

# Body size dimensions in lizard ecological and evolutionary research: exploring the predictive power of mass estimation equations in two Liolaemidae radiations

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Body size influences patterns of variation in several of the most important traits directly linked to fitness. Therefore, the establishment of informative proxies for body size is a critical aim in ecological and evolutionary research. Among lizards, snout–vent length (SVL) is the most widely used proxy for body size. However, since SVL is a linear measure of size, it fails to capture body shape variation. This limitation is largely resolved by the use of body mass, a multidimensional measure of size that is unfortunately rarely considered and reported. To circumvent this restriction, a classic allometric equation (Pough's equation) was proposed to convert SVL into mass. Nevertheless, the predictive power of this equation has been assumed rather than empirically tested for almost three decades. In a recent study on lizard size allometries, additional equations were derived for different groups separately, suggesting that more clade-specific equations are likely to perform better. Here, we investigate the precision of these allometric equations using two sister lizard genera (*Liolaemus* and *Phymaturus*), members of the Liolaemidae radiation, for which SVL and mass have been measured. We found that our equations differ significantly from the two more general equations primarily in intercepts, while the more clade-specific equation derived for Tropiduridae lizards is fully compatible with our equation for *Liolaemus* and showed only a borderline statistical difference with *Phymaturus*. Therefore, although more clade-specific equations may reliably predict body mass, more general equations should be used with caution in lizard ecological and evolutionary research. Previous allometric equations proposed to predict mass from length in other ectotherms should be quantitatively assessed before being employed.

*Key words:* allometry, body mass, lizards, *Liolaemus*, *Phymaturus*

## INTRODUCTION

Ecological and reproductive success among animals are extensively mediated by body size (Peters, 1983; Brown et al., 2004; Fairbairn et al., 2007). Such a strong dependence of fitness on this phenotypic component has repeatedly been illustrated by a number of influential theories spanning a broad diversity of problems in evolutionary biology and ecology (Andersson, 1994; Roff, 2001; Bell, 2008). Therefore, the establishment of both informative and standardized proxies for body size is a major technical aim in the empirical investigation of many of the most important evolutionary and ecological predictions.

Several proxies for body size have been proposed and employed across different animal lineages, given the vast diversity of both developmental and structural characteristics of each particular group (Pough, 1980; Peters, 1983). In lizards, the most extensively used proxy for body size is snout–vent length (SVL) (Meiri, 2008). This

variable has been shown to correlate significantly with a number of important biological parameters, such as ecological, physiological and life-history traits (Pough et al., 2004; Wikelski, 2005; Meiri, 2008). These features make SVL, at least in the absence of alternative proxies, an appropriate estimator for body size, as evidenced by several studies encompassing a wide variety of evolutionary and ecological problems (Losos, 1990, 2009; Ibagüengoytía & Cussac, 2002; Meiri, 2008; Pincheira-Donoso et al., 2008a). However, some important limitations are associated with the use of this variable. Fundamentally, since SVL is simply a linear measure of body length, it does not account for patterns of variation imposed by body shape (Greer & Wadsworth, 2003; Meiri, 2008, 2010). Given the complex polygenic nature of body size as a whole (Falconer & Mackay, 1996; Barsh et al., 2000), the effect of multivariate selection results in different patterns of allometric relationships among different component dimensions of this quantitative trait. For example, comparative analyses based on SVL would fail to detect

differences between species varying dramatically in body weight but not in body length, potentially obscuring or biasing the relationships between body size and other variables of interest.

