

Variation in body size and degree of melanism within a lizards clade: is it driven by latitudinal and climatic gradients?

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Keywords

thermal melanism hypothesis; heat balance hypothesis; body size; Bergmann's rule; ectotherms; lizard.

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Editor: Nigel Bennett

Received 12 May 2014; revised 7 October 2014; accepted 13 October 2014

doi:10.1111/jzo.12193

Abstract

Body size (BS) varies in response to several selective pressures. In ectotherms, thermal inertia may affect thermoregulation, since larger BSs increase heat conservation as Bergmann originally stipulated for endotherms. However, Bergmann's rule is controversial in ectotherms. The heat balance hypothesis states that ectotherms' thermoregulatory capability is relevant for trends in BS. In cold climates, larger BSs would be advantageous for small thermoregulating ectotherms, by increasing heat conservation. However, BS implies a delaying effect on heating too; therefore, ectotherms may need another trait to compensate the later effect. Thermal melanism hypothesis posits that melanism increases heat gain, and may be adaptive for animals inhabiting cold climates. We propose that the higher solar radiation absorption from increased melanism may be such a compensatory trait. We expect BS and melanism to increase with latitude in response to seasonal temperatures and solar radiation. To test this, we studied the monophyletic *Liolaemus goetschi* group of lizard species across its 2200 km (32–48° S latitude) range. We used phylogenetically informed analyses to study geographic variation of BS and melanism (dorsal, ventral and total) in relation to temperatures, thermal amplitude, cloudiness and net solar radiation. Our results show that lizards' BS increases latitudinally in relation to thermal amplitude and temperature. Only ventral melanism varied latitudinally, but all melanism variables varied in response to cloudiness and net radiation. The relationship between BS and melanism was significant and positive in all cases. We suggest thermal inertia may be a fair candidate mechanism explaining geographic variation in BS (heat balance hypothesis), while melanism may influence heat gain according to the thermal melanism hypothesis. However, it remains unclear why latitudinal variation is related to ventral instead of dorsal melanism, and further investigation is needed to clarify the relationship between BS and melanism in light of cold climates.

Introduction

Variation in species morphology and life-history traits are strongly correlated with geographic and climatic characteristics (Ashton, Burke & Layne, 2007). Gradients in body size are among the most studied patterns in animals (Blackburn & Ruggiero, 2001; Meiri, 2011), given that body size is one of the most ecologically integrative characteristics (Peters, 1983; Van Voorhies, 1996). Bergmann's rule, a well-known ecogeographic rule, states that among closely related endothermic species, those inhabiting colder regions are generally

larger than species inhabiting warmer regions (Bergmann, 1847; Blackburn, Gaston & Loder, 1999), in accordance with thermal inertia principles (Bergmann, 1847). There is an extended debate about the interpretation of this rule and its application to different groups and scales beyond Bergmann's original postulation (Blackburn *et al.*, 1999). The inclusion of a mechanism driving the pattern as part of the rule has been also matter of debate (reviews in Watt, Mitchell & Salewski, 2010; Meiri, 2011).

Although Bergmann's rule was originally proposed for endothermic animals (Bergmann, 1847; James, 1970), it was

analysed also in ectothermic species (Ray, 1960; Lindsey, 1966; Ashton & Feldman, 2003; Olalla-Tárraga & Rodríguez, 2007; Pincheira-Donoso & Meiri, 2013). The study of this rule in ectotherms yielded contradictory results, reporting different trends among different groups. Climatic and allometric variables used, phylogenetic scale, representation of the study group and method involved, may account for variability (Ashton, 2004; Cruz *et al.*, 2005; Christian, Tracy & Tracy, 2006; Guillaumet *et al.*, 2008). Yet, body size geographic trends and the mechanism(s) shaping them remain unclear especially for ectotherms (Olalla-Tárraga, 2011).

A larger body size in ectotherms may allow maintaining their optimal activity temperatures (once achieved) for a longer time because of the associated higher thermal inertia (Tracy, 1982; Turner & Tracy, 1984), reducing energy expenditure related to heat conservation (Cruz *et al.*, 2005). Nonetheless, a larger body size also requires longer heating times (Bell, 1980; Herczeg, Török & Korsós, 2007). In 2007, Olalla-Tárraga & Rodríguez proposed the 'heat balance hypothesis' (HBH) for small ectotherms (their small body size does not restrict heat gain in cold environments). For thermoregulators, the HBH states that larger animals will be favoured in cold environments because of their greater heat conservation potential. Conversely, smaller thermoconformers will be favoured in cold areas as their greater surface/volume ratios shorten heating times. Therefore, body size patterns in ectotherms may be determined by their thermoregulatory capacity (Olalla-Tárraga, 2011).

A second (complementary) hypothesis explaining why larger ectotherms may occur in colder environments involves a compensatory attribute to offset the negative effect of large body size on heating rates, that is, morphological, physiological or behavioural traits that increase heat gain (Claussen & Art, 1981; Sagonas *et al.*, 2013). Melanism (dark coloration of animals) may be such a trait. The thermal melanism hypothesis (TMH; Gates, 1980) predicts that dorsally or fully darker animals may be favoured over lighter ones in cold regions because they potentially gain heat faster (Lusis, 1961; Kettlewell, 1973; Clusella-Trullas, Van Wyk & Spotila, 2007). In particular, TMH predicts that (1) melanistic diurnal species should inhabit cooler environments than lighter related species; (2) melanism allows higher performance in cold climates; (3) a trade-off between melanism and body size because colour has smaller effect on temperature of small animals compared with larger ones; (4) there should be co-adaptation between colour patterns, physiology and behaviour (review of TMH in Clusella-Trullas *et al.*, 2007). Evidence for this hypothesis has been mainly provided in arthropods (De Jong, Gussekloo & Brakefield, 1996; Harris, McQuillan & Hughes, 2012; Hegna *et al.*, 2013) and reptiles (Bittner, King & Kerfin, 2002; Clusella-Trullas *et al.*, 2008; Clusella-Trullas, Van Wyk & Spotila, 2009; Tanaka, 2009; Castilla *et al.*, 2013). Additionally, melanism may be also related to intra-specific communication, sexual attributes and disease resistance. Our study system consists of 14 lizard species in the monophyletic *Liolaemus goetschi* group (Abdala, 2007; Moreno Azócar *et al.*, 2013). Species of this clade inhabit Monte and Patagonian steppe regions environments (Cabrera & Willink,

