Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology

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Abstract

Climate change and rising global temperatures pose a serious threat to biodiversity. We assessed the vulnerability to global warming of four genera of iguanian lizards whose distributions include a broad range of environments from the Peninsula of Yucatán to southern Patagonia. Original data on body temperatures (T_b), operative temperatures (T_e, 'null temperatures' for non-regulating animals), thermoregulatory set-point range (preferred body temperatures, T_{set}) and quantitative indices of temperature regulation and quality of the thermal environment (d_b, d_e and E) for *Tropidurus* species were compared to published data for *Anolis*, *Liolaemus* and *Sceloporus*. Our results suggest that thermoregulatory behavior typically increases with latitude and altitude (except for two southernmost liolaemids), and that tropical and lowland lizards generally behave as thermoconformers. In a warming scenario, thermoconformity or poor thermoregulation in environments where large proportions of T_b and T_e exceed the population's T_{set} will cause a reduction in the hours of activity and a higher risk of overheating. These results identify tropical populations as the most vulnerable to rising temperatures, especially the ones inhabiting open and low elevation sites. This indicates that protection of these environments should be a conservation priority. In contrast, Patagonia and montane environments represent potential future thermal refuges for many equator-ward or lowland lizards that, if capable of dispersion, would eventually be forced to retreat to these environments.

Introduction

Rising global temperature is a dimension of climate change projected to have major impacts on the biota (Peñuelas & Filella, 2001; Kerr, 2007; Sinervo *et al.*, 2010) through both direct and indirect effects (Hughes, 2000; Huey *et al.*, 2012). Temperature affects the biota at various levels of biological organization, but processes occurring at the individual level have gained attention as a primary mechanism of impact in animals (Garland & Else, 1987; Andrews, Mathies & Warner, 2000). This is likely to be particularly true for those species whose body temperature depends heavily on environmental temperature. In terrestrial ectothermic vertebrates, for example, body temperature (T_b) is partially dependent on environmental thermal regimes, and thus tend to be sensitive to warming via effects on behavioral and physiological performances (Dunham, 1993; Miles, 1994; Angilletta, 2009; Seebacher & Franklin, 2012). In response to increases in air (environmental; T_a), small heliothermic lizards may vary the amount of time they spend active and basking (Bogert, 1949; Huey, 1982), or alter their phenotype through physio-

logical acclimation (Corn, 1971; Spellerberg, 1972; Hertz, 1981; Somero, 2010). According to the magnitude of climatic shifts and the physiology of organisms, warming may exert different impacts among taxa, eventually benefiting some lineages (Chamaillé-Jammes, Aragón & Clobert, 2006) while causing extirpation or extinction in others (Sinervo *et al.*, 2010). Hence, climate warming may shift the distribution of ectothermic tetrapods, with impacts varying according to physiological sensitivity (e.g. thermal tolerance) and temperature-dependent effects on ecological performance (Huey & Stevenson, 1979; Angilletta, 2009). Therefore, the vulnerability of any given taxon to climate warming may be framed as a compromise between sensitivity and resilience to changes in T_a (Huey *et al.*, 2012).

The concepts of sensitivity and resilience incorporate the notion of adjustment, which occurs at various scales and levels of organization from individual shifts to evolutionary adaptive potential (Williams *et al.*, 2008), including the plasticity of individual responses. The T_b range experienced, particularly during certain periods of life, may influence the integrated performance and fitness of an individual (Huey,

1991; Kingsolver, Izem & Ragland, 2004; Angilletta, 2009). Quantifying fitness is very difficult and research relies on proxy variables such as parameter-specific optimal temperatures (T_o; i.e. the body temperature at which the performance is highest or reaches 80% or 95% of maximum performance breath; Hertz, Huey & Nevo, 1983). In some lineages, particularly marked specialists, T_o is largely inflexible (e.g. species in tropical environments; Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; Huey *et al.*, 2009; McCain, 2009; Sunday, Bates & Dulvy, 2011; Clusella-Trullas, Blackburn & Chown, 2011). However, in other lineages the absolute position and scope of thermal breadths may vary across the geographical clines of a population or even within individuals (Bowler & Terblanche, 2008). Therefore, flexibility of thermal traits may vary according to lineage specialization and environmental traits. Various hypotheses aiming to explain patterns of variation have been tested (Sunday *et al.*, 2011), but broad trends remain elusive. While thermal tolerance breadths increase pole-ward, particularly in terrestrial organisms (Sunday *et al.*, 2011), and the critical thermal minimum (CT_{min}) usually decreases with latitude, no latitudinal variation is observed for the critical thermal maximum (CT_{max}; Addo-Bediako, Chown & Gaston, 2000; Ghalambor *et al.*, 2006; Huey *et al.*, 2009). High variation in seasonal temperature seems to be a significant driver for broadening physiological thermal tolerances (Addo-Bediako *et al.*, 2000; Huey *et al.*, 2009; Sunday *et al.*, 2011). Conversely, warm specialists with low individual variability (e.g. tropical populations) would be more vulnerable to rapid changes (Huey *et al.*, 2009; Logan, Cox & Calsbeek, 2014), with associated enhanced extinction risks (Sinervo *et al.*, 2010; Leal & Gunderson, 2012).

