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Looking at the past to infer into the future: Thermal traits track environmental change in Liolaemidae

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The diversity of habitats generated by the Andes uplift resulted a mosaic of heterogeneous environments in South America for species to evolve a variety of ecological and physiological specializations. Species in the lizard family Liolaemidae occupy a myriad of habitats in the Andes. Here, we analyze the tempo and mode of evolution in the thermal biology of liolaemids. We assessed whether there is evidence of local adaptation (lability) or conservatism (stasis) in thermal traits. We tested the hypothesis that abiotic factors (e.g., geography, climate) rather than intrinsic factors (egg-laying [oviparous] or live-bearing [viviparous], substrate affinity) explain variation in field active body temperature (T_b), preferred temperature (T_p), hours of restriction of activity, and potential hours of activity. Although most traits exhibited high phylogenetic signal, we found variation in thermal biology was shaped by geography, climate, and ecological diversity. Ancestral character reconstruction showed shifts in T_b tracked environmental change in the past ~20,000 years. Thermal preference is 3°C higher than T_b, yet exhibited a lower rate of evolution than T_b and air temperature. Viviparous *Liolaemus* have lower T_bs than oviparous species, whereas T_p is high for both modes of reproduction, a key difference that results in a thermal buffer for viviparous species to cope with global warming. The rapid increase in environmental temperatures expected in the next 50–80 years in combination with anthropogenic loss of habitats are projected to cause extirpations and extinctions in oviparous species.

KEY WORDS: Body temperature, cold climate, Liolaemidae, reproductive mode, thermal preference, viviparity.

Characterizing evolutionary patterns of variation in physiological traits provides the opportunity to predict vulnerability of extant species to global warming (Angilletta et al. 2006; Sinervo et al. 2010; Sinervo et al. 2018). In this regard, analysis of factors that promote or constrain trait evolution requires the integration of the physiological, behavioral, and ecological aspects of organisms (Huey 1991; Muñoz et al. 2014). Since physiological and behavioral traits in ectotherms depend on ambient temperature, selection should favor individuals that can attain physiologically optimal body temperatures to maximize performance capacities associated with growth, reproduction, foraging mode, prey acquisition, predator avoidance, and social behaviors (Huey and Slatkin 1976; Huey 1991; Sinervo and Adolph 1994; Miles 2004; Sears 2005; Miles et al. 2007).

Thermal traits have been considered static (conserved with limited among-individual or population variation), or labile (considerable inter-individual or inter-population variation suggesting adaptation to local environmental conditions, Hertz et al. 1983), and also as a continuum of both (static and labile) responding to the pressures of multiple niche dimensions (Hutchinson 1957; Hertz et al. 1983; Angilletta et al. 2002; Holt 2009; Muñoz and Losos 2018). Moreover, there is a complex interplay among physiological plasticity, environmental constraints or opportunities shaped by habitat physiognomy, mode of reproduction (Esquerré et al. 2019), immune activity (Paranjpe et al. 2014; Duran et al. 2019), diet (Espinoza et al. 2004), and substrate affinity (Schulte et al. 2004; Jiménez-Robles and De la Riva 2019) that affect diversification in thermal traits (Muñoz et al. 2014; Llewelyn et al. 2017; Logan et al. 2018). Another complementary view of static-labile traits considers Behavioral Drive vs. Behavior Inertia as governing labile or static evolutionary changes in traits in relation to regulatory behaviors (Bogert 1949; Huey et al. 2003). In this view, genetic tradeoffs and heritability can accelerate evolution along "genetic lines of least resistance" (Schluter 1996), or allow acclimatization and behavior to limit trait evolution in cases when heritability of traits is low or zero, which is likely for behavioral thermoregulation (Bogert 1949; Sinervo 1990; Sinervo et al. 2010; Paranjpe et al. 2014; Llewelyn et al. 2017; Logan et al. 2018; but see Bestion et al. 2015).

The physiological or behavioral responses of species to environmental stressors are variable and include plasticity, such as shifts in thermal phenotypes in response to climate fluctuations (Hofmann and Todgham 2010; Gilbert and Miles 2019; Domínguez-Guerrero et al. 2020), adaptation to new conditions (i.e., *Sceloporus*, Sinervo et al. 2010; Ibargüengoytía et al. 2020), or habitat tracking in which populations move to environments with conditions similar to their original habitat (i.e., mammals: Raia and Meiri 2011; lizards: *Sceloporus*, Sinervo et al. 2010; *Liolaemus*, Labra et al. 2009; Bonino et al. 2011; Minoli et al. 2013, and *Phrynocephalus*, Sinervo et al. 2018). In the absence of sufficient plasticity, if evolutionary rates of thermal adaptation and dispersal capacity of species cannot keep pace with environmental change (Hoffmann and Sgrò 2011; Quintero and Wiens 2013), extirpation of local populations or species extinction can occur (Kubisch et al. 2016b; Sinervo et al. 2010; Sinervo et al. 2011; Cahill et al. 2012; Vicenzi et al. 2017; Sinervo et al. 2018; Fitzgerald et al. 2018; Riddell et al. 2019). The contemporary increase in temperature during the past 30 years and future projections by 2050 and 2080 exceeds known evolutionary rates (Miles 1994, Morgan et al. 2020) and dispersal capabilities of many species (Sinervo et al. 2010; Hoffmann and Sgrò 2011; Quintero and Wiens 2013; Sinervo et al. 2018). However, effectiveness of physiological and behavioral responses may vary among genera and species. As a consequence, extirpations could be nonrandom with respect to phylogeny, physiology, or geographic locations. For example, vulnerability has been shown to increase for tropical thermoconformers, niche specialists, or endemic species in montane habitats (Tewksbury et al. 2008; Huey et al. 2009; Sinervo et al. 2010).

Montane ecosystems are biodiversity hotspots (Rahbek et al. 2019). The physiographic heterogeneity affects microclimate leading to different adaptative or plasticity responses to the thermal and rainfall regimes of local microhabitats (Theobald et al. 2015). In the Southern Hemisphere montane slopes at low elevation with a northern exposure tend to be warmer than high elevation habitats with a southern exposure (Hannah 2015). Moreover, patterns of rainfall along trans- and cis-Andes promotes dramatic differences in habitat across localities (Whiteman 2000; Jiménez-Robles and De la Riva 2019). These heterogeneous thermal and hydric gradients pose challenges and opportunities for liolaemid species to exploit a variety microhabitats. For example, environmental changes in montane systems modify habitats and leads species to inhabit suboptimal ecological and physiological conditions or promote the invasion into novel niches (Root et al. 2003; Thomas et al. 2006; Jiménez-Robles and De la Riva 2019).

The family Liolaemidae is one the most diverse clades of vertebrates with 331 species (Uetz et al. 2020; Abdala et al. 2021) comprising three genera *Ctenoblepharys*, *Liolaemus*, and *Phymaturus* (Etheridge 1995). Species in this family evolved during different climatic and geological events resulting in an extraordinary model to explore the evolution of ecological and physiological traits. The origin of Liolaemidae dates from ∼62 million years ago (Townsend et al. 2011), and the genera *Liolaemus* and *Phymaturus* are inferred to have split in the early Miocene (∼25-27 million years ago, Ferri Yáñez 2016; Esquerré et al. 2019, respectively). A recent analysis revealed the greatest rate of speciation occurred during consecutive episodes of the Andean uplift during the past ∼25 million years ago (Pincheira-Donoso et al. 2015). The Andes became a barrier to atmospheric circulation resulting in changes of rainfall and seasonal warming patterns.

The shift also was a key reason in the trend of global-cooling observed since the Eocene (Gregory-Wodzicki 2000). The reconstruction of paleoclimates of the Pleistocene versus Eocene temperature regimes indicates that the family Liolaemidae has experienced long-term mean temperatures 6°C lower than and up to 14°C greater than recent means (1960−1990, IPCC 2014; Burke et al. 2018; Ibargüengoytía et al. 2020).

Here, we present the most comprehensive assessment of trait diversity within Liolaemidae focusing on field active body (T_b) and preferred body temperatures (T_p). The latter is obtained from measurements of lizards in a thermal gradient and allowed to thermoregulate, but free from costs associated with the presence of predators, social interactions, and limited access to suitable temperatures. We also include data on substrate affinity (saxicolous, psammophilous, or arboreal), reproductive mode (egg-laying [oviparous] or live-bearing, regardless of the offspring state of maturity, *sensu* Blackburn 1994 [viviparous]), climate (local air temperature, T_a; and rainfall), geographic location (latitude, longitude, and elevation), and operative environmental temperatures (T_e), the equilibrial T_b a non-thermoregulating lizard attains in a given microhabitat (*sensu* Porter et al. 1973; Bakken 1992). Operative temperatures allow the identification of thermal microenvironments suitable for thermoregulation. In addition, considering that climatic disturbances prompt shifts in the thermal niches, we analyzed whether lizards may reduce the potential hours of activity (H_a) and increase the hours of restriction (H_r, see Sinervo et al. 2010; Sinervo et al. 2018). A reduction in the time spent outside of shelters and on critical activities (foraging, courtship) could have a negative impact on a species reproduction and population persistence. Hence, H_r is predicted to affect growth rates, phenology, and structural diversity of populations, resulting in an enhanced risk of extinction (Bickford et al. 2010; Logan et al. 2014). Our sample consists of the monotypic *C. adspersa*, 20 *Phymaturus*, and 105 *Liolaemus* species. We also present new data for *C. adspersa*, two species of *Liolaemus*, and eight species of *Phymaturus*. If the diversification of species in Liolaemidae is associated with thermal specialization, we hypothesize that variation in either T_b or T_p or both may be explained by phylogeny or local climatic conditions. Thus, we predict that T_b and T_p will show phylogenetic signal and a low relationship with geographic and climatic environmental conditions. In addition, species or entire clades that show high inter-specific variability in thermal traits may result in a lower phylogenetic signal and a higher dependence with environmental condition. Since T_p is assumed to represent the temperature selected by an ectotherm to optimize physiological processes (Angilletta et al. 2002; Huey et al. 2003), adaptive shifts in this trait require sufficient genetic variation (Muñoz and Bodensteiner 2018). Furthermore, the dependence of physiological performance on temperature, is expected to constrain adaptive shifts in T_p, which would be manifested by a lower evolutionary rate. In addition, we expect that T_p, despite being a conservative trait, coevolves with T_b in Liolaemidae as observed in other families within the order Squamata (Black et al. 2019). But, we predict the rate of evolution will be slower for T_p than T_b. Based on the integration of the hypotheses presented above and previous studies combining reproductive and thermal physiology characteristics (Andrews et al. 1997; Shine 2004; Sinervo et al. 2018), we expect viviparous liolaemid species to show lower T_b and T_p that result in higher H_r and hence higher vulnerability to climate change than oviparous species (Sinervo et al. 2010).

