Evolutionary Ecology Research, 2014, **16**: 143–152

Thermal tolerances in rodents: species that evolved in cold climates exhibit a wider thermoneutral zone

Francisco Bozinovic[1], Francisco Ferri-Yáñez[2,3,4], Hugo Naya[5],
Miguel B. Araújo[2,3,4] and Daniel E. Naya[6]

[1]Departamento de Ecología and Center of Applied Ecology and Sustainability (CAPES), Facultad de Ciencias Biológicas, Universidad Católica de Chile, Santiago, Chile, [2]Departamento de Biogeografía y Cambio Global, LINCGlobal, Museo Nacional de Ciencias Naturales, Madrid, España, [3]InBIO-CIBIO, Universidad de Évora, Évora, Portugal, [4]Imperial College London, Silwood Park Campus, Ascot, Berkshire, UK, [5]Instituto Pasteur de Montevideo and Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, Montevideo, Uruguay and [6]Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

ABSTRACT

Background: Thermal constraints are often invoked to explain animal distributions. Maximum temperatures are less variable in different biomes around the globe than are minimum temperatures. Considerable information is available for mammals about basal metabolic rate and thermal conductance.

Aims: Evaluate the correlation of lower critical temperature (T_{LC}), upper critical temperature (T_{UC}) or TNZ breadth ($T_{UC} - T_{LC} = TNZ_b$) with three ambient temperatures in rodent species.

Hypotheses: T_{LC}, T_{UC} and TNZ_b should be adjusted by selective processes to the ambient temperature that is most usually experienced by mammal species. TNZ_b should be greater in species inhabiting colder habitats.

Methods: We used T_{LC}, T_{UC} data from published studies of 85 species of rodents. We determined the average annual mean, minimum and maximum temperatures across the distribution of each species. Then, using standard least squares regression with body mass as a covariate, we determined the statistical relationships between the physiological variables and the temperatures. We evaluated the effect of phylogeny using a Bayesian Phylogenetic Mixed Model in addition to Bayesian Model Averaging.

Results: Ambient temperatures correlate positively with T_{LC} and T_{UC}, and negatively with TNZ_b. Species that evolved in cold climates exhibited a greater mass-independent TNZ_b than species from warmer climates. Species that evolved in cold climates exhibited lower T_{LC} and T_{UC} than species from warmer climates. Phylogenetic as well as conventional statistics indicated that there are thermoregulatory constraints across geographic gradients.

Keywords: macrophysiology, energetics, environmental temperature, global ecology, climate change, small mammals.

Correspondence: F. Bozinovic. Departamento de Ecología, CAPES & LINCGlobal, Universidad Católica de Chile, Santiago 6513677, Chile. e-mail: fbozinovic@bio.puc.cl

INTRODUCTION

Understanding the factors that determine the geographic range limits of species is essential to address fundamental questions in ecology, biogeography and evolutionary biology and is particularly pressing because of ongoing environmental global change (Pearson and Dawson, 2003; Martin *et al.*, 2013). Macrophysiology has recently emerged from the integration of physiological ecology and macroecology (Chown *et al.*, 2004) to elucidate the contribution of physiological traits to the geographic distributions of organisms. In other words, macrophysiology is a conceptual convergence between the fields of global ecology and physiology in the study of large spatial- and temporal-scale patterns to explain how high levels of environmental variability affect physiological traits.

Over the past decade, many climate-based hypotheses regarding variation in the distribution range of species have emerged (see Pither, 2003), such as the climate variability hypothesis, the climate extreme hypothesis, and the optimal climate hypothesis. These hypotheses use data on physiological traits of the species, focusing mainly on variation in latitude and altitude (Spicer and Gaston, 1999) and using principally the intrinsic physiological properties of species to predict their responses to climatic variables and how these properties may affect the geographic ranges of assemblages, species and populations (Bozinovic *et al.*, 2011; Naya and Bozinovic, 2012).

