

# Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography

Joseph W. Grigg and Lauren B. Buckley

*Biol. Lett.* 2013 **9**, 20121056, published 16 January 2013

---

## Supplementary data

["Data Supplement"](#)

<http://rsbl.royalsocietypublishing.org/content/suppl/2013/01/15/rsbl.2012.1056.DC1.html>

## References

[This article cites 22 articles, 10 of which can be accessed free](#)

<http://rsbl.royalsocietypublishing.org/content/9/2/20121056.full.html#ref-list-1>

## Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (663 articles)

[evolution](#) (666 articles)

## Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)



## Research

**Cite this article:** Grigg JW, Buckley LB. 2013 Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol Lett* 9: 20121056. <http://dx.doi.org/10.1098/rsbl.2012.1056>

Received: 11 November 2012

Accepted: 14 December 2012

### Subject Areas:

ecology, evolution

### Keywords:

critical thermal limits, environmental niche, space, phylogeny

### Author for correspondence:

Lauren B. Buckley

e-mail: [buckley@bio.unc.edu](mailto:buckley@bio.unc.edu)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2012.1056> or via <http://rsbl.royalsocietypublishing.org>.

## Physiology

# Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography

Joseph W. Grigg and Lauren B. Buckley

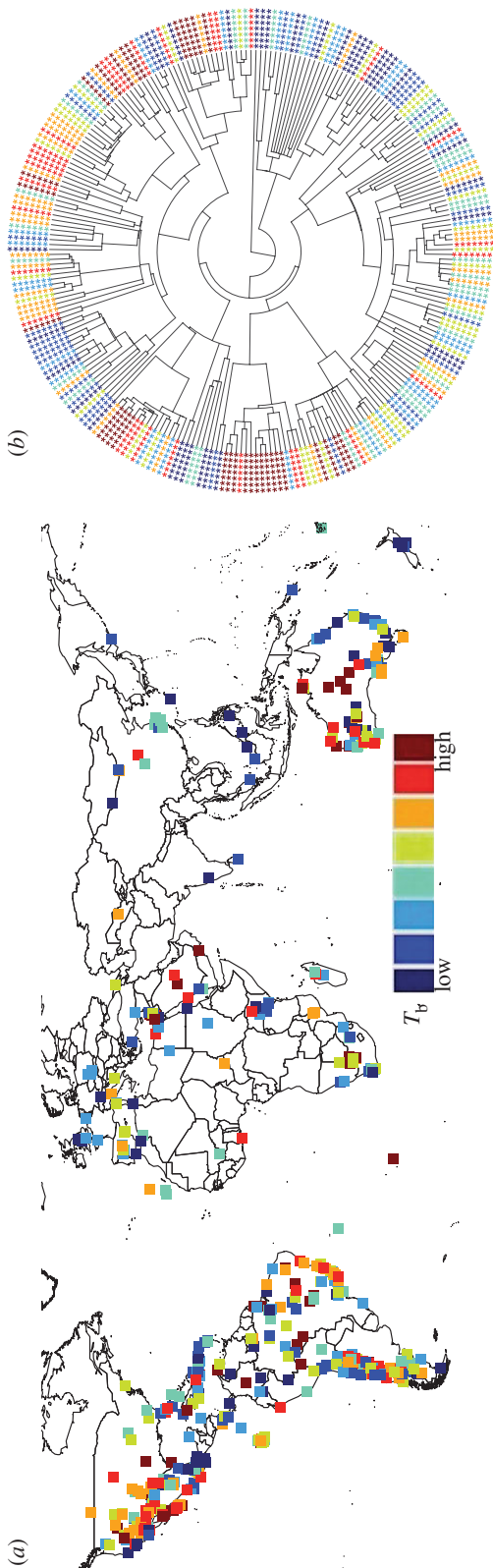
Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

Species may exhibit similar thermal tolerances via either common ancestry or environmental filtering and local adaptation, if the species inhabit similar environments. We ask whether upper and lower thermal limits (critical thermal maxima and minima) and body temperatures are more strongly conserved across evolutionary history or geography for lizard populations distributed globally. We find that critical thermal maxima are highly conserved with location accounting for a higher proportion of the variation than phylogeny. Notably, thermal tolerance breadth is conserved across the phylogeny despite critical thermal minima showing little niche conservatism. Body temperatures observed during activity in the field show the greatest degree of conservatism, with phylogeny accounting for most of the variation. This suggests that propensities for thermoregulatory behaviour, which can buffer body temperatures from environmental variation, are similar within lineages. Phylogeny and geography constrain thermal tolerances similarly within continents, but variably within clades. Conservatism of thermal tolerances across lineages suggests that the potential for local adaptation to alleviate the impacts of climate change on lizards may be limited.