1980). These habitats have a similar vegetation structure consisting of patches of large bushes separated by extended areas of bare sandy soil and similar values of primary productivity (42–54 g m⁻² month⁻¹, 260–290 g m⁻² per season). On the contrary, thermal characteristics vary among environments (Moreno Azócar *et al.*, 2013, Supporting Information Table S1). The species share several life-history traits, as all of them are oviparous, arenicolous (Abdala, 2007), and heliothermic active thermoregulators (Moreno Azócar *et al.*, 2013). Body size of the studied *Liolaemus* species ranges from 60 to 105 mm snout-vent length (SVL; *L. donosobarrosi* and *L. casamiquelai*, respectively). Species also show different dorsal (melanic stripes or dots, or head melanism) and ventral patterns (throat, belly or the whole ventral surface may be homogeneously melanic). They are distributed across a wide latitudinal and altitudinal range (from 28° to 48° south; 8 to 1650 m above the sea level).

Bergmann's rule was previously studied and supported for *Liolaemus* species by Cruz *et al.* (2005). Later, Pincheira-Donoso, Tregenza & Hodgson (2007) reassessed the model finding no pattern. However, species compositions and phylogenetic relationships differed between these studies, leading to conflicting results. Unfortunately, the phylogenetic tree used by Pincheira-Donoso, Hodgson & Tregenza (2007, 2008) was combined from several sources (phenetic and cladistics) and may not be reproducible (Lobo, Espinoza & Quinteros, 2010), affecting data analyses what may lead to bias the outcome (Freckleton, 2009). Here, we gather data from a monophyletic species group that shows variation in body size and degree of melanism, while shown to be conservative for several ecological traits. This study group provides a good case because it allows us to discard some alternative hypotheses, such as those related to diet and reproduction. Additionally, we can 'control' for factors that may affect the results like habitat differences, heating strategies, etc. Given the positive relationship between body size and thermal inertia observed in some *Liolaemus* lizards (Carothers *et al.*, 1997) and effectiveness of thermoregulation (E) observed for all the species studied here (Moreno Azócar *et al.*, 2013), we consider that Bergmann's rule (and the first part of the HBH) as well as the TMH may be plausible to be held up in these lizards.

Therefore, we aim to explore, first, the geographic variation in body size and melanism among the species of the *L. goetschi* clade in relation to climatic variables. We predict larger and darker lizards will inhabit higher latitudes, with cooler climates and lower solar radiation. Then, it is expected that body size and melanism will evolve in concert with some aspects of thermal physiology because of its influence on body temperature (Clusella-Trullas *et al.*, 2008). To analyse this, we tested the relationship of body size and melanism with preferred temperatures and the effectiveness of thermoregulation.

The primary questions we aim to address are (1) do *Liolaemus* of the *L. goetschi* clade follow an interspecific Bergmann's pattern?; (2) is this pattern related to a particular climatic factor?; (3) is there any relationship between latitude or climatic factors and degree of melanism?; (4) is there any relationship between body size and the degree of melanism?;

and (5) did body size, melanism and thermal physiology (preferred temperatures and effectiveness of thermoregulation) co-evolve?

Material and methods

A total of 259 adult lizards representing 14 species of the *L. goetschi* clade were caught from San Juan to Santa Cruz Province (2200 km north to south), in Argentina (sample sizes per species and localities in Supporting Information Table S1). Captured lizards were transported to the laboratory in cloth bags, without mixing specimens of different species. All captures were authorized by the corresponding provincial fauna offices or national parks (see Acknowledgements). After finishing all trials, individuals were euthanized (under the ethic convention of CONICET and National Parks ethics bureaus) and used for other studies.

Species distribution and characterization of the environment

Every species collection point was georeferenced. Climatic data are maximum and minimum seasonal air temperatures (TMAX and TMIN) and mean seasonal thermal amplitude (TA) as a measure of climatic variability. The latter was estimated as the average of the daily differences between maximum and minimum air temperatures. These parameters were calculated for the activity season of lizards (October–April). Maximum and average seasonal cloudiness (MAX_CLOUD, AVG_CLOUD) and minimum and average

net solar radiation (MIN_RAD, AVG_RAD) were also estimated. Climatic variables were obtained from available daily data at the NASA website (<http://power.larc.nasa.gov/>) for a 27-year period (1983–2010), while cloudiness and net radiation values for 2006 to 2010 were obtained from the NEO project of NASA (<http://neo.sci.gsfc.nasa.gov/>).

Measurements of body size and melanism

Body size (SVL) was measured with a Vernier digital calliper (Mitutoyo 500, Mitutoyo, Tokyo, Japan; accuracy 0.01 mm). To estimate degree of melanism of the species, we took pictures of all specimens' dorsal and ventral surfaces, and then estimated the melanic proportion of body surface (BS; Fig. 1). For detailed methodology, see Supporting Information Appendix S1. Total, dorsal and ventral melanic surfaces (MSs) were coded as a proportion of MS over the whole surface (total, dorsal or ventral surface) to standardize and make these variables comparable between species (Supporting Information Appendix S1).