Environmental temperature exerts an influence on most levels of biological hierarchy, and thermal physiology is one key factor underpinning the ecological and evolutionary success of animals. Thermal conditions vary over space and time, and thus populations and species are continuously challenged to maintain homeostasis. Individuals are expected to evolve physiological adaptations, physiological tolerances and acclimatization to local conditions in different and likely heterogeneous environments along geographic ranges. Accordingly, thermoregulatory and energetic constraints factors often have been invoked to explain animal distributions (Lovegrove, 2000; Rezende *et al.*, 2004). However, few studies have examined the relationship between plasticity of energetic traits, other than oxygen consumption, and the distribution of endotherms (but see Rodriguez-Serrano and Bozinovic, 2009; Araújo *et al.*, 2013; Naya *et al.*, 2013a, 2013b; Khalik *et al.*, 2014). The thermoneutral zone (TNZ) limits provide an index of an endotherm's temperature comfort range. Within the limits of TNZ are the basal metabolic rates, i.e. endotherms do not have to expend large amounts of energy to maintain thermoregulatory homeostasis. At the lower limit of the thermoneutral zone is the T_{LC} (lower critical temperature) and at the upper limit is the T_{UC} (upper critical temperature; see Fig. 1). Recently, Riek and Geiser (2013) provided the first phylogenetic analyses on scaling of T_{LC}, T_{UC} and TNZ in mammal species. Also, they demonstrated that mammalian TNZ breadth (TNZ_b) varied from nearly 1°C to as high as 21°C, a range that is not only affected by body mass but also by thermal conductance.

Here we evaluate the correlation between T_{LC}, T_{UC} and TNZ_b ($= T_{UC} - T_{LC}$) and three different ambient temperatures for 85 rodent species, using a model selection approach to compare the predictive power of different statistical models. We hypothesize that since basal metabolic rate and thermal conductance are both sensitive to climatic variables (Naya *et al.*, 2013b), and these physiological traits are mainly adjusted – in an evolutionary sense – by selective processes to ambient temperature (Bozinovic *et al.*, 2011; Naya *et al.*, 2013a), then T_{LC}, T_{UC} (Araújo *et al.*, 2013) and TNZ_b should also be correlated with geographic temperature. In addition, given that minimum temperatures show a much steeper change across the globe

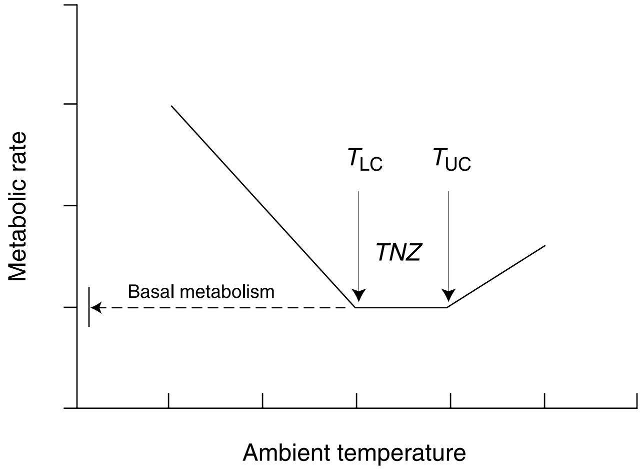

Fig. 1. Fundamental relationships between ambient temperature and metabolic rate for endotherms. The thermoneutral zone (*TNZ*) limits provide an index of an endotherm's temperature comfort range. Within the limits of *TNZ* is basal rate of metabolism. At the lower limit of the thermoneutral zone is the T_{LC} (lower critical temperature) and at the upper limit is the T_{UC} (upper critical temperature).

than maximum temperatures, we expect TNZ_b to be wider in species inhabiting colder habitats (see Araujo *et al.*, 2013).