## 1. Introduction

Similarities in species' thermal niches across evolutionary history (phylogenetic niche conservatism [1]) and geography can aid in forecasting responses to climate change. Thermal physiology and the magnitude of recent warming successfully predict patterns of recent lizard extinction, potentially owing to climate change restricting the activity of species with low upper thermal limits [2]. Lizard thermal physiologies exhibit conservatism across both phylogeny and geography as some forest-dwelling, non-basking lineages remaining restricted to the tropics and open-habitat, basking lineages extending into temperate zones [3]. Lineages with phylogenetically conserved thermal tolerances may be unlikely to adapt locally to climate change. Species with strong geographical gradients in thermal tolerance may be more likely to use dispersal and adaptation to track their environmental niches through climate change.

Does evolutionary history or geography better explain global patterns of lizard thermal physiology? We use a statistical method [4] to partition variance into spatial and phylogenetic contributions for the following four thermal metrics. We consider the upper and lower thermal limits on performance ( $CT_{max}$  and  $CT_{min}$ ), which ranges from 33.4°C to 51.0°C and 1.9°C to 14.1°C respectively, as well as the distance (°C) between these limits (thermal tolerance breadth, TTB).  $CT_{max}$  and  $CT_{min}$  determine how the environment influences fitness as well as susceptibility to acute thermal stress [5]. We additionally consider activity body temperature ( $T_b$ ), which range from 14.5°C to 42.1°C. While  $T_b$  is sometimes used as a more readily available proxy for thermal tolerances [2], it is additionally influenced by microclimate selection.



**Figure 1.** Activity body temperatures ( $T_b$ ) for lizards are less conserved across (a) geography than (b) phylogeny (with blue to red depicting eight quantiles from low to high).

The propensity for such thermoregulatory behaviour may be phylogenetically conserved, and may enable coping with climate change through environmental buffering [6]. Conversely, this buffering may reduce selection for elevated  $CT_{max}$  [7] and ultimately preclude the evolutionary responses necessary to cope with long-term climate change.

Broad-scale patterns of temperature means and seasonality both pose strong selection on thermal physiology [3,5,8]. Indeed, the  $CT_{max}$  of reptiles relates to thermal variability, whereas  $CT_{min}$  relates to mean annual temperature [9]. The limited temperature seasonality in the tropics selects for reduced TTB [3,5]. We first use distance as a proxy ('geographical space') for environmental similarity as location captures trends in both means and seasonality. We then examine environmental similarity directly.