In this paper, we ask whether vulnerability to climate warming in lizards is inversely related to latitude and altitude under scenarios of increased T_a. Our argument is based on thermal constraints, as deduced from the effects of rising T_a on key aspects of thermal biology. We present original data on four populations of two species in the genus *Tropidurus* from the Brazilian Cerrado. We analyze our results in the context of published data from sample of populations in the genera *Anolis*, *Liolaemus* and *Sceloporus* distributed from southern Patagonia to Mexico and the Caribbean. On the basis of this expanded dataset, we examine how T_b, T_e, T_p and effectiveness of thermoregulation (E) relate to (1) altitude, (2) latitude and (3) assess whether vulnerability to predicted global warming decreases with latitude and altitude.

Materials and methods

This study includes field and laboratory temperatures and thermoregulation indices (after Hertz, Huey & Stevenson, 1993) of four iguanian families: Dactyloidae, Liolaemidae, Phrynosomatidae and Tropiduridae (*sensu* Pyron, Burbrink & Wiens, 2013). We gathered data from the literature on the first three, specifically the species *Anolis cooki*, *A. cristatellus*, *A. gundlachi* (Huey & Webster, 1976; Hertz, 1992a,b; Hertz *et al.*, 1993), *Liolaemus albiceps*, *L. irregularis*, *L. multicolor*, *L. yanalcu* (Valdecanto *et al.*, 2013),

L. bibronii (Medina *et al.*, 2009), *L. boulengeri*, *L. lineomaculatus* (Medina *et al.*, 2011), *L. elongatus* (Ibargüengoytía, 2005), *L. magellanicus*, *L. sarmientoi* (Ibargüengoytía *et al.*, 2010), *L. pictus argentinus* (Gutiérrez, Krenz & Ibargüengoytía, 2010), *Sceloporus mucronatus* and *S. serrifer* (Sinervo *et al.*, 2011). To these, we added unpublished data on *Tropidurus catalanensis*, *T. torquatus* (*sensu* Kunz & Borges-Martins, 2013) and *T. oreadicus* that was collected between 2011 and 2013 following the same methodology (i.e. Hertz *et al.*, 1993). Together, these species inhabit a range of ecological settings such as the deserts of Yucatan, the Brazilian Cerrado, the lowlands of southern Patagonia steppe, the rainforests of Puerto Rico and the Nothofagus forests in Tierra del Fuego (Supporting Information Table S1). The combined data were analyzed for patterns of vulnerability associated to the environment the lizards occupy, as well as their thermal biology.

Body and operative temperature data

Four populations of the genus *Tropidurus* were collected from four sites, across three localities along a latitudinal gradient in the Cerrado biome. These were 22 lizards of *T. catalanensis* in Piracicaba, SP (554 m a.s.l; −22.7357, −47.6485; April 2011 and September 2013); 22 specimens of *T. torquatus* (*sensu* Kunz & Borges-Martins, 2013) in Arinos, MG (526 m a.s.l; −15.9095, −46.1107; March 2012); 32 specimens of *T. torquatus* (*sensu* Kunz & Borges-Martins, 2013) in the gallery forests in the proximities of Formoso do Araguaia, TO (192 m a.s.l; −11.7469, −49.9267; September 2012) and 26 *T. oreadicus* inhabiting the urban areas of Formoso do Araguaia, TO (265 m a.s.l.; −11.8428, −49.5233; September 2012).

Specimens were collected by hand or with the aid of a noose between 8:00 to 18:00 only when active (i.e. outside the burrows, performing any behavior related to thermoregulation, feeding and/or breeding activities). Body temperatures (T_b) were measured during the hours of activity immediately after specimens were captured (*sensu* Pough & Gans, 1982) using a Sper Scientific 4 Channel Datalogging thermometer (Mod. # 800024; Fisher Scientific, Pittsburgh, PA, USA) and a catheter probe of 1.62 mm diameter (Sper Scientific Mod. # 800077; Fisher Scientific). Individuals were handled by the head to avoid heat transfer and the T_b was recorded within 10 s of handling inserting *c*. 1 cm inside the cloaca.