MATERIALS AND METHODS

Dataset

Data relating to T_{LC}, T_{UC} and the breadth of TNZ_b (calculated as $T_{UC} - T_{LC}$) from published studies on 85 species of rodents from different families and latitudes are available upon request together with data on habitat temperature (T_{med}, mean annual temperature; T_{min}, minimum temperature of coldest month; and T_{max}, maximum temperature of warmest month). A synthetic metric of ambient temperature was calculated as the average temperature across the distribution of a species. Species distributions were obtained from Hijmans *et al.* (2005) and climatic variables were obtained from the WorldClim dataset (Holt *et al.*, 2013) at 2.5 arc minutes resolution. Species distributions and environmental variables were processed using the software Qgis 1.8.0-Lisboa (QGIS Development Team, 2013).

Data analyses

The relationships between thermal variables (T_{LC}, T_{UC} and TNZ_b) and ambient temperatures (T_{med}, T_{min} and T_{max}) were evaluated through standard least squares regression techniques, using body mass as a covariate. We ran single regression models with one ambient temperature (in addition to log body mass), and also multiple regression models with two ambient temperatures (in addition to log body mass). We estimated the goodness of fit of each model and used the Bayesian Information Criterion (BIC) to compare among them. Specifically, a model was selected as a 'good model' if its BIC value did not differ from the overall best model BIC value (which represents, by definition, the lowest BIC value) by more than 2.3 units (Raftery *et al.*, 1997). All these analyses were performed using the R package leaps (Raftery *et al.*, 1997). The effect of phylogeny on the relationship between thermal variables and ambient temperatures was evaluated using a Bayesian Phylogenetic Mixed Model (Bayesian PMM) (Naya *et al.*, 2006; Lumley and Miller, 2009), as well as Bayesian Model Averaging (BMA) (Raftery *et al.*, 1997). A phylogenetic tree was built up by combining the tree published by Lovegrove (2003) with the tree published by Huchon and Douzery (2001) (hystricognath rodents). Species that were not present in any of these trees were included at the best resolution level, according to the family or genus to which they belong. We decided to incorporate phylogenetic uncertainty in the calculations using BMA because: (1) branch lengths are not known for our super-tree, and (2) there are several soft polytomies associated with (1). Consequently, we included phylogenetic uncertainty by generating 1000 trees in which polytomies were randomly resolved (by transforming all multichotomies into a series of dichotomies with one or several branches of length zero), and branch lengths were randomly sampled from a uniform distribution (ranging between 0.01 and the maximum branch length). For each comparative model, the effect of ambient temperatures on thermal variables was calculated through linear mixed models, using body mass as a covariate. Then, to estimate the effect of each ambient temperature on T_{LC}, T_{UC} and TNZ_{b}, we calculated the proportion of posterior estimates larger than zero (gt0). In short, gt0 can be viewed as the probability of observing a positive (if gt0 > 0.5) or negative (if gt0 < 0.5) association between each thermal variable and each ambient temperature. Note that when a thermal variable is unaffected by an ambient temperature, the probability is equal to 0.5 (i.e. the distribution of the regression coefficients is centred on zero). All comparative analyses were performed using the software R, through packages ‘APE’ (http://cran.r-project.org/web/packages/ape/index.html) and ‘bmaMCMCanalysis’ (L. Spangenberg *et al.*, submitted, available upon request).

RESULTS

The relationships between thermal variables (in °C) and body mass (m_{b} in g) were highly significant for T_{LC} and TNZ_{b}, but not for T_{UC}. The allometric relationships were described by the following functions:

$$T_{\mathrm{LC}} = 36.03\, m_{\mathrm{b}}^{-0.0687} \tag{1}$$

$$(r = -0.66,\ \text{d.f.} = 83,\ P = 1.0\mathrm{E}^{-11})$$

$$T_{\mathrm{UC}} = 34.48\, m_{\mathrm{b}}^{-0.0072} \tag{2}$$

$$(r = -0.16,\ \text{d.f.} = 83,\ P = 0.16)$$

$$TNZ_{\mathrm{b}} = 2.45\, m_{\mathrm{b}}^{0.1957} \tag{3}$$

$$(r = 0.54,\ \text{d.f.} = 83,\ P = 1.2\mathrm{E}^{-7})$$

Regarding the effect of ambient temperatures, we found that ambient temperatures were positively correlated with T_{LC} and T_{UC} (Tables 1 and 2; Fig. 2a,b) and negatively correlated with TNZ_{b} (Tables 1 and 2; Fig. 3). In addition, based on the BIC values the best models to explain variation in T_{LC} and T_{UC} were those that only included the effect of T_{med} (even though the model that only includes the effect of T_{min} also comprises a ‘good model’ for T_{UC}), while the best model to explain variation in TNZ_{b} was the one that only included the effect of T_{max} (even though the model that only includes the effect of T_{med} also comprises a ‘good model’ for TNZ_{b}).

Table 1. Results of single- and multiple-factor models with ambient temperature, in addition to body mass

	$\text{Log}_{10}\, m_b$		T_{med}		T_{min}		T_{max}		
	r	P	r	P	r	P	r	P	BIC
T_{LC}	−0.75	2.3E^{-17}	0.47	2.8E^{-9}	—	—	—	—	405.54
T_{LC}	−0.78	2.0E^{-16}	—	—	0.43	2.2E^{-7}	—	—	414.36
T_{LC}	−0.64	7.8E^{-14}	—	—	—	—	0.41	1.3E^{-7}	413.36
T_{LC}	−0.73	9.1E^{-16}	0.74	0.002	−0.30	0.21	—	—	408.30
T_{LC}	−0.73	1.8E^{-15}	0.36	0.004	—	—	0.12	0.30	408.83
T_{LC}	−0.72	4.0E^{-15}	—	—	0.26	0.005	0.25	0.008	410.29
T_{UC}	−0.24	0.02	0.39	0.0003	—	—	—	—	377.91
T_{UC}	−0.27	0.01	—	—	0.40	0.0003	—	—	378.03
T_{UC}	−0.15	0.16	—	—	—	—	0.28	0.008	384.15
T_{UC}	−0.26	0.02	0.22	0.53	0.19	0.59	—	—	382.05
T_{UC}	−0.26	0.02	0.46	0.01	—	—	−0.08	0.66	382.14
T_{UC}	−0.26	0.02	—	—	0.35	0.01	0.07	0.57	382.13
TNZ_b	0.69	2.2E^{-12}	−0.27	0.002	—	—	—	—	416.26
TNZ_b	0.69	8.9E^{-12}	—	—	−0.22	0.01	—	—	420.15
TNZ_b	0.62	2.5E^{-11}	—	—	—	—	−0.28	0.001	415.04
TNZ_b	0.65	6.7E^{-11}	−0.69	0.01	0.45	0.10	—	—	417.93
TNZ_b	0.65	1.2E^{-10}	−0.11	0.43	—	—	−0.19	0.18	418.82
TNZ_b	0.64	1.8E^{-10}	—	—	−0.06	0.58	−0.247	0.02	419.15

Finally, results obtained by phylogenetically informed analyses were similar to those obtained by conventional statistical methods, such that all the correlations that were significant by conventional methods were also significant by phylogenetically informed methods (Table 2).

DISCUSSION

Phylogenetic as well as conventional statistics indicated that there is a clear correlation between physiological variables and ambient temperatures along geographic gradients. Riek and Geiser (2013) suggested that TNZ_b is related to the apparent thermal conductance and it is consequently possible that basal metabolism at different body masses is a function of both the heat exchange within *TNZ* and that encountered below and above the *TNZ* to allow thermoregulatory homeostasis. Recently, Khalik *et al.* (2014) studied the global variation in thermal tolerances and vulnerability of birds and mammals to climate change. Surprisingly, these authors found support for the climatic variability hypothesis in birds but not in mammals. According to Khalik *et al.* (2014), species are presently experiencing temperatures within their limits of tolerance, whereas in the future they will be able to tolerate temperatures estimated for different scenarios of global warming. Nevertheless, they highlight tropical regions are highly vulnerable to global warming.

