



Thermal sensitivity of cold climate lizards and the importance of distributional ranges

Marcelo F. Bonino^{a,*}, Débora L. Moreno Azócar^a, James A. Schulte II^b, Cristian S. Abdala^c, Félix B. Cruz^a

^a Laboratorio de Fotobiología, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), CONICET-UNCOMA, Quintral 1250, Bariloche 8400, Río Negro, Argentina

^b Department of Biology, Clarkson University, Potsdam, NY, USA

^c Facultad de Ciencias Naturales e I. M. Lillo (UNT), Tucumán, Argentina

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ABSTRACT

One of the fundamental goals in macroecology is to understand the relationship among species' geographic ranges, ecophysiology, and climate; however, the mechanisms underlying the distributional geographic patterns observed remain unknown for most organisms. In the case of ectotherms this is particularly important because the knowledge of these interactions may provide a robust framework for predicting the potential consequences of climate change in these organisms. Here we studied the relationship of thermal sensitivity and thermal tolerance in Patagonian lizards and their geographic ranges, proposing that species with wider distributions have broader plasticity and thermal tolerance. We predicted that lizard thermal physiology is related to the thermal characteristics of the environment. We also explored the presence of trade-offs of some thermal traits and evaluated the potential effects of a predicted scenario of climate change for these species. We examined sixteen species of *Liolaemus* lizards from Patagonia representing species with different geographic range sizes. We obtained thermal tolerance data and performance curves for each species in laboratory trials. We found evidence supporting the idea that higher physiological plasticity allows species to achieve broader distribution ranges compared to species with restricted distributions. We also found a trade-off between broad levels of plasticity and higher optimum temperatures of performance. Finally, results from contrasting performance curves against the highest environmental temperatures that lizards may face in a future scenario (year 2080) suggest that the activity of species occurring at high latitudes may be unaffected by predicted climatic changes.

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1. Introduction

A species' geographic range is considered the fundamental unit of macroecology (Brown et al., 1996; Gaston, 2003; Whitton et al., 2012) and can vary in relation to many different factors (such as climate, competition, diseases, resource types and abundances). Ectothermic animals constitute the vast majority of terrestrial biodiversity (Wilson, 1992) and are expected to be sensitive to climatic variations, making them an interesting group to test the relationships between climatic variables and the distribution of species throughout time and space. The occurrence of these organisms in physiographically variable environments can be explained by different aspects; for example, behavioral regulation, physiological

plasticity or genetic differentiation among populations (Hertz et al., 1983). Therefore, discerning the role of physiological or behavioral plasticity in the context of climatic change is an important task. To appropriately address these alternatives in species with different geographic ranges, first we need to elucidate species distribution patterns and geographic variation in physiological traits. Then, we need to derive the mechanisms or characteristics underlying the ecological and evolutionary patterns observed (Gaston et al., 2009; Naya et al., 2012). Recent studies explicitly relate physiological traits of species and their geographic distribution ranges (e.g., Buckley, 2008, 2010; Kearney and Porter, 2009). Additionally, since the recognition of rapid and recent global climate change (Solomon et al., 2007), numerous studies have emphasized the potential risks and responses of species facing climate change (e.g., Parmesan et al., 1999, 2000; Huey and Tewksbury, 2009; Huey et al., 2010; Sinervo et al., 2010; Hanna, 2012).

* Corresponding author. Tel.: +54 0351155498031.

E-mail address: boninom@gmail.com (M.F. Bonino).

One of the hypotheses related to species distribution across environmental gradients is the climatic variability hypothesis (Gaston and Blackburn, 2000), which states that the range of climatic fluctuation experienced by terrestrial animals increases with latitude and/or elevation (and their combinations) and implies broader tolerance ranges and acclimation ability for species persisting in these sites (Gaston and Chown, 1999; Cruz et al., 2005; Ghalambor et al., 2006; Deutsch et al., 2008; Naya et al., 2012 and citations therein). Direct evidence supporting the climatic variability hypothesis has been obtained during the last fifty years (Brattstrom, 1968; Brett, 1970; Snyder and Weathers, 1975; van Berkum, 1988; Addo-Bediako et al., 2000; Cruz et al., 2005; Naya et al., 2012). Thus, there is support for predicting an association between a flexible thermal physiology and climatic variability.

Thermal tolerance capability and thermal sensitivity are strongly linked to physiological performance and environmental conditions (Hertz et al., 1983; Crowley, 1985). Thermal tolerance is the body temperature range within which an organism can survive or recover (Carothers et al., 1997; Cruz et al., 2005). Thermal sensitivity, often described as a curve, is the extent to which physiological capabilities are influenced by variation in thermal conditions within the tolerance range (Crowley, 1985; van Berkum, 1988; Hochachka and Somero, 2002; Pörtner, 2002; Gunderson and Leal, 2012). These performance curves have an area generally depicted as a left-skewed Gaussian bell curve (Huey and Kingsolver, 1989; Angilletta, 2006; Bulté and Blouin-Demers, 2006) and are described by several key parameters: the thermal optimum (T_o ; temperature at which maximum performance is reached); the optimal temperature range (known as B95); the thermal performance breadth (also known as B80); the thermal limits, referred to as the critical thermal minimum and the critical thermal maximum; and the maximal performance (Hertz et al., 1983; Angilletta, 2009). Running ability is frequently used as a performance measurement strongly related to thermal physiology (Hertz et al., 1983; Crowley, 1985; Huey and Bennett, 1990; Garland and Losos, 1994; Bauwens et al., 1995) and may have potential consequences on fitness (Wright, 1932; Arnold, 1983; Huey and Bennett, 1987), although this is not fully demonstrated.

Understanding the relationship between thermal physiology and climate requires a better knowledge of an individual's maximum performance as it depends on its optimum temperature (Angilletta et al., 2010). Barcroft (1934) and Hochachka and Somero (1973) argue that genotypes adapted to higher temperatures have greater performance ability than cold-adapted ones, since higher temperatures accelerate chemical reactions ("hotter is better"). On the other hand, Clarke (2003), Frazier et al. (2006) and Angilletta et al. (2010) suggest that biochemical adaptation may compensate the effects on thermodynamic performance, assuming that species adapted to low temperatures may present the same levels of performance compared to species adapted to high temperatures, thus turning the discussion about thermal physiology controversial.

Another interesting question is whether an organism with broad thermal tolerance has an evolutionary advantage over species with narrower thermal tolerance. Physiological and biomechanical theory suggests that design characteristics necessary for maximizing the performance of different traits can be difficult to reconcile in one phenotype (Vanhooydonck et al., 2001). Thus, theoretical models in this field are based on the assumption that the "jack of all trades is master of none" (MacArthur, 1972; Huey and Slatkin, 1976; Pianka, 1978; Huey and Hertz, 1984). Then, the performance curve of ectotherms (level of performance at different temperatures) can be viewed as a reaction norm and may allow identification of trade-offs (compromises) between the breadth

(plasticity) and the maximum level of specialization (performance; Angilletta et al., 2003).

In the present study we attempt to explore the issues expounded above in Patagonian lizards. Patagonia is characterized by a rigorous climate with strong winds and low temperatures (Páruelo et al., 1998). We studied 16 species of Patagonian Liolaemini, a species-rich clade with 257 recognized species of *Liolaemus* (Abdala and Quinteros, 2014) and nearly 40 *Phymaturus* species (Lobo et al., 2013; Avila et al., 2014). These 16 species vary considerably in the size of their distribution ranges: from microendemic species that are known only from the type locality or very few localities covering a small area (e.g., *Liolaemus kolengh*), to widespread species covering areas larger than 150,000 km² (e.g., *Liolaemus fitzingerii* and *Liolaemus elongatus*). Our aim was to evaluate the effect of their thermal tolerance and sensitivity given their distinct geographic ranges and phylogenetic relationships in an attempt to elucidate evolutionary patterns of ecophysiological traits.