## 2. Material and methods

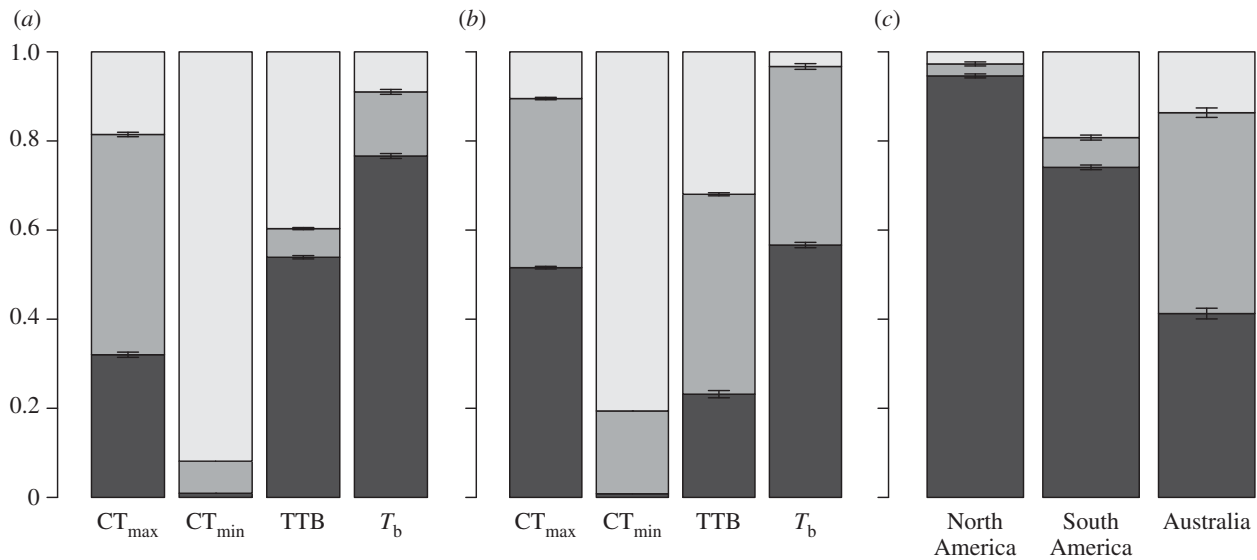
We analysed 481  $T_b$  measures for 254 lizard species from 34 families [2] (see the electronic supplementary material, table S1). We expanded a previous database [8] to include  $CT_{max}$ ,  $CT_{min}$  and TTB values for 68, 60 and 60 species, respectively (see the electronic supplementary material, table S2). We used a supertree of squamate reptiles constructed using matrix representation parsimony analysis and dated based on fossils and molecular data [10]. For each observation, we extracted annual means of daily minimum, mean and maximum air temperatures as well as seasonality calculated as the variance of monthly mean temperatures ( $0.5^\circ$  resolution, which is sufficient resolution to account for broad elevational differences, IIASA database A03). We additionally combined these measures into a single principle component describing the environment ('temperature space').

We conducted our analysis in R v 2.13.1 [11] using the package APE [12]. We determined the relative contribution of space and phylogeny to variation in each metric using a method derived from phylogenetically independent contrasts (PIC) [4]. The following method (equation (2.7) of [4]) produces three positive parameter estimates ( $\varphi$ ,  $\lambda'$  and  $\gamma$ ), which sum to 1 and describe the variance in the metric as follows:

$$V(\varphi, \lambda) = \gamma \mathbf{h} + \lambda' \Sigma + \varphi \mathbf{W}. \quad (\text{eqn 2.7 in [4]})$$

Here,  $\varphi$  represents the relative contribution of spatial effects,  $\lambda' = (1 - \varphi)\lambda$  represents the relative phylogenetic contribution, and  $\gamma = (1 - \varphi)(1 - \lambda)$  represents the relative contribution of effects independent of both phylogeny and space.  $\mathbf{V}$ ,  $\Sigma$  and  $\mathbf{W}$  are variance-covariance matrices describing the expectation, phylogenetic distances and spatial distances, respectively.  $\mathbf{h}$  is a vector of the heights of tips on the phylogeny. The  $\lambda$  used in calculating  $\lambda'$  is Pagel's [13] estimate of phylogenetic signal. We additionally estimate Blomberg's  $K$  because it is a commonly implemented metric that indicates the amount of phylogenetic signal in the tip data relative to the expectation ( $K = 1$ ) for a trait that evolved by Brownian motion [14]. We assessed significance by comparing the variance of independent contrasts for 1000 randomized (tip-swapped) trees with that of the observed trees (phylosignal function in R package picante). We computed PIC to examine correlations between the thermal metrics (R package APE). Correlations were estimated based on 1000 iterations to account for randomization.

Because the analysis requires a binary phylogeny, we resolved polytomies using a birth-death model of diversification (methods follow [15]) and repeated the analyses over 2500 potential phylogenies.  $T_b$  values were randomly selected (when multiple values were available for a single species) for each of the potential phylogenies. We estimated  $\varphi$ ,  $\lambda'$  and  $\gamma$  assuming



**Figure 2.** The stacked contributions of phylogeny ( $\varphi$ , black) and space ( $\lambda'$ , grey) to patterns of thermal tolerance vary by metric (unaccounted for variance:  $\gamma$ , light grey). 95% CIs across the randomizations are depicted. We depict the contributions when characterizing both (a) geographical and (b) (mean annual) temperature space. We additionally analyse the determinants of body temperature ( $T_b$ ) within continents.

that the traits followed a gradual Brownian motion model of evolution (branch lengths proportional to time).