Species in *Liolaemus* and *Phymaturus* differ in the magnitude of variation in both reproductive mode and substrate use (Cei 1986; 1993; Boretto et al. 2018). Previous surveys have shown that viviparous and oviparous species differ in their thermal traits, with the former characterized by lower values for T_b (Sinervo et al. 2010). Moreover, thermal opportunities are known to differ between arboreal, saxicolous, and psammophilous substrates (Bakken 1989; Logan et al. 2014; Pincebourde et al. 2016). Because all species of *Phymaturus* are viviparous and saxicolous we predict they should be more conserved in thermal evolution (Donoso-Barros 1966; Cei 1986; 1993; Scolaro 2005; 2006; Corbalán et al. 2013; Boretto et al. 2018). In contrast, *Liolaemus* have evolved to exploit different substrate types and exhibit different modes of reproduction (oviparous and viviparous; Donoso-Barros 1966; Cei 1986; 1993; Scolaro 2005; 2006), hence we predict thermal traits in *Liolaemus* should be more labile. Differences in thermal traits between *Phymaturus* and *Liolaemus* have been suggested in previous studies, focusing on either *Liolaemus* (Labra 1998; Rodríguez-Serrano et al. 2009; Medina et al. 2012; Moreno Azócar et al. 2012; Ferri-Yañez 2016) or *Phymaturus* (Cruz et al. 2009). These studies showed that thermoregulation of *Liolaemus* is labile and reflects adaptation to environmental constraints with a clear relationship between thermal and climatic traits (Labra 1998; Rodríguez-Serrano et al. 2009; Cruz et al. 2009; Medina et al. 2012; Moreno Azócar et al. 2012). In contrast, *Phymaturus*, being ecologically constrained has been shown to be more conservative suggesting the genera shows stasis as an evolutionary mode (Cruz et al. 2009).

The present study presents the first global analysis on Liolaemidae comprising the three genera *Ctenoblepharys*, *Phymaturus*, and *Liolaemus*, which allows a reassessment of lability in thermal traits in *Liolaemus* and conservatism in *Phymaturus* in a phylogenetic context. We also reconstruct ancestral character states for the thermal traits to predict possible evolutionary pathways species could follow in altered thermal environments due to anthropogenic climate change.

Materials and Methods

STUDY AREA AND SPECIES

We captured individuals of *Phymaturus spurcus* (N = 45), *P. etheridgei* (N = 9), *P. sinervoi* (N = 46), *P. manuelae* (N = 14), *P. tenebrosus* (N = 21), and *P. ceii* (N = 33) from the Patagonian steppe during December 2010 in Ingeniero Jacobacci, Comallo, and Pilcaniyeu (from –40° 22´ to –41° 35´ S; from –69° to –70° 37´ W, between 836 and 1146 m asl) Río Negro Province, Argentina. We also captured individuals of *Phymaturus punae* (N = 35), *Liolaemus montanezi* (N = 21), and *L. eleodori* (N = 55) from the Andes mountains in the San Guillermo Biosphere Reserve (29°26' S to 29°33' S; 69°11' W to 69°25' W, between 2190 and 3627 m asl), San Juan Province, Argentina from November 2017 to March 2018. *Ctenoblepharys adspersa* lizards (N = 13) were captured between San Fernando and San Juan de Marcona in July 2012 and January 2013 (15˚06'42.5'' S 75˚19'56.0'' W; 644 m asl) and between Nazca and Bella Unión in January 2013 (15˚22'56.5'' S and 75˚03'52.8'' W, 172 m asl).

FIELD WORK AND DATA RECORDED

Lizards were caught by hand or lasso only when active (i.e., performing any behavior related to feeding or basking activities, or both). Body temperature (T_b) was measured with a thermocouple (TP-K01, 1.62 mm diameter) inserted ca. 10 mm within the cloaca connected to a TES 1302 thermometer (TES® Electrical Electronic corp., Taipei, Taiwan, ±0.01°C). We handled lizards to avoid heat transfer (grasping them by a hindlimb) and temperature was recorded within 20 s of capture. Capture localities were georeferenced with a GPS (Garmin GPSMap® 60csx). Animals were released at their site of capture within 4 days after capture.

THERMAL PREFERENCE

We measured thermal preference in an indoor laboratory located near the field site within 2 days of capture in a thermal gradient. We used a wooden track consisting of six lanes, (16×20×100 cm for each lane), with a 75 watt incandescent lamp suspended at one end to generate a temperature gradient of 20-50°C. Body temperatures were recorded using ultra-thin (1 mm) thermocouples inserted approximately 10 mm within the cloaca and taped at the base of the lizard's tail to prevent the thermocouple from being dislodged. The temperature of each lizard were recorded every 2 min for a period of 2.5 h with a 24-channel Data Logger (TM1033, 1000 Series Squirrel Meter/Logger GEN2 transmitters).

THERMAL-NICHE BUFFER

We derive a new index, the "Thermal-niche buffer" (TNB), which is the difference between mean T_p and mean T_b (Mean T_p - Mean T_b). The TNB describes the potential of a species to resist or tolerate low or high perturbations in environmental temperatures. Positive values refer to species that show a great buffering capacity and negative values those with low buffering capacity to environmental changes.

DATA FOR *PHYMATURUS* AND *LIOLAEMUS* – LITERATURE REVIEW AND UNPUBLISHED DATA

We also obtained T_b and T_p of *P. patagonicus* (N = 35) from the unpublished data of Erika Kubisch and Alejandro Scolaro using lizards captured at Dolavon Chubut Province, Argentina (43° 45´S and 66° 11´ W, 276 m asl). Additional data on T_b and T_p were obtained from the literature. We extracted the geographic location (latitude, longitude, and elevation), air temperature (T_a), rainfall and substrate affinity for 20 species of *Phymaturus*, and 105 species of *Liolaemus* from each publication (Supplemental material; Table S1). Due to the diversity and complexity of habitats occupied by liolaemid species, substrate affinities were established considering the main substrate used by the lizards to perform most vital activities (feeding, reproduction, and performing territorial defense) following three categories: saxicolous (weathered or boulder rocks), psammophilous (ground dwelling on sandy environments, claylike or salty soils) or arboreal (used of trunk, branch or twig substrates in forest or grassland habitats with leaf litter soils). Latitude, longitude, and elevation (m asl) correspond to the locations from where the thermal values were measured. The midpoint coordinate was used when the publications referred to ranges of the species distribution. The mean air temperatures (T_a) and monthly rainfall of each locality during the activity period of lizards (September to April) were obtained from CONICET (historical data registered for studies of global warming for Argentina, 3CN database, Investigation Center of the sea and atmosphere, http://3cn.cima.fcen.uba.ar/index1.php from 1960 to 2010), the National Service of Meteorology and Hydrography of Peru (SENAMHI; https://www.senamhi.gob.pe from 1960 to 2010), the National Meteorology Institute of Brazil (INMET; http://www.inmet.gov.br/ from 1961 to 1990), and Climatic sciences and resilience center of Chile (CR^2; http://explorador.cr2.cl from 1940 to 2018).

We conducted a critical evaluation of each publication to obtain the data used in the present study. We examined each source for accuracy in geographic coordinates, elevation, identification, and natural history of each species, especially from those with republished datasets. We did this to avoid replicating underlying errors perpetuated in subsequent publications. As a consequence, we amended all unreliable geographic and taxonomic data based on the revision of original descriptions and data inquiries from herpetological collections where possible. Unreliable data were expunged from the database. We replaced missing information on reproductive mode and habitat based on our unpublished data or the original species description (Table S1).

STATISTICAL ANALYSIS

Phylogenetic hypothesis

We used the recently published phylogeny of Esquerré et al. (2019) as our core tree for evolutionary relationships of *Ctenoblepharys*, *Phymaturus*, and *Liolaemus*, pruned to include only species for which we had data on T_b and T_p. However, our analysis included taxa not included in Esquerré et al. (2019). We used Mesquite version 3.31 (Maddison and Maddison 2017), to place the new taxa on Esquerré et al.'s core tree based on recent phylogenies for *Phymaturus* (Lobo et al. 2016; Lobo et al. 2018), and *Liolaemus* (Abdala 2007; Breitman et al. 2011; Abdala et al. 2012; Abdala and Juárez Heredia 2013; Portelli and Quinteros 2018; Abdala et al. 2020).

Phylogenetic conservatism in thermal ecology

All phylogenetic comparative analyses used the statistical programming language R 3.5.3 (R Core Team 2018). We estimated phylogenetic signal (i.e., consistency between the phylogenetic topology and distribution of a phenotypic trait) for the continuous traits (e.g., T_b, T_p, elevation) using Pagel's lambda (Pagel 1999; Freckleton et al. 2002). Lambda is a common statistic to calculate phylogenetic signal and performs well assuming a Brownian motion model of evolution (Münkemüller et al. 2012). Values of lambda were obtained using the function phylosig in the package phytools (Revell 2012). We used a likelihood ratio test to determine whether values of lambda differed from 0. We determined estimates of phylogenetic signal for discrete traits, reproductive mode, and substrate affinity, using the function fitDiscrete in the package geiger (Pennell et al. 2014) applying a lambda transformation. We evaluated whether lambda differed from 0 by fitting the data and fixing lambda equal to 0. We compared the likelihoods of the two models to assess whether the estimated value of lambda differed significantly from 0.

Ancestral character state reconstruction

We used a maximum likelihood model to estimate ancestral character states for thermal traits T_b, T_p, elevation, H_r and H_a in liolaemids. We generated ancestral character states using the function contMap in the package phytools (Revell 2013). We used stochastic character mapping to generate estimates of ancestral character states for the discrete traits. We compared a Brownian motion model, Ornstein-Uhlenbeck and Pagel's Lambda using the AICc scores and likelihood ratio tests using the function *fitDiscrete* in the package *geiger* (Pennell et al. 2014). The OU model provided the best fit to the data. We used the function make.simmap in the package phytools to generate the character estimates for nodal values. We also estimated the transition matrix, Q, by a Bayesian Markov Chain Monte Carlo simulation to generate transition probabilities among character states (Bollback 2000). Simulations ran for 100,000 generations and sampled every 100 generations. Our estimate of ancestral characters at the tree root, *pi*, was derived from the results of the MCMC simulations. The proportion of time each node spent in a particular character state was summarized using pie diagrams and visualized with plot.simmap in the package phytools (Revell 2013).

Geographic and environmental predictors and effects of reproductive mode and substrate affinity on T_b, T_p, and TNB

We assessed roles of geographic and environmental variables in explaining interspecific variation in two thermal traits, T_b and T_p. We used a phylogenetic generalized least squares (PGLS) analysis to test whether T_b and T_p variation reflected plasticity or local adaptation to climatic conditions or best explained by geographical attributes. We first determined the appropriate model of evolution characterizing T_b and T_p to use in the PGLS. As above, we used three covariance structures for each regression: Brownian Motion (BM), Pagel's lambda (λ), and Ornstein-Uhlenbeck. A comparison of AIC scores and likelihood ratio tests again supported the OU model of evolution. Multiple regressions were performed using PGLS (Grafen 1989; Mundry 2014; Symonds and Blomberg 2014) based on the packages ape (Paradis et al. 2001) and nlme (Pinheiro et al. 2018) using the corMartins and gls functions. We used corMartins to generate a correlation structure that modeled trait evolution as an OU process. We performed a multiple regression with T_b as the response variable and latitude, longitude, elevation, T_a, rainfall as predictor variables. Our analysis for T_p included the same predictors, but we also included T_b. We compared the means for T_b or T_p for species that differed in reproductive mode or substrate affinity using phylogenetic *t*-tests or one-factor PGLS. It is possible the results from the PGLS could be influenced by spatial autocorrelation. Because both latitude and longitude exhibit significant phylogenetic signal (see below), we suggest the results would remain unaltered by the spatial proximity of species.

