *L. goetschi* group, we performed multiple linear regressions (by using stepwise backward method) using T_{air} and $Range_{air}$ as independent variables, and T_b, CT_{min}, T_{pant}, CT_{range}, T_{pref}, $T_{pref\ min}$ and $T_{pref\ max}$ as dependent variables. All multiple linear regressions run with IC were forced through the origin (Garland et al.

Table 1 Environmental variables for every collection site and thermal variables of the *Liolaemus goetschi* species

Species	Latitude	Altitude m asl	T_{air}	$Range_{air}$	T_b	Tolerance range			Preferred temperatures		
						CT_{min}	T_{pant}	CT_{range}	T_{pref}	$T_{pref\ min}$	$T_{pref\ max}$
L. canqueli	43°50′S	498	11.0	11.4	33.3 ± 2.1 (18)	6.7 ± 1.7 (22)	41.2 ± 1.2 (18)	35.3	35.2 ± 1.9 (16)	33.1	37.1
L. casamiquelai	40°26′S	668	15.7	11.8	36.0 ± 1.8 (11)	5.9 ± 1.6 (18)	42.6 ± 1.1 (18)	33.9	35.3 ± 1.4 (17)	33.2	37.3
L. cuyanus	32°23′S	595	19.0	12.8	37.5 ± 0.7 (5)	9.7 ± 3.1 (35)	41.3 ± 1.6 (28)	35.3	34.1 ± 0.9 (27)	32.9	35.3
L. donosobarrosi	36°46′S	1,105	16.2	13.4	35.0 ± 2.1 (8)	5.2 ± 2.2 (8)	39.2 ± 1.3 (8)	34.6	37.4 ± 0.7 (8)	35.4	39.8
L. cf fitzingeri	46°18′S	273	16.1	8.9	35.0 ± 2.2 (10)	8.1 ± 1.1 (23)	41.4 ± 1.0 (19)	31.6	33.0 ± 1.5 (9)	30.5	35.1
L. fitzingeri	48°56′S	389	6.9	8.5	34.7 ± 2.5 (10)	4.6 ± 0.9 (10)	41.6 ± 0.5 (10)	36.7	35.9 ± 0.7 (8)	34.5	37.5
L. goetschi	38°45′S	997	18.6	12.6	34.0 ± 2.1 (18)	6.4 ± 1.8 (10)	41.0 ± 1.4 (12)	36.1	35.1 ± 1.1 (15)	33.8	36.6
L. josei	35°45′S	1,841	12.4	14.1	35.0 ± 0.9 (4)	5.2 ± 1.0 (8)	40.5 ± 1.5 (5)	35.8	36.5 ± 1.3 (16)	34.8	38.5
L. mapuche	38°55′S	771	15.2	13.6	33.9 ± 1.9 (6)	6.9 ± 0.8 (17)	42.2 ± 1.9 (8)	34.4	36.6 ± 1.0 (7)	35.3	37.9
L. martorii	40°49′S	8	18.4	12.3	36.1 ± 1.5 (8)	5.0 ± 1.2 (13)	41.1 ± 0.7 (10)	34.6	35.6 ± 1.0 (9)	33.7	37.4
L. melanops	42°10′S	558	15.8	11.7	33.8 ± 1.1 (10)	6.9 ± 1.2 (14)	41.5 ± 1.4 (7)	33.2	36.0 ± 0.9 (6)	35.0	37.0
L. morenoi	40°14′S	592	10.8	11.7	34.7 ± 1.2 (4)	4.9 ± 1.8 (7)	40.7 ± 0.7 (7)	33.4	35.6 ± 1.5 (9)	34.1	37.2
L. xanthoviridis	43°24′S	180	16.1	8.9	36.4 ± 2.0 (13)	7.5 ± 1.8 (19)	40.7 ± 0.7 (14)	37.0	36.7 ± 1.0 (8)	35.6	37.9

All the thermal variables are measured in degrees Celsius

Variables are shown ± standard deviation, numbers in parentheses are sample sizes

T_{air} air annual mean temperatures, $Range_{air}$ seasonal thermal amplitude. Thermal variables: T_b field body temperature, CT_{min} minimum critical temperature, T_{pant} panting temperature, T_{pref} preferred temperatures in an experimental thermal gradient, $T_{pref\ min}$ and $T_{pref\ max}$, first and third inter-quartile of the preferred temperature (used for effectiveness calculations)

1992). Additionally, we evaluated how thermal variables (CT_{min}, T_{pant}, T_{pref}, and T_b) evolved on the phylogeny, by running ancestral character state reconstruction in Mesquite 2.74 (Maddison and Maddison 2010) using parsimony criterion.