The distribution of the operative temperatures (T_e) represents the 'null' distribution of T_b that non-regulating animals would experience in their microhabitats (Heath, 1964; Bakken, 1992; Hertz *et al.*, 1993). In the published studies, this distribution was also collected during the hours of activity at each capture event using plastic models made of gray PVC pipes of 10–15 cm filled with silicone (for a detailed description, see Sinervo *et al.*, 2010) connected to data loggers (HOBO U12 4-Channel External Data Logger – U12-008; Onset, Bourne, MA, USA). Although 60 models were used to sample the distribution of T_e at the *Anolis*' sites (Hertz, 1992b), other studies deployed between 6 (Valdecanto *et al.*, 2013) and 20 (Gutiérrez *et al.*, 2010) models at

each site. Based on this range, in this study we deployed a minimum of 14 and a maximum of 22 models in potential microenvironments that *Tropidurus* lizards might occupy at the pole-ward ($N = 14$), central ($N = 22$) and equator-ward ($N = 22$) localities. The size and color of the models were determined based on calibrations against real specimens for previous studies (Piantoni, Ibargüengoytía & Navas, unpublished data), which used two catheter probes of 1.62-mm diameter (Sper Scientific Mod. # 800077) to simultaneously register the temperatures of both the models and the lizards. The best models for *Tropidurus catalanensis*, *T. torquatus* and *T. oreadicus* were selected by comparing the R^2 obtained from the regression between each model and specimens' T_b (regression of living lizard's T_b vs. model's T_e, $R^2 = 0.96$, $F_{708,1} = 15\ 237.836$, $P \leq 0.001$; $b = 1.001$, $t_{709} = 123.442$, $P \leq 0.001$; CI = 0.985–1.017).

Preferred temperature and set-point range

Back in the laboratory, the lizards were conditioned in terraria with food (cockroaches and crickets) and water *ad libitum*. During the experiments that lasted not more than 3 weeks, lizards were kept in average natural conditions of T_e and photoperiod. Preferred body temperature (T_p) and set-point temperature range (T_{set}, which represents the 'target' T_b range that animals would achieve in environments where the cost of thermoregulation is zero; Heath, 1965; Hertz *et al.*, 1993) were estimated using photothermal gradients of $100 \times 45 \times 16$ cm where lizards were placed individually. A lamp was used as the heat source at one end of each terrarium and it was adjusted to achieve a linear T_a gradient of 23–45°C (well above lethal limits). Ultrathin catheter thermocouples (1 mm, Product code: 5SC-TT-T-40-72; Omega Engineering Inc., Stamford, CT, USA) were taped to the lizard's vent and body temperatures were recorded at 2-min intervals for 2 h, by connecting the thermocouple to a USB-based 8-channel TC input module (MCC DAQ Measurement Computing; Measurement Computing Corporation, Norton, MA, USA). Lizards would start thermoregulating after approximately 20 min of being placed in the gradients so these data were omitted in the calculations. Preferred temperatures, as well as the lower and upper T_{set} (the temperatures bounding the interquartile range of the observed T_p), were estimated from the T_b recorded in the thermal gradients for each lizard, and used to calculate T_p and T_{set} for the populations.

Effectiveness of temperature regulation

The efficiency of temperature regulation (*sensu* Hertz *et al.*, 1993) was calculated as: $E = 1 - (\text{mean } d_b/\text{mean } d_e)$, in which d_b is the average of the absolute distance of T_b from the set-point range of each individual and d_e is the deviation between T_e and T_{set} which specifies the average thermal quality of a microenvironment from the organism's standpoint (Hertz *et al.*, 1993). Therefore, thermoregulation is considered effective when E is close to 1, thermoconforming when E is close to 0 and moderately effective when E is

close to 0.5 (Hertz *et al.*, 1993; Bauwens, Hertz & Castilla, 1996). Negative E-values occur if animals actively avoid favorable thermal microhabitats, perhaps due to predation risk or prey availability (Hertz *et al.*, 1993).

Results

Latitude and thermoregulation trends in *Liolaemus*, *Anolis* and *Sceloporus*

In Patagonia, *Liolaemus bibronii*, *L. boulengeri*, *L. lineomaculatus*, *L. magellanicus* and *L. sarmientoi* exhibit T_bs ranging from 26 to 29°C, but their T_ps are significantly higher, from 34 to 36°C (Medina *et al.*, 2009; Supporting Information Table S2). In the southernmost liolaemids (*L. sarmientoi* and *L. magellanicus*) high percentages (92% and 100% respectively) of the T_bs fall below the T_{set} (Supporting Information Fig. S1a and S1b). Toward the equator, inter-populational studies reveal that the average extent to which *L. bibronii*, *L. boulengeri* and *L. lineomaculatus* experience T_b outside the T_{set} range (d_b) increases with latitude (Medina *et al.*, 2009; Ibargüengoytía *et al.*, 2010; Medina *et al.*, 2011; Supporting Information Table S2; Fig. S2). In contrast, the deviation of the T_b from T_{set} in *L. pictus argentinus* increases with altitude (Gutiérrez *et al.*, 2010; Supporting Information Fig. S3a). In open environments, such as rocky lakeshore or the steppe outcrops, most T_bs experienced by *L. p. argentinus* and *L. elongatus* fall outside the T_{set} range (Ibargüengoytía, 2005; Gutiérrez *et al.*, 2010; Supporting Information Table S2), mainly exceeding their thermal preference. For example, in *L. elongatus*, 26% of T_bs were included within the T_{set}, while 42% fell above this range (Ibargüengoytía, 2005; Supporting Information Fig. S3b). The indices obtained by comparing T_e and T_b with the T_{set} range characterize most of the pole-ward species as moderate thermoregulators (E-values range from 0.30 to 0.59; Supporting Information Table S2), whereas in Patagonia liolaemids in open habitats behave as constrained thermoregulators (negative E-values and close to zero; Supporting Information Table S2).

