

Energetics in Liolaemini lizards: implications of a small body size and ecological conservatism

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Abstract Liolaemini lizards occur in southern South America in a variety of dietary habits across a broad latitudinal and altitudinal distribution. We studied standard metabolic rates of 19 Liolaemini species and analyzed these data using both conventional and phylogenetically informed statistics. Oxygen consumption showed a significant and positive relationship with body mass ($\text{SMR} = 0.109 \times \text{body mass}^{0.876 \pm 0.023}$), with a higher slope than that expected on the basis of the three-quarter power law

model. After phylogenetically informed and conventional analyses, no significant differences in metabolic rates were found to be related to diet or elevation. We hypothesize that small body size, ecological conservatism and physiological compensation may explain the lack of differences in metabolic rates observed among these lizards.

Keywords Energetics · Body mass · Distribution · Diet · Liolaemini lizard · Comparative analysis

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Introduction

The balance of energy through the life-span of organisms is diverse. Components of an energy budget may be conserved in some vertebrates, as is the case for maintenance, foraging and body temperature regulation in mammals and birds (Wunder 1978). In contrast, the energy used for movement may be relatively trivial in some vertebrates, whereas in others it can represent a substantial proportion of the energy budget (Antinuchi et al. 2007). However, in all cases energy for maintenance represents a significant proportion of the annual energy budget (Angilletta Jr 2001).

Basal metabolic rate (BMR) has been used as a proxy of minimal energy use in mammals, with body mass as the most often studied factor influencing its variability and magnitude within and among species. Body mass is a major correlate of metabolic rate (West et al. 1997; Riisgard 1998; Luna et al. 2009). In the case of ectotherms, standard metabolic rate (SMR) is a good predictor of minimal metabolism and, as in mammals, body mass also determines metabolic rate (Andrews and Pough 1985). Previous authors have investigated how different factors, besides body mass, such as diet (McNab 1992; Simandle et al.

2001), elevation (Sears 2005), life cycle (Christian et al. 1999), tissue lipid composition (Simandle et al. 2001), and tissue synthesis (Dial and Fitzpatrick 1981; Naya and Bozinovic 2006; Naya et al. 2008) may be related to variation in energetic demands in reptiles. Identifying factors influencing maintenance costs is a central issue in ecological and evolutionary physiology (McNab 2002; Chappell and Hammond 2004).

Several studies of the relationship between metabolic rates and body mass predict slopes that should be either 0.67 or 0.75 (West et al. 1997; White et al. 2006; Glazier 2010). However, there are exceptions to this allometric metabolic scaling (Glazier 2005; Chown et al. 2007) making it difficult to accept it as a general principle. Deviations from the 0.75 proportion of the allometric metabolic scaling may be due to several factors, such as taxonomic affiliation, food habits, age and biogeography (Glazier 2010).

Lizards show a wide range of life styles, despite the intrinsic constraints influencing their ectothermic physiology. Distribution, elevation range, diet and reproductive mode show variation across Liolaemini lizard species (Espinoza et al. 2004; Schulte et al. 2004; Cruz et al. 2005; O'Grady et al. 2005) in southern South America (Cei 1993). In contrast, some ecological and morphological attributes are particularly conservative in Liolaemini lizards (Schulte et al. 2004; Cruz et al. 2009; Tulli et al. 2009). The availability of a robust series of phylogenetic hypotheses (Schulte et al. 2000; Etheridge 2000; Lobo 2001; Lobo and Quinteros 2005; Avila et al. 2006; Abdala 2007) and extensive data on the natural history and distributional range of Liolaemini (Espinoza et al. 2004; Schulte et al. 2004; Cruz et al. 2005; O'Grady et al. 2005) make this an ideal group to conduct phylogenetically informed studies of ecology and physiology, which may help to elucidate processes involved in the resulting phenotypes.

In the current study, we measured the metabolic rates of 19 Liolaemini species (four *Phymaturus* species and 15 *Liolaemus*) distributed over a broad latitudinal (23–41.5°S) and elevational range (~700–4,000 m), from the high Andes in Salta to the Patagonian steppe in Rio Negro, Argentina. We evaluated the relationship between SMR and body mass, climatic conditions at the geographical midpoint distribution, and diet using both conventional and phylogenetically informed statistics. Our main predictions were: (a) metabolic rate would scale to the three-quarter power law model (West et al. 1997; Banavar et al. 1999; Ginzburg and Damuth 2008) as previously reported for some lizards (Maxwell et al. 2003); (b) lizards from higher elevations would show lower metabolic rates than lizards from lower elevations as lower metabolic expenditure is advantageous in harsh climatic conditions such as those

characterizing high elevation habitats (Sears 2005); (c) herbivorous lizards would show lower metabolic rates (in contrast to omnivores and insectivores) due to the typically lower available energy content of plant material (Pough 1973; McNab 1986; Anderson 1993).