Comparing evolutionary rates of T_b and T_p

We compared evolutionary rates between T_b and T_p using the method of Adams (2013). This approach provides a powerful means of detecting when evolutionary rates differ between traits, thereby extending the likelihood framework for evaluating comparative patterns in evolutionary biology using a phylogenetic perspective. Compared to other existing approaches based on phylogenetically independent contrasts and methods that compare confidence intervals for model parameters, the likelihood-based method exhibits superior statistical properties for a wide range of simulated conditions. We used the R code presented in Adams (2013) to determine whether evolutionary rates varied among thermal traits (T_b and T_p).

Determination of H_r and H_a

We used the model of extinction risk presented in (Sinervo et al. 2018) to estimate the H_r and H_a for liolamid lizards. The equations for calculting H_r include estimates of operative environmental temperature (T_e) computed from microclim rasters for 24-h periods (Kearney et al. 2014). Because our focus in this analysis is on phylogenetic inference of trait evolution and not local species extirpations we used the published location data from the literature and present data for T_b ($N = 119$) and T_p records ($N = 99$) and not all known occurrence records as in Sinervo et al. (2018). Details regarding the calculation of H_r and H_a are presented in the Supporting Information.

The indices H_a and H_r are derived from the integration of biophysical variables with ecophysiological traits (Sinervo et al. 2010; Kearney et al. 2014, Sinervo et al. 2018). We computed H_a and H_r to include phenological (seasonal) changes in abiotic factors, which are adjusted for latitude and elevation. Thus, our method captures the influence of temperature on growth (Sinervo and Adolph 1994) and reproduction (Adolph and Porter 1993).

We used PGLS with an OU model of evolution to determine whether summation of H_r or H_a across the year (12 months of WorldClim rasters and adjusting for days per month) can be predicted from latitude, longitude, elevation, T_a, and rainfall. Our statistical analysis had the goal of determining the main variables linked with vulnerability to global warming in liolaemid species. We restricted analysis of H_r and H_a to those taxa with T_p, given that field T_b retains variation in operative environmental temperature, whereas T_p is carried out in the laboratory and avoids the confounding effects of T_b or T_e. Nevertheless, the new metric H_a, which builds in a family level average for $T_{b,\,minActivity}$ (the minimum temperature at which animals are voluntarily active, obtained from the minimum T_b of animals in the field that are active), allows us to use the climate surface metric T_{min} (daily minimum air temperature) to compute hours of potential activity period, while also using the climate surface metric T_{max} (daily maximum air temperature) with T_p to compute the H_r. These ecophysiological equations decouple potential issues of multicollinearity in our metrics, given a lack of independence of the underlying data, while also maximizing climate surface data by using both T_{max} and T_{min}.

The R code in the supplement to Sinervo et al. (2018) was modified to run R routines in parallel using the doParallel library for a High Performance Computing Cluster (Hummingbird, UC Santa Cruz, running SLURM batch processing in the UNIX environment, to be posted on GitHub once the manuscript is accepted for publication).

Results

PHYLOGENETIC SIGNAL

All variables (T_b, T_a, rainfall, latitude, longitude, elevation, substrate affinity, reproductive mode), with the exception of T_p, exhibited significant values for phylogenetic signal for all species in the Liolaemidae and estimated using only species in the genus *Liolaemus* (Table 1). Both, H_r and H_a had significant values for phylogenetic signal in Liolaemidae. We found only rainfall, latitude, and elevation had significant values for phylogenetic signal for species in the genus *Phymaturus* (Table 1).

ANCESTRAL CHARACTER STATES OF THERMAL TRAITS (T_b AND T_p), AND ELEVATION OF LIOLAEMIDAE

Thermal traits

The ancestral reconstruction of T_b showed that T_b tends to increase from the basal nodes to the terminal clades, and varied from a low T_b of 31.21°C at the ancestral node (A) of *C. adspersa*, 31.71°C for *Liolaemus* (node B), 32.56 °C for the *Liolaemus* subgenus (node C), 31.50°C for the *Eulaemus* subgenus (node D), 31.33°C for *Phymaturus* (node E), 31.49°C for the *P. patagonicus* group (node F), and 31.03°C (node G) for the *P. palluma* group (Fig. 1). The highest values of T_b (37.5°C) occur in the subgenus *Eulaemus* (e.g., *L. wiegmannii* group, *L. grosseorum* clade), and in certain species within the *Liolaemus* subgenus (e.g., *L. monticola* and *L. tenuis*, Fig. 1). In contrast, the ancestral T_p was 34.84°C (node A), which corresponds to *C. adspersa*, 34.88°C for *Liolaemus* (node B), 34.93°C for *Liolaemus* subgenus (node C), 34.87°C for *Eulaemus* subgenus (node D). Genus *Phymaturus* T_p corresponded to 34.9°C (node E), 34.63°C for *P. patagonicus* group (node F), and 35.22°C for *P. palluma* group (node G). The highest values can also be found within *Eulaemus* subgenus with tip values of up to 38°C (Fig. 2).

Elevation

The ancestral reconstruction revealed a mid-elevation origin for the family Liolaemidae. Several clades radiated into high elevation habitats from a mid-elevation ancestor, including the *L. montanus* group, *L. ornatus* clade within the *Eulaemus* subgenus, and some species from different clades within *Liolaemus* subgenus such as *L. chaltin*, *L. alticolor* and *L. puna*, and one clade within *P. palluma* group (Fig. 3). In contrast, *C. adspersa* and entire clades have radiated into low elevations such as the *L. lineomaculatus* group, *L. nigromaculatus* group, *L. melanops* group, *L. anomalus, L. wiegmanii,* and the entire *P. patagonicus* group (Fig. 3).

Table 1. Phylogenetic signal estimates for body temperature variables (T_b and T_p), climate [air temperature (T_a) and rainfall], geographic location (latitude, longitude, elevation), substrate affinity, reproductive mode (viviparous and oviparous), hours of restriction of activity (H_r) and hours of activity (H_a).

	λ Liolaemidae		λ *Liolaemus*		λ *Phymaturus*	
Variable	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value
T_b	0.69	< 0.0001	0.76	< 0.0001	<0.0001	1.00
T_p	0.22	0.39	<0.0001	1	0.18	0.56
T_a	0.80	< 0.0001	0.72	< 0.0001	0.11	0.61
Rainfall	0.50	< 0.001	0.41	0.0004	1.00	< 0.0001
Latitude	1.00	< 0.0001	0.97	<0.0001	1.00	< 0.0001
Longitude	0.78	< 0.0001	0.73	< 0.0001	<0.0001	1.00
Elevation	0.95	< 0.0001	0.93	< 0.0001	1.00	< 0.0001
Substrate affinity*	0.58	< 0.001	0.75	< 0.0001	–	–
Reproductive Mode[a,b]	0.98	< 0.001	0.99	< 0.0001	–	–
Hours of restriction	0.58	< 0.002	–	–	–	–
Hours of activity	0.46	< 0.001	–	–	–	–

The *P*-values represent the results of tests that the estimate of lambda exceeds 0. Significance threshold is $P < 0.05$.

[a] All *Phymaturus* species are saxicolous

[b] All *Phymaturus* species are viviparous

GEOGRAPHICAL AND CLIMATE PREDICTORS OF T_b, T_p, AND TNB

In the Liolaemidae, T_b decreased toward southern latitudes and to the west, with lower T_a, and with the interaction between southern latitudes and low T_a (Table 2). We found that variation in T_b was not predicted by elevation or rainfall. Preferred temperatures (T_p) increased at southern latitudes, with higher elevations and with field T_b (Table 2). Furthermore, there is a significant correlation between T_p and T_b ($r = 0.64$, $P < 0.001$, $N = 92$; Table 2). The TNB increases at southern latitudes and higher elevations (Phylogenetic ANOVA, $F_{latitude} = 19.87$, $b = 0.2114 \pm 0.047$, $P < 0.0001$; $F_{elevation} = 5.30$, $b = 0.0007 \pm 2.06$; $P < 0.023$; $df = 1$; $N = 89$), and there was no significant relationship with the interaction between elevation and latitude ($P > 0.05$). Negative values of TNB were exhibited by species within *L. melanops* group: *L. cuyanus*, *L. casamiquelai*, *L. rothi*, and *L. martorii*; *L. wiegmannii*group: *L. multimaculatus*, *L. riojanus*, *L. salinicola*, and *L. scapularis*; *L. montanus* group: *L. scrocchii* and *L. multicolor*, and in only one species of the *L. walkeri* group, *L. fuscus*. Only one *Phymaturus*, *P. sinervoi*, showed negative value of TNB (Fig. 4A).

Body temperature (T_b) showed no significant relationship with any of the geographical or climatic variables when the analysis included only the genus *Liolaemus*. However, T_p increased at southern latitudes, higher elevation, and with higher T_b (Table 2). In *Phymaturus* T_b increased with southern latitudes and decreased toward the West but T_p could not be predicted by any geographic (latitude, longitude, and elevation) or climatic variables (T_a and rainfall; Table 2).

In the genus *Phymaturus*, none of the geographical or climate variables were related to T_b of the species in the *P. patagonicus* group. However, T_p increases at southern latitudes, higher elevation, and with lower rainfall (Table 3). In the *P. palluma* group higher values of T_b occurred in locations with low rainfall; T_p did not show any relationship with the geographic or climatic variables (Table 3).

RELATIONSHIP BETWEEN REPRODUCTIVE MODE AND THERMAL CHARACTERISTICS (T_b, T_p, AND TNB)

Values for T_b and T_p did not differ between oviparous and viviparous species at the family level (Table 4). An analysis restricted to species within the genus *Liolaemus* supported a pattern of oviparous species having a higher T_b than viviparous species. We found no differences among viviparous and oviparous species for T_p (Table 4). The T_a of environments occupied by oviparous species was higher than those of viviparous species when the analysis included all liolaemid species or was restricted to the genus *Liolaemus*. We found that the distribution of oviparity was in eastern longitudes, and lower elevations (Table 4). However, rainfall in the environments occupied by oviparous species was no different than those of the viviparous (Table 4). Viviparous liolaemids showed higher TNB than oviparous species (ANOVA, $F = 9.77$, $P < 0.002$, $df = 1$, $N = 84$, Fig. 4D).