The intrinsic analytical limitations of SVL can largely be resolved with the use of body mass, a phenotypic measure whose implicit multidimensional nature takes into account variation in body shape components (Pough et al., 2004; Meiri, 2008, 2010). Moreover, body mass exhibits additional advantages such as its potential to satisfactorily capture most of the variation in life-history traits and metabolic processes (Hedges, 1985; Brown et al., 2004; Shine, 2005). Therefore, under several circumstances body mass is a more desirable measure of body size than SVL. Unfortunately, body mass is rarely recorded or reported in lizard studies, which makes it challenging to acquire this information, for example from the literature, for ecological or evolutionary analyses. As a result, SVL often remains the only available proxy for body size (Meiri, 2008, 2010). A potential solution to this problem was suggested three decades ago in an insightful and now classic paper by Pough (1980). In that study, Pough proposed a general allometric equation for lizards ( $\text{mass} = 3.1 \times 10^{-2} (\text{SVL}^{2.98})$ , where mass is expressed in grams and SVL in centimetres; Pough's equation hereafter) for predicting body mass from SVL (additional formulae were also proposed for legless lizards and for other ectotherms in the same work). However, some limitations are inherent in this equation. First, it is aimed at predicting mass in lizards in general. Second, since Pough's dataset is unavailable, it is not possible to evaluate the precision of this equation. Similarly, the equation lacks error and fit measures (Meiri, 2010). Despite these limitations, Pough's equation has traditionally been implicitly assumed to reliably predict lizard mass among a considerable diversity of groups, rather than empirically tested. Since lizards have played a significant role in most ecological and evolutionary fields (Huey et al., 1983; Pianka & Vitt, 2003; Reilly et al., 2007; Losos, 2009), it is of crucial importance to empirically evaluate the predictive power of this equation. In a recent paper, Meiri (2010) presented a large-scale study where Pough's equation was contrasted against empirically derived equations for major lizard groups. This author presented a number of new equations that he suggested might provide more accurate estimations of mass. However, at lower hierarchical phylogenetic levels in a given clade, important variation in body shape even among closely related lineages may result in inaccurate predictions of mass. Given that several questions rely on the use of particular genera or more inclusive levels, a detailed test of Meiri's (2010) equations is warranted. Indeed, Meiri (2010) himself suggested that more clade-specific allometric equations might provide better predictive performance.

In this study, we investigate the predictive power of Pough's and Meiri's allometric equations using two sister genera of the Liolaemidae family (*Liolaemus* and *Phymaturus*) as model systems (Pincheira-Donoso et al., 2008b). These iguanians, particularly *Liolaemus*, have been the subject of an increasing number of ecological and evolutionary studies where body size variation has

been of primary importance (Fox & Shipman, 2003; Espinoza et al., 2004; Schulte et al., 2004; Cruz et al., 2005; Pincheira-Donoso et al., 2007, 2008a, 2009). However, these studies have invariably used SVL as the proxy for body size, mainly because of the limited availability of body mass measures for species of this genus. *Liolaemus* and *Phymaturus* lizards offer an interesting opportunity to explore this problem as they are species-rich sister lineages (more than 200 species are known in *Liolaemus*, and more than 20 in *Phymaturus*) differing substantially in patterns of body length–mass variation (Ceï, 1986; Scolaro, 2005; Pincheira-Donoso et al., 2008b; Scolaro & Pincheira-Donoso, 2010). While *Liolaemus* consists primarily of slender species, *Phymaturus* species are stout and flattened. Although the causes behind these body differences between *Liolaemus* and *Phymaturus* are unknown, it might be argued that they relate to different evolutionary and ecological dynamics known for each lineage. For example, while *Liolaemus* is a prominent adaptive radiation where remarkable adaptive and ecological differences have repeatedly evolved (Schulte et al., 2000, 2004; Espinoza et al., 2004; Pincheira-Donoso et al., 2008a, 2009; Labra et al., 2009), *Phymaturus* species are likely to have undergone a nonadaptive radiation (Scolaro & Pincheira-Donoso, 2010). *Phymaturus* species live in cold environments (Andes and Patagonia), inhabit ranges largely isolated from each other (with some exceptions) and are consistently saxicolous, viviparous and herbivorous (Ibargüengoytia et al., 2008; Pincheira-Donoso et al., 2008b; Díaz-Gómez, 2009; Scolaro & Pincheira-Donoso, 2010). These evolutionary differences appear to match the magnitude of intragenetic variation in body size conformation, with *Liolaemus* species ranging from proportionally heavy and short (e.g. *L. anomalus*, *L. kolongh*) to proportionally long and slim species (e.g. *L. gracilis*, *L. lemniscatus*), while in *Phymaturus* body shape and length are conserved much more among species (e.g. Ceï, 1986; Scolaro, 2005). Hence, these lizards offer ideal models to reflect how mass predictions at lower levels in a lineage can require more specific equations. Given these differences in the allometry of body size dimensions in these two clades, we predict that the power of Pough's and Meiri's equations will differ between them. Specifically, we predict that the quality of fit of Liolaemidae allometric regressions to Pough's and Meiri's equations will decrease with increasing phylogenetic coarseness, i.e. Meiri's equation for Tropicuridae will fit better than Meiri's general equation for legged lizards, which will in turn fit better than Pough's equation for lizards in general. Finally, we expect to show that allometric equations for mass predictions should be used cautiously when attempting to draw evolutionary and ecological conclusions, and that group-specific predictions may be required in some cases.