Materials and methods

Animal collection and preferred temperature determination

One hundred and thirty-five active adult lizards were used in this study (74 males and 61 females). Our purpose was to compare metabolic rates among several phylogenetically related species. Because, some of these species are viviparous and some other are oviparous, we chose to avoid potential physiological differences due to reproductive condition. For this reason, all lizards were non-reproductive (gonads were in repose in males and no females were pregnant or had yolked follicles) as lizards were collected out of their reproductive season (see “Appendix”; March 2005 for oviparous species, October 2005 for viviparous species; sensu Ramírez Pinilla 1991). Among the 19 Liolaemini species included here, nine occur over 2,000 m above sea level and ten below that elevation; five species are herbivores, eight insectivores, and six omnivores.

Lizards were captured by hand or noose and collected from different localities in Argentina from the northern Puna to the Patagonian steppe (Table 1). Once captured, lizards were transferred to the lab within 2–4 days. First, we determined the preferred body temperature (T_{sel}) of each species in the lab (Table 1). To estimate this parameter, we placed each lizard individually in a thermal gradient (temperature in the gradient varied from 18 to 46°C). Individuals were able to freely select a place with a particular ambient temperature. Tank dimensions were 1.2 m long, 0.6 m wide and divided into five 0.12 m lanes. Temperature corresponded to ambient controlled temperature (approximately $18 \pm 1^\circ\text{C}$) and 100 W IR bulbs placed at one end that generated the gradient as described by Cruz et al. (2009). We obtained body temperatures of lizards hourly with a type K ($\pm 0.1^\circ\text{C}$) thermocouple (Extech 421502, Waltham, Massachusetts) during the photophase of three consecutive days.

Metabolic rate determination

Previous to oxygen consumption trials in the laboratory of Ecophysiology at Universidad Nacional de Mar del Plata, lizards were housed in individual cages ($0.30 \times 0.40 \times 0.25$ m) for 10 days ($24 \pm 1^\circ\text{C}$ Ta, 12L:12D). Depending on diet type, each lizard was fed every 2 days with

Table 1 List of *Liolaemus* (L.) and *Phymaturus* (P.) species studied

Species	N	Lat.	Elev.	C. Ind.	Diet	Mass (\pm SD)	SMR (\pm SD)	ms-SMR (\pm SD)	Tsel
<i>L. abaucan</i>	9	27°43'	1,800	29.79	Ins	5.51 (\pm 1.27)	0.57 (\pm 0.14)	0.11 (\pm 0.03)	34.7
<i>L. albiceps</i>	8	24°05'	3,540	19.32	Her	12.08 (\pm 4.21)	0.88 (\pm 0.39)	0.08 (\pm 0.03)	34.9
<i>L. calchaqui</i>	9	26°17'	3,575	19.64	Omn	5.78 (\pm 2.17)	0.49 (\pm 0.19)	0.09 (\pm 0.04)	34
<i>L. chacoensis</i>	7	28°25'	700	34.65	Ins	1.21 (\pm 0.28)	0.16 (\pm 0.04)	0.15 (\pm 0.06)	33.1
<i>L. crepuscularis</i>	3	27°15'	2,950	19.70	Omn	2.11 (\pm 0.24)	0.32 (\pm 0.09)	0.15 (\pm 0.03)	35.4
<i>L. cuyanus</i>	7	29°31'	1,200	28.64	Omn	14.83 (\pm 3.29)	1.70 (\pm 0.53)	0.12 (\pm 0.04)	32.3
<i>L. darwini</i>	10	31°35'	1,250	23.18	Ins	5.67 (\pm 1.24)	0.85 (\pm 0.20)	0.15 (\pm 0.04)	33.6
<i>L. espinozai</i>	7	27°06'	2,600	23.74	Ins	4.85 (\pm 0.69)	0.50 (\pm 0.10)	0.10 (\pm 0.02)	34.6
<i>L. irregularis</i>	4	23°58'	4,030	16.34	Omn	15.88 (\pm 5.83)	1.56 (\pm 0.53)	0.10 (\pm 0.02)	35.8
<i>L. koslowskyi</i>	10	28°47'	1,625	29.30	Ins	6.68 (\pm 1.59)	1.00 (\pm 0.38)	0.15 (\pm 0.04)	34.1
<i>L. laurenti</i>	7	28°13'	950	33.02	Ins	3.70 (\pm 0.43)	0.51 (\pm 0.14)	0.14 (\pm 0.03)	34.5
<i>L. lavillai</i>	10	24°43'	3,050	19.62	Omn	3.79 (\pm 1.15)	0.31 (\pm 0.12)	0.08 (\pm 0.02)	35.4
<i>L. olongasta</i>	10	30°35'	1,335	29.96	Ins	4.51 (\pm 1.16)	0.86 (\pm 0.44)	0.18 (\pm 0.05)	32.9
<i>L. ornatus</i>	9	23°18'	3,400	17.85	Omn	4.07 (\pm 1.52)	0.79 (\pm 0.34)	0.20 (\pm 0.05)	36.5
<i>L. quilmes</i>	10	26°37'	2,300	26.45	Ins	5.12 (\pm 0.73)	0.68 (\pm 0.20)	0.13 (\pm 0.04)	34.1
<i>P. dorsimaculatus</i>	3	37°48'	2,025	18.70	Her	43.39 (\pm 10.65)	3.51 (\pm 0.18)	0.08 (\pm 0.02)	34.1
<i>P. exelsus</i>	5	41°32'	1,140	21.15	Her	20.53 (\pm 2.35)	1.19 (\pm 0.47)	0.06 (\pm 0.02)	32.1
<i>P. spectabilis</i>	3	41°39'	950	21.91	Her	15.81 (\pm 7.79)	1.25 (\pm 0.56)	0.08 (\pm 0.03)	32.8
<i>P. tenebrosus</i>	4	41°05'	915	22.28	Her	24.85 (\pm 3.09)	2.85 (\pm 0.68)	0.11 (\pm 0.02)	31.1*