Phylogenetic framework

A phylogenetic tree was constructed using aligned DNA sequences and a maximum likelihood analysis partitioned *a priori* for the 14 species of the *Liolaemus goetschi* clade (Fig. 2). Details of DNA sequences samples, spanning and alignment, as well as estimation and evaluation of the tree can be found in Supporting Information Appendix S1. Aligned

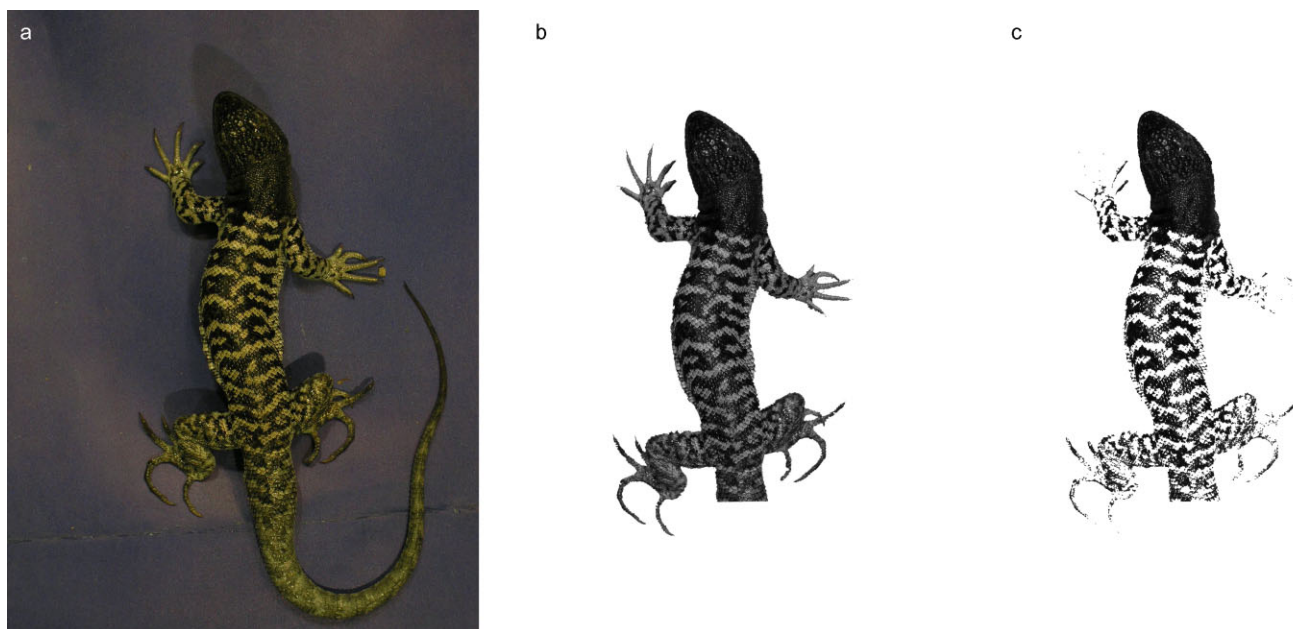


Figure 1 Image illustrating how melanism was measured showing the dorsal melanism measurement in a specimen of *Liolaemus canqueli*. (a) Picture taken under standardized light and camera conditions. (b) Background and tail deletion. (c) Extraction of the melanistic surface of the specimen.

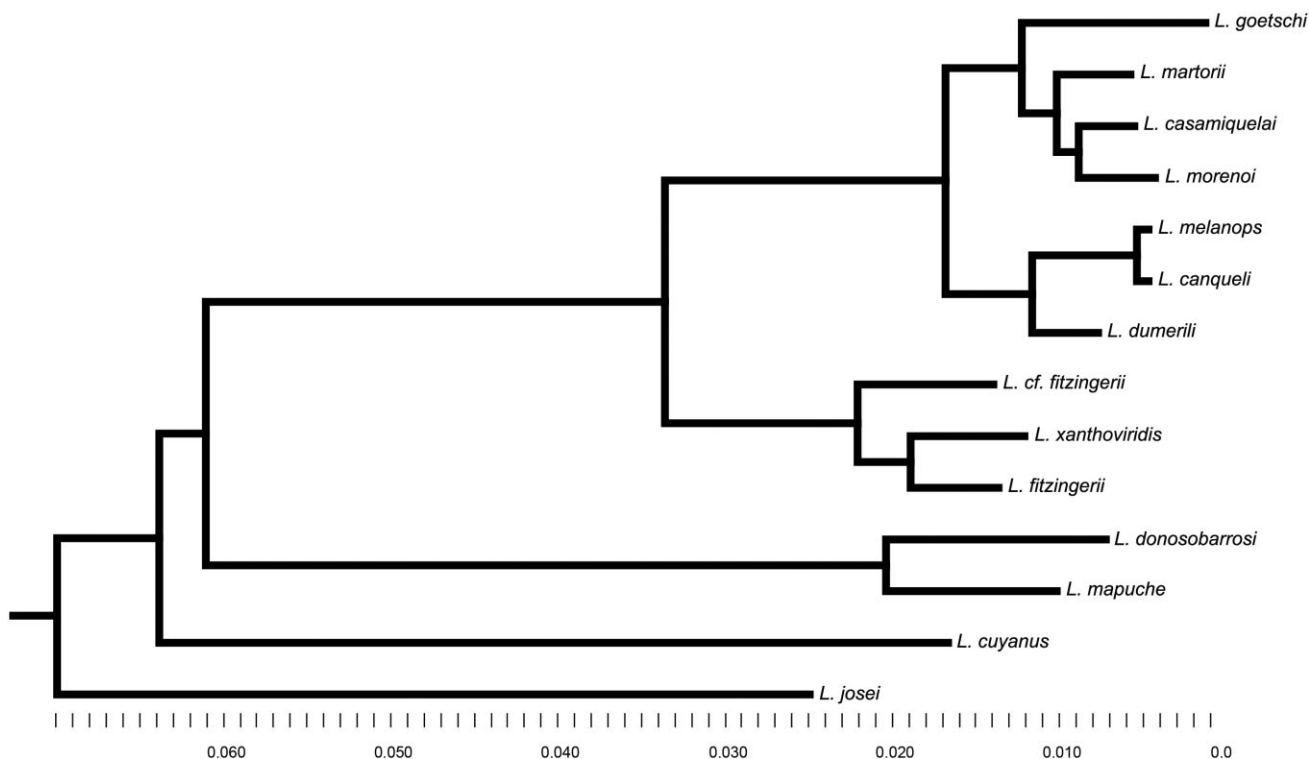


Figure 2 Phylogenetic relationships of *Liolaemus goetschi* species inferred using mtDNA sequence data spanning the region from ND1-COI and maximum likelihood criterion. Branch lengths scale is shown below the tree.

