A Journal of Macroecology

Global Ecology and Biogeography

RESEARCH PAPER

The influence of temperature seasonality on elevational range size across latitude: a test using *Liolaemus* lizards

Kimberly S. Sheldon[1]*, Adam D. Leaché[2,3] and Félix B. Cruz[4]

[1]*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA, [2]Department of Biology, University of Washington, Seattle, WA 98195, USA, [3]Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98195, USA, [4]Laboratorio de Fotobiología, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), CONICET-UNCOMA, Quintral 1250, Bariloche, 8400 Río Negro, Argentina*

ABSTRACT

Aim Identifying factors that limit species distributions is a fundamental question in ecology with implications for understanding global biodiversity patterns and species responses to environmental change. Theory suggests that temperature seasonality may affect range size. Species at higher latitudes and elevations experience greater temperature variation, which should lead to broader thermal tolerances and elevational ranges. Research suggests that realized seasonality, or the seasonality species experience when active, may be a better predictor of distributions than annual seasonality. We tested the seasonality hypothesis by examining relationships between environmental factors and elevational range.

Location Argentina.

Methods We gathered data on ecology and thermal physiology for 33 *Liolaemus* lizards (Liolaemidae) and analysed data in phylogenetic comparative analyses using mitochondrial DNA sequences. We used 1000 tree structures and ran phylogenetic generalized least squares analyses on all 33 species and on 23 species in the *boulengeri* clade to determine if the elevational range of lizards shows a positive relationship with annual and realized seasonality, thermal tolerance, latitude and elevational midpoint of the species distribution.

Results Latitude and elevational midpoint were good predictors of elevational range in all models. Annual seasonality was a good predictor of elevational range in models containing 33 species. Variation in phylogenetic tree structure led to differences in the best-fit statistical models. Thermal tolerance and realized seasonality were not good indicators of elevational range.

Main conclusions Our findings support some, but not all, of the predictions of the seasonality hypothesis. Species at higher latitudes and elevations have larger elevational ranges, and annual seasonality is partly responsible for this increase. Yet, adult thermal tolerance shows no relationship with elevational range, suggesting that distributions may depend on the physiology of other *Liolaemus* life stages. Differences in phylogenetic tree structure and the number of species included in analyses can lead to different conclusions regarding the seasonality hypothesis.

Keywords

Climatic variability, distributions, geographic range size, Liolaemidae, Rapoport's rule, thermal physiology, thermotolerance.

*Correspondence: Kimberly S. Sheldon, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.
E-mail: kimberlyssheldon@gmail.com

INTRODUCTION

Understanding the factors that limit species ranges is a fundamental goal in ecology (Sexton *et al.*, 2009) and has become increasingly important for predicting species responses to environmental change (Wilson *et al.*, 2005). Though many factors may shape species distributions, scientists have long recognized that temperature, which affects a host of biological processes

(Park, 1954; Dillon & Frazier, 2013), may play a large role in dictating where organisms can survive and reproduce (Sexton et al., 2009).

Rapid changes in temperature are causing many species to shift their geographic ranges, yet species responses are not uniform (Wilson et al., 2005). Differential responses among taxa are likely to derive from both spatial and temporal variation in the direction and magnitude of temperature change and from species responses to those changes (Deutsch et al., 2008; Mair et al., 2012). The impacts of current temperature change on species and communities may depend strongly on latitude, as factors such as life history and thermal specialization vary with distance from the equator (Huey et al., 2009; Sheldon & Tewksbury, 2014). Thus, knowledge of the impacts of temperature on species distributions at different latitudes is essential for an understanding of the effects of climate warming.

Janzen (1967) suggested that annual temperature variation should effect elevational range sizes by constraining ranges where temperature variation is minimal and expanding ranges where temperature variation is large. Specifically, species at lower latitudes and elevations experience minimal variation in temperature over time, resulting in narrower thermal tolerance (i.e. thermal specialists). Thus, thermal specialists should have reduced dispersal along temperature gradients (i.e. up or down mountains), since they are only adapted to handle a narrow range of temperatures. Reduced dispersal should result in narrower geographical ranges. Conversely, species at higher latitudes and elevations should experience large variation in temperature over time and, therefore, should have broader thermal tolerance (i.e. thermal generalists), greater dispersal and, thus, larger ranges compared with thermal specialists (Janzen, 1967; Huey, 1978; Stevens, 1992; Gaston & Chown, 1999; Sheldon & Tewksbury, 2014). This theory, often called the 'seasonality hypothesis' (Gaston & Chown, 1999), has been broadly applied in studies of both latitudinal and elevational range size (e.g. Huey, 1978; Rapoport, 1982; Stevens, 1992; Gaston & Chown, 1999).