Mean latitude (*Lat.*) is in S°; mean elevation (*Elev.*) is in m above sea level; climatic index (*C. Ind.*, *sensu* Espinoza et al. 2004); type of diet (*Ins* insectivore, *Omn* omnivore, *Her* herbivore); body mass (g), mean standard metabolic rate (*SMR*, ml O₂ g⁻¹ h⁻¹); mean mass-specific standard metabolic rate (*ms-SMR*, ml O₂ g⁻¹ h⁻¹); number of individuals (*N*) and preferred body temperature (*Tsel*) of the species studied here; *SD* standard deviation

* *Tsel* data from Ibargüengoytia (2005)

mealworms (*Tenebrio monitor* larvae), daisy flowers or both. After each individual lizard ate it was located in a terrarium with a heating stone for a lapse of at least 2 h. Finally, once lizards accomplished acclimation, they were used in trials having fasted for between 48 and 56 h.

After acclimation, oxygen consumption measurements were taken from each specimen at their specific *Tsel* during daytime (Table 1), using an individual closed respirometry system (see Vleck 1987) based on a dynamic injection technique for constant volume respirometry (see Lighton 2008). We used this technique because it allowed us to use several individual chambers to estimate O₂ consumption for each individual at the same time, minimizing possible effects of circadian rhythm on metabolic rate (Aschoff and Pohl 1970).

Lizards were placed into a respirometric chamber, made of transparent acrylic to observe if lizards were moving or jerking, in which case we removed the individual and repeated the trial the day after. Because lizards were different sizes we used chambers of two volumes (148 and 463 ml). For both chamber types, an additional chamber (without animal, Control 1) was used to control for any possible change in atmospheric oxygen concentration. Chambers were cylindrical with a concave threaded lid at

one end and inlet–outlet air valves at the opposite end. Into the concave lid, a measured quantity of CO₂-absorbent (IQB®) and water scrubber (Silica Gel) was placed and retained with a wire mesh.

First, individuals were placed inside the chamber. Air free of CO₂ and H₂O was flushed through the chambers using an air pump. Whereas air was flushing into the chamber, an air sample was taken using a 60 ml syringe connected to it (Control 2). Syringe was closed using a stopcock, chambers closed, and start time recorded. The same procedure was used for control chamber (Control 1). The initial air samples were flushed through the O₂ analyzer (see description below). Given that we flow free CO₂ and H₂O air, no evidence of differential O₂ concentration between initial air sample and the baseline (20.95% O₂) was observed. Lizards remained in the chambers for 30–45 min, depending on the temperature and body size. To control ambient temperature, chambers were placed in a modified incubator consisting of a double aluminum wall with polyurethane between the walls. Heat was interchanged with the outside automatically by two Peltier intercoolers (Melcor, model CP-1.4-127-061) connected to a PC and controlled by custom written software. Air

temperature inside the chamber was maintained with an accuracy of 0.1°C. Previously estimated preferred temperature of each species was used to set the ambient temperature during each trial. Animals that moved within the chamber during the measurements were excluded from the analysis, and the measurement of O₂ consumption was repeated the next day. After each trial, the outlet valve of the chamber was connected to a 60 ml syringe, the valve opened, and the gas in the chamber was mixed by pumping the syringe repeatedly (three times). Finally, a sample of air was collected with the syringe and the time recorded. This procedure was also carried out using Control 1 and no difference with baseline was observed.