DNA sequence datasets for species sampled here are available in TreeBASE (study accession number = 13386; matrix accession number = M14405).

Statistical analysis

We calculated the mean values for each variable for every species. SVL data were \log_{10} transformed (LOG_SVL). Total, ventral and dorsal melanism proportions (MELTOT, total MS/total BS; MELVEN, ventral MS/ventral BS; MELDOR, dorsal MS/dorsal BS) were transformed to the arcsine of the square root of each value.

Species cannot be considered as independent data points because of their phylogenetic relationships (Harvey & Pagel, 1991). Therefore, we estimated Pagel's phylogenetic signal (λ) from the residual errors simultaneously on the regression parameters of phylogenetic generalized least squares models (PGLS) analyses. Analyses were done in 'caper' (Orme *et al.*, 2012) and 'ape' (Paradis, Claude & Strimmer, 2004) packages, both developed in R (R Development Core Team, 2011). This procedure is preferred as it has been shown to outperform or to be equivalent to phylogenetic or non-phylogenetic procedures depending on the λ value obtained (Revell, 2010).

To analyse geographic variation in body size, we ran PGLS using models with latitude and altitude as predictor variables (LAT + ALT + c; LAT + c, ALT + c, with c = constant) and

LOG_SVL as dependent variable, as well as the relationship of range size (RANGE) on body size. To study the relationship of body size and climatic variables, models included TMAX, TMIN and TA as predictor variables, and LOG_SVL as dependent variable. To ensure the regression model provided the best fit among the candidate models (Angilletta, 2006), we used the Akaike information criterion (AIC). We used Akaike weights as a measure of strength of evidence for each model, indicating the probability that a given model is the best among a series of candidate models (Burnham & Anderson, 2004).

Geographic variation and environmental influence on melanism were analysed in the same way as for body size, using each melanism measurement (total, ventral and dorsal melanism) as dependent variables. Additionally, we studied the influence of cloudiness (CLOUD_AVG, CLOUD_MAX) and net solar radiation (AVG_NETRAD, MIN_NETRAD) on melanism proportion, following similar procedures. We also explored the relationship between body size and proportion of melanism by using PGLS models, with LOG_SVL as the predictor variable of melanism.

Finally, we tested for possible co-evolution between morphology and physiology, by evaluating the influence of body size and melanism on preferred temperatures (T_{pref}) and effectiveness of thermal regulation (Hertz, Huey & Stevenson, 1993). T_{pref} and E values were taken from Moreno Azócar *et al.* (2013, details in Supporting Information Table S2).

T_{pref} is the mean value of the temperatures selected by the animals in a thermal gradient without restrictions. Effectiveness of thermoregulation is calculated as $E = 1 - db/de$, where db is the mean deviation between field body temperature and T_{pref} , and de is the mean deviation between operative temperatures and T_{pref} . Thus, we ran PGLS models using separately LOG_SVL and every melanism variables as predictors, with T_{pref} or E as dependent variable.

Results

Analyses of Bergmann's pattern in the sampled lizard species showed that body size increases with latitude (adjusted $r^2 = 0.45$, Table 1). Variability of body size in PGLS models was better explained by TA and TMAX and their combination (adjusted $r^2 = 0.36$, 0.27 and 0.41 respectively, Table 1). Phylogenetic signal (Pagel's λ) in all the analyses performed for LOG_SVL was equal to zero.

We observed latitudinal variation only for MELVEN (Table 2), but melanism variation was in all cases related to a combination of CLOUD_AVG and MIN_NETRAD (adjusted r^2 : MELTOT = 0.58, MELVEN = 0.67, MELDOR = 0.66, with λ values higher than 0.6 in all cases, Table 3).

The relationship between each melanism variable and body size was positive and significant in all cases (adjusted r^2 values higher than 0.60). While MELTOT and MELDOR relationships with LOG_SVL indicated a phylogenetic component in

these regression models, with lambda values above 0.95; MELVEN-LOG_SVL analyses showed phylogenetic independence ($\lambda = 0.00$; Table 4).

Finally, PGLS models run to evaluate the relationship of body size and melanism with preferred temperature and effectiveness of thermoregulation indicated that morphological variables do not affect T_{pref} , while effectiveness showed a significant relationship with melanism (all three measurements, Table 5), specially dorsal melanism, according to the AIC values.

Discussion

Our results show that body size increases with latitude in the lizard species of the *L. goetschi* group in response to environmental temperature variables (TA and TMAX), in accordance with Bergmann's rule and HBH, but these relationships are not very strong. Heat conservation may be related to body size variation in these ectotherms (Olalla-Tárraga & Rodríguez, 2007), although body size is probably influenced by other selective pressures as well, what would explain the shallow slopes of the regression relationships. Regarding melanism patterns, only ventral melanism varied with latitude and we found no influence of environmental temperature variables. It is possible that ventral melanism (that independently evolved three times within the studied clade in seven species) is more related to other aspects rather than acquiring temperature

Table 1 Phylogenetic generalized least squares regression models evaluating geographic variation in body size and climatic influence in the *Liolaemus goetschi* clade (14 species)