COMPARISONS OF T_b, T_p, AND T_a, AND H_a AND H_r AMONG SPECIES WITH DIFFERENT SUBSTRATE AFFINITIES

There were no differences in T_b, T_p, T_a, rainfall, H_r or H_a among arboreal, psammophilous, or saxicolous lizards when

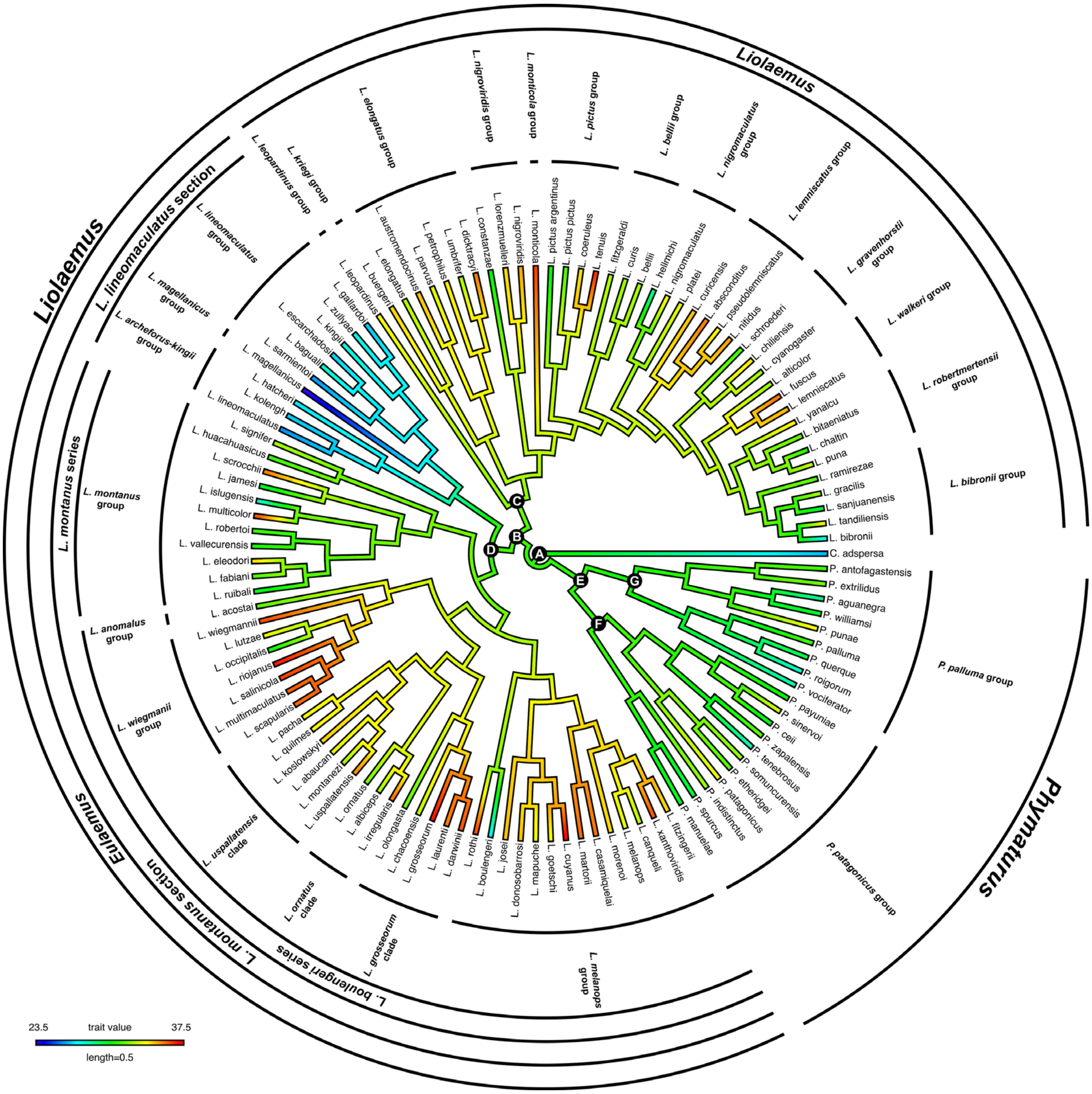

Figure 1. Maximum likelihood reconstruction of ancestral character states for body temperature (T_b) of 119 species of Liolaemidae using the function contMap. Cool colors indicate species with low field active body temperatures (T_b) and warmer colors designate species with higher values of T_b. Letters A, B, C, D, E, F and G correspond to the nodes of the main clades.

comparing all liolaemid species. The analysis restricted to the genus *Liolaemus* showed no differences among T_b, T_p, T_a, H_r, or H_a. The sole exception was rainfall, which was higher in the environments inhabited by arboreal species, but was not different between saxicolous and psammophilous (Table 5).

COMPARING THE EVOLUTIONARY RATES OF T_b AND T_p IN LIOLAEMIDAE

Estimated rates of evolution for T_b and T_p were 1.35 (AICc = 558.44) and 0.28 (AICc = 366.53), respectively. Likelihood ratio tests showed that T_b had greater evolutionary rate than T_p ($\lambda^2 = 383.82$, $P < 0.0001$).

COMPARISON BETWEEN T_b AND T_p

The mean T_b in the family was 32.70 ± 2.98 (coefficient of variation, CV = 0.09) and mean T_p was 35.18 ± 1.39 (CV = 0.04). T_b was significantly lower than T_p (Phylogenetic paired *t*-test, $t_{89} = 5.69$, $P < 0.0001$, $\lambda = 0.86$).

GEOGRAPHY, CLIMATE, T_b, AND REPRODUCTIVE MODE AS PREDICTORS OF H_r AND H_a

Among Liolaemidae, H_r increases at northern latitudes and with higher T_a, but did not show any significant relationship with the remaining climatic or geographic variables. Potential hours of activity (H_a) increased at northern latitudes, at higher elevation, in environments with lower T_a, and lower rainfall. We also found

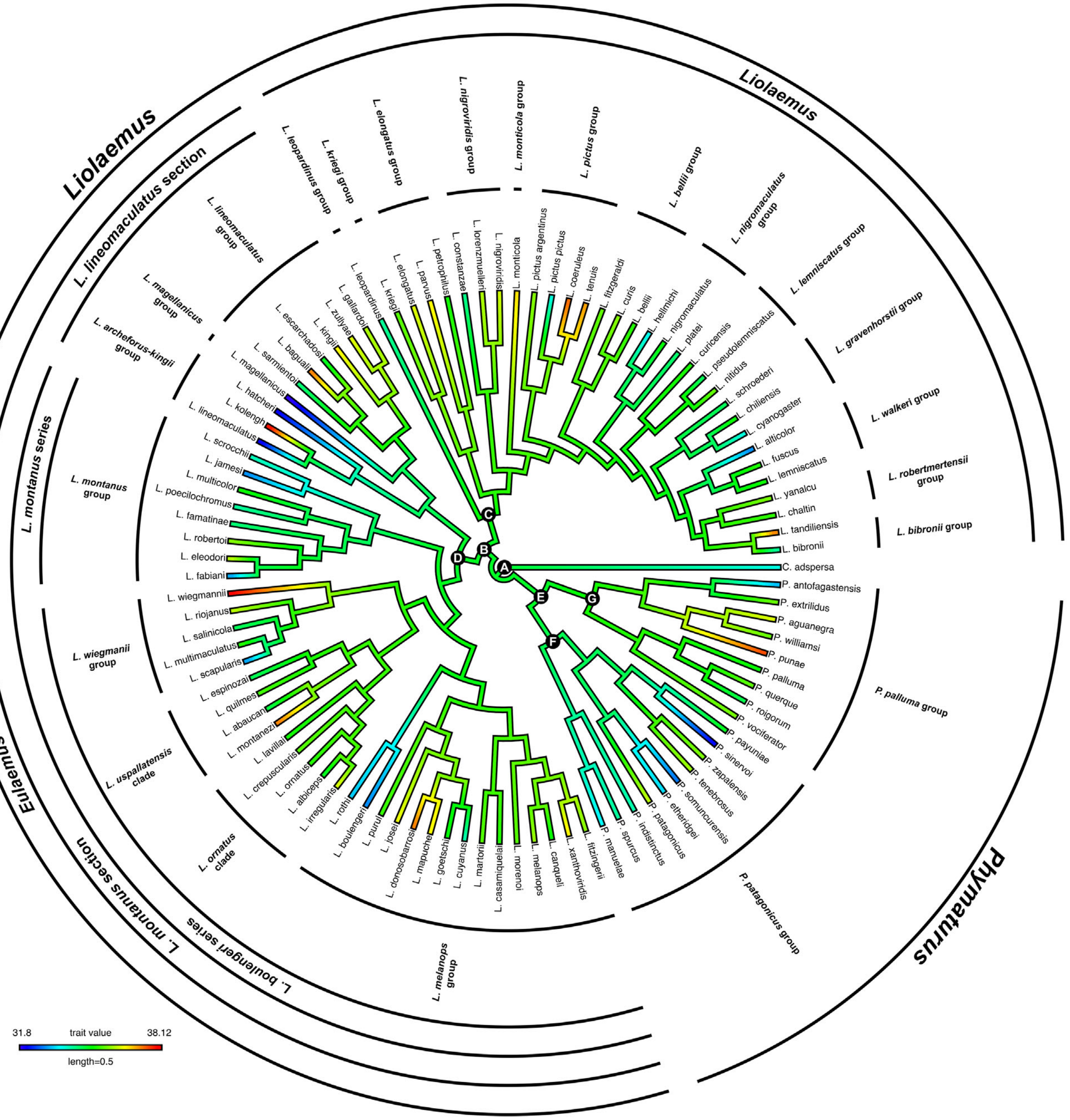

Figure 2. Maximum likelihood reconstruction of ancestral character states for thermal preference of 99 species of Liolaemidae using the function contMap. Cool colors indicate species with low preferred body temperatures (T_p) and warmer colors designate species with higher values of T_p. Letters A, B, C, D, E, F and G correspond to the nodes of the main clades.

no evidence that the combined effect of latitude:longitude predicted H_r (Table 6). The H_r was higher in oviparous than in viviparous Liolaemidae (Table 4). Overall, the oviparous clades such as *L. melanops* (*Eulaemus* subgenus) and *L. nigromaculatus* (*Liolaemus* subgenus) exhibit highest values of H_r than those viviparous clades within *Liolaemus* or *Phymaturus* (Fig. 5). In contrast, the H_a are greater for viviparous species compared to oviparous species (Fig. 6; Table 4).