Oxygen concentration was measured with an FC-1B Oxygen Analyzer (Sable Systems, Las Vegas). To measure O₂ concentration, outside air passed through a CO₂-absorbent (IQB[®]) and water scrubber (Silica Gel) before passing through the analyzer at a flow rate 90 ml min⁻¹ (baseline), fitted at a constant O₂ concentration of 20.95% (atmospheric O₂ concentration). Flow rate was generated by a flow controller (Sable Systems, Las Vegas) located upstream from the analyzer. Gas samples were injected by hand at a faster rate (~120 ml min⁻¹) into the tubing leading to the analyzer. The injected air sample was passed also through the CO₂ and H₂O scrubber. Data on O₂ concentration were recorded every 1 s by a Datacan V system (Sable System, Las Vegas). Typically, air samples produce a similar pattern to those described in Lighton (2008) and Simandle et al. (2001). Subtraction of a differential O₂ concentration of 0.2095 was used to obtain air sample O₂ concentration. Rate of O₂ consumption was calculated according to Vleck (1987, eq. 9), described elsewhere by Lighton (2008, eq. 4.18). Because chambers contained Silica Gel and IQB[®], the initial volume of H₂O and CO₂ was zero (Vleck 1987, and see above Control 1 and 2). The total volume of the chamber was estimated by subtracting the volume occupied by each lizard (assuming 0.98 g = 1 ml, De Vera and Hayes 1995), and H₂O and CO₂ scrubber volumes from the volume of the corresponding respirometric chamber. Before each metabolic trial, body mass of individuals was measured using an electronic balance (AND, model FX-3000, ±0.01 g).

We measured SMR of Liolaemini at their Tsel because it has profound ecological and physiological implications on ectotherms such as lizards and provides us with biologically meaningful data. However, for comparative purposes, we standardized the metabolism to an ambient temperature of 30°C using the Q₁₀ equation (McNab 2002, p. 47). In the case where it was available, we used specific Q₁₀ data (Table 2), or else we used a Q₁₀ of 2.33 (estimated based on the Q₁₀ of Liolaemini species used in this study plus other *Liolaemus* species not included here, such as *L. lineomaculatus*, *L. escarchadosi*, *L. sarmiento*, *L. zullyi*,

Table 2 Q₁₀ taken at 30–35°C for SMR values for ten species of Liolaemini studied here

Species	Q ₁₀
<i>Liolaemus chacoensis</i>	2.52
<i>L. espinozai</i>	2.60
<i>L. koslowskyi</i>	2.20
<i>L. laurenti</i>	2.85
<i>L. ornatus</i>	0.98
<i>L. quilmes</i>	1.30
<i>Phymaturus dorsimaculatus</i>	1.22
<i>P. exelsus</i>	2.34
<i>P. spectabilis</i>	1.20

L. magellanicus, *L. hatcheri*, *L. coeruleus*, *L. baguali*, *L. elongatus*, *L. fitzingerii*, *L. kingii* and *L. xanthoviridis*). The latter 12 species were used in an unrelated study of thermal sensitivity (Cruz et al., unpublished data). The range of ambient temperatures where Q₁₀ was estimated ranged between 22 and 38°C. After comparing both data sets we detected no significant differences ($t = -0.640$; $df = 5$; $P = 0.550$), and thus assumed a Q₁₀ value of 2.33 as being a valid number for Liolaemini. Moreover, it was similar to that determined for reptiles, in general (2.4, Andrews and Pough 1985).

To estimate the effect of body mass and distribution (elevation and climatic index) on SMR, we used multiple regressions, as well as simple regression analyses. Before analyses, SMR and body mass were log₁₀-transformed. Diet, elevation and climatic index were considered as factors for comparisons.

Temperature and climatic conditions are dependent on latitude and elevation which are independent variables. We used the Espinoza et al. (2004) equation to obtain temperature indexes after regression of air temperatures and corrected for latitudinal and elevational deviations based on climatic lapse-rate functions. Thus, the index regression for latitude is $y = 25.79 + 0.28263x - 0.017708x^2 + 0.000010727x^3$, where y is the corrected temperature (climatic index) for latitude x . The lapse-rate function to correct air temperatures at sea level to those at different elevations decreases 0.65°C every 100 m. The addition of the products of each equation minus the starting temperature (here, 20°C) resulted in a single index for a given latitude and elevation.

Statistical analyses

To address evolutionary patterns across species, we used both conventional and phylogenetically informed statistics (ANCOVAs and regressions). Specifically, for conventional statistics we used InfoStat (Di Rienzo et al. 2008)