In the Puna, *Liolaemus albiceps*, *L. irregularis*, *L. multicolor* and *L. yanalcu* achieve T_bs that range from 34.2 to 36.6°C, of which 39.5–63.6% (mean = 46.5) fall within the T_{set} (Supporting Information Table S2; Fig. S4). Mean proportions of 25% and 28% of T_bs were below and above the T_{set} respectively (Supporting Information Fig. S4). T_bs were higher overall, but close to (low d_b) the mean T_e registered in their environments (Supporting Information Table S2; Fig. S4). In fact, 63.4–87.8% of the T_e recordings fall below the T_{set} range in all sites (Supporting Information Fig. S4). Low d_b (given by the proximity of T_b and T_e) and high d_e (due to the high proportions of T_e below the T_{set}) result in high values of E, which range from 0.88 to 0.97 (Supporting Information Table S2).

In Puerto Rico, *Anolis* species experience T_b values (19.4–32.1°C; Supporting Information Table S2) that are usually below the T_p (25.1–30.6°C; Supporting Information Table S2). More than 95%, 58–95% and 73–80% of the T_e recordings fall below the T_{set} range at high elevation (1130–

1150 m a.s.l.), low elevation (90–210 m a.s.l.) and in the desert (5 m a.s.l.), respectively (Supporting Information Fig. S5). For example, at 210 m a.s.l., *A. gundlachi* occupies microenvironments where almost 50% of all T_e readings are below the T_{set}, while the proportion rose to more than 95% at 1130 m a.s.l. (Supporting Information Fig. S5c). Moreover, lizards of this species thermoregulate more efficiently in summer ($E = 0.14-0.21$), when mean T_e is above T_{set}, than in winter ($E = 0.00-0.08$; Supporting Information Table S2). *Anolis cristatellus* also shows more efficiency in the desert in summer ($E = 0.64$) than in winter or mesic sites in either season (Supporting Information Table S2). In xeric lowlands, *A. cooki* also prefers and is active at high T_bs, however *A. gundlachi* and *A. cristatellus* appear to thermoregulate more effectively in winter than in summer (Supporting Information Table S2).

In Mexico, *Sceloporus mucronatus*, from both upland (Ajusco – 3400 m a.s.l.) and montane (Tecocomulco – 2500 m a.s.l.) sites and *S. serrifer* from a lowland tropical forest site (Yucatan – 10 m a.s.l.) exceed their T_{set} (Supporting Information Fig. S6), even though most registered values of T_e fall below the T_{set} range (Sinervo *et al.*, 2010).

Thermoregulation in four populations of the genus *Tropidurus*

In southern Brazilian Cerrado (pole-ward site; lat. −22.7357), *Tropidurus catalanensis* maintains its T_b within and close to its preferred temperature range (Table 1). Here, most of the T_b recordings fall below the T_{set} range, while T_b typically exceeded this range (by 0.9–1.7°C) in most of the recordings of the central and equator-ward sites of the biome (Table 1). Also at the pole-ward site, 59% of the T_e values fall below the T_{set} range (Fig. 1a). At the central site, most T_es exceed the upper T_{set} (Table 1; Fig. 1b), while closer to the equator (lat. −11.7469) 13% and 58% of the T_es fall within and below this range respectively (Table 1; Fig. 1c). The index d_b was close to 2 in all populations, but d_e was significantly higher at the pole-ward site, which results in a higher efficiency in thermoregulation for this population ($E = 0.69$). At the central and equator-ward sites, *T. torquatus* behaves as a thermoconformer and as a constrained thermoregulator, respectively, reflected in the near zero and/or negative E-values (Table 1).

Variation in the thermoregulatory behavior with latitude and altitude

The d_b and d_e indices of the populations included herein, as well as their respective standard deviations, were all positively correlated with latitude and altitude, with the exception of d_b and altitude (Table 2; Fig. 2a and b). The correlation between E and latitude was significant when *L. magellanicus* was removed from the analyses, but became weak when included (Table 2; Fig. 2c and d).