Model	λ	Adj. r^2	AICc	Δ_i	W_i	Independent variables	Slope	SE	P	d.f.
LOG_SVL ~ LAT	0.000	0.454	-42.169	0.000	0.789	Intercept	1.405	0.130	0.000	1, 13
						LAT	0.011	0.003	0.005	
LOG_SVL ~ ALT	0.000	0.137	-35.761	6.407	0.032	Intercept	1.891	0.028	0.000	1, 13
						ALT	0.000	0.000	0.106	
LOG_SVL ~ LAT + ALT	0.000	0.407	-38.939	3.230	0.157	Intercept	1.435	0.181	0.000	2, 12
						LAT	0.010	0.004	0.027	
						ALT	0.000	0.000	0.808	
LOG_SVL ~ RANGE	0.000	-0.073	-32.715	9.454	0.007	Intercept	1.853	0.021	0.000	1, 13
						RANGE	-7E-08	2E-07	7E-01	
LOG_SVL ~ TMAX	0.000	0.268	-38.064	1.967	0.145	Intercept	2.041	0.081	0.000	1, 13
						TMAX	-0.009	0.004	0.034	
LOG_SVL ~ TMIN	0.304	0.071	-34.654	5.378	0.026	Intercept	1.893	0.050	0.000	1, 13
						TMIN	-0.007	0.005	0.184	
LOG_SVL ~ TA	0.000	0.364	-40.032	0.000	0.387	Intercept	2.118	0.093	0.000	1, 13
						TA	-0.023	0.008	0.013	
LOG_SVL ~ TMAX + TA	0.000	0.406	-38.907	1.124	0.221	Intercept	2.162	0.096	0.000	2, 12
						TMAX	-0.005	0.004	0.200	
						TA	-0.017	0.009	0.077	
LOG_SVL ~ TMIN + TA	0.000	0.406	-38.910	1.122	0.221	Intercept	2.162	0.096	0.000	2, 12
						TMIN	-0.005	0.004	0.200	
						TA	-0.022	0.008	0.014	

In bold, the best models after considering r^2 , AIC and W_i values. Body size varies latitudinally in response to TMAX and TA.

Δ_i , Akaike differences; λ , phylogenetic signal (Pagel's); AIC, Akaike information criterion; ALT, altitude; LAT, latitude; LOG_SVL, snout-vent length logarithm; r^2 , correlation coefficient; RANGE, range size; SE, standard error; TA, thermal amplitude; TMAX, maximum seasonal temperatures; TMIN, minimum seasonal temperatures; W_i , Akaike weights.

Table 2 Phylogenetic generalized least squares models evaluating geographic (LAT, latitude; ALT, altitude) and environmental influences (TMAX and TMIN, maximum and minimum seasonal temperature; TA, thermal amplitude) on melanism (MELTOT, total melanism; MELVEN, ventral melanism; MELDOR, dorsal melanism) in the *Liolaemus goetschi* clade studied (14 species)

Model	λ	Adj. r^2	AICc	Δ_i	W_i	Independent variables	Slope	SE	P	d.f.
MELTOT ~ LAT	0.000	0.088	-1.832	0.000	0.321	Intercept LAT	-0.559 0.020	0.550 0.014	0.329 0.160	1, 13
MELTOT ~ ALT	0.000	0.083	-1.764	0.068	0.310	Intercept ALT	0.377 0.000	0.095 0.000	0.002 0.166	1, 13
MELTOT ~ LAT + ALT	0.000	0.051	0.803	2.635	0.086	Intercept LAT ALT	-0.196 0.013 0.000	0.747 0.017 0.000	0.798 0.455 0.477	2, 12
MELVEN ~ LAT	0.000	0.351	-4.982	0.000	0.735	Intercept LAT	-1.160 0.034	0.492 0.012	0.036 0.015	1, 13
MELVEN ~ ALT	0.000	0.084	-0.159	4.823	0.066	Intercept ALT	0.349 0.000	0.101 0.000	0.005 0.164	1, 13
MELVEN ~ LAT + ALT	0.000	0.293	-1.699	3.283	0.142	Intercept LAT ALT	-1.096 0.033 0.000	0.683 0.015 0.000	0.137 0.056 0.889	2, 12
MELDOR ~ LAT	0.000	-0.083	1.978	0.919	0.206	Intercept LAT	0.294 0.000	0.630 0.016	0.650 0.978	1, 13
MELDOR ~ ALT	0.000	-0.083	1.977	0.918	0.206	Intercept ALT	0.279 0.000	0.109 0.000	0.025 0.971	1, 13
MELDOR ~ LAT + ALT	0.000	-0.181	5.282	4.223	0.039	Intercept LAT ALT	0.330 -0.001 0.000	0.876 0.020 0.000	0.714 0.955 0.951	2, 12
MELTOT ~ TMAX	0.338	-0.013	-0.834	0.000	0.319	Intercept TMAX	0.463 -0.012	0.308 0.014	0.160 0.380	1, 13
MELTOT ~ TMIN	0.370	-0.039	-0.450	0.384	0.263	Intercept TMIN	0.293 -0.011	0.172 0.015	0.114 0.489	1, 13
MELTOT ~ TA	0.000	0.003	-0.598	0.235	0.284	Intercept TA	0.647 -0.033	0.382 0.032	0.116 0.327	1, 13
MELTOT ~ TMAX + TA	0.276	-0.093	2.293	3.127	0.067	Intercept TMAX TA	0.601 -0.009 -0.016	0.465 0.016 0.041	0.223 0.575 0.697	2, 12
MELTOT ~ TMIN + TA	0.276	-0.093	2.292	3.126	0.067	Intercept TMIN TA	0.601 -0.009 -0.026	0.465 0.016 0.037	0.223 0.575 0.496	2, 12
MELVEN ~ TMAX	0.213	0.113	-1.080	0.388	0.286	Intercept TMAX	0.654 -0.022	0.305 0.014	0.053 0.129	1, 13
MELVEN ~ TMIN	0.363	0.014	0.375	1.844	0.138	Intercept TMIN	0.314 -0.017	0.177 0.016	0.102 0.298	1, 13
MELVEN ~ TA	0.000	0.166	-1.469	0.000	0.347	Intercept TA	0.919 -0.059	0.370 0.031	0.029 0.083	1, 13
MELVEN ~ TMAX + TA	0.000	0.158	0.749	2.218	0.114	Intercept TMAX TA	1.045 -0.015 -0.043	0.395 0.016 0.036	0.023 0.365 0.263	2, 12
MELVEN ~ TMIN + TA	0.000	0.158	0.749	2.217	0.115	Intercept TMIN TA	1.044 -0.015 -0.058	0.395 0.016 0.032	0.023 0.365 0.094	2, 12
MELDOR ~ TMAX	0.000	-0.080	1.931	0.285	0.260	Intercept TMAX	0.343 -0.003	0.339 0.016	0.331 0.844	1, 13
MELDOR ~ TMIN	0.000	-0.061	1.680	0.034	0.295	Intercept TMIN	0.362 -0.009	0.179 0.018	0.067 0.620	1, 13
MELDOR ~ TA	0.000	-0.058	1.646	0.000	0.300	Intercept TA	0.057 0.019	0.414 0.035	0.894 0.601	1, 13
MELDOR ~ TMAX + TA	0.247	-0.098	4.479	2.833	0.073	Intercept TMAX TA	0.039 -0.012 0.038	0.497 0.018 0.044	0.938 0.517 0.406	2, 12
MELDOR ~ TMIN + TA	0.247	-0.098	4.478	2.832	0.073	Intercept TMIN TA	0.039 -0.012 0.026	0.497 0.018 0.039	0.938 0.517 0.515	2, 12