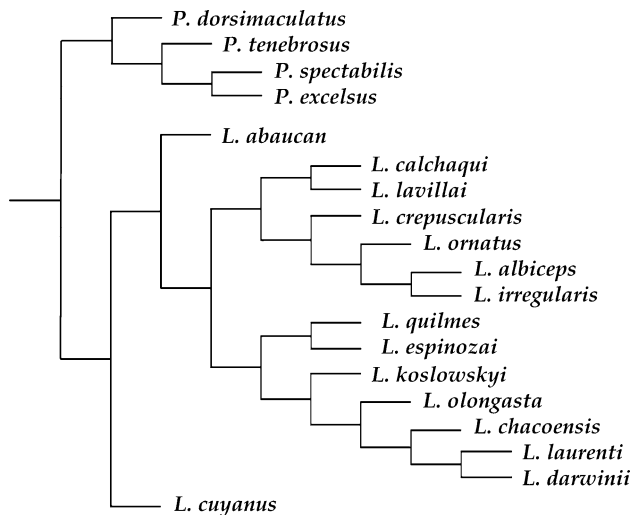


Fig. 1 Metatree constructed for the studied species, based on phylogenetic analyses provided in Lobo and Quinteros (2005) and Abdala (2007). Branch lengths were set equal to one in our analysis

and for independent contrasts calculations (Felsenstein 1985) we used the PDAP module (Midford et al. 2008) in Mesquite 2.5 (Maddison and Maddison 2008). To compute contrasts, we used a combination of a much larger number of species belonging to two phylogenetic analyses, Lobo and Quinteros's (2005) morphology-based phylogenetic tree for *Phymaturus* species and Abdala's (2007) tree for *Liolaemus* species that resulted from a combination of morphology and gene sequences. In the combination of these topologies (Fig. 1), we arbitrarily set branch lengths to one, as branch lengths based on molecular studies were not available for all species in our analyses. Moreover, independent contrast analyses are robust to variation in branch lengths (Díaz-Uriarte and Garland 1998).

Next, we performed phylogenetic ANCOVAs (PDAP, PDANOVA, Midford et al. 2008) to test for differences between metabolic rates of high (above 2,000 m) versus low elevation lizards (1,800 m and below), and among the three dietary groups, using \log_{10} transformed body mass as a covariate. With regard to elevation, the limits between groups are based on Sears (2005). An empirical null distribution of F -statistics that takes phylogeny into account was generated using PDSIMUL and analyzed with PDANOVA (Garland et al. 1993). For each thermal variable we ran 1,000 simulations under a speciation model of evolution. Significant differences among categories (type of diet or elevation) were considered if the original F value was higher than the F_{95} value derived from the empirical distribution. The speciation model sets all branch lengths to one in PDSIMUL, thus assuming only one character change per branch (Martins and Garland 1991).

We calculated the phylogenetic signal in our data set using the randomization test (Blomberg et al. 2003) and

computed the K statistic as an indicator of phylogenetic signal for the following log transformed variables using PHYSIG (available upon request from T. Garland, University of California, Riverside): body mass, metabolic rate, mean elevation and climatic index. Diet was coded as follows: 1 = herbivore, 2 = omnivore and 3 = insectivore.

Due to the small sample size, and to make sure the regression model provided the best fit among the candidate models (Angilletta Jr 2006), we used the Akaike Information Criterion differences (Δ_i): the lowest Akaike information Criterion (AIC) and a Δ_i value of zero were considered the best models. Additionally, we used Akaike weights (W_i) as a measure of the strength of evidence for each model, indicating the probability that a given model is the best among a series of candidate models (Burnham and Anderson 2002). AIC analysis was performed separately for conventional statistics and standardized independent contrasts.

Results

The standard allometric equation relating metabolic rate to body mass obtained for the *Liolaemini* species studied here was (Fig. 1):

$$\text{SMR}(\text{ml O}_2 \text{ h}^{-1}) = 0.109 \times \text{body mass}^{0.876 \pm 0.023}$$

$$r^2 = 0.81, F_{1,17} = 1.426, P < 0.001,$$

Where ± 0.023 is the SE of the exponent (95% CI = 0.921–0.831). *Phymaturus* species show high values of SMR; however, their mass-specific SMR dropped as a consequence of their large body size (Table 1) and noticeably *P. excelsus* showed the lowest mass-specific SMR ($0.06 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) among all the species studied here. A few species showed a mass-specific SMR higher than $0.15 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, among them *Liolaemus olongasta* and *L. ornatus*, but these two species show differences in their diet habits, elevation range and are not closely related.

Body mass was a good predictor of SMR ($\text{ml O}_2 \text{ h}^{-1}$) after conventional ($r^2 = 0.88$, slope = 0.78; Fig. 2) and phylogenetically informed simple regressions ($r^2 = 0.79$, slope = 0.88; Fig. 2), showing a significant and positive trend in both cases. Overall, multiple regression analyses (using two or three independent variables) of mass-specific SMR showed only non-significant trends (Table 3). The same pattern was observed when we used independent contrasts, finding no significant trends for any of the regression analyses was performed (Table 3).