Table 1 Mean ± standard error or median and range of body (T_b) and preferred (T_p) temperatures, set-point range (lower and upper T_{set}), operative temperatures (T_e), d_b and d_e indices and effectiveness of thermoregulations (E) of *Tropidurus catalanensis*, *T. torquatus* (sensu Kunz & Borges-Martins, 2013) and *T. oreadicus*

	T_b	T_p	T_{set} Lower	T_{set} Upper	T_e	d_b	d_e	E
Tropidurus catalanensis – Brazil								
Savanna, 22°S	36.1 (30.6–39.3; 43)	34.4 ± 0.02 (43)	33.6 ± 0.2 (43)	35.2 ± 0.2 (43)	37.3 ± 0.3 (14)	1.6 ± 0.2 (41)	5.3 ± 1.3 (13)	0.69
T. torquatus (sensu Kunz & Borges-Martins, 2013)								
Savanna, 15°S	35.8 (30.4–39.3; 22)	33.9 ± 0.01 (22)	33.1 ± 0.2 (22)	34.7 ± 0.2 (22)	36.1 ± 0.6 (20)	1.9 ± 0.3 (22)	0.9 (0–6.6; 20)	0.06
Gallery forest in savanna, 11°S	36.2 ± 0.3 (32)	34.6 (30.3–37; 32)	34.1 (30–36.3; 32)	35.3 (30.4–39.1; 32)	33.5 (31.5–39.4; 7)	1.7 ± 0.2 (32)	1.7 ± 0.7 (7)	−0.01
T. oreadicus								
Savanna, 11°S	38.1 (30.1–41.3; 26)	35.3 (30.7–37; 26)	34.8 (29.6–37; 26)	36 (30.8-37.5; 26)	39.6 ± 1.2 (15)	3.2 ± 0.4 (26)	4.5 ± 0.9 (15)	0.29

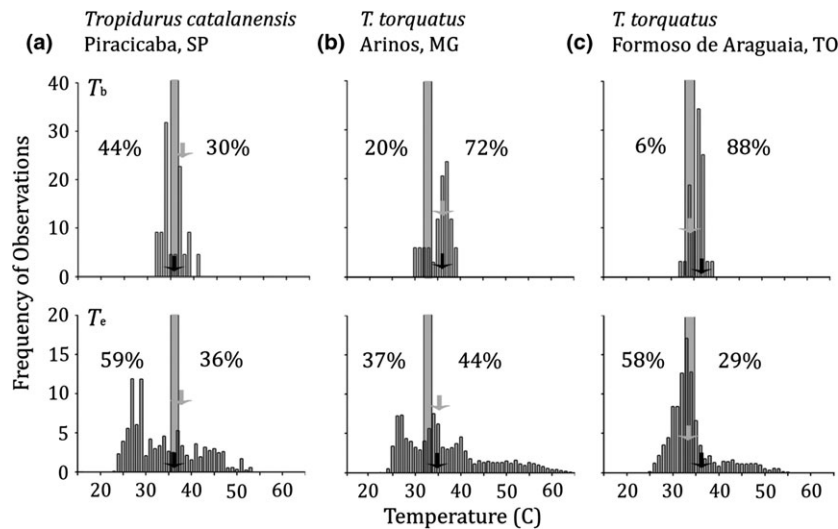Sample size is indicated between brackets.

Figure 1 Distribution of body temperatures (T_b; upper graphs) and operative temperatures (T_e; lower graphs) of *Tropidurus catalanensis* in (a) Piracicaba (pole-ward site) and *T. torquatus* in (b) Arinos (central site) and (c) Formoso de Araguaia (equator-ward site). The black and gray arrows indicate the mean T_b and mean T_p respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature. Percentages of the observation below and above the T_{set} range are specified.

Table 2 Results of the correlation (Spearman rank order statistic and *P*-value) and regressions [when the correlations were significant ($P < 0.05$); *b* coefficient, *t*-test and analysis of variance statistics and equation] among latitude, altitude, indices of thermoregulation (d_b, d_e and E) and the correspondent standard deviation (SD)