In bold, the best models after considering r^2 , AIC and W_i values. Only MELVEN varies latitudinally, and there is no influence of climatic variables on melanism.

Δ_i , AIC differences; λ , phylogenetic signal (Pagel's); AIC, Akaike information criterion; r^2 , correlation coefficient; SE, standard error; W_i , AIC weights.

Table 3 Phylogenetic generalized least squares models evaluating incident solar radiation on melanism of the *Liolaemus goetschi* lizards clade (14 species)

Model	λ	Adj. r^2	AICc	Δ_i	W_i	Independent variables	Slope	SE	P	d.f.
MELTOT ~ CLOUD_AVG	0.000	0.169	-3.139	5.489	0.034	Intercept	-0.120	0.206	0.572	1, 13
MELTOT ~ CLOUD_MAX	0.000	0.375	-7.136	1.492	0.252	CLOUD_AVG	0.010	0.005	0.081	1, 13
MELTOT ~ CLOUD_MAX						Intercept	-0.591	0.291	0.065	
MELTOT ~ CLOUD_MAX						CLOUD_MAX	0.014	0.005	0.012	
MELTOT ~ AVG_NETRAD	0.297	-0.019	-0.777	7.851	0.010	Intercept	3.498	3.785	0.374	1, 13
MELTOT ~ AVG_NETRAD						AVG_NETRAD	-0.021	0.024	0.400	
MELTOT ~ MIN_NETRAD	0.000	0.044	-1.180	7.448	0.013	Intercept	1.739	1.169	0.163	1, 13
MELTOT ~ MIN_NETRAD						MIN_NETRAD	-0.014	0.011	0.230	
MELTOT ~ CLOUD_AVG + AVG_NETRAD	0.000	0.094	0.159	8.787	0.007	Intercept	0.292	4.364	0.948	2, 12
MELTOT ~ CLOUD_AVG + AVG_NETRAD						CLOUD_AVG	0.010	0.006	0.132	
MELTOT ~ CLOUD_AVG + AVG_NETRAD						AVG_NETRAD	-0.003	0.027	0.926	
MELTOT ~ CLOUD_AVG + MIN_NETRAD	0.794	0.577	-8.628	0.000	0.531	Intercept	-12.801	3.292	0.003	2, 12
MELTOT ~ CLOUD_AVG + MIN_NETRAD						CLOUD_AVG	0.055	0.013	0.001	
MELTOT ~ CLOUD_AVG + MIN_NETRAD						MIN_NETRAD	0.104	0.027	0.003	
MELTOT ~ CLOUD_MAX + AVG_NETRAD	0.000	0.328	-4.014	4.615	0.053	Intercept	-2.098	3.935	0.605	2, 12
MELTOT ~ CLOUD_MAX + AVG_NETRAD						CLOUD_MAX	0.015	0.006	0.020	
MELTOT ~ CLOUD_MAX + AVG_NETRAD						AVG_NETRAD	0.009	0.024	0.708	
MELTOT ~ CLOUD_MAX + MIN_NETRAD	0.000	0.386	-5.294	3.335	0.100	Intercept	-2.563	1.812	0.185	2, 12
MELTOT ~ CLOUD_MAX + MIN_NETRAD						CLOUD_MAX	0.020	0.007	0.018	
MELTOT ~ CLOUD_MAX + MIN_NETRAD						MIN_NETRAD	0.015	0.014	0.294	
MELVEN ~ CLOUD_AVG	0.000	0.436	-6.955	4.416	0.083	Intercept	-0.353	0.180	0.073	1, 13
MELVEN ~ CLOUD_AVG						CLOUD_AVG	0.015	0.005	0.006	
MELVEN ~ CLOUD_MAX	0.000	0.443	-7.113	4.257	0.090	Intercept	-0.741	0.291	0.026	1, 13
MELVEN ~ CLOUD_MAX						CLOUD_MAX	0.016	0.005	0.006	
MELVEN ~ AVG_NETRAD	0.312	0.084	-0.674	10.696	0.004	Intercept	5.761	3.789	0.154	1, 13
MELVEN ~ AVG_NETRAD						AVG_NETRAD	-0.035	0.024	0.165	
MELVEN ~ MIN_NETRAD	0.000	0.255	-3.042	8.328	0.012	Intercept	2.776	1.094	0.026	1, 13
MELVEN ~ MIN_NETRAD						MIN_NETRAD	-0.025	0.011	0.038	
MELVEN ~ CLOUD_AVG + AVG_NETRAD	0.000	0.395	-3.875	7.495	0.018	Intercept	1.257	3.778	0.746	2, 12
MELVEN ~ CLOUD_AVG + AVG_NETRAD						CLOUD_AVG	0.014	0.005	0.019	
MELVEN ~ CLOUD_AVG + AVG_NETRAD						AVG_NETRAD	-0.010	0.023	0.678	
MELVEN ~ CLOUD_AVG + MIN_NETRAD	0.688	0.661	-11.370	0.000	0.758	Intercept	-11.778	3.036	0.003	2, 12
MELVEN ~ CLOUD_AVG + MIN_NETRAD						CLOUD_AVG	0.056	0.012	0.001	
MELVEN ~ CLOUD_AVG + MIN_NETRAD						MIN_NETRAD	0.094	0.025	0.003	
MELVEN ~ CLOUD_MAX + AVG_NETRAD	0.000	0.396	-3.888	7.483	0.018	Intercept	0.271	3.953	0.947	2, 12
MELVEN ~ CLOUD_MAX + AVG_NETRAD						CLOUD_MAX	0.015	0.006	0.019	
MELVEN ~ CLOUD_MAX + AVG_NETRAD						AVG_NETRAD	-0.006	0.024	0.802	
MELVEN ~ CLOUD_MAX + MIN_NETRAD	0.000	0.394	-3.848	7.522	0.018	Intercept	-0.390	1.908	0.842	2, 12
MELVEN ~ CLOUD_MAX + MIN_NETRAD						CLOUD_MAX	0.015	0.008	0.079	
MELVEN ~ CLOUD_MAX + MIN_NETRAD						MIN_NETRAD	-0.003	0.015	0.856	
MELDOR ~ CLOUD_AVG	0.000	-0.081	1.949	5.617	0.038	Intercept	0.238	0.247	0.355	1, 13
MELDOR ~ CLOUD_AVG						CLOUD_AVG	0.001	0.006	0.876	
MELDOR ~ CLOUD_MAX	0.000	0.005	0.785	4.453	0.068	Intercept	-0.118	0.386	0.765	1, 13
MELDOR ~ CLOUD_MAX						CLOUD_MAX	0.007	0.006	0.322	
MELDOR ~ AVG_NETRAD	0.000	-0.083	1.978	5.646	0.038	Intercept	0.179	4.465	0.969	1, 13
MELDOR ~ AVG_NETRAD						AVG_NETRAD	0.001	0.028	0.983	
MELDOR ~ MIN_NETRAD	0.000	-0.071	1.814	5.482	0.041	Intercept	-0.213	1.301	0.873	1, 13
MELDOR ~ MIN_NETRAD						MIN_NETRAD	0.005	0.013	0.713	
MELDOR ~ CLOUD_AVG + AVG_NETRAD	0.000	-0.178	5.247	8.915	0.007	Intercept	-0.243	5.234	0.964	2, 12
MELDOR ~ CLOUD_AVG + AVG_NETRAD						CLOUD_AVG	0.001	0.007	0.863	
MELDOR ~ CLOUD_AVG + AVG_NETRAD						AVG_NETRAD	0.003	0.032	0.928	
MELDOR ~ CLOUD_AVG + MIN_NETRAD	0.732	0.458	-3.668	0.000	0.632	Intercept	-13.991	3.975	0.005	2, 12
MELDOR ~ CLOUD_AVG + MIN_NETRAD						CLOUD_AVG	0.054	0.015	0.005	
MELDOR ~ CLOUD_AVG + MIN_NETRAD						MIN_NETRAD	0.117	0.033	0.005	
MELDOR ~ CLOUD_MAX + AVG_NETRAD	0.000	-0.057	3.721	7.388	0.016	Intercept	-2.937	5.187	0.583	2, 12
MELDOR ~ CLOUD_MAX + AVG_NETRAD						CLOUD_MAX	0.008	0.007	0.278	
MELDOR ~ CLOUD_MAX + AVG_NETRAD						AVG_NETRAD	0.017	0.031	0.597	
MELDOR ~ CLOUD_MAX + MIN_NETRAD	0.310	0.258	-0.930	2.738	0.161	Intercept	-5.063	2.188	0.041	2, 12
MELDOR ~ CLOUD_MAX + MIN_NETRAD						CLOUD_MAX	0.021	0.008	0.032	
MELDOR ~ CLOUD_MAX + MIN_NETRAD						MIN_NETRAD	0.039	0.017	0.044	