Because behavioural temperature regulation of an organism may influence its physiology, selection should favour some combination of thermal sensitivity and thermoregulatory behaviour (Huey and Bennett 1987). Thus, we explored the relationship between physiological and behavioural traits and hence possible co-evolution. We ran simple linear regressions of the independent contrasts of T_{pref} as behavioural (dependent) variable versus CT_{min} and T_{pant} as physiological (independent) variables individually (e.g. T_{pref} vs. CT_{min} and T_{pref} vs. T_{pant}).

Finally, to evaluate the influence of the phylogenetic relationships on the analysed variables ($Range_{air}$, T_{air}, T_b, T_{pref}, CT_{min}, T_{pant} and CT_{range}), we performed phylogenetic signal estimation (PHYSIG; Blomberg et al. 2003) by using the two phylogenetic trees, TEV and ML. Three models were used to estimate the phylogenetic signal: one with branch lengths kept constant (CBL), and two in which branch lengths were transformed using Ornstein–Uhlenbeck (OU) transformations with $d = 0.8$ and $d = 0.2$, respectively (Blomberg et al. 2003). Each one of these transformations represent the power of stabilizing selection, where a low value of OU transformation ($d = 0.2$) turns the data towards a more "adaptive" scenario, and an OU transformation close to 1 (in this case $d = 0.8$) tending towards Brownian motion (Blomberg et al. 2003). This way, using a d value equal to 0.2 simulates a more star-like topology, and a d value equal to 0.8 simulates a more hierarchical topology (Blomberg et al. 2003). We also wanted to evaluate if trends obtained for the *L. goetschi* group are also valid at a larger scale, and if hierarchical scales affect the relationships between thermal biology and phylogeny. To do so, we applied the same statistical methods (PHYSIG, IC, and multiple linear regressions) on data available for *Liolaemus* species using T_b and T_{pref} (68 species), CT_{min} (62 species), T_{pant} (47 species), and CT_{max} and CT_{range} (38 species) as dependent variables, and T_{air} and $Range_{air}$ as predictor variables.

Results

Evolutionary flexibility of thermal characteristics in *L. goetschi* group

The environmental variables of every collection site and thermal variables for the 13 studied species are shown in Table 1. Our analysis of thermoregulatory effectiveness

Table 2 Effectiveness of thermoregulation of *Liolaemus goetschi* group

Species	$d_b \pm$ SD (n)	$d_e \pm$ SD	E
L. canqueli	0.39 ± 0.57 (11)	4.14 ± 5.74	0.91
L. casamiquelai	0.20 ± 0.26 (11)	2.83 ± 2.95	0.93
L. cuyanus	2.19 ± 0.71 (5)	4.28 ± 7.44	0.49
L. donosobarrosi	1.16 ± 1.21 (8)	6.90 ± 4.34	0.83
L. cf fitzingeri	0.83 ± 1.22 (11)	2.45 ± 3.11	0.66
L. fitzingeri	0.86 ± 1.51 (10)	10.03 ± 4.52	0.91
L. goetschi	0.77 ± 1.06 (18)	4.15 ± 2.37	0.81
L. josei	0.20 ± 0.28 (4)	6.22 ± 4.30	0.97
L. mapuche	1.47 ± 1.79 (6)	5.13 ± 3.34	0.71
L. martorii	0.23 ± 0.64 (8)		
L. melanops	1.18 ± 1.05 (10)	4.68 ± 2.81	0.75
L. morenoi	0.03 ± 0.05 (4)	5.34 ± 4.08	0.99
L. xanthoviridis	0.82 ± 0.77 (13)	2.83 ± 2.95	0.71

d_b Mean values of individual variation of field body temperature from selected temperatures, d_e deviation of the operative temperatures with respect to selected temperatures for every species, E effectiveness of thermal regulation observed for every species, calculated according to Hertz et al. (1993)

was only available for 12 of the 13 species and showed low values of the d_b index (all below 3 °C), indicating that T_b of the individuals are close to T_{pref}, although there is variation in the range of preferred temperatures between 2 and 4 °C according to the difference of $T_{pref\ max}$ and $T_{pref\ min}$. In contrast, d_e showed a deviation of the operative temperatures from the T_{pref} ($T_{pref\ max} - T_{pref\ min}$) values between 2.5 and 10 °C. Finally, E was high in most species analysed here, except *L. cuyanus* and *L. cf. fitzingeri* (Table 2).