## MATERIALS AND METHODS

### Data

We collected individual data for SVL and body mass across a large sample of Liolaemidae lizards comprising 1,715 *Liolaemus* individuals belonging to 29 species

**Table 1.** Sample of species and specimens used in this study. The entire sample consists of adult individuals only.

Genus	Species	<i>n</i>	SVL (mm)	Weight (g)
<i>Liolaemus</i>	<i>bellii</i>	153	72.83	11.96
	<i>bibroni</i>	108	52.21	4.26
	<i>boulengeri</i>	114	56.63	5.75
	cf. <i>bellii</i>	12	66.77	9.83
	cf. <i>elongatus</i>	4	78.42	17.25
	<i>constanzae</i>	32	62.33	7.03
	<i>cuyanus</i>	32	79.43	17.98
	<i>chacoensis</i>	21	47.80	3.45
	<i>chiliensis</i>	6	75.78	13.60
	<i>darwinii</i>	66	53.34	4.50
	<i>elongatus</i>	8	73.70	12.37
	<i>fuscus</i>	173	46.72	2.81
	<i>gununakuna</i>	2	73.68	13.50
	<i>koslowskyi</i>	12	59.41	5.80
	<i>laurenti</i>	6	41.33	3.00
	<i>lemniscatus</i>	175	47.69	2.80
	<i>leopardinus</i>	83	86.24	19.67
	<i>lineomaculatus</i>	131	54.63	4.78
	<i>magellanicus</i>	9	56.77	5.59
	<i>monticola</i>	158	60.70	6.68
	<i>nigromaculatus</i>	8	65.95	12.12
	<i>nigroviridis</i>	140	66.64	9.06
	<i>nitidus</i>	67	83.17	21.04
	<i>olongasta</i>	23	54.60	5.38
	<i>parvus</i>	13	63.15	7.69
	<i>pictus</i>	47	56.91	5.39
<i>sarmientoi</i>	60	74.86	11.13	
<i>schroederi</i>	36	56.93	5.26	
<i>tenuis</i>	16	52.23	4.43	
<i>Phymaturus</i>	<i>antofagastensis</i>	27	89.61	29.53
	cf. <i>palluma</i>	20	92.96	25.99
	<i>payunia</i>	29	86.94	27.06
	<i>punae</i>	19	93.61	32.10
	<i>roigorum</i>	28	102.37	49.42
	<i>tenebrosus</i>	32	93.14	29.46
	<i>zapalensis</i>	53	81.34	21.17