Metabolic rate was not different between species inhabiting low and high elevations (above 2,500 m), when considering conventional ANCOVA ($F_{1,18} = 0.82$; $P = 0.38$)

Fig. 2 Relationship between \log_{10} -transformed body mass to \log_{10} -transformed standard metabolic rate (ml oxygen consumed per hour, O_2 ml h^{-1}) using raw data (left, black symbols) or independent contrast (right, white symbols)

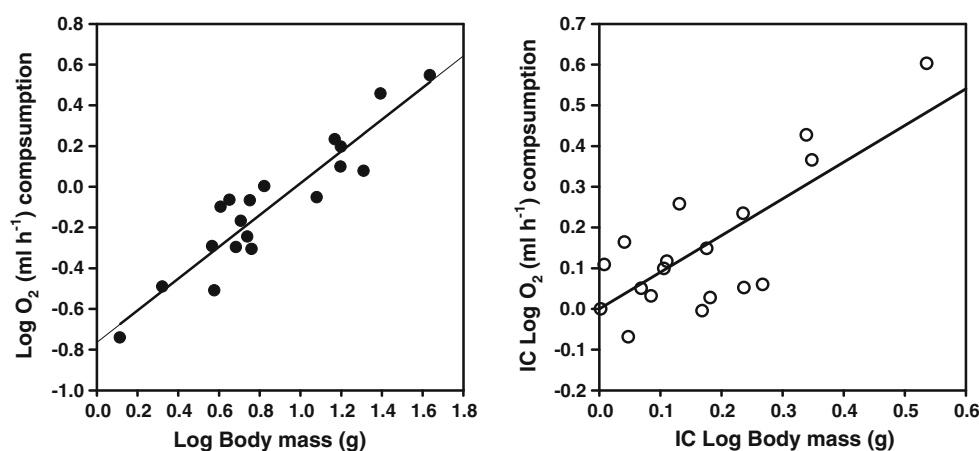


Table 3 Akaike information criterion values (AIC), differences (Di) and Akaike weights (Wi) for different models using conventional statistics (CS) and standardized independent contrasts (IC)

Variables in the model	AIC	Di	Wi	r^2	P
CS ClimInd	24.82	0.14	0.43	0.16	0.09
CS Elevation	24.67	0.00	0.46 [‡]	0.02	0.64
CS Elevation, ClimInd	27.38	2.71	0.12	0.21	0.15
IC ClimInd	24.91	0.00	0.51 [‡]	0.00	0.92
IC Elevation	24.92	0.01	0.50	0.01	0.65
IC Elevation, IC ClimInd	27.49	2.58	0.12	0.04	0.76

Standard metabolic rate was the dependent variable. r^2 is the determination coefficient

ClimInd climatic index *sensu* Espinoza et al. (2004)

[‡] Best fit from CS and IC models, respectively

Table 4 K Statistics (an indicator of phylogenetic signal) and P values for Liolaemini using constant branch lengths (CBL) and Ornstein–Uhlenbeck (OU) transformed branch lengths for the tree topology

Variable	CBL		OU ($d = 0.2$)		OU ($d = 0.8$)	
	K	P	K	P	K	P
Body mass	0.55	0.027	0.93 [‡]	0.561	0.75 [‡]	0.189
Metabolic rate	0.39 [‡]	0.126	0.10 [‡]	0.157	0.65 [‡]	0.116
Climatic index	0.24 [‡]	0.987	0.86 [‡]	0.851	0.42 [‡]	0.929
Diet	0.47	0.040	0.95 [‡]	0.363	0.67 [‡]	0.099
Elevation	0.29 [‡]	0.795	0.89 [‡]	0.689	0.49 [‡]	0.920

[‡] Variables for which closely related species are less similar than expected based on a Brownian motion model of evolution and phylogenetic signal is non-significant

or phylogenetically informed ANCOVA ($F_{1,17} = 0.02$; $P = 0.49$). We found no significant differences among the three different types of diet either, in the case of conventional ANCOVA ($F_{2,18} = 1.78$; $P = 0.20$) or phylogenetically informed ANCOVA ($F_{2,17} = 0.20$; $P = 0.44$).

Body mass and type of diet showed significant phylogenetic signal, but K statistics were not high (less than 1.0; Table 4). Other variables, such as metabolic rate, climatic index and elevation also showed K values lower than one, suggesting that adaptive variation could be present (Table 4). However, note that the 19 species included in this study lie below the suggested sample size minimum (20) for this type of analysis (see Blomberg et al. 2003) and thus, the phylogenetic signal obtained should be interpreted with caution.

Discussion

Although SMRs in reptiles have been studied extensively, this aspect of physiology has been scarcely studied in

Liolaemini despite their wide geographic distribution, variation in habitat use, and diet. Recent studies on *L. nitidus* and *L. belli* have examined how SMR is affected by tail regeneration and season (Naya and Bozinovic 2006; Naya et al. 2007, 2008). Our interspecific comparative data indicate that elevation and type of diet did not explain the observed variation in metabolic rate, after using both conventional and phylogenetically informed analyses. Phylogenetic signal analyses showed mixed results. Body mass and diet type showed significant signal, but K values were lower than 1 indicating less signal than expected given the topology. We are aware of the relative amount of variation present at the various taxonomic levels, as well as the low power of our analysis and the use of a pruned tree. To test whether our results may have been biased by low sample sizes for some species, we reran the analyses excluding species with less than four specimens. Results were quite similar, for example SMR was positively related to body mass (conventional analysis $r^2 = 0.81$; $P < 0.001$, IC analysis $r^2 = 0.73$; $P < 0.001$). Moreover, in all cases (multiple and simple regressions of raw data and IC of

ms-SMR vs. ecological variables) we were unable to detect any significant relationships.