Multiple linear regressions models with T_{air} and $Range_{air}$ as predictor variables showed different results depending on tree topology and evolutionary model used. The analyses performed with the raw data and the TEV IC showed similar tendencies, with no significant partial correlations of the environmental variables with T_b, T_{pant} or T_{pref} (Table 3) while in the case of ML IC analysis, T_b showed a significant positive partial correlation with T_{air} (Table 3c). In the first two cases (i.e. raw data and TEV), we found a significant positive partial correlation of CT_{min} with T_{air}, and a negative association between CT_{range} and T_{air}.

The ancestral state reconstruction showed that the thermal tolerance ranges in the *L. goetschi* group increased slightly with respect to the ancestral state except for *L. donosobarrosi* and *L. cuyanus*. In the case of T_{pref}, values were similar to the ancestral state (Fig. 2). It seems that extant lizards are tolerant to a slightly wider range of temperature than their ancestors, but most variables remain similar to the ancestral state.

Is there co-evolution between thermal preferences and thermal tolerances?

Our test of co-evolution between the thermal variables also showed different results depending on the evolutionary model and tree topology used. By using raw data and the TEV tree, we observed a significant negative relationship between CT_{min} and T_{pref}, but not between T_{pant} and T_{pref} (Table 4). Analyses based on ML tree showed no significant relationships between these variables (Table 4).

Are the results affected by the number of species or hierarchical scale, phylogenetic approaches, or evolutionary models used?

The analysis at a higher phylogenetic scale for 68 *Liolaemus* species shows that the environmental characteristics of the locations where the species occur are variable (Online resource 2). T_{air} varies between 3.9 and 21.9 °C, and $Range_{air}$ between 4.6 and 16.6 °C as a consequence of a wider geographic range compared to the *L. goetschi* group. Thermal biology variables of the 68 species also varied over a wider range than the study group (Online resource 2). Multiple linear regressions showed that this thermal biology variability is associated with environmental disparity, although associations depended on the phylogenetic tree and the information used (Table 5). When using the raw data for *Liolaemus*, we observed significant relationships with $Range_{air}$ in most of the variables analysed (T_b, CT_{max}, CT_{range} and T_{pref}), while CT_{min} was related to T_{air}. Differently, although TEV analyses also showed significant models in most cases (except for T_{pref}), in this case T_b and CT_{range} were associated to T_{air}, CT_{max} was again related to $Range_{air}$, while CT_{min} was influenced by both environmental variables. Finally, ML analyses showed a significant regression model for CT_{min}, that was related to T_{air}, while CT_{max} was related to $Range_{air}$ but the regression model was not significant (Table 5).

Ancestral character states of the analyzed variables for the 68 species with available thermal data within the *Liolaemus* genus are shown in Fig. 3. Interestingly, the southernmost group—*L. lineomaculatus* (*L. kolengh*, *L. lineomaculatus*, *L. magellanicus*, *L. zullyi*, *L. gallardoi*, *L. baguali*, *L. escarchadosi*, *L. sarmientoi*)—showed lower thermal values than the rest of the groups; even lower than the ancestral states. The *L. boulengeri* series showed the highest values in the genus, while the *L. goetschi* group (nested within it) is intermediate (Fig. 3).