In this framework we expected to find that (i) species with broader distribution ranges, where climatic fluctuations are present, will show broader thermal tolerance and performance curves compared to species with restricted distributions (Cruz et al., 2005); (ii) genotypes adapted to higher temperatures have greater performance ability than cold-adapted ones ("hotter is better"; Barcroft, 1934; Hochachka and Somero, 1973); (iii) species with broad plasticity levels have lower levels of performance (trade-off between performance level and amplitude indicators (Huey and Bennett, 1987; Garland et al., 1991; Bauwens et al., 1995; Bonino et al., 2011); and (iv) physiological thermal characteristics indicative of thermal breadth should be directly related to environmental thermal amplitude and the area occupied, rather than to mean environmental temperature in accordance with the climatic variability hypothesis (Gaston and Blackburn, 2000). We also explore the potential effects of predicted climate change based on performance breadths and future climatic predictions.

2. Materials and methods

2.1. Study animals

We studied 16 Liolaemini lizard species with very distinct geographic range sizes (see Table S1 in the supplementary online Appendix): *Liolaemus baguali*, *Liolaemus ceii*, *Liolaemus coeruleus*, *Liolaemus elongatus*, *Liolaemus fitzingerii*, *Liolaemus gallardoi*, *Liolaemus hatcheri*, *Liolaemus kingii*, *Liolaemus kolengh*, *Liolaemus magellanicus*, *Liolaemus multimaculatus*, *Liolaemus shitan*, *L. sp.* (a new and unnamed species), *Liolaemus zullyi*, *Liolaemus xanthoviridis* and *Phymaturus tenebrosus*. Distribution area estimates for each species were obtained through minimum convex polygons from our own collection data, as well as georeferenced data from the literature and museum collections for each studied species (see Table S2 in the supplementary online Appendix).

In all, 319 lizards were collected from different Patagonian localities (covering Neuquén, Río Negro, Chubut and Santa Cruz provinces in Argentina; see Table S1) and the Buenos Aires coast during different field trips between February 2009 and March 2010. After capture, the lizards were transported to the laboratory in cloth bags with moist material to avoid stress and desiccation. In the laboratory, the lizards were released in glass terraria (1.2 m × 0.6 m, subdivided into five lanes of 1.2 m × 0.12 m) where a thermal gradient (20–40 °C) was provided by three infrared lamps of 150 W at one end, so they were able to select their preferred temperature and be fed. Lizards were offered live crickets (*Achaeta domestica*), tenebrio larvae (*Tenebrio molitor*), flower buds and water ad libitum. Lizards that lost 20% or more of their original weight were not included in the experiments.

2.2. Thermal sensitivity and locomotor performance

To determine the thermal tolerance range we measured both critical minimum (CT_{min}) and critical maximum temperatures (CT_{max}). The critical temperature is defined as the temperature at which an organism loses motor coordination, failing to get back to its normal posture after being set in supine position (Carothers et al., 1997; Cruz et al., 2005); thus, individual lizards were exposed to temperatures close to their critical temperature until they lost coordination and the trial was stopped. Procedures for obtaining critical temperatures are identical to those described in Bonino et al. (2011).

To obtain thermal sensitivity data we conducted races of lizards on a horizontal 1.2 m length racetrack with seven LED sensors arranged every 0.155 m, connected to a timer circuit and an electronic data collector. Cork substrate was used to provide grip and traction. To prevent the escape of lizards, 10 cm high panels were placed on both sides. Although several studies use race tracks of up to 2 m length, there is no consensus regarding the length of the track necessary to obtain maximum speed for small lizards (snout–vent length: 60–95 mm). The running speed in lizards is usually explosive, reaching its maximum speed within the first 0.6 m after the start of a trial (Huey and Hertz, 1982; Irschick and Jayne, 1998). In fact, near 73.3% (5127/6990) of the maximum velocities registered on our racetrack were recorded by the first four LED sensors (first 0.465 m of 1.2 m total). Furthermore, it has been observed that some *Liolaemus* lizards generally do not run for a sustained distance greater than 1 m (Petriek et al., 2009). Therefore, a 1.2 m track is a reliable length to allow measurement of running speed trials.

For each run, the lizards were placed at one end of the track and released; gentle taps on the sacral region were used as stimuli until the entire track was completed (Angilletta et al., 2002; Aguilar and Cruz, 2010; Bonino et al., 2011). The speed of the lizards was measured between consecutive sensors (0.155 m). The runs were performed at five discrete body temperatures within specific CT_{mix} and CT_{max} temperatures (22 °C, 26 °C, 30 °C, 34 °C and 38 °C). Lizards were heated to the desired test temperatures in an incubator chamber (Semedic FT 290; Semedix, Buenos Aires, Argentina). Runs were conducted on consecutive days, at one temperature per day, which was assigned randomly. Each trial was ranked as “excellent” (lizards ran all the way without interruption), “good” (lizards ran with some interruption) or “poor” (lizards refused to run or escaped before the end of the run) depending on the performance and physical condition of the lizard at the time of running. 250 of the 319 collected lizards met the criteria for reliability in running performance. Each specimen completed six runs on the track for each of the five temperatures, following Losos et al. (2002); thus, each lizard ran 30 times within a period of 5 days. No more than six runs per day were made per individual, and they were divided into three series of two races, with an interval between them of at least 2 h for the lizards to rest. Body temperature of the specimens was recorded (prior to each race) with an ultra-thin K-type thermocouple connected to a digital thermometer (Extech 421502; Extech Instruments, Waltham, MA, USA). From the six runs for each discrete temperature we retained the highest speed value recorded between two of seven consecutive LED sensors (0.155 m intervals), which was considered the maximum speed (m/s) at each temperature. Then, once the series of speed points for each temperature for each individual of each species had been obtained, performance curves were constructed using CT_{min} and CT_{max} (CT_{min} and CT_{max} were the same for all individuals within a species) as extreme values. While Angilletta (2006, 2009) proposed that the simple Gaussian function provides a more acceptable description than other, more complex models under the Akaike criterion, we based the model selection on the Bayesian approach, which would enable us to use prior information about the shape

of a performance curve (Ellison, 2004), our previous experience (Bonino et al., 2011), and high r^2 values (>0.9 for all specimens). Under these criteria we used the exponentially modified Gaussian model that, as Angilletta (2006) described, is a familiar biological function with left skewness.

From the curves, we obtained for each lizard maximum sprint speed (V_{max}) and optimum temperature (T_o), defined as the temperature at which the individual reaches its maximum speed. Then we standardized the performance for each lizard species, obtaining the relative velocity at each temperature (instantaneous velocity at each temperature/maximum speed reached). After this, for each lizard we calculated the optimal temperature range and the thermal performance breadth, defined as body temperature ranges over which the lizard can run at 95% (B95) or 80% (B80) of its maximum speed (V_{max}), respectively (Hertz et al., 1983).

2.3. Geographic ranges and climate

Every species collection point was georeferenced. From each collection site we characterized the environmental thermal conditions as follows: mean temperature (T_{mean}) and environmental temperature variation (T_{ampl}, the average of the daily differences between maximum and minimum air temperatures), the latter as a measure of temperature harshness and climatic variability. Both variables were taken with consideration of the lizards' activity season (from October to the end of March). These variables were based on daily data available on the NASA website (<http://power.larc.nasa.gov/>) for a 27-year period (1983–2010).

Additionally, we obtained climate data to evaluate the impact of predicted climate change given the performance breadths of the investigated species. Data were obtained from the global meteorological database Worldclim (<http://www.worldclim.org/>) to test if thermal physiology may be affected by temperature changes of various future scenarios. We used the maximum temperature of warmest month (MTWM) for the localities of each species in the present conditions and the corresponding MTWM for the climatic change scenario A1B for 2080 (Solomon et al., 2007), which represents a drastic, but not the most extreme scenario for the future.

2.4. Data analysis

We implemented a phylogenetically informed analysis of variance (ANOVA). For this purpose we used the PhyloANOVA package in Phytools (Revell, 2012) developed in R (R Development Core Team, 2011), with 1000 simulations. Species cannot be considered as independent data points because of their phylogenetic relationships (Harvey and Pagel, 1991). Therefore, we estimated Pagel's phylogenetic signal (λ ; Pagel, 1999) from the residual errors simultaneously with the regression parameters of phylogenetic generalized least squares (PGLS) models. These analyses were carried out in the ‘caper’ (Orme et al., 2012) and ‘ape’ (Paradis et al., 2004) packages, both developed in R (R Development Core Team, 2011). This procedure is preferred as it has been shown to outperform, or to be equivalent to, phylogenetic or nonphylogenetic procedures depending on the λ value obtained (Revell, 2010).