### 3. Results and discussion

We find that body temperatures are less conserved across geography than evolutionary history (figure 1). Phylogeny accounts for most of the variation in  $T_b$  patterns ( $\varphi = 0.087$ ,  $\lambda' = 0.877$  and  $\gamma = 0.036$ , figure 2). The strong phylogenetic signal of  $T_b$  ( $K = 1.075$ ,  $p = 0.001$ ) is notable because one would expect body temperatures to be strongly influenced by air and surface temperatures, which exhibit pronounced geographical gradients. However, many lizard species are able to maintain their preferred body temperatures through behavioural thermoregulation and habitat selection [16–18]. The propensity for thermoregulatory behaviour varies between lineages [3], but its phylogenetic conservatism has not been formally assessed.

The influence of phylogeny and geography varies between thermal tolerance metrics. Space accounts for more variation in  $CT_{\max}$  than phylogeny ( $\varphi = 0.549$ ,  $\lambda' = 0.270$  and  $\gamma = 0.181$ ; figure 2a).  $CT_{\min}$  shows little conservatism across either phylogeny or space ( $\varphi = 0.073$ ,  $\lambda' = 0.009$  and  $\gamma = 0.917$ ). Interestingly, TTB shows a greater contribution of phylogeny than either  $CT_{\max}$  or  $CT_{\min}$  ( $\varphi = 0.083$ ,  $\lambda' = 0.547$  and  $\gamma = 0.369$ ).  $CT_{\max}$  ( $K = 0.585$ ,  $p = 0.001$ ),  $CT_{\min}$  ( $K = 0.427$ ,  $p = 0.02$ ) and TTB ( $K = 0.458$ ,  $p = 0.002$ ) exhibit significant phylogenetic conservatism, but to a lesser extent than  $T_b$ . A previous, counterintuitive result is that both  $CT_{\min}$  and  $CT_{\max}$  increase with latitude, because many temperate lizards are basking species that inhabit warm and thermally variable desert environments [3]. The conservation of thermoregulatory behaviour across lineages may alter selection and thus geographical patterns of thermal tolerance. Patterns of conservatism are similar when we consider temperature space rather than geography (see figure 2b and electronic supplementary material, table S3) with several exceptions. Habitat selection may cause more

thermal similarity than would be expected based on geography and account for these exceptions. Indeed, environmental temperatures account for more of the variation in  $T_b$  and TTB than geography.

We used PIC (standardized) to investigate why TTB exhibits greater phylogenetic conservatism than  $CT_{\max}$  or  $CT_{\min}$  (see the electronic supplementary material, figure S1). We find that lizards have a broad TTB owing to either a low  $CT_{\min}$  ( $F_{1,52} = 117$ ,  $p < 10^{-15}$  and  $r^2 = 0.69$ ) or high  $CT_{\max}$  ( $F_{1,52} = 18.2$ ,  $p < 10^{-4}$  and  $r^2 = 0.26$ ). However,  $CT_{\min}$  and  $CT_{\max}$  are not correlated ( $p = 0.70$ ). We find that  $T_b$  is positively correlated with  $CT_{\max}$  ( $p < 0.01$ ,  $r^2 = 0.56$ ) but is not related to  $CT_{\min}$  ( $p = 0.4$ ). These findings suggest that narrow TTB, which confers sensitivity to climate warming, is not associated with a particular range of thermal tolerance. The importance of the thermal metrics as determinants of activity time and thermal stress varies latitudinally, and is likely to shift through climate warming:  $CT_{\min}$  may become less important as a constraint on activity in temperate areas, whereas  $CT_{\max}$  is likely to become increasingly important as a determinant of thermal stress in the tropics [6].

Is  $T_b$  conservatism similar within geographical and phylogenetic subsets (see figure 2c and electronic supplementary material, table S3)? The importance of phylogeny persists within North America ( $n = 71$ ,  $\varphi = 0.027$ ,  $\lambda' = 0.946$  and  $\gamma = 0.027$ ) and South America ( $n = 40$ ,  $\varphi = 0.067$ ,  $\lambda' = 0.741$  and  $\gamma = 0.192$ ). Greater conservatism across geographical and temperature space occurs in Australia, perhaps owing to its pronounced aridity gradient ( $n = 62$ ,  $\varphi = 0.451$ ,  $\lambda' = 0.413$  and  $\gamma = 0.136$  for geographical space). Patterns of conservatism are more variable across clades (defined by Sites *et al.* [19]). Conservatism was substantially stronger across phylogeny than geography for the Anguimorpha ( $n = 23$ ) and Scincoidea ( $n = 67$ ) clades, and somewhat stronger for Lacertoidea ( $n = 36$ ). Estimates of conservatism varied between geographical and temperature space for Iguania ( $n = 96$ ), and were generally low for Gekkota ( $n = 27$ ). These results suggest that thermoregulatory behaviours diverged deep within the lizard phylogeny and have persisted through colonization and

radiations on different continents. The thermal niches of ants ( $\lambda \sim 0.9$ ) [20] and amphibians [21] also exhibit phylogenetic conservatism, whereas geography is more important for mammals [22].