Results of our analyses of co-evolutionary patterns between T_{pref} and the tolerance range for the 68 species of *Liolaemus* showed different results depending on the tree structure. TEV data indicated a negative and significant relationship between T_{pref} and CT_{min}, while the other two

Table 3 Multiple linear regressions of thermal variables of the *Liolaemus goetschi* species using raw data

(a) Raw data							
Included variables	T_b –	CT_{min} –	T_{pant} –	CT_{range} –	T_{pref} –	$T_{pref\ min}$ –	$T_{pref\ max}$ –
Model							
r	0.494	0.601	0.218	−0.558	0.470	0.402	0.517
gl	2, 12	2, 12	2, 12	2, 12	2, 12	2, 12	2, 12
F	1.610	2.830	0.249	2.260	1.417	0.963	1.828
P	0.248	0.106	0.784	0.155	0.287	0.414	0.211
(b) Total evidence tree							
Included variables	T_b –	CT_{min} T_{air}	T_{pant} –	CT_{range} T_{air}	T_{pref} –	$T_{pref\ min}$ –	$T_{pref\ max}$ –
Model							
r	0.196	0.595	0.131	−0.658	0.377	0.307	0.425
gl	2, 12	1, 12	2, 12	1, 12	2, 12	2, 12	2, 12
F	0.200	6.014	0.087	8.402	0.830	0.520	1.105
P	0.822	**0.032**	0.917	**0.014**	0.464	0.610	0.368
(c) Maximum likelihood							
Included variables	T_b T_{air}	CT_{min} –	T_{pant} –	CT_{range} –	T_{pref} –	$T_{pref\ min}$ –	$T_{pref\ max}$ –
Model							
r	0.607	0.493	0.288	0.231	0.231	0.391	0.196
gl	1, 12	2, 12	2, 12	2, 12	2, 12	2, 12	2, 12
F	6.403	1.608	0.454	0.282	0.282	0.902	0.199
P	**0.028**	0.248	0.648	0.760	0.760	0.436	0.833

Independent contrasts (IC) based on TEV and IC based on ML both IC regressions forced through the origin. Independent variables are air temperature (T_{air}) and seasonal thermal range ($Range_{air}$). Dependent variables are field body temperature (T_b), minimum critical temperature (CT_{min}), panting temperature (T_{pant}), thermal tolerance (CT_{range}), preferred temperature (T_{pref}), and the preference limits ($T_{pref\ min}$, $T_{pref\ max}$)

Bold values indicate significant results

Table 4 Co-evolution estimation between preferred temperatures and thermal tolerances of the *L. goetschi* species (13 species) and for the *Liolaemus* genus, including the *L. goetschi group*

	Raw data		TEV tree		ML tree	
	r	*P*	*r*	*P*	*r*	*P*
L. goetschi group						
T_{pref} versus CT_{min}	−0.538	0.058	−0.599	**0.030**	−0.385	0.193
T_{pref} versus T_{pant}	−0.384	0.195	−0.088	0.324	−0.095	0.757
Liolaemus genus						
T_{pref} versus CT_{min} (68 spp)	−0.099	0.439	−0.373	**0.001**	−0.073	0.576
T_{pref} versus T_{pant} (33 spp)	0.284	0.050	0.205	0.287	−0.081	0.594
T_{pref} versus CT_{max} (33 spp)	0.314	0.051	0.197	0.261	−0.079	0.644

Analyses are performed over the raw data, independent contrasts based on a total evidence (*TEV*) tree, and on a maximum likelihood tree (*ML*)

Bold values indicate significant results

models did not show a significant or strong relationship (Table 4).

Our analyses of phylogenetic signal show that tree structure (and data matrix) and evolutionary model used, greatly affect the results (Table 6). When we analyzed the *L. goetschi* traits, we observed that only ML tree with CBL showed significant *k* values ($P < 0.05$), but only for $Range_{air}$, CT_{min}, and CT_{range}, and these were below 1 for all the

Table 5 Multiple linear regressions between thermal variables of the 68 *Liolaemus* species using raw data; independent contrasts (IC) based on TEV and IC based on ML both IC regressions forced through the origin