To study the relationship between thermal variables, range size, and climatic variables, the PGLS models included environmental temperature variation (T_{ampl}), mean temperature (T_{mean}) and geographic range (Area) as predictor variables; the variables were used individually, combined in pairs, and all three together. Then, all thermal variables (TTR, B95 range, B80 range, B80 and B95 inferior and superior limits, CT_{min}, CT_{max}, V_{max} and T_o) were used as dependent variables. To ensure the regression model provided the best fit among the candidate models (Angilletta, 2006) we used the Akaike information criterion (AIC). We used Akaike weights (W_i) as a measure of strength of evidence for each model, indicating

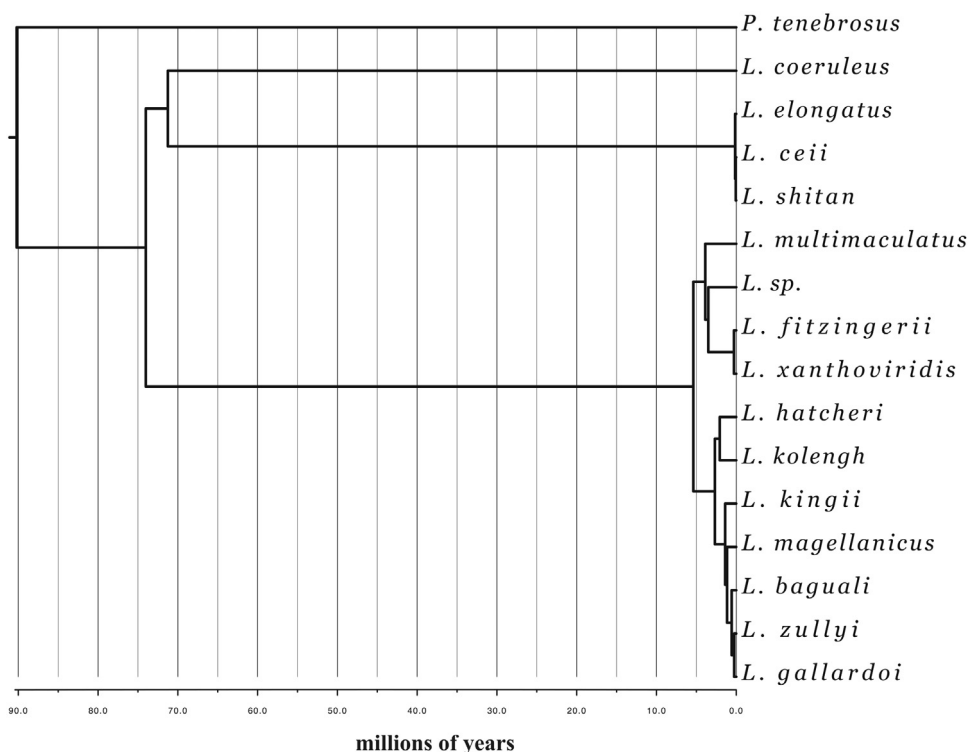


Fig. 1. Phylogenetic relationships among the investigated species obtained by the maximum likelihood method.

the probability that a given model is the best among a series of candidate models (Burnham and Anderson, 2002).

Phylogenetic analyses were based on a hypothesis inferred from mitochondrial DNA sequences spanning the protein-coding gene regions ND1 to COI, sequenced and aligned using the molecular protocols and alignment structures described in Schulte et al. (2000). 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) combined and one partition for combined tRNA and noncoding 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 therein, partitioning by codon position most often explains the data better than other partitioning schemes using likelihood ratio tests or Bayes factor estimates. The aligned DNA sequences for species included in the sample are available in TreeBASE (<http://purl.org/phylo/treebase/phyloWS/study/TB2:S13386>). The phylogenetic tree was estimated using a maximum likelihood (ML) criterion with a mixed model analysis of a priori partitioned data for the 16 Liolaemini species (Fig. 1).

3. Results

Thermal tolerance values (the difference between mean CTmax and mean CTmin values per species) of all studied species are summarized in Table 1. Thermal tolerance values varied between 38.84°C (*L. baguali*) and 30.10°C (*P. tenebrosus*). In relation to the physiological responses (locomotor responses), the highest and lowest B80 and B95 range corresponded to

L. sp. (B80 = 14.3 ± 0.89°C; B95 = 7.0 ± 0.50°C) and *P. tenebrosus* (B80 = 7.7 ± 1.52°C; B95 = 3.6 ± 0.81°C), respectively. The highest and lowest optimum temperature (To) values corresponded to *L. kolengh* (36.1 ± 2.21°C) and *L. magellanicus* (31.2 ± 1.26°C), respectively. Finally, the fastest species were *L. coeruleus* (2.42 ± 0.37 m/s), *L. kingii* (2.42 ± 0.39 m/s) and *L. sp.* (2.42 ± 0.35 m/s) and the slowest one was *L. magellanicus* (1.04 ± 0.49 m/s) (Table 1).

When comparing the thermal parameters between widespread species with an area of occurrence larger than 15,000 km² and species with a restricted distribution smaller than 13,000 km², widespread species possessed significantly broader B80 and B95, but not a broader thermal tolerance (Table 2). Additionally, when comparing To and Vmax between widespread and restricted distribution species, only To showed significant differences (Table 2).

PGLS models of thermal characteristics (To, CTmin, CTmax, B80 and B95 limits) showed better fits (based on their Wi) with thermal amplitude (Tamp; Table S3 in the supplementary online Appendix) in the case of CTmin and B80 inferior limit, whereas the rest of the variables showed better fits with mean air temperature (Tmean) of the collection sites (Table S3). Only CTmax showed a globally significant relationship (regarding intercept and slope) with Tmean (Table 3).

The trade-off analysis showed that thermal optimum (To) had a negative and significant relationship with thermal performance breadth (B80) and optimal temperature range (B95; Angilletta, 2009), but B80 was the best model (Table 4). Maximum sprint speed (Vmax) did not show a clear trend when compared to B80, B95 and To (Table 4).

To test the climatic variability hypothesis we ran PGLS in which climatic variables and geographic distribution were used as predicting variables and thermal tolerance range (TTR), thermal performance breadth (B80) and optimal temperature range (B95) were used as response variables (Table 5). Environmental thermal variation (Tamp) showed the steepest slopes among the variables in most of the models (Table 5 and Table S4 in the supplementary online Appendix). However, none of the models resulted in

Table 1
Summary of physiological parameters and thermal tolerance for the species under study.