Naya *et al.* (2013a, 2013b) demonstrated that mean and minimum temperatures plus accumulated rainfall were the main predictors of mass-independent variation in basal

Table 2. Parameter estimation (*B*), standard deviation (SD) and proportion of posterior estimates greater than zero (gt0) for single- and multiple-factor models, according to phylogenetically informed analysis

	T_{med}			T_{min}			T_{max}		
	B	SD	gt0	*B*	SD	gt0	*B*	SD	gt0
T_{LC}	0.2146	0.0401	0.9999	—	—	—	—	—	—
T_{LC}	—	—	—	0.1338	0.0292	0.9999	—	—	—
T_{LC}	—	—	—	—	—	—	0.2793	0.0594	0.9999
T_{LC}	0.3436	0.1264	0.9964	−0.0958	0.0891	0.1397	—	—	—
T_{LC}	0.1702	0.0716	0.9907	—	—	—	0.0767	0.1033	0.7731
T_{LC}	—	—	—	0.0781	0.0374	0.9816	0.1761	0.0765	0.9889
T_{UC}	0.1145	0.0335	0.9995	—	—	—	—	—	—
T_{UC}	—	—	—	0.0770	0.0237	0.9994	—	—	—
T_{UC}	—	—	—	—	—	—	0.1183	0.0499	0.9908
T_{UC}	0.1083	0.1073	0.8455	0.0045	0.0757	0.5235	—	—	—
T_{UC}	0.1494	0.0605	0.9930	—	—	—	−0.0604	0.0874	0.2425
T_{UC}	—	—	—	0.0681	0.0312	0.9851	0.0284	0.0641	0.6732
TNZ_b	−0.1043	0.0433	0.0084	—	—	—	—	—	—
TNZ_b	—	—	—	−0.0592	0.0311	0.0291	—	—	—
TNZ_b	—	—	—	—	—	—	−0.1679	0.0618	0.0037
TNZ_b	−0.2479	0.1393	0.0368	0.1065	0.0980	0.8622	—	—	—
TNZ_b	−0.0247	0.0769	0.3716	—	—	—	−0.1384	0.1108	0.1043
TNZ_b	—	—	—	−0.0110	0.0401	0.3899	−0.1528	0.0821	0.0318

Note: Body mass contribution was significant in all cases ($gt0 < 0.05$).

metabolism. These authors also reported a significant and positive relationship between mass-independent thermal conductance and mean annual temperature plus accumulated rainfall/aridity (or aridity), concluding that the same exogenous factors are affecting the evolution of both thermal conductance and metabolic rate among rodent species (Naya *et al.*, 2013a, 2013b). Indeed, in the present study we found that temperatures were positively correlated with T_{LC} and T_{UC}, and negatively correlated with TNZ_b. Therefore, species that evolved in cold climates exhibited lower mass-independent T_{LC} and T_{UC} than species from warmer habitats. Also, rodents that evolved in cold climates exhibited a wider mass-independent TNZ_b than species from warmer habitats

There may be two not completely exclusive (statistical) reasons why TNZ_b is negatively correlated with ambient temperature while T_{LC} and T_{UC} are positively correlated with temperature. One possibility is that high environmental temperatures are less variable than cold temperatures (Addo-Bediako *et al.*, 2000; Boher *et al.*, 2010), so that perfect tracking of T_{UC} to high temperatures would imply less variation than perfect tracking of T_{LC} to low temperatures. The second possibility is that it is more difficult to increase T_{UC} because of a high probability of a destabilizing effect of high temperature on cell membranes and protein structure and function than to decrease T_{LC}, and thus, although both correlate with ambient temperature, T_{LC} would be more strongly correlated (higher slope) with ambient temperature than T_{UC}. Although a higher geographical variation of minimum temperatures