| | Correlation | Regression | | | | | | | |
	S	P	b	t-test	P	r^2	F	P	Equation
Latitude									
d_b	0.382	<0.05	0.111	$t_{33} = 5.039$	<0.001	0.442	$F_{1,32} = 25.388$	<0.001	$d_b = -0.325 + (0.111 \times \text{Lat.})$
SD of db	0.618	<0.05	0.0105	$t_{33} = 0.855$	0.399	0.0223	$F_{1,32} = 0.73$	0.399	SD of $d_b = 0.38 + (0.0105 \times \text{Lat.})$
d_e	0.678	<0.05	0.150	$t_{33} = 3.122$	0.004	0.239	$F_{1,32} = 9.746$	0.004	$d_e = 2.262 + (0.15 \times \text{Lat.})$
SD of d_e	0.706	<0.05	0.818	$t_{33} = 0.975$	0.334	0.0424	$F_{1,32} = 0.975$	0.334	SD of $d_e = 0.818 + (0.0656 \times \text{Lat.})$
E	0.27	0.127	–	–	–	–	–	–	–
Altitude									
D_b	−0.16	0.365	–	–	–	–	–	–	–
SD of d_b	0.629	<0.05	0.0003	$t_{33} = 3.49$	0.001	0.276	$F_{1,32} = 12.177$	0.001	SD of $d_b = 0.295 + (0.0003 \times \text{Lat.})$
D_e	0.673	<0.05	0.00181	$t_{33} = 4.987$	<0.001	0.445	$F_{1,32} = 24.872$	<0.001	$d_e = 4.295 + (0.00181 \times \text{Lat.})$
SD of d_e	0.799	<0.05	0.00183	$t_{33} = 21.18$	<0.001	0.953	$F_{1,32} = 448.607$	<0.001	SD of $d_e = -0.118 + (0.00183 \times \text{Lat.})$
E	0.423	<0.05	0.00017	$t_{33} = 5.622$	<0.001	0.505	$F_{1,32} = 31.611$	<0.001	$E = 0.238 - (0.00017 \times \text{Lat.})$

Discussion

The results presented here corroborate the hypotheses that there is greater susceptibility to warming in species from lower latitudes and lowlands, and thus contributes to the debate over climate-related risks of extinction in lizards (Deutsch *et al.*, 2008; Huey *et al.*, 2009). Lizards from colder regions (i.e. higher latitudes and montane populations), where most T_es fall below the T_{set} of the species, face reduced opportunities for thermoregulation that, within limits, may be compensated by behavior (Fuentes & Jaksic, 1979; Ibargüengoytía *et al.*, 2008, 2010). In contrast, lizards from warmer environments (i.e. lower latitude and lowlands) show a tendency to thermoconformity. Most low-elevation Patago-

nian *Liolaemus* thermoregulate poorly (Medina *et al.*, 2009, 2011; Gutiérrez *et al.*, 2010). However, their counterparts from the mountains and plateaus display moderate to high thermoregulatory efficiency (Gutiérrez *et al.*, 2010; Ibargüengoytía *et al.*, 2010; Valdecanto *et al.*, 2013). Given the high proportion of T_e below T_{set} observed in most of the cold and temperate environments inhabited by *Liolaemus* and *Anolis*, and the broad thermal tolerance described for, for example *Liolaemus* (Cruz *et al.*, 2005), warming could be neutral or beneficial to these populations, which can thus be considered to be at lowest risk. *Anolis* also display variation in thermoregulation behavior across the genera. For example, *A. cooki* from xeric lowlands behaves as a moderate thermoregulator, whereas *A. cristatellus* exhibits an increasing
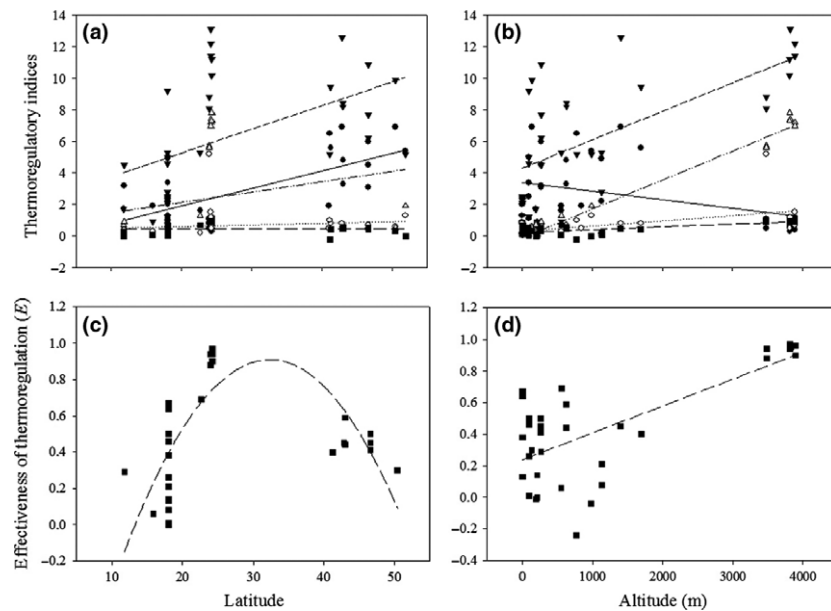
Figure 2 Variation in thermoregulatory indices (*sensu* Hertz *et al.*, 1993) with latitude (a) and altitude (b) for the populations of *Anolis*, *Liolaemus*, *Sceloporus* and *Tropidurus* included in the paper. Index d_b, solid circles and lines; standard deviation of d_b, empty circles and dotted lines; d_e, solid triangles and medium dashed lines; standard deviation of d_e, empty triangles and dash-dot-dotted lines; and the effectiveness of thermoregulations (*E*), solid squares and long dashed lines.