In bold, the best models after considering r^2 , AIC and W_i values. Average cloudiness and minimum net radiation influence all melanism variables.

Δ_i , AIC differences; λ , phylogenetic signal (Pagel's); AIC, Akaike information criterion; AVG_NETRAD and MIN_NETRAD, average and minimum seasonal net radiation; CLOUD_AVG and CLOUD_MAX, seasonal average and maximum cloud cover; MELTOT, MELVEN, MELDOR, total, ventral and dorsal melanism; r^2 , correlation coefficient; SE, standard error; W_i , AIC weights.

Table 4 Relationship between body size and melanism values in species of the *Liolaemus goetschi* clade

Model	λ	Adj. r^2	F	P-value
MELTOT ~ LOG_SVL	1.00	0.873	91.6	<0.001
MELVEN ~ LOG_SVL	0.00	0.604	20.9	<0.001
MELDOR ~ LOG_SVL	1.00	0.785	48.6	<0.001

We show the values of the simple linear regressions using body size as independent variable and melanism as the dependent variable. There is a positive relationship between all melanism variables and body size.

Table 5 Phylogenetic generalized least squares regression models evaluating influence of body size (snout-vent length logarithm, LOG_SVL) and total, ventral and dorsal melanism (MELTOT, MELVEN, MELDOR) on preferred temperatures and effectiveness of thermal regulation of the *Liolaemus goetschi* clade studied (14 species)

Model	λ	Adj. r^2	AIC	Δ_i	W_i
TPREF ~ LOG_SVL	0.000	0.160	43.815	0.000	0.644
TPREF ~ MELTOT	0.000	-0.060	47.066	3.252	0.127
TPREF ~ MELDOR	0.000	-0.083	47.367	3.552	0.109
TPREF ~ MELVEN	0.000	-0.067	47.160	3.346	0.121
E ~ LOG_SVL	0.762	-0.090	-10.312	2.694	0.104
E ~ MELTOT	1.000	0.539	-12.121	0.884	0.257
E ~ MELDOR	1.000	0.570	-13.005	0.000	0.399
E ~ MELVEN	1.000	0.535	-11.986	1.020	0.240

Preferred temperatures are influenced by body size, while effectiveness of thermoregulation is affected by melanism.