Discussion

PHYLOGENETIC TRENDS IN THERMAL BIOLOGY IN RELATION TO GEOGRAPHY AND CLIMATE

The uplift of the Andes during the Miocene and accompanying climate change over the last ~25-27 million years ago generated a variety of novel thermal and humidity environments for lizards (Blisniuk et al. 2005; Esquerré et al. 2019). The ecological opportunities arising from the shift in climate and heterogeneous

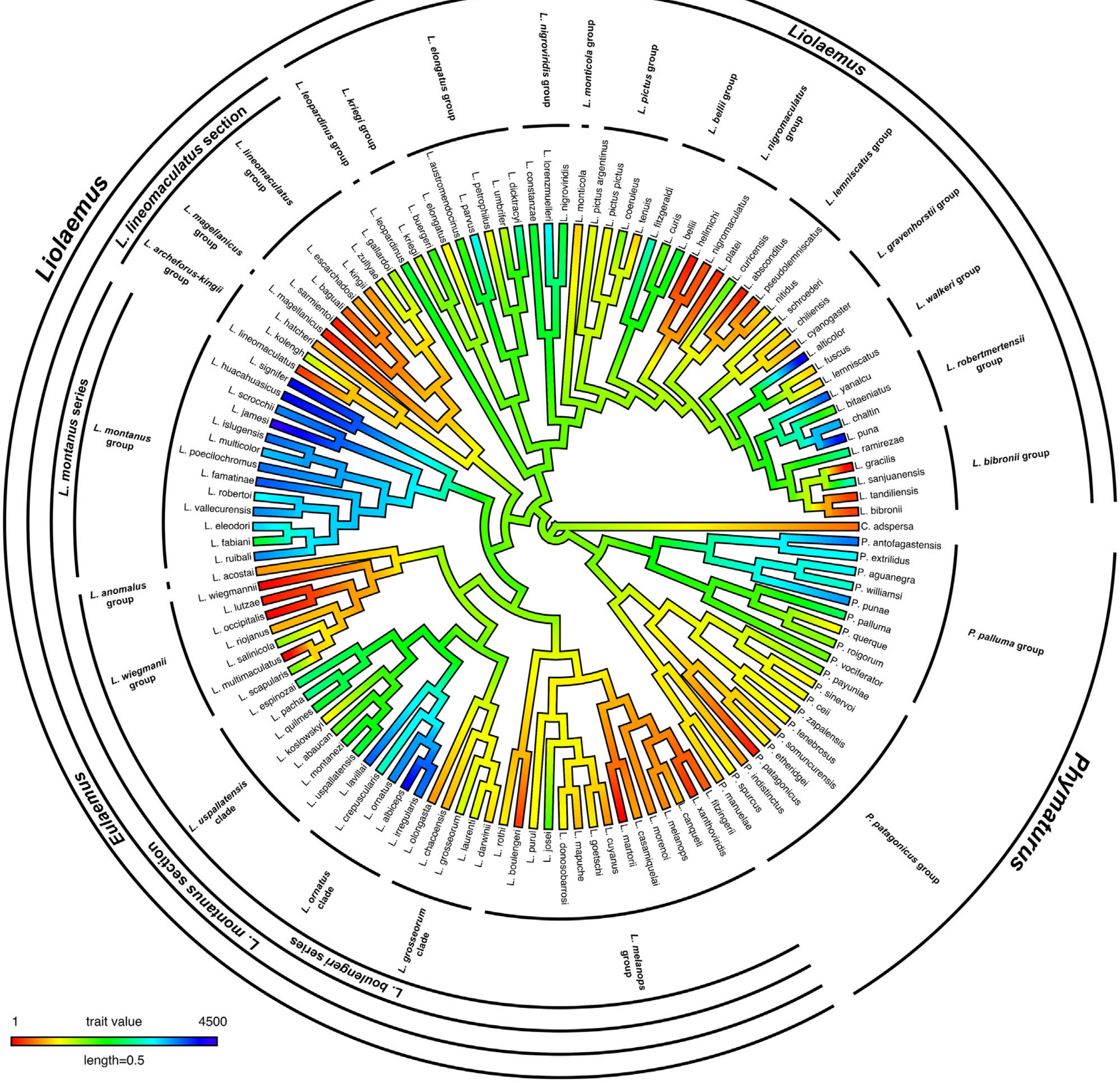

Figure 3. Maximum likelihood reconstruction of ancestral character states for elevation in the Liolaemidae. Cool colors indicate species with at high elevations and warmer colors designate species at lower elevations.

topography facilitated the colonization of diverse environments (Ferri Yáñez 2016; Esquerré et al. 2019), promoted the evolution of different thermoregulatory behaviors (Ibargüengoytía et al. 2010; Medina et al. 2012; Valdecantos et al. 2013; Piantoni et al. 2016), feeding habits (Espinoza et al. 2004), substrate affinities (Schulte et al. 2004; Jiménez-Robles and De la Riva 2019), and mode of reproduction (Schulte et al. 2000; Esquerré et al. 2019). The diversification of Liolaemidae is an outcome of historical biogeography (Olave et al. 2020), and evolutionarily labile thermal physiology, but this is more remarkable in *Liolaemus*, because trait evolution has been more conservative in *Phymaturus* and *Ctenoblepharys*.

In Liolaemidae, and within the genus *Liolaemus* variation in T_b, geographic variables (latitude, longitude and elevation), climate (T_a, rainfall), substrate affinity, and reproductive mode was explained by phylogeny. High values of phylogenetic signal (λ) indicate that different clades in the family and within the genus *Liolaemus* evolved in distinct environments and explains, in part, the current diversity in T_b and T_p. In the family Liolaemidae, mean T_b is lower at southern latitudes, but increases at lower

Table 2. Results from a multiple regression based on a phylogenetic generalized least square analysis (PGLS) using an Ornstein-Uhlenbeck model of evolution for either body temperature (T_b) and preferred temperature (T_p) *versus* geographic location (latitude, longitude, elevation), climate [air temperature (T_a), rainfall] and T_b.

Variable	β ± SE	*t*	*P*-value	Variable	β ± SE	*t*	*P*-value
A. Liolaemidae (*Ctenoblepharys*, *Liolaemus* and *Phymaturus*)							
Response variable: T_b ($N = 121$)				Response variable: T_p ($N = 92$)			
Intercept	322.54 ± 126.9	2.54	0.013	Intercept	31.59 ± 5.75	5.49	< 0.001
Latitude	–3.77 ± 1.76	–2.14	0.034	Latitude	0.077 ± 0.029	2.67	0.009
Longitude	–3.98 ± 1.84	–2.15	0.032	Longitude	–0.085 ± 0.063	–1.33	0.18
Elevation	–0.02 ± 0.016	–0.97	0.33	Elevation	0.0005 ± 0.0022	2.36	0.02
T_a	–7.51 ± 3.24	–2.32	0.02	T_a	0.086 ± 0.04	1.97	0.052
Rainfall	–0.53 ± 0.28	–1.92	0.06	Rainfall	0.0863 ± 0.009	0.25	0.80
Latitude:T_a	–0.03 ± 0.011	–2.38	0.02	T_b	0.1480 ± 058	2.52	0.014
B. *Liolaemus*							
Response variable: T_b ($N = 105$)				Response variable: T_p ($N = 77$)			
Intercept	37.81 ± 6.39	5.91	< 0.001	Intercept	31.54 ± 5.94	5.31	< 0.001
Latitude	–0.03 ± 0.057	–0.67	0.51	Latitude	0.11 ± 0.03	3.39	0.0012
Longitude	–0.07 ± 0.087	–0.82	0.41	Longitude	–0.12 ± 0.07	–1.82	0.073
Elevation	0.0009 ± 0.00043	0.24	0.80	Elevation	0.0005 ± 0.0002	2.32	0.023
T_a	0.06 ± 0.07	0.95	0.35	T_a	0.06 ± 0.05	1.29	0.21
Rainfall	–0.003 ± 0.01	–0.22	0.83	Rainfall	–0.005 ± 0.01	–0.53	0.60
				T_b	0.21 ± 0.06	3.25	0.002
C. *Phymaturus*							
Response variable: T_b ($N = 20$)				Response variable: T_p ($N = 19$)			
Intercept	75.58 ± 25.69	2.94	0.01	Intercept	34.78 ± 28.91	1.27	0.22
Latitude	0.69 ± 0.28	2.38	0.03	Latitude	–0.08 ± 0.33	–0.26	0.80
Longitude	–1.09 ± 0.39	–2.78	0.02	Longitude	0.009 ± 0.42	0.02	0.98
Elevation	0.03 ± 0.0014	2.21	0.05	Elevation	0.0009 ± 0.002	0.05	0.96
T_a	0.02 ± 0.11	0.17	0.87	T_a	0.15 ± 0.09	1.58	0.13
Rainfall	–0.01 ± 0.03	–0.50	0.62	Rainfall	0.006 ± 0.03	0.18	0.86
				T_b	–0.03	0.21	0.88

The results of the regression analysis include; predictor variables, β ± standard error (SE), Student *t*-test, and probability values (*P*-value) for the family Liolaemidae (A, *Ctenoblepharys*, *Liolaemus* and *Phymaturus*), the genus *Liolaemus* (B) and genus *Phymaturus* (C) are indicated. Significance threshold is $P < 0.05$.

elevations and to the more xeric eastern environments. However, we failed to detect a correlation with T_b and geographic or climatic variables in the genus *Liolaemus*, suggesting that behavioral thermoregulation compensates for the gradient in T_a as observed in other families (behavioral inertia; Huey et al. 2003; Muñoz and Losos 2018). In addition to plasticity, gene flow can reduce the opportunity for local adaptation (Lenormand 2002). In this regard, future studies should explore the case of *L. pictus argentinus*, a widespread species with continuous populations along environmental gradients that maintain similar T_b by means of thermoregulation (Gutiérrez et al. 2010).

We found that latitude and elevation exhibited significant phylogenetic signal in *Phymaturus*. This pattern reflects the near allopatric distribution of the two main clades. Species in the *P. palluma* group are found at high elevation habitats in the northern and central Andes of Chile and adjacent western Argentina, whereas species in the *P. patagonicus* group have a distribution restricted to mid-elevation sites in the south east of the Patagonian steppe of Argentina. The two groups are sympatric only in northern Patagonia, near Neuquén (*Phymaturus zapalensis* and *Phymaturus querque*), and in Mendoza (*P. roigorum* and *P. payuniae*). The increase in T_b toward southern latitudes and to the east in *Phymaturus* can also be explained by the differences between the environments where the two main groups prevail, since T_b does not show a relationship with geography or climate within *P. patagonicus* or *P. palluma* groups. The only observed trend is for a higher T_b in the *P. palluma* group inhabiting environments with lower rainfall. In addition, the *P. patagonicus* group lives in low-elevation, steppe environments of Patagonia and experiences milder conditions than species living at high elevations in