(a) Raw data					
Predictor	T_b	CT_{min}	CT_{max}	CT_{range}	T_{pref}
Included variables	T_{air} $Range_{air}$	T_{air}	$Range_{air}$	–	$Range_{air}$
Model					
r	0.768	0.368	0.640	0.343	0.315
F	48.043	4.698	12.516	2.394	3.683
df	2, 69	2, 62	2, 38	2, 38	2, 69
P	**<0.001**	**0.013**	**<0.001**	0.106	**0.030**
(b) Total evidence					
Predictor	T_b	CT_{min}	CT_{max}	CT_{range}	T_{pref}
Included variables	T_{air}	T_{air} $Range_{air}$	$Range_{air}$	–	–
Model					
r	0.283	0.395	0.562	0.468	0.016
F	3.211	6.098	7.149	4.493	0.009
df	2, 76	2, 68	2, 33	2, 34	2, 76
P	**0.046**	**0.004**	**0.003**	**0.019**	0.991
(c) Maximum likelihood					
Predictor	T_b	CT_{min}	CT_{max}	CT_{range}	T_{pref}
Included variables	–	T_{air}	$Range_{air}$	–	–
Model					
r	0.258	0.366	0.354	0.264	0.204
F	2.318	4.497	2.436	1.271	1.406
df	2, 67	2, 60	2, 36	2, 36	2, 67
P	0.107	**0.015**	0.103	0.294	0.252

Independent variables are: air temperature (T_{air}) and seasonal thermal range ($Range_{air}$). Dependent variables and field body temperature (T_b), minimum critical temperature (CT_{min}), panting temperature (T_{pant}), thermal tolerance (CT_{range}), and preferred temperature (T_{pref})

Significant results are shown in bold

thermal biology variables (Table 6). TEV analyses, on the contrary, did not show any significant *k* value. With regard to branch length transformations, it was observed that most of the thermal characteristics in the *L. goetschi* group show stabilizing selection as *k* values are higher for $d = 0.2$. However T_b using the TEV tree showed signs of Brownian motion. It is important to take into account that power of the *k* statistic is limited when used for less than 20 species (here we analyzed 13 species for the *L. goetschi* group). Data analyses of the 68 *Liolaemus* species, showed more significant results (several *P* values are <0.05) according to the increased power due to a bigger sample. Additionally and similarly to the *L. goetschi* group, several thermal variables showed *k* values higher than 1 when used O.U. transformations with $d = 0.2$, while in all cases the *k* values increased in association to a more star-like tree (Table 6). This contrasting result is probably due to phylogenetic clustering within each major clade of *Liolaemus* species or because of incomplete data (we have data on 68 out of more than 220 species of *Liolaemus*). It was also noted that stabilizing selection seems to be strong in most thermal characteristics of the extended sample of *Liolaemus* species (for ML and TEV trees). On the contrary, and differently of what observed for the *L. goetschi* species, in the case of T_b in the ML tree, Brownian motion seems to be more important in light of higher *k* values when $d = 0.8$.

Discussion

Is the thermal biology of *L. goetschi* group modelled by the environment or the result of phylogenetic constraints?

Our results show that the focal group of species shows clear signs of effective thermoregulation. The 13

Table 6 Phylogenetic signal analysis of the studied variables for the *L. goetschi* group and the 68 species of *Liolaemus* using a maximum likelihood model of the molecular data and a maximum parsimonia tree based on total evidence characters (Abdala 2007)