Species		B80 (°C)			B95 (°C)			To (°C)	Vmax (m/s)	CTmin (°C)	CTmax (°C)	TTR (°C)
		t° low.	t° up.	Range	t° low.	t° up.	Range					
<i>Liolaemus baguali</i>	\bar{X}	28.7	39.0	10.3	32.5	37.2	4.7	35.1	2.29	5.24	43.52	38.84
	SD	3.79	1.99	2.71	3.60	2.59	1.42	3.21	0.41	1.81	0.73	
	(N)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(11)	
<i>L. ceii</i>	\bar{X}	27.9	38.0	10.1	31.3	36.0	4.7	33.8	2.10	7.6	43.67	36.07
	SD	3.87	1.68	2.80	3.42	2.26	1.44	2.82	0.60	0.78	0.82	
	(N)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(16)	(12)	
<i>L. coeruleus</i>	\bar{X}	29.6	38.8	9.3	32.9	37.2	4.2	35.3	2.42	9.22	43.36	34.15
	SD	2.24	1.31	1.85	2.16	1.66	0.95	1.96	0.37	1.31	0.56	
	(N)	(22)	(22)	(22)	(22)	(22)	(22)	(22)	(22)	(20)	(10)	
<i>L. elongatus</i>	\bar{X}	28.4	39.0	10.6	32.1	37.0	4.9	34.8	2.36	7.42	44.32	36.79
	SD	2.89	1.57	2.22	2.68	1.96	1.13	2.33	0.52	1.98	0.63	
	(N)	(55)	(55)	(55)	(55)	(55)	(55)	(55)	(55)	(59)	(25)	
<i>L. fitzingerii</i>	\bar{X}	27.7	38.1	10.4	31.2	36.0	4.8	33.9	2.13	6.36	44.36	37.39
	SD	2.53	1.95	2.36	2.39	2.07	1.22	2.22	0.66	1.93	0.55	
	(N)	(23)	(23)	(23)	(23)	(23)	(23)	(23)	(23)	(44)	(27)	
<i>L. gallardoi</i>	\bar{X}	26.8	37.7	10.9	30.2	35.5	5.2	33.0	1.69	8.52	44.1	35.58
	SD	2.43	1.38	1.88	2.18	1.61	0.94	1.93	0.59	1.01	0.28	
	(N)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(6)	(5)	
<i>L. hatcheri</i>	\bar{X}	27.8	38.4	10.6	31.5	36.4	4.9	34.3	1.69	7.02	43.23	36.11
	SD	2.7	1.34	1.92	2.41	1.69	1.04	2.10	0.21	0.88	0.37	
	(N)	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(6)	(6)	
<i>L. kingii</i>	\bar{X}	27.0	38.6	11.6	30.9	36.4	5.5	33.9	2.42	7.37	44.22	37.16
	SD	2.61	1.59	2.12	2.43	1.90	1.16	2.17	0.39	1.98	0.46	
	(N)	(39)	(39)	(39)	(39)	(39)	(39)	(39)	(39)	(40)	(22)	
<i>L. kollegh</i>	\bar{X}	28.8	39.7	10.9	33.2	38.0	4.8	36.1	1.21	5.46	44.05	38.59
	SD	2.65	1.55	2.09	2.39	1.90	0.97	2.21	0.42	0.71	0.21	
	(N)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	
<i>L. magellanicus</i>	\bar{X}	24.3	36.7	12.5	28.0	34.0	6.0	31.2	1.04	8.3	43.59	35.29
	SD	1.38	1.39	2.00	1.16	1.37	1.05	1.26	0.49	0.56		
	(N)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(3)	(1)	
<i>L. multimaculatus</i>	\bar{X}	24.4	37.6	13.2	28.4	34.8	6.4	31.8	1.31	6.96	45.10	38.14
	SD	2.08	1.45	2.13	1.82	1.53	1.11	1.62	0.25	1.62	0.43	
	(N)	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(8)	(8)	
<i>L. sp.</i>	\bar{X}	23.3	37.6	14.3	27.6	34.6	7.0	31.4	2.42	7.57	44.12	36.55
	SD	1.84	1.51	0.89	1.99	1.83	0.50	1.96	0.35	2.37	0.42	
	(N)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)	(5)	
<i>L. shitan</i>	\bar{X}	24.2	37.7	13.5	28.2	34.8	6.6	31.7	2.40	7.48	45.33	37.85
	SD	3.24	1.17	3.02	2.67	1.49	1.59	2.01	0.52	2.03	0.56	
	(N)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)	(6)	
<i>L. xanthoviridis</i>	\bar{X}	26.4	37.7	11.3	30.1	35.4	5.3	33.0	1.79	6.61	44.32	37.35
	SD	3.35	2.16	2.29	3.22	2.59	1.17	2.93	0.33	2.29	0.71	
	(N)	(14)	(14)	(14)	(14)	(14)	(14)	(14)	(14)	(24)	(12)	
<i>L. zullyi</i>	\bar{X}	27.1	38.5	11.4	30.9	36.4	5.4	33.9	1.68	8.38	43.95	35.57
	SD	2.19	1.45	1.44	2.25	1.78	0.80	2.06	0.30	0.66	1.23	
	(N)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(6)	(5)	
<i>Phymaturus tenebrosus</i>	\bar{X}	30.3	38.0	7.7	33.4	36.9	3.6	35.4	2.36	9.80	39.90	30.10
	SD	2.12	0.61	1.52	1.72	0.91	0.81	1.31	0.34	2.7	1.5	
	(N)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(15)	(14)	

Source: Data on CTmin and CTmax for *P. tenebrosus* were obtained from [Ibargüengoytia et al. \(2008\)](#).

Mean (\bar{X}), standard deviation (SD). B80, thermal performance breadth; B95, optimal temperature range (t° low., t° up., range, corresponding to lower, upper limits and range of B80 and B95, respectively); To, optimum temperature; Vmax, maximum sprint speed; CTmin, critical temperature minimum; CTmax, critical temperature maximum; TTR, thermal tolerance range obtained by difference of mean CTmax and CTmin of the species.

steep and significant slopes (Table 5 and Table S4). Additionally, trends were negative in many cases, contrary to what was expected (Table 5).

To explore the impact of predicted climate change while taking into consideration the performance breadths of the species studied here, we compared the B80, B95 boundaries with the maximum temperature of warmest month (MTWM) for localities where species were collected under present-day conditions and in the climatic change scenario A1B for 2080 (Solomon et al., 2007; Fig. 2). In all cases (for current and future conditions) MTWM is lower than the B80 and B95 upper limits. MTWM is only higher than the B80 and B95 lower limits for some species (*L. ceii*, *L. multimaculatus*, *L. sp.*, *L. shitan*, *L. xanthoviridis*, Fig. 2). This result indicates that our sampled species are not likely to be threatened by warmer

temperatures projected for 2080 under the A1B scenario of the IPCC (Solomon et al., 2007).

4. Discussion

Locomotor performance curves are considered an ecologically important index as running speed is considered an indicator of survival and therefore of fitness (Christian and Tracy, 1981; Hertz et al., 1983; van Berkum, 1988; Jayne and Bennett, 1990). However, whether this aspect is related to geographic range amplitude remains scarcely explored. In our results, thermal sensitivity of locomotor performance varied among species. We observed a broader B80 and B95 in widespread species, supporting the idea that higher physiological plasticity allows species to achieve a

Table 2

Phylogenetically informed analysis of variance (ANOVA) comparing thermal tolerance, thermal performance breadth, optimal temperature range, thermal optimum and maximum performance of widespread species (15,000 km² or larger area of occurrence) and species with a restricted distribution (13,000 km² or smaller area of occurrence).

Parameter	F	P
B80	3.834	0.004
B95	4.164	0.005
TTR	0.438	0.615
To	5.276	0.002
Vmax	0.059	0.856

B80, thermal performance breadth; B95, optimal temperature range; TTR, thermal tolerance range; To, optimum temperature range; Vmax, maximum sprint speed. Bold face denotes significant differences, with B80 and B95 being broader and To lower in widespread species.

wider distribution compared to species with restricted distribution. Analogous results were found in a study with 8 North American lizards (of 4 genera) where species with narrower thermal activity ranges had more restricted distributions (Buckley, 2010). We did not find differences in TTR between widespread and restricted species. A wide thermal performance breadth and optimal temperature range are thermal characteristics related directly to lizards' activity patterns, and therefore are ecologically relevant (e.g., Hertz

et al., 1983; van Berkum, 1988). For example, foraging, escaping from predators, and reproduction typically take place within these ranges. Thermal tolerance is a physiology-related trait allowing life at different climatic regimes. It is probable that TTR evolved early in the radiation of Liolaemini (Moreno Azócar et al., 2013; Cruz et al., 2014). TTR in these species is associated with environmental variability, but not significantly (Cruz et al., 2014; present study). Thus, the capacity of these lizards to survive at different environmental conditions is similar despite the different environmental conditions where they occur today. This thermal tolerance would allow Liolaemini species to survive at a wide range of climatic conditions, while B80 and B95 probably play a role in the success of these species to expand their range limits. Liolaemini species that occur at wider geographic ranges also show a To that differs from that of restricted species. Additionally, species with restricted distribution show a higher To and a narrower performance amplitude, suggesting a degree of thermal specialization. However, maximum sprint speed (Vmax) shows no differences between widespread and restricted species (Table 2), indicating that species are adapted to the habitats in which they occur, and are capable of feeding, reproducing and escaping from predators in a similar way. It has to be considered that other factors, such as morphological traits, may play a role in the speeds that these species can reach (Bonino et al., 2011; Tulli et al., 2012).

Table 3

Summary of the best fitting PGLS models for physiological thermal variables (Ctmin, B80, B95, CTmax and To; see Table S3 in the supplementary online Appendix for all models) and thermal characteristics of the environment (Tmean and Tampl).