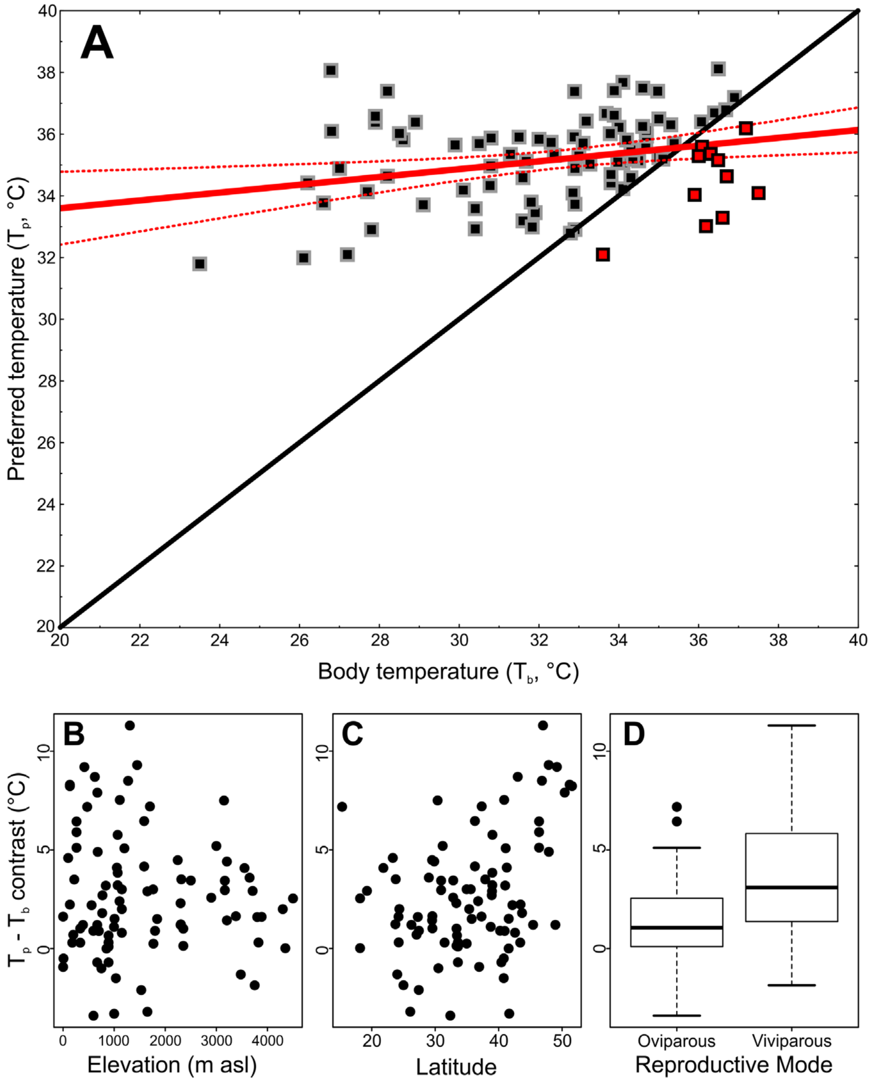

Figure 4. Thermal-niche buffering in liolaemids. Relationships between of T_p vs T_b (A, regression and 95 % confidence intervals are indicated in red, black line is the best fit 1:1; red squares indicated the species whose T_b exceed T_p). Thermal-niche buffer index (TNB) versus elevation (B) and versus latitude (C). Box plot shows the difference in TNB between oviparous and viviparous species (D).

the northern Andes (Díaz-Gómez 2007; Garreaud 2009; Cabezas-Cartes et al. 2019).

COMPARISON OF EVOLUTIONARY TRENDS IN T_b AND T_p: RELEVANCE OF OPTIMIZATION OF DIFFERENT PHYSIOLOGICAL TRAITS

Ancestral character reconstructions show there is a trend in the evolution of T_b toward higher temperatures in most clades (T_b from 31.21°C to 37.5°C), with the exception of conservatism in T_b among species in the *L. lineomaculatus* section and in *Phymaturus* as proposed in previous studies (Ibargüengoytía et al. 2008; Labra et al. 2009; Cruz et al. 2009). The trend in T_b is similar to the observed rise in environmental temperature of 6°C in the last ~20000 years (Marcott et al. 2013; Figs. 1 and 2) when considering the low T_b of *C. adspersa* (31.21°C). Our estimate is lower than the reconstructed temperature for the common ancestor of Liolaemidae (34.0 ± 5.8°C) as calculated by Espinoza et al. 2004; based on 67 taxa). As mentioned above, an evolutionary trend toward lower T_b occurred only in the *L. lineomaculatus* section from high latitudes in southern Patagonia (Fig. 1). The low T_b, but similar T_p compared with ancestors in the *L. lineomaculatus* clade (Figs. 1 and 2) provides evidence the species have constrained opportunities for thermoregulation. In fact, *L. lineomaculatus, L. magellanicus* and *L. sarmientoi* inhabit sub-optimal thermal conditions in the cold environment at southern latitudes in Argentina and Chile (Ibargüengoytía et al. 2020). According to eco-physiological studies of this clade, some species show limitations in the effectiveness of thermoregulation, which seems to be related to their environments and substrate affinity (Ibargüengoytía et al. 2010; Fernández et al. 2011; Medina et al.

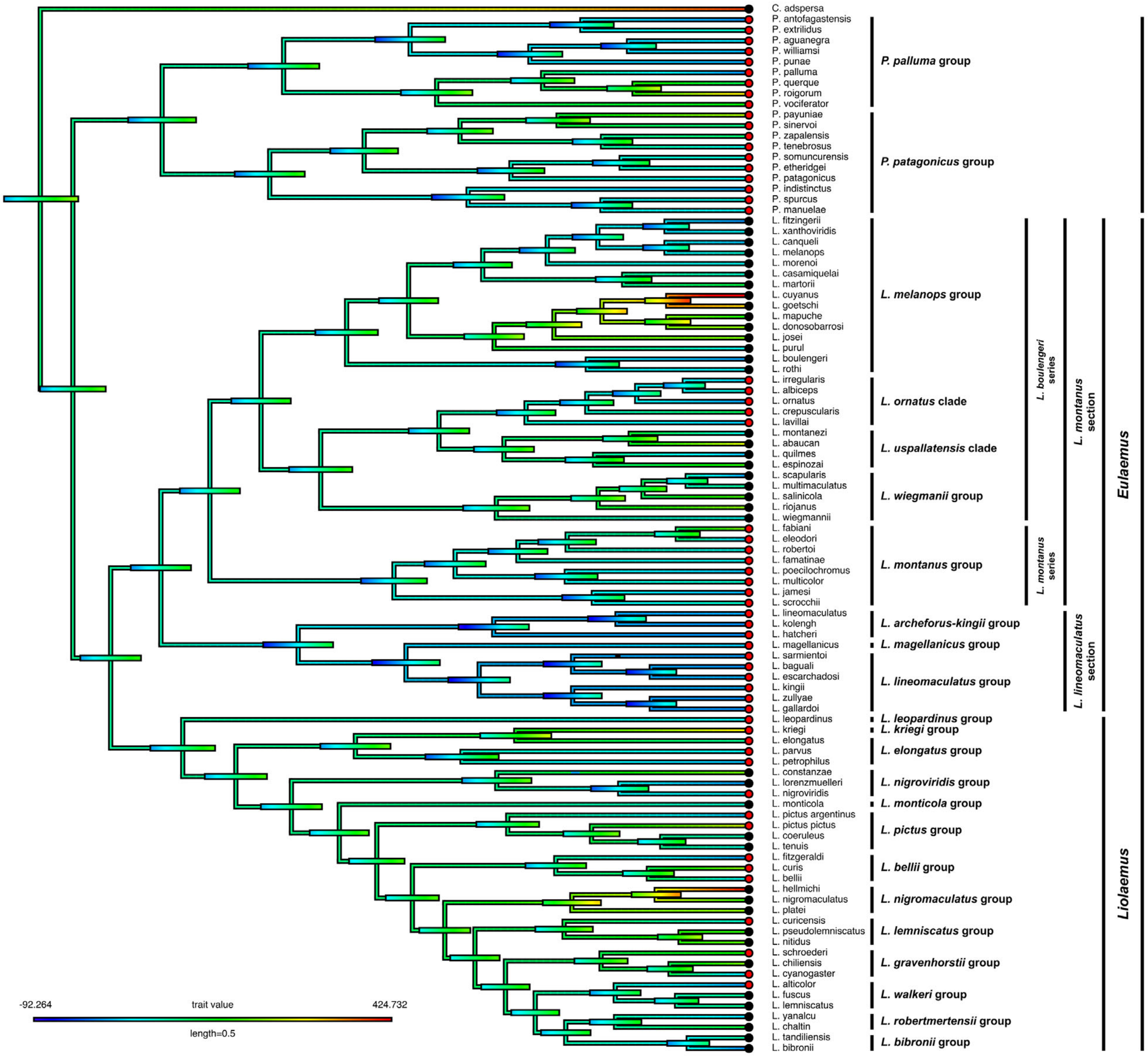

Figure 5. Ancestral state reconstruction of hours or restriction of activity (H_r). Tip labels indicate Reproductive Mode of each species. Red = Viviparous, Black = Oviparous. Cool colors indicate species with low H_r and warmer colors designate species with high H_r.

2011). In particular, the lowest T_bs correspond to the southernmost lizards of the world, the viviparous *L. magellanicus* and *L. sarmientoi* that are sympatric in part of their distribution and inhabit the Magellanic steppe (from 50.11° to 53.9° and 48.67 to 52.31°S, respectively; Ibargüengoytía et al. 2010). In *Phymaturus*, fewer species show lower T_b than the most recent common ancestor, which is a reflection of conservatism in most life-history traits (Fig. 1). In particular, the southernmost species within the *P. palluma* group, which includes *P. roigorum* (1587 m asl; Corbalán et al. 2013), and *P. vociferator* (1700 m asl; Vidal et al. 2010) that inhabits the highlands on either side of the Andes, and *P. tenebrosus* (belonging to *P. patagonicus* group) that inhabits mid-elevation tablelands in central Patagonia (1110 m asl; present study).

Results from the ancestral reconstruction show limited variation in T_p perhaps reflecting low or maladaptation to prevailing environments. Values for T_p fluctuate about a mean of 34°C with a tendency for lower temperatures manifested at tip taxa (as low as 31.8°C) and increasing in only a few taxa. One species, the psammophilous *L. wiegmannii*, has an extreme T_p of up to 38.0°C (Fig. 2) and inhabits the oceanic temperate environment of the Atlantic coast of Argentina (Stellatelli et al. 2013). We note that T_p increases at southern latitudes and higher elevations, which could be explained by several species. First, the occurrence of the saxicolous species *L. baguali* and *L. kolengh*, found at high latitudes and moderate elevation (49.18°S, 417 m asl and 46.99°S, 1307 m asl, respectively). These two species have low T_b but unexpected higher T_p than most liolaemids. Second, *L. coeruleus*