	Constant BL		OU 0.8		OU 0.2	
	K	*P*	*K*	*P*	*K*	*P*
Maximum likelihood tree with molecular data of the *L. goetschi* group						
T_{air}	0.101	0.676	0.551	0.793	0.979	0.917
$Range_{air}$	1.630	**0.000**	1.698	**0.002**	1.052	**0.011**
CT_{min}	0.373	**0.028**	0.724	0.275	0.983	0.878
T_{pant}	0.167	0.396	0.598	0.728	0.997	0.520
CT_{range}	0.370	**0.023**	0.751	0.323	0.988	0.795
T_{pref}	0.176	0.309	0.648	0.467	0.994	0.612
$T_{prefmin}$	0.091	0.766	0.538	0.909	0.982	0.861
$T_{prefmax}$	0.340	**0.045**	0.785	0.146	1.006	0.239
T_b	0.319	0.057	0.792	0.195	0.996	0.480
E	0.168	0.320	0.784	0.149	0.992	0.614
Total evidence tree (Abdala 2007) *L. goetschi* group						
T_{air}	0.463	0.808	0.722	0.885	0.944	0.836
$Range_{air}$	0.342	0.670	0.578	0.751	0.989	0.429
CT_{min}	0.321	0.832	0.579	0.811	0.994	0.347
T_{pant}	0.334	0.730	0.547	0.894	0.971	0.623
CT_{range}	0.323	0.829	0.566	0.845	0.986	0.441
T_{pref}	0.339	0.866	0.579	0.909	0.973	0.598
$T_{prefmin}$	0.441	0.649	0.735	0.646	0.988	0.488
$T_{prefmax}$	0.291	0.930	0.494	0.967	0.952	0.708
T_b	0.809	0.293	1.114	0.327	0.942	0.850
E	0.356	0.904	0.608	0.915	0.972	0.616
Maximum likelihood tree with molecular data of *Liolaemus*						
T_{air}	0.167	**0.036**	0.964	**0.000**	1.083	**0.002**
$Range_{air}$	1.545	**0.000**	1.281	**0.000**	1.128	**0.000**
CT_{min}	0.305	**0.000**	0.808	**0.001**	1.017	**0.047**
T_{pant}	0.231	**0.002**	0.844	**0.003**	1.135	**0.001**
CT_{max}	0.155	0.219	0.776	**0.039**	1.020	0.062
CT_{range}	0.374	**0.000**	0.843	**0.000**	1.063	**0.008**
T_{pref}	0.189	**0.016**	0.604	0.130	0.984	0.469
T_b	0.573	**0.000**	1.774	**0.000**	1.215	**0.000**
Total evidence tree (Abdala 2007) *Liolaemus*						
T_{air}	0.311	**0.004**	0.549	**0.028**	0.935	0.170
$Range_{air}$	0.653	**0.000**	1.104	**0.000**	1.093	**0.000**
CT_{min}	0.270	**0.013**	0.559	**0.010**	1.050	**0.002**
T_{pant}	0.218	0.130	0.615	**0.000**	1.108	0.058
CT_{max}	0.311	**0.023**	0.491	0.206	0.920	0.377
CT_{range}	0.321	0.053	0.519	0.327	0.909	0.401
T_{pref}	0.243	0.503	0.488	0.699	0.871	0.753
T_b	0.422	**0.000**	0.728	**0.000**	1.101	**0.000**

We applied three evolutionary models: Constant branch length (*BL*), Ornstein–Uhlenbeck transformation (*OU*) = 0.8 and 0.2

Analyzed variables are: T_{air} mean air temperature for the activity season (September–April), $Range_{air}$ mean thermal range for the same season, CT_{min} critical thermal minimum, T_{pant} panting temperature, CT_{max} critical thermal maximum, CT_{range} tolerance range (T_{pant}–CT_{min}, and CT_{max}–CT_{min} in *Liolaemus*), T_{pref} preferred temperatures, $T_{pref\ min}$ 25 % interquartile of T_{pref}, $T_{pref\ max}$ 75 % interquartile of T_{pref}, T_b field body temperature, *E* effectiveness

P values <0.05 indicate that *k* statistic value is significant (showing or not phylogenetic signal), and are shown in bold

Liolaemus species of the *L. goetschi* group inhabit environments with very different average air temperatures and wide thermal amplitudes (Cruz et al. 2005), and it is observed that thermal characteristics of the species vary. For example, in most species (with the exception of *L. cuyanus*), we observed low values of CT_{min}, which are expected for species inhabiting cold Patagonian environments. Also, the interspecific variation of this trait was

higher than that of panting and preferred body temperatures, which were more conservative. Notably, there is evidence from interspecific as well as intraspecific studies on ectotherms supporting the idea that upper thermal limits show less geographic variation than lower ones (Lutterschmidt and Hutchison 1997; Gaston and Chown 1999; Huang and Tu 2008). Similar trends have been found in other Patagonian lizard groups (*L. lineomaculatus* section, Bonino et al. 2011; *Phymaturus*, Cruz et al. 2009). The lower flexibility of T_{pant} may reflect physiological constraints, such as the strong effect of high temperatures (in this case T_{pant}) on proteins and cell membrane stability (Hochachka and Somero 2002; Angilletta 2009). In addition to this, it was suggested that CT_{min} is more difficult to avoid behaviourally than CT_{max} (Spellerberg 1972), and therefore CT_{min} should be adjusted by increasing the tolerance to low temperatures in cold environments.