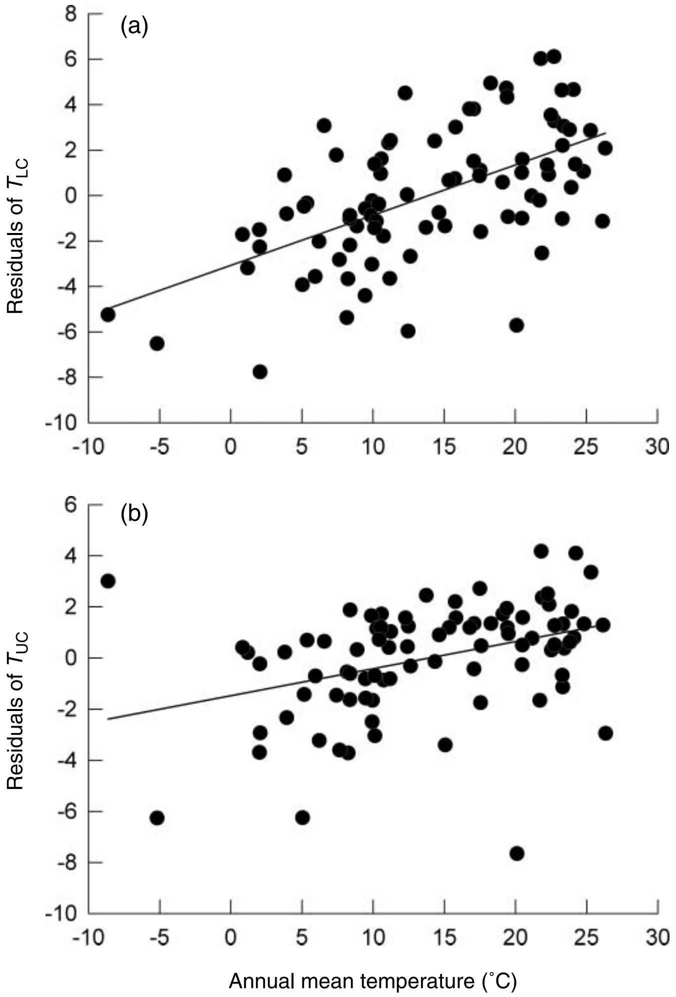

Fig. 2. Relationship between (a) residuals of lower critical temperature, T_{LC} (with regard to body mass) and (b) residuals of upper critical temperature, T_{UC} (with regard to body mass) and mean annual temperature.

than maximum temperatures has been reported (Sunday *et al.*, 2013), the results of the phylogenetically informed analysis in Table 2 show that the correlations between T_{LC} and environmental temperature are always higher than those between T_{UC} and environmental temperature, which provides support for the second hypothesis and is in line with the pattern recently reported for several taxa (Araújo *et al.*, 2013). In other words, the heat tolerance of rodents is more conserved with little variation by latitude and environmental temperature, but cold tolerance decreases significantly with environmental temperature and latitude and exhibits marked variability.

Araújo *et al.* (2013) asked if species adapt physiologically to climate warming. These authors analysed thermal tolerances of a large number of terrestrial ectotherms, endotherms and plant species across the world, and found that tolerance to heat is largely