Previous work on latitudinal range sizes supports the seasonality hypothesis. Species from higher latitudes have broader thermal tolerances and larger latitudinal ranges (Addo-Bediako et al., 2000; Cruz et al., 2005). Studies have also demonstrated that species with larger elevational ranges are found at higher latitudes and elevations (Huey, 1978; Gaston & Chown, 1999; Sheldon et al., 2011) and have a broader thermal tolerance (Gaston & Chown, 1999; Sheldon & Tewksbury, 2014). However, the role of temperature seasonality in determining elevational range sizes, as outlined by Janzen (1967), has rarely been tested across latitude using phylogenetic comparative methods that account for the confounding effects of shared ancestry in species comparisons (but see Pincheira-Donoso, 2011; Cruz et al., 2014). Studies that have tested the impact of seasonality in temperature on elevational range size using phylogenetic comparative methods have used a single phylogeny in analyses. Because phylogenies are working hypotheses that are subject to error, using only one tree structure does not account

for uncertainty in the relationships among species and could bias results (Rezende & Diniz-Filho, 2012; Moreno Azócar et al., 2013).

Most studies examining Janzen's hypothesis have used latitude as a substitute for annual seasonality in temperature (but see Quintero & Wiens, 2013; Cruz et al., 2014; Sheldon & Tewksbury, 2014). Because annual seasonality in temperature does not vary linearly with latitude, direct estimates of temperature are needed to test Janzen's hypothesis (Sheldon & Tewksbury, 2014). In addition, recent work shows that realized seasonality, or the temperature variation adults experience when active, is a better predictor of elevational range size than annual seasonality (Sheldon & Tewksbury, 2014). Thus, combining actual temperature data with ecological data in a well-studied group that occurs across broad latitudinal and elevational gradients, while simultaneously accounting for phylogenetic uncertainty, provides a powerful approach for testing the seasonality hypothesis.

The genus Liolaemus (Iguania: Liolaemidae) is the most species-rich genus of lizards in southern South America, with more than 150 species occurring in Argentina alone (Abdala et al., 2012). Liolaemus live in arid and semi-arid habitats (Avila et al., 2000) from sea level to over 5000 m in elevation, and the genus has one of the largest distributions of any lizard on Earth (Cei, 1986; Pincheira-Donoso et al., 2008). Ecological and phylogenetic data are available for broad-scale comparative analyses thanks to extensive research on the group (e.g. Carothers et al., 1998; Avila et al., 2000; Schulte et al., 2000; Labra & Bozinovic, 2002; Morando et al., 2003; Espinoza et al., 2004; Ibargüengoytía et al., 2010; Breitman et al., 2011; Pincheira-Donoso, 2011; Moreno Azócar et al., 2013). Previous work examining aspects of the seasonality hypothesis in Liolaemus has produced mixed results, perhaps owing to the fact that studies included different numbers of species and different phylogenetic trees (e.g. Cruz et al., 2005, 2014; Pincheira-Donoso et al., 2008)