Model	AICc	λ	r^2	Intercept	Tmean	Tampl	Pp	Wi	Pt
Ctmin ~ Tampl	49.316	0.000	0.150	4.655		0.265	0.131	0.434	0.131
B80 t ^o low. ~ Tampl	68.632	0.000	0.014	24.649		0.242	0.362	0.211	0.362
B80 t ^o low. ~ Tmean	67.601	0.000	0.053	29.846	-0.216		0.238	0.353	0.238
B80 t ^o up. ~ Tmean	36.798	0.000	0.034	39.218	-0.071		0.396	0.407	0.396
B95 t ^o low. ~ Tmean	64.555	0.000	0.088	33.729	-0.223		0.204	0.427	0.204
B95 t ^o up. ~ Tmean	48.533	0.000	0.092	37.862	-0.133		0.239	0.469	0.239
Ctmax ~ Tmean	37.751	0.914	0.276	41.179	0.122		0.037	0.589	0.037*
To ~ Tmean	58.019	0.000	0.100	36.159	-0.188		0.205	0.462	0.205

Ctmin, critical temperature minimum, CTmax, critical temperature maximum; B80, thermal performance breadth; B95, optimal temperature range; t^o low., lower limit; t^o up., upper limit; To, optimum temperature; AICc, Akaike information criterion for small samples; λ , lambda; Wi, Akaike weights; Tampl, environment temperature variation; Tmean, mean temperature. Pp, partial P value for each variable; Pt, P value for the complete model.

* Significant result (<0.05).

Table 4

PGLS models for trade-off between thermal characteristics among species.

Models	AICc	λ	r^2	Intercept	Slope	Wi	P
To ~ B95	40.88	0.00	0.67	42.67	-0.79	0.07	<0.001**
To ~ T80	35.80	0.00	0.77	41.91	-1.54	0.93	<0.001**
To ~ Vmax	57.13	0.00	0.04	32.55	0.64	0.00	0.433
Vmax ~ B95	22.55	0.00	0.03	2.69	2.68	0.52	0.505
Vmax ~ B80	22.74	0.00	0.04	2.50	2.50	0.48	0.444

To, optimum temperature; B95, optimal temperature range; B80, thermal performance breadth; Vmax, maximum sprint speed; AICc, Akaike information criterion for small samples; λ , lambda; Wi, Akaike weights. P = P value for the model.

** Significant relationship.

Table 5

Best fitted PGLS models for the climatic variability hypothesis. See Table S4 in the supplementary online Appendix for all possible models.

Model	AICc	λ	r^2	Intercept	Area	Tmean	Tampl	Pp	Wi	Pt
TTR ~ Tampl	62.102	0.832	0.065	35.477				0.812	0.227	0.812
TTR ~ Tmean	61.434	0.843	0.019	33.248		0.093		0.284	0.317	0.284
TTR ~ Area	61.987	0.835	0.057	34.395	<-0.000			0.812	0.240	0.812
B80 ~ Tampl	60.647	0.000	0.033	13.783			-0.252	0.251	0.245	0.251
B80 ~ Tmean	60.003	0.498	0.079	8.230		0.165		0.133	0.339	0.133
B95 ~ Tampl	42.914	0.000	0.005	6.487			-0.119	0.316	0.178	0.316
B95 ~ Tmean	42.266	0.435	0.091	3.786		0.092		0.136	0.202	0.136
B95 ~ Tmean + Tampl	41.451	0.000	0.103	5.558		0.099		0.136	0.270	0.195
							-0.148	0.184		

TTR, thermal tolerance range; Tampl, environment temperature variation; Tmean, mean temperature; B80, thermal performance breadth; B95, optimal temperature range; AICc, Akaike information criterion for small samples; λ , lambda; Wi, Akaike weights. Pp, partial P value for each variable; Pt, P value for the complete model.

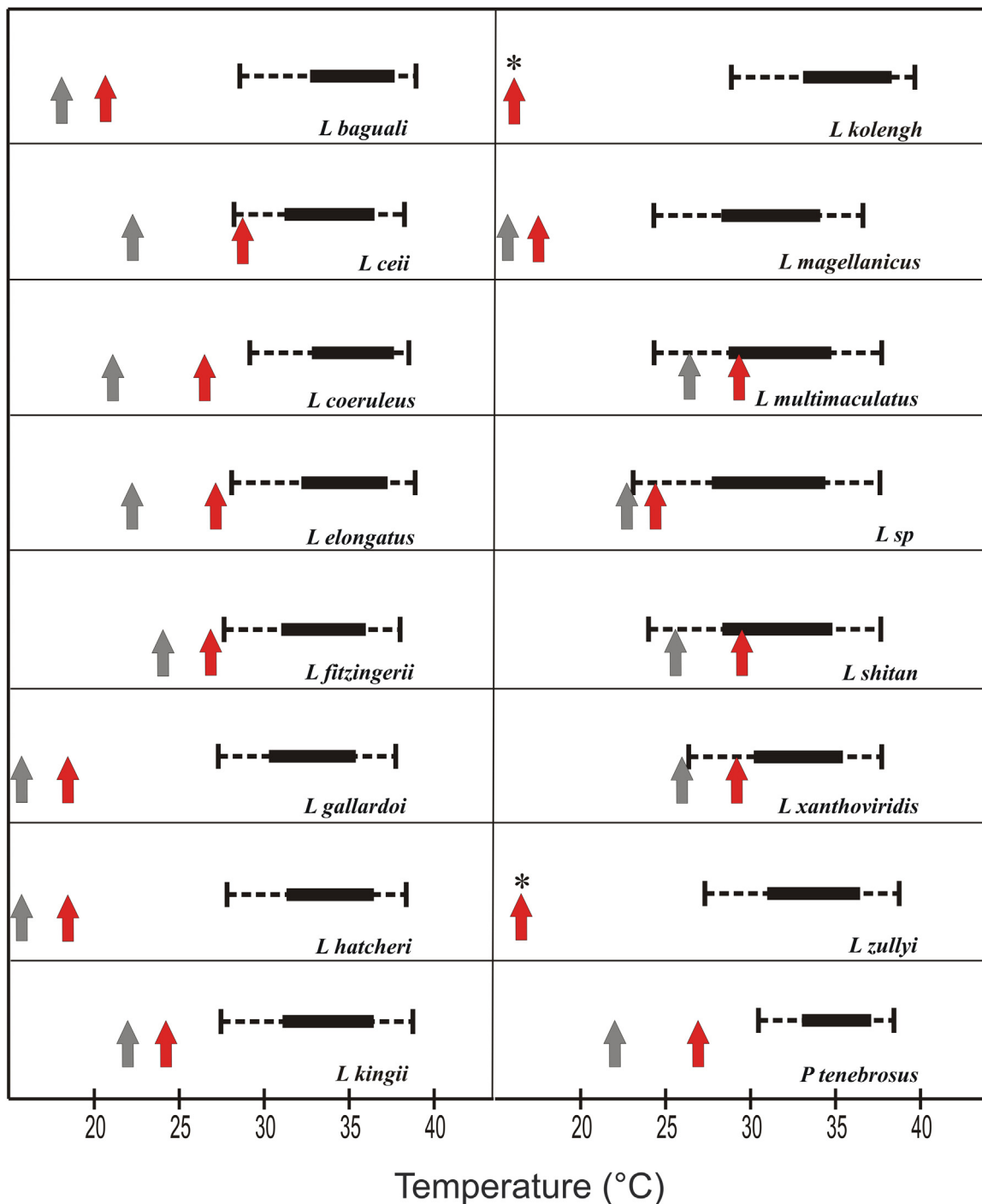


Fig. 2. Comparing lizard performance breadths and environmental temperatures: thermal performance breadth (B80, horizontal dashed lines), and optimal temperature range (B95, horizontal black bars). Maximum temperature of the warmest month (MTWM) for the localities of each species was obtained from global data sets in WorldClim for the present (gray arrows) and for the 2080 A2B scenario (red arrows) proposed by the IPCC (Solomon et al., 2007). Asterisks (*) indicate present MTWM lower than the minimum temperature in the scale. It is observed that most species experience today, and even in the future scenario, suboptimal temperatures.