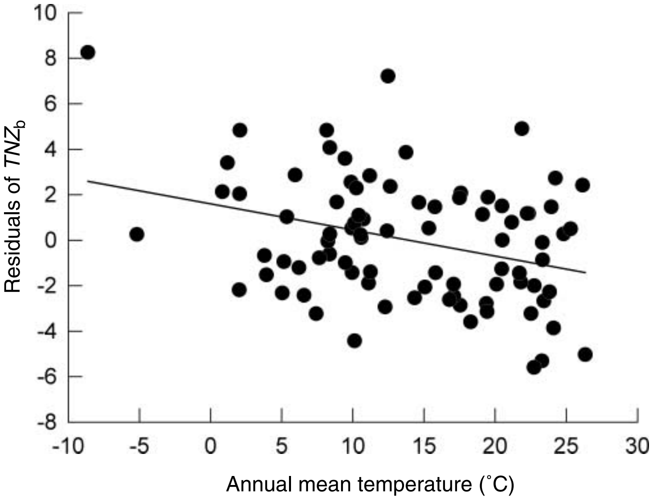

Fig. 3. Relationship between residuals of the breadth of the thermoneutral zone, TNZ_b (with regard to body mass) and mean annual temperature.

conserved across lineages, but tolerance to cold varies between and within species. This pattern challenges the classic view that physiological tolerances of species change continuously across climatic gradients, and portrays an alternative view in which the thermal component of climatic niches would overlap across species more than expected. One consequence of this conservatism of upper tolerances is that the upper thermal limits for cold-adapted species will likely be underestimated, so potentially inflating assessments of risk from climate change. In contrast, species whose climatic preferences are close to their upper thermal limits are unlikely to evolve physiological tolerances to increased heat, and could predictably be more affected by global warming.

Finally, our study provides good evidence that long-term average temperatures could affect small mammals' – in our case rodent species' – thermoregulatory capabilities on an evolutionary scale. However, it is important to note that energetic traits can change among populations within each species and also within a single individual throughout its life [developmental plasticity, seasonal flexibility (e.g. Johnston and Bennett, 1996; McKechnie, 2008)]. Thus, a basic assumption of our study is that intraspecific variation in energetic traits is of a lower magnitude than interspecific variation. Unfortunately, at the present time, there are not enough data to empirically test this assumption, but data on basal metabolic rates suggest that this is indeed the case (Naya *et al.*, 2013a). In addition, the fact that we were able to detect a clear pattern of variation even though we did not control for several sources of intraspecific variation (e.g. we used environmental data averaged throughout a species' distributional range and not for each specific site of collection) indicate that the reported global trend is a strong one. Further work is needed to estimate the relative importance of different sources of intra-specific variation in *TNZ* in small endotherms. A second restriction arises from the character of the study itself. Indeed, comparative studies must trade off precision for generality, and ours is no exception. The use of coarse meteorological variables, for instance, may not accurately reflect those microclimates that species are really experiencing in the field as well as the whole geographic range of each species. The significant relationships between T_{LC}, T_{UC}, and TNZ_{b} and temperature obtained with such a conservative approach suggests, however, that behavioural traits cannot totally compensate differences in thermal environments estimated with weather station data. On the other hand, our taxonomic database is just a small sample of the vast diversity of rodent species. Future studies should not only assess the generality of our results, but also the mechanistic basis that could account for these patterns as well as a large database of species and habitat diversity.

ACKNOWLEDGEMENTS

This research was partially funded by FONDECYT 1130015 and Fondo Basal FONDECYT FB-002 (line 3) to F.B. We also acknowledge a CSIC-UC-LINCGlobal grant to F.F.-Y., M.B.A. and F.B.

REFERENCES

Addo-Bediako, A., Chown, S.L. and Gaston, K. J. 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B*, **267**: 739–745.

Araújo, M.B., Ferri-Yañez, F., Bozinovic, F., Chown, S.L., Marquet, P.A. and Valladares, F. 2013. Heat freezes niche evolution. *Ecol. Lett.*, **16**: 1206–1219.

Boher, F., Godoy-Herrera, R. and Bozinovic, F. 2010. The interplay between thermal tolerance and life-history is associated with the biogeography of *Drosophila* species. *Evol. Ecol. Res.*, **13**: 973–986

Bozinovic, F., Calosi, P. and Spicer, J.I. 2011. Physiological correlates of geographic range in animals. *Annu. Rev. Ecol. Evol. Syst.*, **42**: 155–179.