Body mass correlated with SMR, but with an exponent that is higher than expected for the 3/4 power model of West et al. (1997). Despite the fact that 3/4-power scaling appears to be common (e.g. a slope of 0.76 was observed for reptiles in the studies by White et al. 2006; Glazier 2010), a variety of other scaling relationships have been observed (Glazier 2005). For example, in Squamate reptiles, in general, the average exponent is approximately 2/3 (Andrews and Pough 1985; Zari 1993). Apparently, extrinsic and intrinsic factors (the taxa involved, body-size ranges and ecological types) are involved in driving such variations (Glazier 2005). Thus, our results support the idea that 3/4 power scaling is not universal; variations in power scaling between 2/3 and 1 (even more than 1) are observed in a variety of organisms (Glazier 2010). Interestingly, the intercept (metabolic level) is similar to those proposed for reptiles (Glazier 2010), favoring the idea of being considered a group-specific component of metabolism.

Different species, to some extent, may respond differently depending on the environmental conditions despite being ectotherms, and consequently, macrophysiological patterns may be related to ecological conditions (Chown et al. 2004), or alternatively may be shaped by particular physiological constraints. Unexpectedly, our results do not support the predictions of either the influence of geographic climatic conditions or elevation range on SMR in the Liolaemini species studied here. However, the relationship between oxygen consumption and body mass was positively correlated both after conventional and phylogenetically based statistical analyses. An explanation for the lack of patterns in our analyses may be that body mass and type of diet have significant phylogenetic signals, despite the fact that the calculated *K* statistics are low. Indeed, within subclades these traits may be less variable and consequently distribution of these traits is phylogenetically clustered reducing our power to detect significant adaptive trends (Vanhooydonck and Van Damme 1999). Interestingly, *Liolaemus nitidus* and *L. bellii* from Chile despite belonging to a different clade (*L. chiliensis* group) showed SMR similar to those observed in the present study (see Naya and Bozinovic 2006; Naya et al. 2007). Among several small-bodied diurnal lizards (mass less than 30 g), *Liolaemus* species SMR ranges between 0.065 and 0.2 ml O₂ g⁻¹ h⁻¹, and this includes some *Anolis* species, sceloporines, gekkonids, scincids and even varanid species (Andrews and Pough 1985; Dial and Grismer 1992; Hare et al. 2006; Clemente et al.

2009). On the contrary, active Teiid lizards show metabolic ranges above 0.23 ml O₂ g⁻¹ h⁻¹ (Cullum 1997).

Generally, the relationship between animal diversity and ecosystem functioning remains poorly understood (Chown et al. 2004). A few recent studies found evidence of macroecological and macrophysiological differences in the structure and function of southern and northern Hemisphere ecosystems (Blackburn and Gaston 1996; Addo-Bediako et al. 2000; Royer et al. 2003). The dominance of ocean masses in the southern hemisphere is thought to result in a decreased climatic effect on the ecology (and physiology) of terrestrial organisms (Ruggiero and Lawton 1998; Cruz et al. 2005). South America remains poorly explored. As such, the lack of information about macroecological (and macrophysiological) patterns in the southern Hemisphere, potentially weak climatic effects, and seasonality (see Angilletta 2009) must be considered in interpreting the outcome of the present study. It is important to note that the number of species used in this study, in addition to the broad elevational and latitudinal ranges, precluded the present study to consider a seasonal variation of SMR as a factor to be included in the analysis. As such, further studies are needed to assess this effect within Liolaemini group.

Another explanation for the lack of a relationship between geographic and climatic conditions and metabolic rates may be the strong association between these variables and phylogeny. For example, in the case of mammals both diet and phylogeny are strongly implicated in explaining variation in metabolic rates (Cruz-Neto et al. 2001). However, in our study all *Phymaturus* species studied are distributed in Patagonia, while the six *Liolaemus* species belonging to the *L. ornatus* clade (Abdala 2007) live exclusively at high elevations. This may result in colinearity of the data as a result of species sampling; reducing the statistical power of our analyses (Garland et al. 1993; Vanhooydonck and Van Damme 1999). Additionally, *Phymaturus* species are particularly conservative in many aspects of their biology, including thermal biology (Cruz et al. 2009), diet (Espinoza et al. 2004) and body shape, while *Liolaemus* species generally show greater variation (Cruz et al. 2005, 2009).