Regarding critical temperatures, on the one hand our results show that CTmax was the only variable related to environmental temperature (Table 3). Moreover, it was the only variable with strong phylogenetic signal ($\lambda = 0.91$), suggesting a strong phylogenetic pattern. On the other hand, CTmax appears to be the least variable parameter between the thermal limits both at the intraspecific and interspecific level; only CTmax of *P. tenebrosus* is substantially lower than that of other species (see Table 1). This point is not surprising given CTmax reaches temperatures close to those that negatively affect proteins and cell membrane stability

and show (in many lizard species) less plasticity, geographic and evolutionary variation than lower thermal limits (Lutterschmidt and Hutchinson, 1997; Addo-Bediako et al., 2000; Angilletta, 2009; Sunday et al., 2011; Allen et al., 2012; Grigg and Buckley, 2013; Hoffmann et al., 2013; Muñoz et al., 2014). Previous studies with *Liolaemus* show the same pattern (Cruz et al., 2005; Kubisch et al., 2011; Araújo et al., 2013; Moreno Azócar et al., 2013). On the other hand, CTmin is suggested as a temperature behaviorally difficult to avoid compared to CTmax (Spellerberg, 1972), which potentially puts the lower critical temperature under strong selective pressure.

We are aware that relatively new models have been developed linking ecology, physiology and other traits to species distribution ranges. Among these challenging and innovative models is the one by Buckley (2008) who developed an ecophysiological model capable of producing spatially explicit maps of parameters, such as potential activity hours and food requirements to meet the target species' energetic costs. These models require, among other aspects, assumptions about the potential energy intake (including activity patterns, reproductive potential, metabolic rates, prey abundance, and development rate) to predict distributions (Buckley, 2008, 2010; Kearney and Porter, 2009; Buckley et al., 2011; Ceia-Hasse et al., 2014). Although these models have the advantage and novelty of linking distribution to specific processes, the baseline information is rare, especially when one attempts to work with large numbers of species. Moreover, our data can still challenge and improve the correlative approach that, as Buckley (2010) suggests, may underpredict climate-induced range shifts.

With regard to our prediction that genotypes adapted to higher temperatures have greater performance ability than cold-adapted ones ("hotter is better"; Barcroft, 1934; Hochachka and Somero, 1973), we did not find sufficient supporting evidence. Although we found a positive relationship between performance level and temperature, this relationship was not significant (Table 4). Our results suggest that biochemical adaptation may partially compensate the effects on thermodynamic performance in species living at different temperatures (Frazier et al., 2006; Angilletta et al., 2010). Surprisingly, Bonino et al. (2011) found evidence for the "hotter is better" hypothesis exclusively for the *L. lineomaculatus* section. It is thus possible that different lineages have experienced different evolutionary patterns regarding the temperature–performance relationship. Moreover, this may also depend on the way in which the level of locomotor performance contributes to the actual fitness and broader aspects of an organism's life history (Angilletta, 2009). For example, physiological performance likely depends on several other factors in addition to temperature.

A central topic when evaluating the biology of organisms is whether an adaptive benefit of having a generalist over a specialist phenotype exists (Huey and Hertz, 1984; Gilchrist, 1995; Angilletta, 2009; Tulli et al., 2012). Our results show a significant and negative relationship between performance breadth and optimum temperature. However, since we did not find a strong relationship between optimal temperature and maximum performance level, we must be cautious in drawing conclusions. Other studies found trade-offs in traits related to locomotion, for example between speed and endurance (Huey and Hertz, 1984; Vanhooydonck et al., 2001), between speed and surefootedness (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Macrini and Irschick, 1998), between speed and clinging ability (Losos et al., 1993) or between sprint speed and bite force (Cameron et al., 2013). This type of evidence, in agreement with the trends documented here, supports the idea there is a trade-off between broad levels of plasticity and higher levels of performance. However, a previous study on the relationship between morphology and performance in nearly 40 species of *Liolaemus* (Tulli et al., 2012) suggests that these lizards with a generalized morphology do not fit the concept that a "jack of all trades is master of none", since no trade-offs were found. As we see, the genus *Liolaemus* shows a complex mixture of conservative and variable characters, making it very difficult to make generalizations.

According to the climatic variability hypothesis (Gaston and Blackburn, 2000) species experiencing a broader range of climatic fluctuations (at higher altitudes, latitudes or their combination) may be expected to exhibit higher tolerance ranges and acclimation capacity to survive in such conditions (Janzen, 1967; Stevens, 1989; Gaston and Chown, 1999; Ghalambor et al., 2006). Available evidence from terrestrial ectothermic vertebrates supports the climatic variability hypothesis, for example in anurans (Brattstrom,

1968; Snyder and Weathers, 1975) and squamates (van Berkum, 1988; Cruz et al., 2005). For the species studied here, we did not find any evidence linking climatic variability with higher thermal tolerance ranges; we even observed a negative relationship between thermal tolerance and thermal environmental amplitude, contrary to our predictions. Likewise, other studies with similar or even larger sample sizes do not unequivocally support the climatic variability hypothesis in *Liolaemus* lizards. Cruz et al. (2005) failed to reject this hypothesis only when their analysis was restricted to 19 lizard species belonging to the *L. boulengeri* group, yet after analyzing a larger sample of 34 *Liolaemus* species corresponding to different clades the hypothesis was rejected. In that study, the authors mention that the inclusion of multiple outgroups tended to obscure macroecological patterns. Recently, after analyzing an even larger sample of *Liolaemus* lizards (47 species), the climatic variability hypothesis was not fully supported (Cruz et al., 2014). It is interesting that *Liolaemus* lizards were shown to be efficient thermoregulators (Moreno Azócar et al., 2013), which may mask the effect of the selective pressure from different environments. In the present study each species shows a particular distributional range and geographic characteristics that may lead to a bias in the results. Further we must keep in mind that other factors not considered in the framework of this hypothesis may be important for the evolution of these species' tolerance ranges, for example, phenology, species–species interactions, food availability, starvation resistance (Gaston and Blackburn, 2000; Sexton et al., 2009), or behavioral shifts that require less genetic changes than physiological shifts (Blomberg et al., 2003; Muñoz et al., 2014).

Our analyses show that present-day environmental temperatures are lower than the temperatures that most lizards require to achieve optimal functioning, thus these species may be experiencing suboptimal temperatures. If we consider that MTWM provides the hottest temperature in the future scenario for 2080 these organisms might face in their respective localities, we propose that these species will be unaffected by the maximum environmental temperatures expected under this scenario. Thus, in contrast to the less optimistic projections that mention a large number of extinctions in relation to global climate change (e.g., Sinervo et al., 2010) we believe that predicted climatic changes in terms of temperature will not be a threat for these Patagonian lizards. However, several other aspects should be taken into account, for example that there might be changes in food and water availability that may lead to negative consequences (Cahill et al., 2012).

Our results show a link between physiological plasticity indicators and geographic distribution range. We found a clear relationship between broad levels of plasticity and wider distributions, as well as trade-offs between broad levels of plasticity and higher optimum temperatures. Finally, our data in relation to future climatic scenarios suggest that *Liolaemini* lizards occurring in Patagonia are not under a severe threat due to a global temperature increase. However, other aspects should be considered, such as increases in competition, parasitism and predation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2015.03.001>