Using 33 species of Liolaemus lizards from Argentina (Fig. 1), we tested Janzen's seasonality hypothesis with phylogenetic comparative analyses to evaluate the factors determining elevational range size. Our primary goal was to evaluate the hypotheses that elevational range size increases with annual seasonality in temperature, realized seasonality in temperature, thermal tolerance, latitude and elevation. A second goal was to examine how differences in species number and phylogenetic tree structure alter results. We answered the following questions.
1. As suggested in Janzen's seasonality hypothesis, does elevational range size increase with both annual seasonality in temperature and breadth of thermal tolerance? Support for the seasonality hypothesis would be indicated by significant positive relationships between elevational range size and these two factors.
2. Is realized seasonality in temperature a better predictor of elevational range size than annual seasonality in temperature? Recent work suggests the most relevant temperature variation for physiology and distributions may be restricted to the period in which species are active (Sheldon & Tewksbury, 2014).
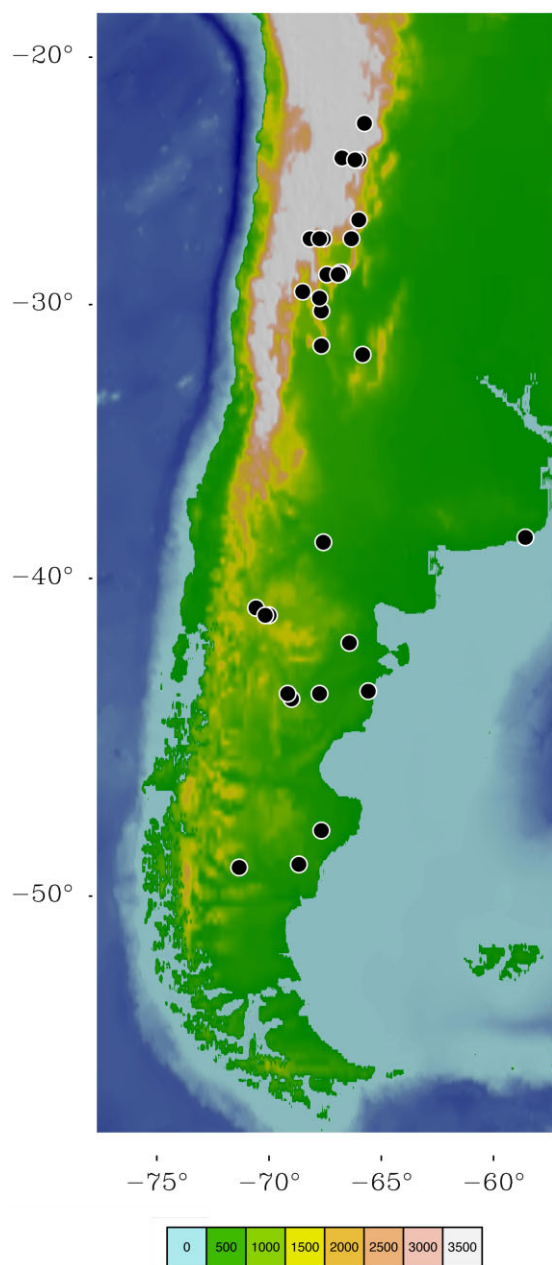
Figure 1 Map of southern South America showing the location of 33 *Liolaemus* species from Argentina. Note that some points are obscured due to overlap among species. Points represent the populations used for thermal tolerance tests and thus the locations for which we obtained geographical and temperature data. Map colours/shades represent elevation (m a.s.l.).

3. Do species at higher latitudes and elevations have larger elevational range sizes than species at lower latitudes and elevations? Temperature is not the only factor that varies along latitudinal and elevational gradients. Other biotic and abiotic factors, such as species diversity and precipitation, can vary with latitude and elevation and could affect elevational range size. If we find that seasonality in temperature is not a good predictor of

elevational range size, but latitude and elevation are, then factors other than temperature may be affecting range size.

4. How are results affected when we incorporate both a different number of species and phylogenetic uncertainty in analyses?

MATERIALS AND METHODS

Data collection

To test the seasonality hypothesis, we obtained information for 33 *Liolaemus* species including the annual and realized seasonality they experience, the latitude of study populations, elevational range size and breadth of thermal tolerance. We include two populations of *Liolaemus darwinii* in our analysis (northern and southern samples) that we count as two separate species based on recent species delimitation work suggesting that these populations are distinct species (Camargo *et al.*, 2012). We used previously collected estimates of elevational range size and adult thermal tolerance for all 33 species (see methods and data in Cruz *et al.*, 2005). For each species, adult thermal tolerance from a single study population was defined as the difference between the critical thermal maximum and critical thermal minimum, or the point at which individuals lost their righting ability in hot and cold temperatures, respectively (see methods in Cruz *et al.*, 2005).

Following Sheldon & Tewksbury (2014) we used the latitudinal and longitudinal coordinates for the populations from the thermal tolerance tests to obtain climate data experienced by study populations for the years 1961 to 1990 from the Climatic Research Unit CL 2.0 high-resolution dataset (New *et al.*, 2002). Because our measures of thermal tolerance are evolved differences not plastic responses we expect that small changes in temperature between 1990 and 2005, when we measured thermal tolerance, would not alter the broader relationship between environmental temperature variation and breadth of thermal tolerance. Following Deutsch *et al.* (2008), we calculated annual seasonality as the standard deviation (SD) of mean monthly temperatures for the entire year and realized seasonality as the SD of mean monthly temperatures only for the months when adults of each *Liolaemus* species are active. We also calculated the overall temperature range experienced by animals (mean maximum – mean minimum temperatures).

We used the latitude of the study populations and the midpoint of the elevational range of each species (hereafter 'elevational midpoint') for analyses (see below). Elevational midpoint is a measure of whether a species is found higher or lower on a mountain relative to other species. We ran phylogenetic comparative analyses on all 33 taxa as well as on 23 species in the *boulengeri* clade (Abdala, 2007).