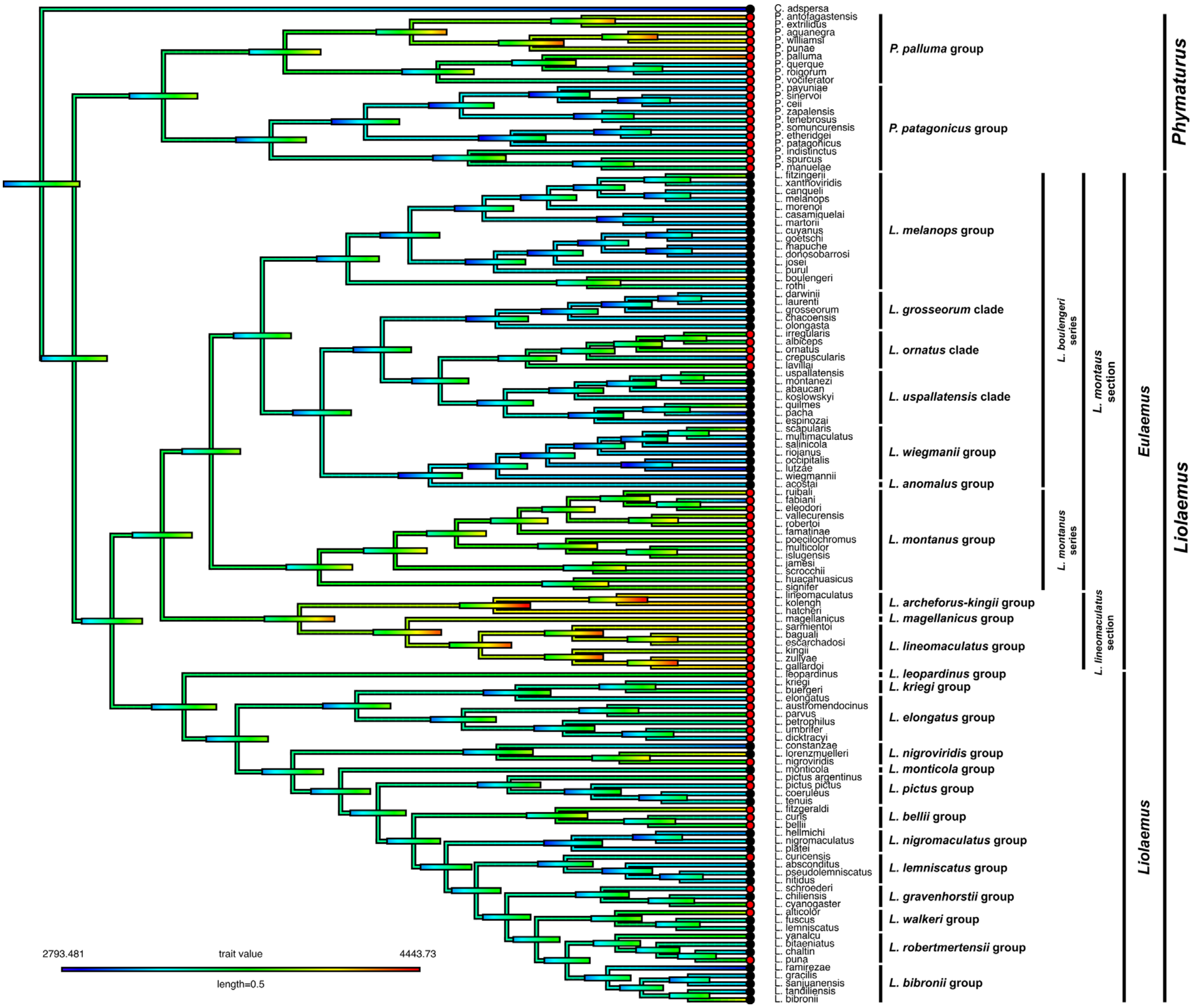

Figure 6. Ancestral character state reconstruction of H_a. Tip labels indicate Reproductive Mode of each species. Red = Viviparous, Black = Oviparous. Cool colors indicate species with low H_a and warmer colors designate species with high H_a.

and *L. tenuis* inhabiting rocky or forest highlands of the Andes in northern Patagonia (38.95°S, 1650 m asl and 33.58°S, 890 m asl, respectively) also have high T_p. Third, *P. punae* also found at mid-latitude, but high elevation habitats in the Andes (29°S, 3650 m asl) have the highest value for T_p in the genus *Phymaturus* (37.69°C; Table S1). There is not an evident relationship among phylogeny, mode of reproduction or substrate affinity to explain the high T_p of these species living at high latitudes or elevations.

The correlation between T_p with T_b suggests evolutionary constraint between the traits as observed for several species of lizards, including *Liolaemus* (Labra et al. 2009; Black et al. 2019; García-Porta et al. 2019). Consistent with our prediction and despite the family-wide diversification in several thermal traits, rates of environmental change may outpace rates of trait evolution (Miles 1994), considering that there is a difference of ~3°C to 4°C between field active T_b and T_p in the family Liolaemidae. This difference is higher than what was observed for most lizard families (Black et al. 2019). Lizards in Patagonia show T_p values higher than the T_b lizards attain in nature (Labra et al. 2008; Medina et al. 2012; Duran et al. 2018; Cabezas-Cartes et al. 2019; Ibargüengoytía et al. 2020). Lower evolutionary rates of T_p than T_b could represent different constraints for thermoregulation under natural conditions in T_b, and a compromise for optimizing multiple physiological processes that differ in both the thermal performance optima (T_{opt}) and performance breadths (*sensu* Huey 1982). A potential result is a relaxation of the different constraints for thermoregulation under natural conditions coupling between T_{opt} and T_b and partial coadaptation (Angilletta 2009). So, one species can be well adapted for one trait and maladapted for another trait in the present conditions (Huey 1982). The case of liolaemids living in Patagonia that show differences

Table 3. PGLS analysis with geographic location and climatic variables as predictors for the genus *Phymaturus* [*P. patagonicus* group (A) and *P. palluma* group (B)].

Source	β	SE	t	P – value
A. *P. patagonicus* group				
E.1. Response variable: T_b ($N = 10$)				
Intercept	–17.56	143.15	0.12	0.91
Latitude	2.81	11.00	0.26	0.81
Longitude	–1.05	8.20	0.13	0.91
Elevation	0.01	0.04	0.30	0.78
T_a	–0.05	0.75	0.07	0.95
Rainfall	–0.04	0.05	0.73	0.52
$\lambda = 0$, $R^2 = 0.62$, $F_{5,3} = 0.97$, $P = 0.54$				
E.2. Response variable: T_p ($N = 10$)				
Intercept	–13.63	24.98	0.55	0.64
Latitude	9.79	1.94	5.06	0.04
Longitude	–5.10	1.43	3.56	0.07
Elevation	0.04	0.007	5.20	0.04
T_a	–0.54	0.13	4.18	0.05
Rainfall	–0.05	0.01	4.72	0.04
T_b	–0.14	0.10	1.39	0.30
$\lambda = 0$, $R^2 = 0.98$ $F_{6,2} = 16.43$, $P = 0.06$				
B. *P. palluma* group				
E.1. Response variable: T_b ($N = 11$)				
Intercept	–7.71	40.32	0.19	0.86
Latitude	–0.39	0.32	1.24	0.13
Longitude	0.89	0.53	1.69	0.17
Elevation	–0.003	0.002	1.40	0.23
T_a	0.35	0.34	1.03	0.36
Rainfall	–0.44	0.19	4.36	0.02
$\lambda = 1.00$, $R^2 = 0.89$, $F_{5,4} = 6.63$, $P = 0.05$				
E.2. Response variable: T_p ($N = 11$)				
Intercept	28.30	33.92	0.83	0.47
Latitude	0.32	0.32	0.99	0.39
Longitude	–0.14	0.55	0.26	0.81
Elevation	0.0006	0.002	0.30	0.79
T_a	0.72	0.31	2.34	0.10
Rainfall	0.17	0.18	0.96	0.41
T_b	–0.30	0.36	0.83	0.47
$\lambda = 0$, $R^2 = 0.84$, $F_{6,3} = 4.10$, $P = 0.14$				

in T_{opt} for traits related to fitness and in many cases the T_{opt} is lower than the T_p (Bonino et al. 2011; Kubisch et al. 2011; Fernández et al. 2011; Fernández et al. 2017; see also Vicenzi et al. 2018). For example, in *L. sarmientoi* the 90% of values for T_b are lower than the interquartile of T_p ($T_{set} = 33$–37°C Ibargüengoytía et al. 2010), and T_{opt} varies from 27°C in sprint runs to 36°C in long runs. Sprint speed represents the distance usually used for evasive behaviors, for example when liolaemids are basking close to their refuges (on the ground or by crevices) and suddenly flee from a predator (Fernández et al. 2017; Higham 2019; Vicenzi et al. 2019). Long runs correspond to distances observed to be used for social activities (territorial defense – i.e., patrolling rock promontories), feeding, and predator avoidance (Fernández et al. 2011; Cabezas-Cartes et al. 2014; Higham 2019).

On the other hand, T_b is determined by different constraints for thermoregulation under natural conditions (García-Porta et al. 2019). For example, lizards in the Andes Valleys are exposed to high solar radiation during midday and contrasting cold temperatures during the rest of the day when the sun is occluded by mountain ridges (Corte and Espizúa 1981; Garreaud 2009; Vicenzi et al. 2017; Vicenzi et al. 2018). These constraints include risks of overheating during hotter periods of the day and reduction in H_a (Vicenzi et al. 2017; Vicenzi et al. 2018; Laspiur et al. in press). In saxicolous lizards, where basking during midday could result in overheating as the substrate temperature exceeds 40°C these constraints become particularly important. Moreover, substrate temperatures above T_p can last for several hours due to thermal inertia of the rocks (Huey 1991; Vicenzi et al. 2017; Duran et al. 2018; Vicenzi et al. 2019; Laspiur et al. in press). Hence, in many liolaemids there is avoidance of thermoregulatory behavior for several hours of the day resulting in high H_r (e.g., *P. tenebrosus*, Sinervo et al. 2010; *P. querque*, *P. zapalensis*, *L. elongatus*, Duran et al. 2018; *P. palluma*, Vicenzi et al. 2017).

THERMOREGULATION, H_a AND H_r

Previous studies of the thermal ecology of Liolaemidae showed that thermoregulation effectiveness increases at southern latitudes and higher elevations, suggesting that liolaemids closer to the tropics may be more vulnerable to global warming than temperate species (Sinervo et al. 2010; Piantoni et al. 2016; Cabezas-Cartes et al. 2019). In tropical environments, liolaemids behave like thermoconformers or poor thermoregulators and have T_bs similar to ambient temperatures that in many cases exceed their T_p (Piantoni et al. 2016). Viviparous liolaemids occur in colder environments and in contrast with our prediction, they show lower H_r and higher H_a as in *Phymaturus*, the *L. lineomaculatus* section, and most of the high-elevation species within the *L. montanus* section (*L. montanus* and *L. ornatus* groups; Fig. 5). Instead, the oviparous clades exhibited the highest H_r and the lowest H_a such as the *L. melanops* group (*Eulaemus*) from arid habitats in central Monte and Patagonia, Argentina, and the *L. nigromaculatus* group from central-to-northern Chile. In addition, when analyzing the TNB, all species exhibiting low values are distributed along the "arid diagonal" from southern South America, that runs from north-west (10–30°S) to the south east (30–45°S). Most of these species are psammophilous according to our prediction, including members belonging to the *L. montanus* and *L. walkeri* groups in the northern part of the diagonal; *L. wiegmannii* group at middle latitudes, and species from *L. melanops* group, plus the single *Phymaturus* species,

Table 4. Comparison of body temperature (T_b), preferred temperature (T_p), air temperature (T_a), rainfall, latitude (degrees south), longitude (degrees west), elevation (m asl), and hours of restriction (H_r) and activity (H_a) between oviparous and viviparous species in the Liolaemidae and within genus *Liolaemus* using Ornstein-Uhlenbeck model of evolution (OU).