Our analyses of the environmental influence on thermal biology traits show different associations depending on what phylogenetic analyses were used, if any. Raw data and TEV tree analyses showed an influence of T_{air} on CT_{min}, while the ML tree analysis did not. After exploring trees and contrasts, the ML tree shows that the ancestor of *L. canqueli* and *L. melanops* lowers the correlation coefficient, therefore affecting the results. Variation in CT_{min} (lower values in colder climates; Table 3) suggests that these lizards have been at some point adapted to the cold climatic conditions in the Patagonian habitats where they mostly occur, as observed by Cruz et al. (2005) in congruence with TEV tree.

Variation in preferred body temperatures in the *L. goetschi* group was narrow and was not associated with environmental variables in any of our analyses, supporting the static hypothesis of lizard thermal physiology (Hertz et al. 1983; Andrews et al. 1999). This is also observed in our ancestral reconstruction analyses (both in the 68 species of *Liolaemus* and the *L. goetschi* group). Thermal preferences are usually related to temperatures at which physiological performance is also near optimal (Huey and Bennett 1987; Angilletta 2001) in some *Liolaemus* species (Bonino et al. 2011). Therefore, we predict this variable is less plastic than other thermal variables, and evolutionarily constrained (Kohlsdorf and Navas 2006; Angilletta et al. 2010). Our results on thermal preferences together with the high values of effectiveness of thermoregulation may be associated with the physiological needs related to performance. However, environmental characteristics may also influence thermal preferences. For example, patchiness of the environment favours precise behavioural thermoregulation (Huey and Slatkin 1976), and it may buffer selection pressure on T_{pref} (Huey et al. 2003). The *L. goetschi* group species, for example, inhabit open areas interrupted by patches of big shrubs, offering different microenvironments. This heterogeneity represents good opportunities for thermoregulation. Our results support the conservative character of T_{pref}, in contrast to findings reported by Labra et al. (2009), who found variation in T_{pref} associated with ambient temperature for 32 species of *Liolaemus*. It has to be noted that most of Labra et al.'s (2009) species (26 of 32 species) correspond to the *L. chiliensis* group, whereas our sample is broader and balances several other radiations (e.g. the *L. boulengeri* and the *L. lineomaculatus* series); additionally, our sample corresponds to a broader latitudinal range. In addition, environmental temperatures measured by Labra and colleagues (T_e) are lower than T_e measured by us in the *L. goetschi* group habitats, and differ from T_{air} temperatures used here. Despite this, and according to our findings, evolution of thermal biology is not sufficiently clear to establish general patterns, but it seems to be a continuum between the two extreme proposed patterns of flexible and static thermal traits (Hertz et al. 1983; Andrews et al. 1999; Angilletta et al. 2002; Rodríguez-Serrano et al. 2009).

Is there co-evolution between behavioural thermoregulation and thermal physiology?

Coevolutionary studies of thermal variables in ectotherms have provided contradictory evidence, showing that some species show co-evolution of certain thermal traits (Garland et al. 1991; Bauwens et al. 1995) whereas others found no evidence for co-adaptation or obtained equivocal results in other species (Angilletta et al. 2002; Cruz et al. 2009; Labra et al. 2009; Bonino et al. 2011). The present work is not an exception; we infer co-evolution between T_{pref} and CT_{min} when using TEV tree analyses only, both within the *L. goetschi* group and within *Liolaemus*. Contrary to our expectations, high T_{pref} correspond to low CT_{min}.

Our results are consistent with Labra et al. (2009) and Bonino et al. (2011), who found no co-evolution between critical thermal maximum and T_{pref} traits in *Liolaemus*, which seems to be a common pattern in this genus. It is possible that different evolutionary trajectories of thermal traits lead to different combinations between thermal physiology and thermal behaviour to reach a successful thermoregulatory strategy, without changes in preferences. Behavioural adjustments should incur less cost than physiological ones. For example, adjustments in time of basking, or the use of the environment (basking earlier in the morning, or for longer times), may allow lizards to keep similar thermal preferences. This adjustment would avoid changes in thermal preferences, which should be more "expensive" for the animals, due to its relationship with performance optima (Angilletta et al. 2002; Angilletta 2009).

Are the results affected by the number of species or hierarchical scale, phylogenetic approaches, or evolutionary models used?