References

- Abdala, C.S., Quinteros, A.S., 2014. Los últimos 30 años de estudios de la familia de lagartijas más diversa de Argentina. Actualización taxonómica y sistemática de Liolaemidae. *Cuad. Herpetol.* 28, 55–82.
- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B* 1445, 739–745, <http://dx.doi.org/10.1098/rspb.2000.1065>
- Aguilar, R., Cruz, F.B., 2010. Refuge use in a Patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. *J. Herpetol.* 44, 236–241.
- Allen, J.L., Clusella-Trullas, S., Chown, S.L., 2012. The effects of acclimation and rates of temperature change on critical thermal limits in *Tenebrio molitor* (Tenebrionidae) and *Cyrtobagous salvinae* (Curculionidae). *J. Insect Physiol.* 58, 669–678.
- Angilletta, M.J., 2006. Estimating and comparing thermal performance curves. *J. Therm. Biol.* 31, 541–545, <http://dx.doi.org/10.1016/j.jtherbio.2006.06.002>
- Angilletta, M.J., 2009. *Thermal Adaptation. A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford and New York.
- Angilletta, M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27, 249–268, [http://dx.doi.org/10.1016/S0306-4565\(01\)00094-8](http://dx.doi.org/10.1016/S0306-4565(01)00094-8)
- Angilletta, M.J., Wilson, R.S., Navas, C.A., James, R.S., 2003. Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol. Evol.* 18, 234–240, [http://dx.doi.org/10.1016/S0169-5347\(03\)00087-9](http://dx.doi.org/10.1016/S0169-5347(03)00087-9)
- Angilletta, M.J., Huey, R.B., Frazier, M.R., 2010. Thermodynamic effects on organismal performance: is hotter better? *Physiol. Biochem. Zool.* 83, 197–206.
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L., 2013. Heat freezes niche evolution. *Ecol. Lett.* 16, 1206–1219, <http://dx.doi.org/10.1111/ele.12155>
- Arnold, S.J., 1983. Morphology, performance and fitness. *Am. Zool.* 23, 347–361.
- Avila, L.J., Fulvio Pérez, C.H., Minoli, I., Morando, M., 2014. A new lizard of the *Phymaturus* genus (Squamata: Liolaemidae) from Sierra Grande, northeastern Patagonia, Argentina. *Zootaxa* 3793, 99–118.
- Barcroft, J., 1934. *Features in the Architecture of Physiological Function*. Cambridge University Press, Cambridge.
- Bauwens, D., Garland Jr., T., Castilla, A.M., Van Damme, R., 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* 49, 848–863.
- Blomberg, S.P., Garland Jr., T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57, 717–745.
- Bonino, M.F., Azócar, D.L.M., Tulli, M.J., Abdala, C.S., Perotti, M.G., Cruz, F.B., 2011. Running in cold weather: morphology, thermal biology, and performance in the southernmost lizard clade in the world (*Liolaemus lineomaculatus* section: Liolaemini: Iguania). *J. Exp. Zool. A* 315, 495–503, <http://dx.doi.org/10.1002/jez.697>
- Brattstrom, B.H., 1968. Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.* 24, 93–111.
- Brett, J.R., 1970. Temperature – animals – fishes. In: Kinne, O. (Ed.), *Marine Ecology*. John Wiley, London, pp. 515–560.
- Brown, J.H., Stevens, G.C., Kaufman, D.F., 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* 27, 597–623.
- Buckley, L.B., 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am. Nat.* 171, E1–E19, <http://dx.doi.org/10.1086/523949>
- Buckley, L.B., 2010. The range implications of lizard traits in changing environments. *Global Ecol. Biogeogr.* 19, 452–464, <http://dx.doi.org/10.1111/j.1466-8238.2010.00538.x>
- Buckley, L.B., Waaser, S.A., MacLean, H.J., 2011. Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology* 92, 2214–2221, <http://dx.doi.org/10.1890/11-0066.1>
- Bulté, G., Blouin-Demers, G., 2006. Cautionary notes on the descriptive analysis of performance curves in reptiles. *J. Therm. Biol.* 31, 287–291, <http://dx.doi.org/10.1016/j.jtherbio.2005.11.030>
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection, Multimodel Inference: A Practical Information-theoretic Approach*. Springer, New York.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2012. How does climate change cause extinction? *Proc. R. Soc. B* 280, 1890, <http://dx.doi.org/10.1098/rspb.2012.1890>
- Cameron, S.F., Wynn, M.L., Wilson, R.S., 2013. Sex-specific trade-offs and compensatory mechanisms: bite force and sprint speed pose conflicting demands on the design of geckos (*Hemidactylus frenatus*). *J. Exp. Zool. A* 216, 3781–3789, <http://dx.doi.org/10.1242/jeb.083063>
- Carothers, J.H., Fox, S.F., Marquet, P.A., Jaksic, F.M., 1997. Thermal characteristics of ten Andean lizards of the genus *Liolaemus* in central Chile. *Rev. Chil. Hist. Nat.* 70, 297–309.
- Ceia-Hasse, A., Sinervo, B., Vicente, L., Pereira, H.M., 2014. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. *Ecography* 37, 679–688, <http://dx.doi.org/10.1111/j.1600-0587.2013.00600.x>
- Christian, K.A., Tracy, C.R., 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49, 218–223, <http://dx.doi.org/10.1007/BF00349191>
- Clarke, A., 2003. Costs and consequences of evolutionary temperature adaptation. *Trends Ecol. Evol.* 18, 573–581, <http://dx.doi.org/10.1016/j.tree.2003.08.007>
- Crowley, S.R., 1985. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia* 66, 219–225, <http://dx.doi.org/10.1007/BF00379858>
- Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E., Schulte II, J.A., 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J. Evol. Biol.* 18, 1559–1574, <http://dx.doi.org/10.1111/j.1420-9101.2005.00936.x>
- Cruz, F.B., Moreno Azócar, D.L., Bonino, M.F., Schulte II, J.A., Abdala, C.S., Perotti, M.G., 2014. Clima, distribución geográfica y viviparismo en especies de *Liolaemus* (Reptilia: Squamata): cuando las hipótesis se ponen a prueba. *Ecosistemas* 23, 37–45, <http://dx.doi.org/10.7818/ECOS.2014.23-1.06>
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* 105, 6668–6672, <http://dx.doi.org/10.1073/pnas.0709472105>
- Ellison, A.M., 2004. Bayesian inference in ecology. *Ecol. Lett.* 7, 509–520.
- Frazier, M.R., Huey, R.B., Berrigan, D., 2006. Thermodynamics constrains the evolution of insect population growth rates: warmer is better. *Am. Nat.* 168, 512–520.
- Garland Jr., T., Losos, J.B., 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright, P.C., Reilly, S. (Eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago, pp. 240–302.
- Garland Jr., T., Huey, R.B., Bennett, A.F., 1991. Phylogeny and coadaptation of thermal physiology in lizards: a reanalysis. *Evolution* 45, 1969–1975.
- Gaston, K.J., 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Gaston, K.J., Blackburn, T.M., 2000. *Pattern and Process in Macroecology*. Blackwell Science, Malden, MA.
- Gaston, K.J., Chown, S.L., 1999. Why Rapoport's rule does not generalise. *Oikos* 84, 309–312.
- Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S., Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L., Schulte, P.M., Spicer, J.L., Stillman, J.H., Terblanche, J.S., Klunen, M.V., 2009. Macrophysiology: a conceptual reunification. *Am. Nat.* 174, 595–612.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G., 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.* 46, 5–17, <http://dx.doi.org/10.1093/icb/icj003>
- Gilchrist, G.W., 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* 146, 252–270.
- Grigg, J.W., Buckley, L.B., 2013. Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol. Lett.* 9 (2012), 1056, <http://dx.doi.org/10.1098/rstb.2012.1056>
- Gunderson, A.R., Leal, M., 2012. Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. *Funct. Ecol.* 26, 783–793, <http://dx.doi.org/10.1111/j.1365-2435.2012.01987.x>
- Hanna, L., 2012. *Saving a Million Species: Extinction Risk From Climate Change*. Island Press, Washington, DC.
- Harvey, P.H., Pagel, M.D., 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hertz, P.E., Huey, R.B., Nevo, E., 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37, 1075–1084.
- Hochachka, P.W., Somero, G.N., 1973. *Strategies of Biochemical Adaptation*. WB Saunders, Philadelphia.
- Hochachka, P.W., Somero, G.N., 2002. *Biochemical Adaptation*. Oxford University Press, Oxford.
- Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S., 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct. Ecol.* 27, 934–949, <http://dx.doi.org/10.1111/j.1365-2435.2012.02036.x>
- Huey, R.B., Bennett, A.F., 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41, 1098–1115.
- Huey, R.B., Bennett, A.F., 1990. Physiological adjustments to fluctuating thermal environments: an ecological and evolutionary perspective. In: Morimoto, R.I., Tissieres, A., Georgopoulos, C. (Eds.), *Stress Proteins in Biology and Medicine*. CSHL Press, Cold Spring Harbor, pp. 37–59.
- Huey, R.B., Hertz, P.E., 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. Exp. Zool. A* 97, 401–409.
- Huey, R.B., Hertz, P.E., 1984. Is a jack-of-all-temperatures a master of none? *Evolution* 38, 441–444.
- Huey, R.B., Kingsolver, J.G., 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4, 131–135, [http://dx.doi.org/10.1016/0169-5347\(89\)90211-5](http://dx.doi.org/10.1016/0169-5347(89)90211-5)
- Huey, R.B., Slatkin, M., 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 5, 363–384.
- Huey, R.B., Tewksbury, J.J., 2009. Can behavior douse the fire of climate warming? *Proc. Natl. Acad. Sci. U.S.A.* 106, 3647–3648, <http://dx.doi.org/10.1073/pnas.0900934106>
- Huey, R.B., Losos, J.B., Moritz, C., 2010. Are lizards toast? *Science* 328, 832–833, <http://dx.doi.org/10.1126/science.1190374>