	Mean ± SE (121)			
Variable	Oviparous	Viviparous	Phylogenetic ANOVA χ^2 value and *P* value	
Liolaemidae				
T_b	34.06 ± 0.33 (56)	31.48 ± 0.36 (63)	2.27	0.09
Total	32.69 ± 0.27 (119)			
T_p	35.44 ± 0.19 (42)	34.98 ± 0.19 (57)	3.20	0.40
Total	35.18 ± 0.14 (99)			
T_a	15.44 ± 0.56 (58)	10.46 ± 0.50 (68)	33.35	0.001*
Total	12.76 ± 0.43 (126)			
Rainfall	31.87 ± 3.63 (58)	24.58 ± 2.21 (68)	0.98	0.66
Total	27.94 ± 2.07 (126)			
Latitude	33.06 ± 0.90 (58)	34.51 ± 1.08 (68)	0.06	0.81
Total	33.84 ± 0.71 (126)			
Longitude	67.01 ± 0.7 (58)	69.48 ± 0.20 (68)	4.95	0.026*
Total	68.35 ± 0.38 (126)			
Elevation	1118 ± 128.01 (58)	2191 ± 161.36 (68)	16.51	0.001*
Total	1697.87 ± 115.15 (126)			
H_r	211.07 ± 25.60 (58)	75.70 ± 9.57 (68)	13.17	0.001*
H_a	3275.72 ± 38.89 (58)	3629 ± 42.59 (68)	21.20	0.0001*
Liolaemus				
T_b	34.19 ± 0.31 (55)	31.76 ± 0.50 (43)	29.1	< 0.0001*
Total	33.08 ± 0.30 (98)			
T_p	35.49 ± 0.19 (41)	35.02 ± 0.24 (38)	3.18	0.074
Total	35.26 ± 0.15 (79)			
T_a	15.35 ± 0.56 (57)	10.46 ± 0.60 (48)	26.20	<0.0001*
Total	13.12 ± 0.47 (105)			
Rainfall	32.44 ± 3.65 (57)	26.87 ± 2.80 (48)	0.48	0.82
Total	29.89 ± 2.37 (105)			
Latitude	33.37 ± 0.86 (57)	33.35 ± 1.41 (48)	0.014	0.91
Total	33.36 ± 0.80 (105)			
Longitude	66.88 ± 0.70 (57)	69.49 ± 0.27 (48)	4.67	0.03*
Total	68.07 ± 0.42 (105)			
Elevation	1130.18 ± 129.77 (57)	2394.29 ± 198.99 (48)	14.96	< 0.001*
Total	1708.06 ± 130.06 (105)			

Mean ± SE and sample size (*N*) of oviparous and viviparous lizards, and *P* value are shown.

P. sinervoi, in the southern end of the arid diagonal (Fig. 4). Nevertheless, dark-colored individuals (or species as those in the *L. melanops* group) reached high temperatures in a short-time, run faster at lower temperatures, or exhibit faster heating rates than non-melanic species (Moreno Azócar et al. 2016, Moreno Azócar et al. 2020; Literas 2017). Hence, melanism could confer an advantage for species living in cold environments, because individuals could reach T_{opt} at a lower T_a or for species such as those needing to modify their activity patterns due to reach high H_r (Moreno Azócar et al. 2020). Species are expected to exhibit some degree of melanism as a compensatory strategy to cope with a potential reduction in activity patterns, which may pertain to the species within the *L. melanops* clade distributed in warmer habitats along the arid diagonal from Argentina (*L. goetschi* clade in Moreno Azócar et al. 2016). In addition, we cannot discard a role for plasticity in physiological traits among *Liolaemus* species to cope with climate change. But, in the light of the low plasticity observed in some species of *Liolaemus* such as *L. pictus argentinus* (Kubisch et al. 2016a,b) or *L. sarmientoi* (Fernández et al. 2017) we expect that the rates of evolution or plasticity will not be fast enough to outpace the environmental disturbances as observed in several species of the genus *Sceloporus* (Sinervo et al. 2010). In summary, the oviparous liolaemids living in low elevation, arid environments are the

Table 5. Comparison of body temperature (T_b), preferred temperature (T_p), air temperature (T_a), rainfall, hours of restriction (H_r), and hours of activity (H_a) among species with different substrate affinities in Liolaemidae and within genus *Liolaemus* using Ornstein-Uhlenbeck model of evolution (OU).

	Mean ± SE (*N*)				
Liolaemidae					
Variable	Arboreal	Psammophilous	Saxicolous	χ^2 Value	*P* - value
T_b	33.34 ± 1.06 (5)	33.20 ± 0.43 (56)	32.16 ± 0.35 (58)	1.59	0.45
Total	32.70 ± 0.27 (119)				
T_p	35.05 ± 0.66 (5)	34.97 ± 0.22 (45)	35.39 ± 0.19 (49)	3.44	0.18
Total	35.18 ± 0.14 (99)				
T_a	14.09 ± 1.48 (5)	13.71 ± 0. 71 (59)	11.73 ± 0.53 (62)	0.36	0.83
Total	12.76 ± 0.43 (126)				
Rainfall	38.13 ± 15.14 (5)	27.75 ± 3.19 (59)	27.30 ± 2.70 (62)	3.87	0.15
Total	27.94 ± 2.07 (126)				
Liolaemus					
T_b	33.34 ± 1.06 (5)	33.32 ± 0.42 (55)	32.68 ± 0.48 (38)	1.37	0.50
Total	33.08 ± 0.30 (98)				
T_p	35.05 ± 0.66 (5)	34.99 ± 0.22 (44)	35.69 ± 0.21 (30)	1.48	0.39
Total	35.26 ± 0.15 (79)				
T_a	14.09 ± 1.48 (5)	13.59 ± 0.71 (58)	12.34 ± 0.63 (42)	0.98	0.95
Total	13.12 ± 0.47 (105)				
Rainfall	38.13 ± 15.14 (5)	28.23 ± 3.21 (58)	31.21 ± 3.57 (42)	10.07	0.006*(Arb > Psam = Sax)
Total	29.89 ± 2.37 (105)				
H_r	125.66 ± 50.03	171.56 ± 23.78	107.64 ± 22.71	0.19	0.91
H_a	3460 ± 93.90	3417 ± 49.77	3540 ± 55.25-37.50	0.49	0.788
N = 105					

Mean ± SE and sample size (*N*) for arboreal, psammophilous and saxicolous species. χ^2 and *P* - values are shown.

most vulnerable clades to increases in environmental temperature. The occurrence of viviparous lizards in colder environments combined with their high T_p results in lower H_r in viviparous liolaemids. These results contrast with viviparous and montane species of *Sceloporus* in Mexico (Sinervo et al. 2010) and viviparous *Phrynocephalus* of Eurasia on the Qinghai-Tibetan plateau (Sinervo et al. 2018). Therefore, viviparous liolaemids may have a lower vulnerability to climate change rejecting our hypothesis.

Recent predictions suggest a warming between 1.5 and 1.8°C for the period 2045–2065, and an increase in rainfall for the east and central subtropical Argentina (Barros et al. 2015). However, in the region of Patagonia the expected patterns are a reduction in rainfall (between 30 to 50% with respect to current conditions), and glacial retreat (assuming an extreme scenario of CO_2 and other greenhouse gas emissions, RCP "Representative Concentration Pathway" scenario 4.5 and 8.5; Meehl et al. 2007; Barros et al. 2015; IPCC 2018). Patterns of warming are expected to be more intense and faster during summer months (Barros et al. 2015). Under an increase in environmental temperature as expected for southern South America, species could adapt to the new conditions or disperse towards new locations reducing thermoregulatory costs (i.e. habitat tracking). However, the persistence of populations and species will depend on whether they have physiological and behavioral plasticity, vagility, and enough time to respond to environmental changes (Miles 1994; Cahill et al. 2012; Vicenzi et al. 2017; Fitzgerald et al. 2018; Sinervo et al. 2018). The ancestral character reconstruction results show an evolutionary trend toward higher T_bs at the family level. Moreover, we observed an increase of ~ 6°C above ancestral T_bs that coincides with an increase in ambient temperatures in the last ~20,000 years (Marcott et al. 2013). However, our analyses revealed that T_p remains stable in most clades.

Species in the genus *Liolaemus* show lability and reversals in T_b pointing out their resilience to environmental changes and the possibilities to exploit new niches. In contrast, in the genus *Phymaturus* the potential factors responsible for a more conservative character in T_b might relate to the slow life history (Boretto et al. 2018) and the stability of the ecological niche (Debandi

Table 6. Results from a multiple regression based on a phylogenetic generalized least square analysis (PGLS) analyses using Pagel's lambda model of evolution for hours of activity (H_a) and hours of restriction of activity (H_r) *versus* geographic location (latitude, longitude, elevation) and climate (air temperature [T_a], and rainfall).

Variable	β	χ^2	*P* value
Hours of restriction			
Latitude	–40.36	14.22	<0.001
Longitude	–8.55	1.57	0.21
Elevation	–0.071	1.87	0.17
T_a	18.96	38.05	<0.0001
Rainfall	0.49	0.70	0.40
Latitude: Longitude	0.43	1.59	0.21
Latitude: Elevation	0.002	1.54	0.21
$\lambda = 0.31$			
Hours of activity			
Latitude	–68.60	9.16	0.003
Longitude	–37.50	0.02	0.89
Elevation	0.15	5.02	0.03
T_a	–38.74	35.27	<0.0001
Rainfall	–2.89	5.40	0.02
Latitude: Longitude	1.25	2.99	0.08
Latitude: Elevation	–0.003	0.89	0.35
$\lambda = 0.42$			

Variables, β ± standard error (SE), Student *t*-test, and probability values (*P*) for the family Liolaemidae.

et al. 2012) that has retained saxicoly, viviparity (Donoso-Barros 1966; Cei 1986; 1993; Boretto et al. 2018), and feeding habits (Espinoza et al. 2004) since their most recent common ancestor. Nevertheless, there is potential for plasticity in those taxa buffered by a low T_b and relatively high T_p, such as species of *Phymaturus* and viviparous *Liolaemus*. The TNB (Mean T_p - Mean T_b) may counteract the rapid increase in environmental temperatures expected by the next 50 to 80 years due to climate warming. The combination with the anthropogenic reduction of entire habitats could cause extirpations and extinctions in particular in oviparous, endemic species with low vagility and actually living in warmer lowland environments (e.g., where T_p is closer to T_b).

CONFLICT OF INTEREST

There are not conflict of interest to declare.

AUTHOR CONTRIBUTIONS

N.R.I., D.M., B.S., A.L., and M.M. conceived and designed the study, participated in the interpretation of data, and wrote the manuscript. D.M., B.S., Y.F.Q., and N.R.I. contributed to the analysis and interpretation of the data. N.R.I., M.M., A.L., B.S., and D.M. assisted in data curation, contributed to field and experimental design, and acquisition of data. C.A.R.P. contributed to field and experimental design and acquisition of data of *Ctenoblepharys adspersa*. NRI. DM. BS. AL. MM. YFQ. CARP. Revised the manuscript for intellectual content.

All authors have read the manuscript and agreed about submitting it for publication.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Latitude, longitude and elevation (m asl) correspond to the locations from where the thermal values were taken, the midpoint coordinate was used when the articles referred to ranges of the species distribution.