Phylogenetic information

We downloaded the NEXUS file containing mitochondrial DNA (mtDNA) sequence data spanning the protein-coding genes *ND1* to *COI* for *Liolaemus* lizards from TreeBase (Legacy Study ID 1281; Cruz *et al.*, 2005) and realigned DNA sequence data

using MUSCLE v.3.8.31 (Edgar, 2004). We generated posterior distributions of phylogenetic trees using two types of Bayesian phylogenetic analyses. First, we used a relaxed molecular clock obtained with BEAST v.1.6.1 (Drummond & Rambaut, 2007) to get a posterior distribution of phylogenetic trees with branch lengths proportional to time (hereafter 'chrono' trees; Fig. 2a). External calibrations for time were not used, so time is relative. Second, we obtained a Bayesian posterior distribution of phylogenetic trees with branch lengths that represent the expected number of substitutions per site using MRBAYES v.3.1.2 (Ronquist & Huelsenbeck, 2003; hereafter 'phylo' trees; Fig. 2b). The 'phylo' trees from the MRBAYES analysis were rooted prior to conducting comparative analyses. The 33-taxon trees were rooted with *Liolaemus kriegi*, and the 23-taxon trees were rooted with *Liolaemus pseudoanomalus*, which are the most distantly-related species in the respective analyses, thus making them an appropriate outgroup species for rooting the trees.

We applied both 'chrono' and 'phylo' approaches to both the 33 *Liolaemus* species and to 23 species in the *boulengeri* clade for a total of four sets of trees (chrono33, phylo33, chrono23 and phylo23). All phylogenetic analyses assumed the GTR+I + G model of nucleotide substitution (Tavaré, 1986). The relaxed clock analyses assumed the uncorrelated lognormal distribution and a Yule process tree prior with a uniform (0,100) distribution. All Markov chain Monte Carlo analyses were run for 10 000 000 generations, sampling every 5000 steps, to produce 2000 samples from the posterior distribution. We performed convergence diagnostics using TRACER v.1.5 (Rambaut & Drummond, 2009) to check that parameters reached stationarity and that the effective sample size values were ≥ 500. We removed the first 1000 samples as burn-in, and the 1000 remaining trees from the posterior distribution were used in the phylogenetic comparative analyses.

Comparative analyses

Our goal was to evaluate the hypotheses that elevational range size increased with annual seasonality in temperature, realized seasonality in temperature, thermal tolerance, latitude and elevational midpoint. For the purposes of our analyses we treated environmental factors (seasonality, latitude and elevational midpoint) as species traits because species may have inherited adaptations from ancestors that lived in similar habitats (Harvey & Pagel, 1991). We used phylogenetic generalized least squares (PGLS) multiple regression models under a Brownian motion of trait evolution ($\lambda = 1$) (Pagel, 1999) using the caper package (Orme *et al.*, 2012) in R version 3.0.2 (R Development Core Team, 2013). The PGLS approach accounts for the statistical non-independence of interspecific data in comparative analyses by incorporating phylogenetic relatedness of species (Harvey & Pagel, 1991; Pagel, 1999).

We ran PGLS models with elevational range size as the response variable and all combinations of the explanatory variables of annual and realized seasonality in temperature, thermal tolerance, latitude and elevational midpoint across all 1000 phylogenies for all four sets of trees to account for phylogenetic

uncertainty. We included an interaction between latitude and elevational midpoint because species at a high-latitude, low-elevation site may experience a similar thermal environment compared with species at a low-latitude, high-elevation site and, thus, the two species may have similar elevational range sizes. We performed model simplification using Akaike information criterion (AIC) values to choose the most parsimonious model (i.e. the fewest explanatory variables) (Burnham & Anderson, 2004). We also ran models that included the temperature range experienced by species (mean maximum – mean minimum temperatures) in place of annual seasonality in temperature; however, we found no difference in the models (ΔAIC < 1) and therefore did not include temperature range in subsequent analyses.

When we had determined the best-fit model for each set of trees we tested for phylogenetic signal in the data (i.e. phylogenetic dependency of the data; Pagel, 1999) by maximum likelihood (ML) optimization of λ. The optimized λ value ranges from 0, where the phylogeny is not helpful in explaining the distribution of character values among taxa, to 1, which corresponds to data structured according to a Brownian motion model of trait evolution (Pagel, 1999). We show results from PGLS regressions of the best-fit model across all 1000 samples in each of the four sets of trees, and we report the phylogenetic signal (λ) for each best-fit model as an average across all 1000 trees in a set.