- Ibargüengoytia, N.R., Acosta, J.C., Boretto, J.M., Villavicencio, H.J., Marinero, J.A., Krenz, J.D., 2008. Field thermal biology in *Phymaturus* lizards: comparisons from the Andes to the Patagonian steppe in Argentina. *J. Arid Environ.* 72, 1620–1630.
- Irschick, D.J., Jayne, B.C., 1998. Effects of incline on acceleration, body posture, and hindlimb kinematics in two species of lizard, *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Zool. A* 21, 273–287.
- Janzen, D.H., 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101, 233–249.
- Jayne, B.C., Bennett, A.F., 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44, 1204–1229.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350, <http://dx.doi.org/10.1111/j.1461-0248.2008.01277.x>
- Kubisch, E.L., Fernández, J.B., Ibargüengoytia, N.R., 2011. Is locomotor performance optimised at preferred body temperature? A study of *Liolaemus pictus* argentinus from northern Patagonia, Argentina. *J. Therm. Biol.* 36, 328–333, <http://dx.doi.org/10.1016/j.jtherbio.2011.06.006>
- Lobo, F., Laspiur, A., Acosta, J.C., 2013. Description of new Andean species of the genus *Phymaturus* (Iguania: Liolaemidae) from Northwestern Argentina. *Zootaxa* 3683, 117–132.
- Losos, J.B., Sinervo, B., 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Zool. A* 245, 23–30, <http://dx.doi.org/10.1016/j.jtherbio.2011.06.006>
- Losos, J.B., Walton, B.M., Bennett, A.F., 1993. Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Funct. Ecol.* 7, 281–286.
- Losos, J.B., Creer, D., Schulte II, J.A., 2002. Cautionary comments on the measurement of maximum locomotor capabilities. *J. Zool.* 258, 57–61, <http://dx.doi.org/10.1017/S0952836902001206>
- Lutterschmidt, W.I., Hutchinson, V.H., 1997. The critical thermal maximum: history and critique. *Can. J. Zool.* 75, 1561–1574, <http://dx.doi.org/10.1139/z97-783>
- MacArthur, H., 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.
- Macrini, T.E., Irschick, D.J., 1998. An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biol. J. Linn. Soc.* 63, 579–591, <http://dx.doi.org/10.1111/j.1095-8312.1998.tb00330.x>
- Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, New Orleans, pp. 1–8.
- Moreno Azócar, L.D., Vanhooydonck, B., Bonino, M.F., Perotti, M.G., Abdala, C.S., Schulte, J.A., Cruz, F.B., 2013. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. *Oecologia* 171, 773–788, <http://dx.doi.org/10.1007/s00442-012-2447-0>
- Muñoz, M.M., Stimola, M.A., Algar, A.C., Conover, A., Rodriguez, A.J., Landestoy, M.A., Bakken, G.S., Losos, J.B., 2014. Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proc. R. Soc. B* 281, 2433, <http://dx.doi.org/10.1098/rspb.2013.2433>
- Naya, D.E., Spangenberg, L., Naya, H., Bozinovic, F., 2012. Latitudinal patterns in rodent metabolic flexibility. *Am. Nat.* 179, 172–179, <http://dx.doi.org/10.1086/665646>
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., 2012. Caper: Comparative Analyses of Phylogenetics and Evolution in R, Version 0.5. <http://cran.r-project.org/package=caper>
- Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884, <http://dx.doi.org/10.1038/44766>
- Paradis, E., Claude, J., Strimmer, K., 2004. *APE: analyses of phylogenetics and evolution in R language*. *Bioinformatics* 20, 289–290.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., Warren, M., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583, <http://dx.doi.org/10.1038/21181>
- Parmesan, C., Root, T.L., Willig, M.R., 2000. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Mus. Nat. Hist.* 81, 443–450, [http://dx.doi.org/10.1175/1520-0477\(2000\)081<0443:IOEWAC>2.3.CO;2](http://dx.doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2)
- Paruelo, J.M., Beltrán, A., Jobbágy, E., Sala, O.E., Golluscio, R., 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecol. Aust.* 8, 85–101.
- Petrick, A.G., Walker, R.S., Novaro, A.J., 2009. Susceptibility of lizards to predation under two levels of vegetative cover. *J. Arid Environ.* 73, 574–577.
- Pianka, E.R., 1978. *Evolutionary Ecology*. Harper & Row, New York.
- Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol. A* 132, 739–761, [http://dx.doi.org/10.1016/S1095-6433\(02\)00045-4](http://dx.doi.org/10.1016/S1095-6433(02)00045-4)
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org>
- Revell, L.J., 2010. Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* 1, 319–329.
- Revell, L.J., 2012. *Phytools: an R package for phylogenetic comparative biology (and other things)*. *Methods Ecol. Evol.* 3, 217–223.
- Schulte II, J.A., de Queiroz, K., 2008. Phylogenetic relationships and heterogeneous evolutionary processes among phrynosomatine sand lizards (Squamata, Iguanidae) revisited. *Mol. Phylogenet. Evol.* 47, 700–716.
- Schulte II, J.A., Macey, J.R., Espinoza, R.E., Larson, A., 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.* 69, 75–102, <http://dx.doi.org/10.1111/j.1095-8312.2000.tb01670.x>
- Sexton, J.P., McIntyre, P.J., Angert, A.L., Rice, K.J., 2009. Evolution and ecology of species range limits. *Annu. Rev. Ecol. Syst.* 40, 415–436, <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120317>
- Sinervo, B., Losos, J.B., 1991. Walking the tight rope: a comparison of arboreal sprint performance among populations of *Sceloporus occidentalis* lizards. *Ecology* 72, 1225–1233.
- Sinervo, B., Méndez de la Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Duarte Rocha, C.F., Ibargüengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites Jr., J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899, <http://dx.doi.org/10.1126/science.1184695>
- Snyder, G.K., Weathers, W.W., 1975. Temperature adaptations in amphibians. *Am. Nat.* 109, 93–101.
- Solomon, S., Qin, D., Manning, Z., Chen, Z., Marquis, M. (Eds.), 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, New York.
- Spellerberg, I.F., 1972. Temperature tolerances of southwest Australian reptiles examined in relation to reptile thermoregulatory behavior and distribution. *Oecologia* 9, 23–46.
- Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web servers. *Syst. Biol.* 57, 758–771.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* 133, 240–256.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* 278, 1823–1830, <http://dx.doi.org/10.1098/rspb.2010.1295>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* 28, 2731–2739.
- Tavaré, S., 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. *Lec. Math. Life Sci.* 17, 57–86.
- Tulli, M.J., Abdala, V., Cruz, F.B., 2012. Effects of different substrates on the sprint performance of lizards. *J. Evol. Biol.* 215, 774–784, <http://dx.doi.org/10.1242/jeb.065490>
- van Berkum, F.H., 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* 132, 327–343.
- Vanhooydonck, B., Van Damme, R., Aerts, P., 2001. Speed and stamina trade-off in lacertid lizards. *Evolution* 55, 1040–1048, <http://dx.doi.org/10.1111/j.0014-3820.2001.tb00620.x>
- Whitton, F.J.S., Purvis, A., Orme, C.D.L., Olalla-Tárraga, M.A., 2012. Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Global Ecol. Biogeogr.* 21, 179–190, <http://dx.doi.org/10.1111/j.1466-8238.2011.00660.x>
- Wilson, E.O., 1992. *The Diversity of Life*. Harvard University Press, Cambridge, MA.
- Wright, S., 1932. The roles of mutation, inbreeding crossbreeding and selection in evolution. In: Jones, D.F. (Ed.), *Proceedings of the 6th International Congress of Genetics*, 1. Brooklyn Botanic Garden, Menasha, WI, pp. 356–366.