Chown, S.L., Gaston, K.J. and Robinson, D. 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Funct. Ecol.*, **18**: 159–167.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, **25**: 1965–1978.

Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, X.S.A., Araújo, M.B., Dimitrov, D. *et al.* 2013. An update of Wallace's zoogeographic regions of the world. *Science*, **339**: 74–78.

Huchon, D. and Douzery, E.J.P. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of Hystricognath rodents. *Mol. Phylogenet. Evol.*, **20**: 238–251.

Johnston, I.A. and Bennett, A.F., eds. 1996. *Animals and Temperature: Phenotypic and Evolutionary Adaptation*. Society for Experimental Biology, Seminar Series 59. Cambridge: Cambridge University Press.

Khalik, I., Hof, C., Prinzinger, R., Böhning-Gaese, K. and Pfenninger, M. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. R. Soc. Lond. B*, **281**: 20141097 [http://dx.doi.org/10.1098/rspb.2014.1097].

Lovegrove, B.G. 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.*, **156**: 201–219.

Lovegrove, B.G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow–fast metabolic continuum. *J. Comp. Physiol. B*, **173**: 87–112.

Lumley, T. and Miller, A. 2009. *Leaps: Regression Subset Selection*. R package version 2.9 [http://CRAN.R-project.org/package = leaps].

McKechnie, A.E. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. *J. Comp. Physiol. B*, **178**: 235–247.

Martin, Y., van Dyck, H., Dendoncker, N. and Titeux, N. 2013. Testing instead of assuming the importance of land use change scenarios to model species distributions under climate change. *Global Ecol. Biogeogr.*, **22**: 1204–1216.

Naya, D.E. and Bozinovic, F. 2012. Metabolic scope of fish species increases with distributional range. *Evol. Ecol. Res.*, **14**: 769–777.

Naya, D.E., Spangenberg, L., Naya, H. and Bozinovic, F. 2013a. How does evolutionary variation in basal metabolic rates arise? A statistical assessment and a mechanistic model. *Evolution*, **67**: 1463–1476.

Naya, D.E., Spangenberg, L., Naya, H. and Bozinovic, F. 2013b. Thermal conductance and basal metabolic rate are part of a coordinated system for heat transfer regulation. *Proc. R. Soc. Lond. B*, **280**: 20131629 [http://dx.doi.org/10.1098/rspb.2013.1629].

Naya, H., Gianola, D., Romero, H., Urioste, J.I. and Musto, H. 2006. Inferring parameters shaping amino acid usage in prokaryotic genomes via Bayesian MCMC methods. *Mol. Biol. Evol.*, **23**: 203–211.

Pearson, R.G. and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.*, **12**: 361–371.

Pither, J. 2003. Climate tolerance and interspecific variation in geographic range size. *Proc. R. Soc. Lond. B*, **270**: 475–481.

QGIS Development Team. 2013. *Qgis 1.8.0-Lisboa*. Open Source Geospatial Foundation [http://qgis.osgeo.org].

Raftery, A.E., Madigan, D. and Hoeting, J.A. 1997. Bayesian model averaging for regression models. *J. Am. Stat. Assoc.*, **92**: 179–191.

Rezende, E.L., Bozinovic, F. and Garland, T., Jr. 2004. Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution*, **58**: 1361–1374.

Riek, A. and Geiser, F. 2013. Allometry of thermal variables in mammals: consequences of body size and phylogeny *Biol. Rev.*, **88**: 564–572.

Rodriguez-Serrano, E. and Bozinovic, F. 2009. Interplay between global patterns of environmental temperature and variation in non-shivering thermogenesis of rodent species across large spatial scales. *Global Change Biol.*, **15**: 2116–2122.

Spicer, J.I. and Gaston, K.J. 1999. *Physiological Diversity and its Ecological Implications*. Oxford: Blackwell Science.

Sunday, J.M., Bates, A.E. and Dulvy, N.K. 2013. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. Lond. B*, **278**: 1823–1830.