Our analysis suggests that thermal tolerances are conserved deep within evolutionary history rather than being determined by ecological filtering, dispersal, or local adaptation (perhaps due to limits to adaptation). The potential for local adaptation to alleviate the impacts of climate change on lizards may be limited [23] particularly in the

tropics [3,17], where narrow TTBs can correspond to low genetic variation and limited evolutionary potential [24]. However, strong phylogenetic signal in body temperatures suggests that some lineages may effectively use thermoregulation to avoid thermal stress [6].

We thank Rob Freckleton for contributing R code, and J. Kingsolver, G. Thomas, members of the Buckley and Kingsolver research groups and reviewers for comments. Work supported in part by NSF grant no. EF-1065638 to L.B.B.

## References

- Wiens JJ *et al.* 2010 Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)
- Sinervo B *et al.* 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
- Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Álvarez Pérez HJ, Garland T. 2009 Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* **276**, 1939–1948. (doi:10.1098/rspb.2008.1957)
- Freckleton RP, Jetz W. 2009 Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B* **276**, 21–30. (doi:10.1098/rspb.2008.0905)
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
- Kearney M, Shine R, Porter WP. 2009 The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840. (doi:10.1073/pnas.0808913106)
- Huey RB, Hertz PE, Sinervo B. 2003 Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
- Sunday JM, Bates AE, Dulvy NK. 2010 Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830. (doi:10.1098/rspb.2010.1295)
- Clusella-Trullas S, Blackburn TM, Chown SL. 2011 Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am. Nat.* **177**, 738–751. (doi:10.1086/660021)
- Bergmann PJ, Irschick DJ. 2011 Vertebral evolution and the diversification of squamate reptiles. *Evolution* **66**, 1044–1058. (doi:10.1111/j.1558-5646.2011.01491.x)
- R Core Development Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
- Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
- Blomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)
- Kuhn TS, Mooers AØ, Thomas GH. 2011 A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* **2**, 427–436. (doi:10.1111/j.2041-210X.2011.00103.x)
- Seebacher F, Shine R. 2004 Evaluating thermoregulation in reptiles: the fallacy of the inappropriately applied method. *Physiol. Biochem. Zool.* **77**, 688–695. (doi:10.1086/422052)
- Tewksbury JJ, Huey RB, Deutsch CA. 2008 Putting the heat on tropical animals. *Science* **320**, 1296–1297. (doi:10.1126/science.1159328)
- Huey RB, Tewksbury JJ. 2009 Can behavior douse the fire of climate warming? *Proc. Natl Acad. Sci. USA* **106**, 3647–3648. (doi:10.1073/pnas.0900934106)
- Sites Jr JW, Reeder TW, Wiens JJ. 2011 Phylogenetic insights on evolutionary novelties in lizards and snakes: sex, birth, bodies, niches, and venom. *Annu. Rev. Ecol. Syst.* **42**, 227–244. (doi:10.1146/annurev-ecolsys-102710-145051)
- Diamond SE, Sorger DM, Hulcr J, Pelini SL, Toro ID, Hirsch C, Oberg E, Dunn RR. 2012 Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Change Biol.* **18**, 448–456. (doi:10.1111/j.1365-2486.2011.02542.x)
- Hof C, Rahbek C, Araújo MB. 2010 Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography* **33**, 242–250. (doi:10.1111/j.1600-0587.2010.06309.x)
- Cooper N, Freckleton RP, Jetz W. 2011 Phylogenetic conservatism of environmental niches in mammals. *Proc. R. Soc. B* **278**, 2384. (doi:10.1098/rspb.2010.2207)
- Angilletta MJ. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.
- Kellermann V, Van Heerwaarden B, Sgrò CM, Hoffmann AA. 2009 Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* **325**, 1244–1246. (doi:10.1126/science.1175443)