efficiency of thermoregulation with altitude (Hertz *et al.*, 1993). Additionally, the thermoregulatory behavior of *Anolis* may vary seasonally (Hertz *et al.*, 1993), so the risk would not be homogenous through the year. For example, the thermoregulation efficiency of *A. cooki* and *A. cristatellus*, at 5 and 90 m a.s.l, respectively, decreases in summer when the risk of overheating rises. Thus, the vulnerability of these lizards to climate warming is not only linked to the efficiency of thermoregulation but also to the geographic and seasonal variation in their physiology (phenotypic plasticity; Gunderson & Leal, 2012; Logan *et al.*, 2014).

Near the equator, at low elevation, lizards experience minimal annual variations in T_a, and both open and forested environments are thermally stable. Under proper thermal conditions and physiological specialization, such environments may favor thermoconformity and, as seems the case of some *Tropidurus*, lead to a limited capacity to adjust to changes (Huey, Hertz & Sinervo, 2003; Sears, Raskin & Angilletta, 2011). Furthermore, in most tropical open environments T_es exceed CT_{max} (Sunday *et al.*, 2014), which makes them hostile to many species. *Tropidurus* at the equator-ward and pole-ward limits of the Cerrado may find buffering options against warming (e.g. gallery forests with low T_as), but central populations are exposed to T_es exceeding their upper T_{set}, making them vulnerable to warming. In addition, tropical forest lizards may be particularly susceptible to climate change given a high tendency for physiological specialization, derived from the relative thermal stability (Huey *et al.*, 2009). Similarly, substrate temperatures at tropical low-elevation localities may increase with warming, eventually achieving levels that would lead to overheating in the current

populations. Low T_e shelters may benefit lizards in the short term, but the compromise between sheltering and activity time may affect fitness over the long term.

Overheating has already been identified as a distinct risk in some environments, both as a direct driver of death and as a factor-limiting activity (Sinervo *et al.*, 2010). For example, the ground surface temperature of deserts inhabited by *Sceloporus merriami* exceeds the species lethal temperature during most of the day (Grant & Dunham, 1990). Accordingly, Dunham (1993) predicted that a 2°C increase in T_a would even more severely restrict lizard activity, and thus also energy gain and population growth. Furthermore, Sinervo *et al.* (2010) emphasized the vulnerability of *S. merriami*, *S. mucronatus* and *S. serrifer* during the energetically demanding reproductive season, reporting the extinction of 24 populations of this genus between 1975 and 2009. In the forested environments, species like *T. torquatus* and *Sceloporus* avoid overheating in cool refuges and cope with other species from open environments seeking similar refuge (Huey *et al.*, 2009; Buckley, 2012). However, the central population of *Tropidurus torquatus* and *A. gundlachi*, as well as the desert populations of *Anolis cristatellus*, cannot access such refuges and therefore are at greater risk of suffering the effects of warming. A recent study on *A. sagrei* confirmed that some tropical populations might be capable of adapting to warmer and more thermally variable environments (Logan *et al.*, 2014), but it remains unclear whether most ectothermic vertebrates have the genetic plasticity to overcome the rate of global warming (Chevin, Lande & Mace, 2010; Seebacher *et al.*, 2010; Gunderson & Stillman, 2015). Climate change will thus likely drive natural selection

of behavior, physiology and niche preferences in lizard taxa, but specific consequences remain unclear given the few studies on the evolutionary rates for these traits (Kellermann et al., 2012; Logan et al., 2014; Muñoz et al., 2014; Sunday et al., 2014).

A possible generalization based on the variation in lizards' thermal physiology across latitudinal gradients is that continued global warming may be most threatening to populations that are more sensitive to T_a fluctuations (e.g. at sites close to the equator; Deutsch et al., 2008; Tewksbury, Huey & Deutsch, 2008). Moreover, upper tolerances seem to be conserved across many species (Addo-Bediako et al., 2000; Sunday et al., 2011; Kellermann et al., 2012; Grigg & Buckley, 2013; Hoffmann, Chown & Clusella-Trullas, 2013), so populations facing high T_a may simply be unable to evolve the necessary physiological tolerances to warming (Araujo et al., 2013). Furthermore, while T_a is generally exceeded by the physiological thermal tolerance limits, T_e matches or surpasses them. This suggests that threat predictions based on rising T_a generally underestimate the effects of climatic variation on ectotherms (Sunday et al., 2014).