With respect to diet, vertebrate ectotherms show variation in SMR that is related to food quantity (Anderson 1993) and quality (Simandle et al. 2001). For example, Zari (1996) suggested that herbivorous lizards may have low SMR as an adaptation to an energetically poor diet. Anatomically, herbivorous Liolaemini lizards tend to have larger intestines than omnivores and insectivores (O'Grady et al. 2005). Moreover, there is an association between reduced specific activity of digestive organs during periods

of inactivity in small hibernating ectotherms (Tracy and Diamond 2005) and chemical changes in tissue composition occurring throughout the year in *Liolaemus* lizards (Naya et al. 2008). In the case of mammals (Antinuchi et al. 2007), larger digestive tracts (such as in herbivores) may produce similar physiological output to that of species with shorter digestive tracts with a more energetic diet. Consequently, despite subsisting on a potentially low energy diet, animals may achieve similar SMR by compensation.

Our results are congruent with those of Nussear et al. (1998), who observed that ecologically relevant differences in diet quality may have negligible effects on SMR in an herbivorous lizard. Some *Liolaemus* species show physiological flexibility allowing animals to adjust energy acquisition (Naya et al. 2008). This ability may be present across species too; however, a more detailed study is needed to assess this hypothesis.

Herbivorous Liolaemini lizards have slightly lower SMR than omnivores and insectivores; however, this result was not significant. Among species studied here, herbivores did not have higher Tsel than omnivores or insectivores either

(Cruz, unpublished data). Interestingly, Liolaemini lizards are among the smallest known herbivorous species (Espinoza et al. 2004) and the evidence reported in the present study show that Liolaemini lizard species may present particular ecophysiological responses different from what is observed or expected for other lizards. However, the proximate mechanisms driving these patterns still remain obscure.

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Appendix

See Table 5

Table 5 List of *Liolaemus* (L.) and *Phymaturus* (P.) species collected for the present

Species	Province	Department	Locality	Latitude	Longitude	Elevation	Date
<i>L. abaucan</i>	Catamarca	Tinogasta	Near Palo Blanco	27°26'S	67°41'W	1,800	10 October 2005
<i>L. albiceps</i>	Salta	La Poma	Estación Muñano	24°21'S	66°09'W	4,300	25 March 2005
<i>L. calchaqui</i>	Tucumán	Trancas	Hualinchay	26°17'S	65°36'W'	3,575	22 March 2005
<i>L. chacoensis</i>	San Juan	Valle Fertil	Las Tumanas	30°52'S	67°19'W	750	9 October 2005
<i>L. crepuscularis</i>	Catamarca	Andalgala	Near M Capillitas	27°15'S	66°35'W	3,100	17 March 2005
<i>L. cuyanus</i>	San Juan	Caucete	Medanos Grandes	31°36'S	67°41'W	1,200	8 October 2005
<i>L. darwini</i>	San Juan	Caucete	Medanos Grandes	31°36'S	67°41'W	1,200	8 October 2005
<i>L. espinozai</i>	Catamarca	Santa María	Punta Balasto	26°59'S	66°19'W	2,600	16 March 2005
<i>L. irregularis</i>	Salta	Los Andes	15 km W S. A. Cobres	24°02'S	66°16'W	3,450	25 March 2005
<i>L. koslowskyi</i>	La Rioja	Castro Barros	Near Anillaco	28°49'S	66°57'W	1,750	18 October 2005
<i>L. laurenti</i>	La Rioja	Famatina	30 km S Pituil	28°50'S	67°24'W	1,100	18 October 2005
<i>L. lavillai</i>	Salta	La Poma	S of La Poma	24°44'S	66°10'W	2,995	18 March 2005
<i>L. olongasta</i>	La Rioja	Vinchina	35 km S V Unión	29°47'S	67°42'W	1,550	19 October 2005
<i>L. ornatus</i>	Jujuy	Cochinoca	5 km W Abra Pampa	22°42'S	65°43'W	3,350	26 March 2005
<i>L. quilmes</i>	Catamarca	Santa María	Santa María	26°39'S	66°01'W	2,100	20 October 2005
<i>P. dorsimaculatus</i>	Neuquén	Ñorquin	25 km S El Huecú	37°48'S	70°42'W	2,025	5 March 2005
<i>P. exelsus</i>	Río Negro	25 de Mayo	35 km S Jacobacci	41°32'S	69°51'W	1,150	6 March 2005
<i>P. spectabilis</i>	Río Negro	25 de Mayo	45 km S Jacobacci	41°42'S	69°45'W	950	6 March 2005
<i>P. tenebrosus</i>	Río Negro	Pilcaniyeu	Cerro Alto	40°52'S	70°34'W	1,050	6 March 2005

We include information about province, department, locality, coordinates (latitude and longitude), elevation and date of capture

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