Δ_i , Akaike differences; λ , phylogenetic signal (Pagel's); Adj. r^2 , correlation coefficient; AIC, Akaike information criterion; W_i , Akaike weights.

from direct radiation or air temperature. However, the three melanism variables (dorsal, ventral, total) did vary significantly with average cloudiness and minimum net radiation suggesting a potential thermoregulatory function. The high phylogenetic signal observed in our models suggests that evolutionary processes may be influencing melanism variation too, except for ventral melanism.

When considering the conflicting results found regarding Bergmann's pattern in *Liolaemus* lizards (Cruz *et al.*, 2005; Pincheira-Donoso *et al.*, 2007), our results are based on a better representation of the studied clade of lizards (although a smaller species number), and more accurate climatic data, enabling us to achieve more precise results. The composite tree used by Pincheira-Donoso *et al.* (2007) shows less support than ours, being the result of collapsing several trees (Lobo *et al.*, 2010). Additionally, our phylogenetic analysis possesses variable branch lengths important for PGLS and phylogenetic signal detection.

For ectotherms and endotherms, a larger body size leads to increased heat conservation times (Porter & Gates, 1969; Stevenson, 1985); therefore, once a desired body temperature is achieved, it might be maintained for longer times as the result of thermal inertia. However, our study only shows the latitudinal pattern of BS in response to environmental tem-

peratures (significant, although with shallow slopes), and does not prove the mechanism, which remains unresolved.

It has to be considered that thermal inertia may be one among several other mechanisms explaining Bergmann's pattern (Gaston & Blackburn, 1999; Olalla-Tárraga *et al.*, 2010). For example, temperature influences on development (Ray, 1960); body size may vary with maturity (Atkinson & Silby, 1997), longevity or clutch size (Miaud, Guyétant & Faber, 2000); smaller species may show low dispersal capacity (Blackburn & Gaston, 1996); body size may depend on food availability (McNab, 1971; Yom-Tov & Yom-Tov, 2005) or may be related to starvation resistance (Searcy, 1980; Arnett & Gotelli, 1999) and predation or competition pressures may have an effect on body size too (Ashton, 2002). Net primary productivity (NPP) was also suggested as relevant to body size patterns (McNab, 2010). However, NPP is similar across localities and probably not relevant.

The significant, positive relationship between body size and melanism, combined with the significant influence of cloudiness and net radiation on melanism, suggests that this trait may be related to heat gain under unfavourable environmental conditions, and be a possible candidate trait to compensate for the 'negative' influence of body size on heating. The relationship with cloudiness and net radiation, used as indicators of the amount of solar radiation available in the environment, suggests that melanism may actually play a role increasing heat gaining rates in circumstances of low solar radiation, which would be related to the observed influence of melanism on effectiveness of thermoregulation. However, we are aware that our -correlational- study leaves several unfilled gaps to be solved in future studies. We observed the patterns, but we need more evidence in order to completely understand the evolutionary history. In addition, we may ask, how will an increased thermal inertia affect heat uptake? Or is the effect of melanism large enough to compensate for body size effect? And, do large, melanistic lizards differ in the activity times with smaller, lighter coloured ones and how?

Several other factors may influence the degree of melanism, as recently argued by Reguera, Zamora-Camacho & Moreno-Rueda (2014) for the lizard *Psammotromus algirus*. These factors are not exclusive, and therefore, the TMH may be one among several possible explanations for the colour patterns observed, such as predator avoidance (Kettlewell, 1973; Endler, 1984), ultraviolet protection (Gunn, 1998; Calbó, Pagès & González, 2005), sexual selection (Wiernasz, 1989) or the high cost of melanin production (Talloen, Van Dyck & Lens, 2004).

Finally, we observed that body size variation may be explained by the heat conservation hypothesis (Bergmann, 1847; Gaston & Blackburn, 2000), in agreement with the HBH (Olalla-Tárraga & Rodríguez, 2007). The relationship between body size and melanism supports the third TMH assumption of a trade-off among them. However, we failed to find support for the latitudinal variation of melanism (assumption 1), which was observed only for ventral melanism. The lack of information regarding if body size and melanism have an effect on heating and cooling rates prevent us to be conclusive with regard to the TMH (Clusella-Trullas

et al., 2007). Therefore, the next step to disentangle the role of size and melanism on thermoregulation of these lizards is to acquire heating and cooling rates. However, in light of the available information, a combination of the HBH and TMH seems to be possible, but other ecological pressures cannot be discarded.

Acknowledgements

We acknowledge the critical reading of early versions of this paper by A. Herrel, S. Meiri, M. Olalla-Tárraga, A. Ruggiero and V. Corbalán. J. Nori, R. Semhan, V. Juárez and G. Scrocchi helped in the field. PICT (ANPCyT) 06-01205 to F.B.C. partially supported this work. D.L.M.A. and M.F.B. are supported by CONICET fellowships, and received research material from NGC used for this work. D.L.M.A. was supported by EADIC II program. We thank L. Buria (APN, National Parks of Argentina), and Fauna authorities; S. Montanelli (Chubut), L.B. Ortega (Santa Cruz), M. Faillá (Río Negro), F. Lonac (Neuquén), P. Barlanga (Mendoza) and M. Jordán (San Juan) for providing collection permits.

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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:

Table S1. Species lists, number of collected specimens (*N*), collection site coordinates, environmental data, body size and melanism measures for each studied species of the *Liolaemus goetschi* clade.

Table S2. Thermal biology data for each studied species of the *Liolaemus goetschi* clade (taken from Moreno Azócar *et al.*, 2013).

Appendix S1. Methodology applied to obtain the measurements of melanism and to the phylogenetic framework.