RESULTS

For the two sets of trees containing 33 species (chrono33 and phylo33), elevational range size was best predicted by a model that included annual seasonality in temperature, latitude and elevational midpoint (ΔAIC ≥ 2; Table 1, Fig. 3, Appendix S1 in Supporting Information). Phylogeny had a clear effect on the model for the phylo33 trees (mean $\lambda = 0.88$), but only a weak effect on the model for the chrono33 trees (mean $\lambda = 0.17$; Table 1). Annual seasonality in temperature, latitude and elevational midpoint explained approximately 63% of the variation in elevational range size in the phylogenetic trees containing 33 species (Table 1).

For the two sets of trees containing the 23 species in the *boulengeri* clade (chrono23 and phylo23), the model including annual seasonality in temperature, latitude and elevational midpoint had the lowest AIC value. However, removing annual seasonality in temperature only slightly increased the AIC value (ΔAIC = 1); thus, the most parsimonious model that best predicted elevational range size for the phylogenetic trees containing 23 species included only latitude and elevational midpoint (Table 1, Fig. 4, Appendix S1). The two explanatory variables in the best-fit model explained approximately 64% of the variation in elevational range size. For both sets of phylogenetic trees containing 23 species, phylogeny had no effect on the resulting model (mean $\lambda = 0$; Table 1).

Contrary to the seasonality hypothesis, adult thermal tolerance was not a significant predictor of elevational range size. The interaction between latitude and elevational midpoint was not supported for any of the phylogenetic tree sets (Table 1).
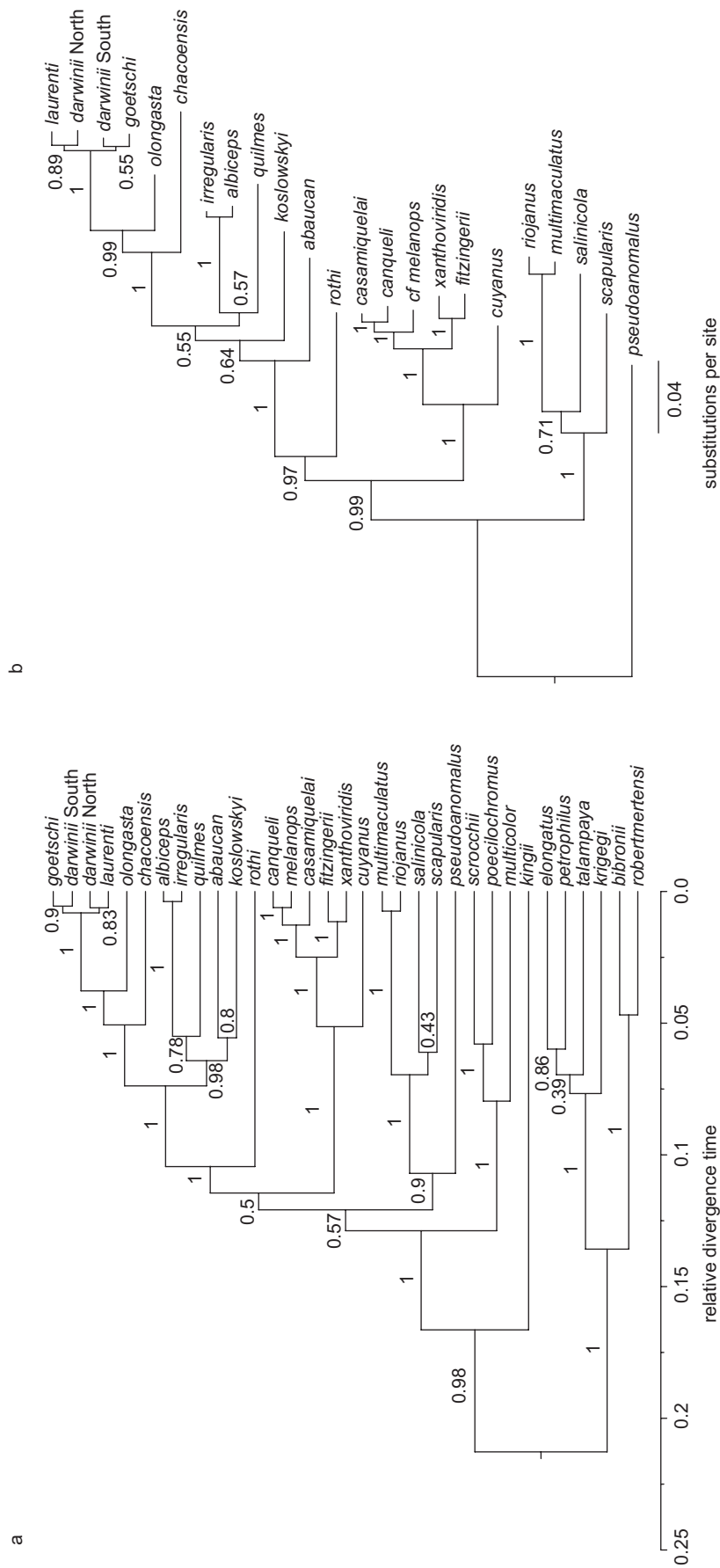
Figure 2 Phylogenetic relationships within *Liolaemus* based on Bayesian phylogenetic analysis of the mitochondrial DNA data for 33 taxa (a) and 23 taxa in the *boulengeri* clade (b). Branch lengths are proportional to relative divergence time (a) or approximate the expected number of substitutions per site (b).