The sensitivity of populations to warming, as noted by Williams et al. (2008), may vary across lineages. Some taxa may be able to adapt to the associated environmental changes (Logan et al., 2014), but others will likely fail as the pace of adaption may simply not be quick enough (Miles, 1994; Sinervo et al., 2010). Additionally, habitat fragmentation and transformation may further constrain the possibilities of dispersal to cooler environments, accelerating extinctions, particularly in montane populations also facing the upward progress of lowland species (Huey et al., 2009). Understanding the processes of adaptation, acclimation and phenotypic plasticity that determine the variation in the physiology among taxa would help assessing lizard vulnerability to climate warming. This challenge entails an integration of physiological, behavioral and evolutionary approaches, and will require testing specific predictions for different traits and lineages.

As a final comment, we must acknowledge the challenging ecological context in which some of the studied populations are located. Overgrazing by sheep together with the pollution of soil and water by oil and mining companies represent the main threats to the biodiversity of Patagonia. Nevertheless, this region contains more than 2.2 million ha. of National Parks (Hopkins, 1995). In contrast, habitat fragmentation represents the major conservation problem in Puerto Rico and Mexico. For example, species like *Anolis cooki* that used to inhabit dry forests have been slowly displaced to areas in sympatry with *A. cristatellus* (Genet, 2002). Despite being considered as a hotspot for conservation (Myers et al., 2000), less than 3% of the Brazilian Cerrado biome is under protection (Ratter, Ribeiro & Bridgewater, 1997). Consequently, the savanna is gradually being replaced by soy fields and cattle ranches, which may locally enhance rises of T_e to levels well above wider predicted values. Paradoxically, the results presented herein suggest that species with the highest vulnerability inhabit the least protected areas, which highlights the urgent need of mitigation measures as the increase in conservation units to protect their underestimated biodiversity.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Distribution of body temperature (T_b; upper graph) and operative temperatures (T_e; lower graph) of (a) *L. sarmientoi* and (b) *L. magellanicus*. The black and gray arrows indicate the mean T_b and mean T_e respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature (modified from Ibargüengoytía *et al.*, 2010). Percentages of the observation below and within the T_{set} range are specified.

Figure S2. Distribution of body temperature (T_b) of (a) *Liolaemus bibronii*, (b) *L. boulengeri* and (c) *L. lineomaculatus* from Esquel (equator-ward site; upper graphs) and Perito Moreno (pole-ward site; lower graphs). The black and gray arrows indicate the mean T_b and mean operative temperatures (T_e) respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature (modified from Medina *et al.*, 2011). Percentages of the observation below and above the T_{set} range are specified.

Figure S3. Distribution of body temperature (T_b) of (a) *Liolaemus pictus argentinus* at 1615–1769 m a.s.l. (Chalhuaco Mountain; upper graph) and at 771 m a.s.l. (Melipal Beach, Lake Nahuel Huapi; lower graph) (modified from Gutiérrez *et al.*, 2010) and for (b) *L. elongatus* at 840 m a.s.l. (modified from Ibargüengoytía, 2005). The black and gray arrows indicate the mean T_b and mean operative temperatures (T_e)

respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature. Percentages of the observation below and above the T_{set} range are specified.

Figure S4. Distributions of body temperature (T_b; upper graphs) and operative temperatures (T_e; lower graphs) of (a) *L. irregularis* from the four sites studied and of (b) *L. multicolor* (left), *L. albiceps* (center) and *L. yanalcu* (right) from sympatric sites with *L. irregularis* (modified from Valdecanto *et al.*, 2013). The black and gray arrows indicate the mean T_b and mean T_e respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature. Percentages of the observation below and above the T_{set} range are specified.

Figure S5. Distributions of body temperature (T_b; upper graphs) and operative temperatures (T_e; lower graphs) of (a) *Anolis cristatellus* from 1150 m a.s.l. collected in August, (b) the same population collected in January and of (c) *A. gundlachi* from 210 m a.s.l. collected in August. The black and gray arrows indicate the mean T_b and mean T_e respectively. The gray area indicates the lower and upper set points (T_{set}) of the preferred body temperature (modified from Hertz *et al.*, 1993). Percentages of the observation below and above the T_{set} range are specified.

Figure S6. Distribution of operative temperature (T_e) for (a) *Sceloporus mucronatus* lizards from an upland site (2500 m a.s.l.), (b) *S. mucronatus* from a montane site (3400 m a.s.l.) and (c) *S. serrifer* from a lowland tropical forest site (10 m a.s.l.). The black and gray arrows indicate the mean body temperature (T_b) and mean T_p respectively. The gray area includes the lower and upper set points (T_{set}) of the preferred body temperature (modified from Sinervo *et al.*, 2011). Percentages of the observation below and above the T_{set} range are specified.

Table S1. Data on the study sites of the species/populations included in the study.

Table S2. Mean ± standard error and, in some cases, range of body (T_b) and preferred (T_p) temperatures, set-point range (lower and upper T_{set}), operative temperatures (T_e), d_b and d_e indices and effectiveness of thermoregulations (E) of species/populations included in the study. Sample size is indicated between brackets.