Our analysis of thermal biology for 68 *Liolaemus* species shows a wider range of variation in the thermo-physiological variables compared to what we observed in 13 species of the *L. goetschi* group, probably due to the increase in the number of species, the variety of habitats they inhabit, and the wider geographical range. As a result, the environmental effect on the thermal biology of a broader sample of *Liolaemus* species differ from the effect observed on the *L. goetschi* group, that shows a more conservative pattern. Probably, this group evolved in comparable similar thermal environments that drove the observed thermal characteristics. For example, in the broader sample of 68 species, CT_{min}, CT_{range} and T_b are modelled by T_{air}, while CT_{max} is related to variation in thermal amplitude ($Range_{air}$). Our results on the variation of T_b explained by the environment are in agreement with results that Rodríguez-Serrano et al. (2009) reported for 20 Chilean species of *Liolaemus*, supporting the labile thermal hypothesis of lizard thermal physiology (Hertz et al. 1983; Andrews et al. 1999). We observe that at a broader scale the regressions between T_b and environmental temperatures show a relationship between geographic range and environmental temperatures. We found species with high T_b in hot environments in northern Argentina as well as low T_b in *Liolaemus* species inhabiting cold environments as observed by Ibargüengoytía et al. (2010). Conversely, the lower variability in T_b observed in the species belonging to the *L. goetschi* group may be associated with the similarity among species in several aspects, including morphology. It is also possible that our results obtained at different hierarchical scales are driven by phylogenetic clustering (Vanhooydonck and Van Damme 1999); for example, all members of the *L. lineomaculatus* clade in our database have equally low body temperatures and lower critical thermal limit (Bonino et al. 2011; this study).

The influence of the phylogenetic and geographical scale on comparative analyses has been noted in other studies (e.g. Cruz et al. 2005). These authors found that different groups nested in a larger clade may obscure results of macroecological patterns, mainly because each one of these groups may show different (or opposite) patterns or tendencies. Here, we observed that the *L. goetschi* group species differ in thermal biology from a broader sample of *Liolaemus* species. These differences may be due to the particular thermal characteristics of some clades, such as the *L. lineomaculatus* section, which is exclusive to Patagonia and shows low T_b and CT_{min} values. Thus, this particular clade may pull the data in a different direction from the *L. goetschi* group, increasing the differences observed here.

The use of phylogenetically based comparative analyses were developed to avoid lack of independence among taxa (Felsenstein 1985; Martins 1996), and different phylogenetic techniques may lead to different tree structures and branch lengths. Our analyses under three different scenarios (raw data, TEV and ML) with different branch lengths recovered mixed results depending on the scale of the phylogenetic tree used, even while testing for phylogenetic signal. When we analysed the focal species (the *L. goetschi* group), data were very sensitive to tree structure, although in general the phylogenetic signal was fairly low. Conversely, when we expanded the tree to 68 species including members of each of the four major clades in *Liolaemus*, that is *L. chiliensis* group, *L. lineomaculatus* section, *L. montanus* series and *L. boulengeri* series (Avila et al. 2006; Abdala 2007; Lobo et al. 2010), we found a strong phylogenetic signal in most variables (except for CT_{max}, probably because it is a physiological limit for most lizards). In agreement with Revell et al. (2008), we believe that differences observed between different scales in the trees are not exclusively a matter of evolutionary rates, they seem to be related to phylogenetic clustering (Vanhooydonck and Van Damme 1999). This was observed in nail features in *Liolaemus* lizards (Tulli et al. 2009). However, we have to consider species sampling or methodological limitations, too. Our sample smaller than 20 species may cause problems with the statistical power of phylogenetic signal analyses (Blomberg et al. 2003).

Our findings lead to several interesting conclusions. First, both phylogenetic and environmental adaptive forces are acting on the thermal biology of *Liolaemus* as well as in the *L. goetschi* group. Second, CT_{min} is more flexible than upper tolerance limit, showing adaptation to low temperatures and also related with T_{pref}. Third, some adaptive patterns are independent of phylogenetic scale while others are not. Thus, thermal biology evolution in *Liolaemus* lizards is apparently not just a consequence of environmental effects or phylogenetic constraints as independent and exclusive processes but also a mixture of both forces that are operating to model the thermal biology of this succesful group of lizards inhabiting a great diversity of environments.

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