Table 1 Results from phylogenetic generalized least squares models for factors that best predict elevational range size in *Liolaemus* lizards. The models took into account annual seasonality in temperature (Seas), realized seasonality in temperature, thermal tolerance breadth, latitude (Lat), elevational midpoint (Mid) and the interaction between latitude and elevational midpoint. The best-fit, most parsimonious models (Best model) are shown for the four sets of phylogenetic trees (Tree set). The number of parameters (Par) and average log-likelihood, λ and R^2 across all 1000 trees are shown for the best-fit model. ΔAIC shows the change between the best and second best models. The coefficients (β) are shown for factors in the best-fit model, and asterisks denote the *P*-values for the coefficients.

| Tree set | Best model | Par | Log-likelihood | λ | ΔAIC | Coefficients (β) | | | R^2 |
						Seas	Lat	Mid	
Chrono33	Seas + Lat + Mid	4	−266	0.17	2	420(*)	101***	1.01***	0.63
Chrono23	Lat + Mid	3	−186	0.00	1	–	82**	0.98***	0.64
Phylo33	Seas + Lat + Mid	4	−266	0.88	2	413*	99***	0.99***	0.64
Phylo23	Lat + Mid	3	−186	0.00	1	–	80**	0.94***	0.65

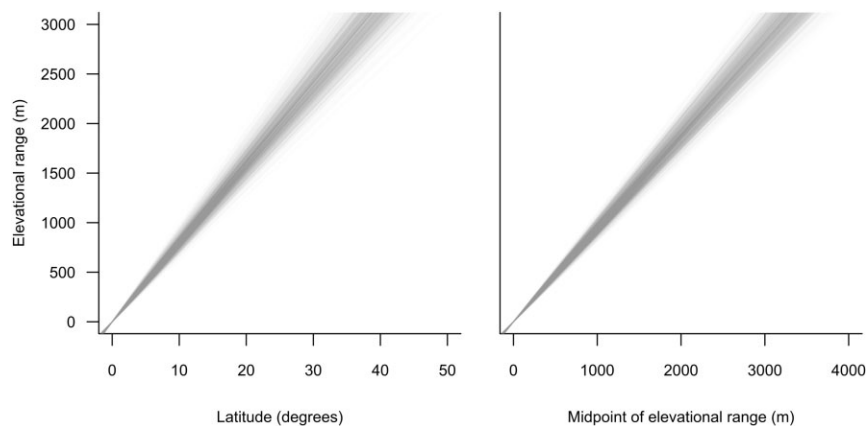(*)$P < 0.06$; *$P = 0.05$; **$P < 0.01$; ***$P < 0.0001$.
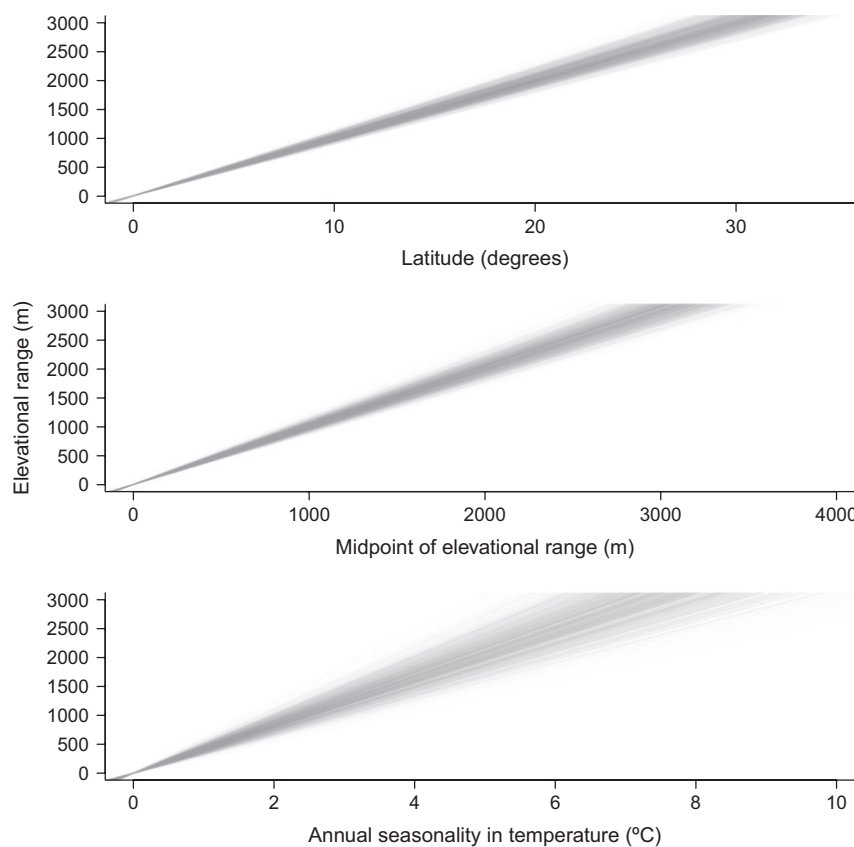
Figure 3 Relationship between elevational range size and annual seasonality, latitude and elevational midpoint based on comparative analyses of 33 *Liolaemus* lizards. Each line represents results from phylogenetic generalized least squares analysis for a single tree from 1000 possible trees in the chrono33 dataset. The density of the lines reflects the uncertainty in the phylogenetic tree, with dense lines reflecting less uncertainty and diffuse lines showing more uncertainty in the tree. The intercept for each line was set at zero.

DISCUSSION

Understanding the role of temperature in limiting species distributions has intrigued biologist for centuries, and has become particularly important in the light of recent changes in the thermal environment. Our results for *Liolaemus* lizards support some, but not all, of the predictions outlined in the seasonality hypothesis (Janzen, 1967). Direct measures of annual seasonality in temperature were a good predictor of elevational range size for the phylogenetic trees containing 33 species of *Liolaemus* (chrono33 and phylo33) but not for the phylogenetic trees containing only the 23 species in the *boulengeri* clade (chrono23 and

Figure 4 Relationship between elevational range size and latitude and elevational midpoint based on comparative analyses of 23 *Liolaemus* lizards in the *boulengeri* clade. Each line represents results from phylogenetic generalized least squares analysis for a single tree from 1000 possible trees in the phylo23 dataset. The density of the lines reflects the uncertainty in the phylogenetic tree, with dense lines reflecting less uncertainty and diffuse lines showing more uncertainty in the tree. The intercept for each line was set at zero.

phylo23). Thus, based on our results, in the broader context of *Liolaemus* the seasonality hypothesis holds; however, within a clade containing fewer but more closely related species (*boulengeri*) it does not.

One challenge in studies of the seasonality hypothesis is determining what aspects of the thermal environment are relevant to the physiologies and distributions of species (Kearney & Porter, 2009). Contrary to our expectations, realized seasonality was not a better predictor of elevational range size than annual seasonality. However, our measures of realized seasonality could not capture how duration of temperature fluctuations and extreme events such as cold spells affect physiology and distributions (Addo-Bediako *et al.*, 2000; Kingsolver *et al.*, 2011). In addition, lizards can take advantage of microhabitats and behavioural shifts to modify the temperatures they experience (Carothers *et al.*, 1998; Labra *et al.*, 2009). With a better measure of the temperature variation experienced by *Liolaemus* species – including microhabitat conditions – we might expect the realized seasonality term to be supported in the best-fit models.

Contrary to the seasonality hypothesis, adult thermal tolerance did not predict elevational range size in our models. Cruz *et al.* (2005) found that thermal tolerance increased with latitude among *Liolaemus* lizards, suggesting that exposure to greater temperature variation at higher latitudes led to greater thermal tolerance in these lizards. Though we expected to see this pattern across elevation, we found no such relationship. This could be due to several reasons. First, our data on thermal tolerance limits and environmental temperatures are from one population of each species, which may not represent the entire range of temperatures experience by the species or the physiological limits of the species. Second, because *Liolaemus* lizards are efficient thermoregulators (Moreno Azócar *et al.*, 2013) they may maintain relatively high body temperatures even in cool, high-elevation habitats (Navas, 2002; Espinoza *et al.*, 2004), which may mean that their distributions are not limited by adult

thermal tolerance (Carothers *et al.*, 1998). Third, environmental temperature may determine the ability of a species to survive and persist in a given location via effects on fitness, indirectly determining range size (e.g. maternal size; Angilletta *et al.*, 2006). Finally, at elevations above 3000 m, lizard ranges may be constrained by thermal effects on ontogeny (Navas, 2002; Medina *et al.*, 2011), such that the life stage that limits ranges precedes the adult stage, as has been shown in *Sceloporus undulatus* where the temperature tolerance of embryos determines geographic range limits (Parker & Andrews, 2007). Viviparity is common in high-elevation lizard species (Lambert & Wiens, 2013) and has evolved multiple times within the genus *Liolaemus* (Schulte *et al.*, 2000). Additionally, high-elevation viviparous *Liolaemus* species show less variation in their body temperature than low-elevation oviparous ones (Cruz *et al.*, 2014), especially in the case of pregnant females (F.B.C., unpublished data). Thus, temperature effects on reproduction and ontogeny may play a larger role in setting elevational distributions than does thermal tolerance of adult lizards (but see Labra & Bozinovic, 2002).

Consistent with Janzen's seasonality hypothesis (Janzen, 1967), elevational range size was greater in *Liolaemus* species found at higher latitudes and elevations. However, our results differ from a previous study that found no relationship between latitude and elevational range size among *Liolaemus* species (Pincheira-Donoso, 2011). This disagreement may reflect differences in incorporation of phylogenetic uncertainty; we used 1000 trees for each analysis rather than one tree structure. To see if this made a difference in our results, we followed Pincheira-Donoso (2011) and generated independent contrasts for all trees in a tree set to test whether elevational range size varied significantly with latitude (see Appendix S2 for details). Depending on the tree set, elevational range size increased significantly with latitude for 55–90% of trees (Appendix S2). Therefore, 10–45% of the trees in each tree set showed no significant relationship between the two variables. In addition,

Pincheira-Donoso (2011) used 68 species of *Liolaemus* to analyse the relationship between latitude and elevational range size. In our analyses, we saw striking differences in phylogenetic signal between tree sets containing 33 and 23 species. Phylogeny had an effect on the resulting model for the 33 species sets, however, the 23 species sets showed no phylogenetic signal. Thus, differences in both tree structure and number of species used in analyses could alter the relationships between environmental factors and elevational range size and may account for differences between our study and previous work (Moreno Azócar *et al.*, 2013). *Liolaemus* is a species-rich clade with over 230 species (Breitman *et al.*, 2011), and this estimate may be less than half of the actual number (Morando *et al.*, 2003). Future phylogenetic comparative analyses that include all described species and incorporate phylogenetic uncertainty are needed to test the relationships between seasonality in temperature, thermal physiology and elevational range size.

Though we found support for the seasonality hypothesis, temperature variation is not the only factor that limits the distribution of ectotherms. Precipitation patterns may strongly restrict species ranges (Hawkins *et al.*, 2003). In addition, biotic factors including competition, predation and mutualisms may also determine range limits (Sexton *et al.*, 2009). These biotic factors, in combination with thermal physiology, are likely to affect the ability of species to shift ranges in response to climate change (Urban *et al.*, 2012). Thus, future studies incorporating physiology and biotic interactions are likely to be the best approach for understanding factors affecting range limits and distributional shifts in response to temperature change.

ACKNOWLEDGEMENTS

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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.

Appendix S1 Additional figures.
Appendix S2 Methods and results for independent contrasts.

BIOSKETCHES

Kimberly S. Sheldon is an NSF post-doctoral research fellow at the University of Wyoming. Her research interests include physiological ecology, biogeography, conservation and natural history.

Adam D. Leaché is an assistant professor of biology at the University of Washington and curator of genetic resources and herpetology at the Burke Museum of Natural History and Culture. He studies phylogenetics, systematics, phylogeography and species delimitation, mostly in lizards.

Félix B. Cruz is a full researcher of CONICET (the Argentine Science Council) in the Laboratorio de Fotobiología, Instituto de Investigaciones en Biodiversidad y Medioambiente in Argentina. His research interests include ecological physiology, macroecology and natural history, mostly in *Liolaemus* lizards.

Editor: Gary Mittelbach