and 208 *Phymaturus* individuals belonging to seven species (Table 1). All measurements were taken from living specimens in the field or shortly after being captured. The sample comprises species representing a vast geographical area of Argentina and Chile, and a large diversity of environments. This variation in the selection regimes across species is likely to be involved in the differences in patterns of allometric scaling observed among these lizards, and hence, to provide a representative magnitude of the overall body shape variation within each lineage. Despite being sister clades, important differences in body shape are observed between *Liolaemus* and *Phymaturus*, as detailed above (Scolaro, 2005; Scolaro et al., 2008; Scolaro & Pincheira-Donoso, 2010). The robust body shape conformation of *Phymaturus* in relation to body length (compared to *Liolaemus*), leads us to expect that Pough's

and Meiri's equations will not predict body mass with the same accuracy in these two lineages. However, it does not seem appropriate to regard *Phymaturus* as a "body shape–body length" outlier lineage among lizards in general, as similar relationships between shape and length are likely to be found in a number of lizard groups in other areas of the world (e.g. *Diplolaemus*, *Phrynosoma*, *Sauromalus*, *Uromastyx*, among others).

### Statistical analyses

For quantitative analyses we used the mean value of SVL and body mass of each species. Prior to statistical tests, all data were  $\log_{10}$ -transformed on both sides of the allometric equations to linearize the power-law relationship between body mass and snout–vent length in the standard way, from  $y = ax^b$  to  $\log(y) = \log(a) + b\log(x)$ , where  $y$  is body mass,  $x$  is SVL, and  $a$  and  $b$  are the parameters of the equation, namely the intercept and the slope, respectively (Peters, 1983; Harvey & Pagel, 1991). Hence, Pough's equation, for example, was linearized from  $\text{mass} = 0.031\text{SVL}^{2.98}$ , to  $\log_{10}(\text{mass}) = -1.509 + 2.98\log_{10}(\text{SVL})$ . Meiri's (2010) allometric equations are presented in Table 2. The same log-transformation also serves to reduce skew and equalize variance of residuals in regression analyses (Miles & Ricklefs, 1984; Zar, 2009).

We then proceeded to investigate the predictive power of allometric equations previously derived to calculate lizard body masses from SVL by Pough (1980) and Meiri (2010), through comparisons with our genus-specific equations obtained from actual SVL and mass data in our *Liolaemus* and *Phymaturus* samples (Meiri's equations are also based on actual SVL and mass data, although our samples are considerably larger and hence more representative of the magnitude of allometric variation within both genera). While we performed comparisons with the single general equation proposed for lizards by Pough (1980), our analyses compared our Liolaemidae equations with the more specific equations derived by Meiri (2010) for Tropicuridae and legged lizards (which both contain *Liolaemus* and *Phymaturus*), in two separate stages. First, to assess the fit of Pough's equation to our own measurements in *Liolaemus* and *Phymaturus*, we calculated the residual  $\log_{10}(\text{mass})$  of each species from their predicted values. We then regressed these residuals against  $\log_{10}(\text{SVL})$  and tested the deviation of the resulting regression slope and intercept from zero. This procedure is equivalent to using an offset to compare our observed linear regression of  $\log_{10}(\text{mass})$  against  $\log_{10}(\text{SVL})$  with Pough's equation (Crawley, 2007).

Second, we compared our allometric regressions with the equations derived by Meiri (2010). This was facilitated by the availability of original datasets in his paper's appendix S1. For these comparisons, we performed analyses of covariance, with  $\log_{10}(\text{mass})$  as a common response variable,  $\log_{10}(\text{SVL})$  as a common covariate, and data source ("Meiri's data" vs. "our data") as a categorical explanatory variable. This allowed for a precise test of differences between slopes, tested using the interaction between data source and  $\log_{10}(\text{SVL})$ . We then used an offset term to force the common slope for the two data sources to be equal to Meiri's slope for the relevant liz-

**Table 2.** Allometric relationships between the mass and SVL body size dimensions in the Liolaemidae genera *Liolaemus* and *Phymaturus* (this study; see results), and allometric equations from ordinary least-square regressions (OLS) provided by Meiri (2010) for legged lizards in general and for the Tropicuridae family, which in this study included *Liolaemus* and *Phymaturus*. SE = standard error; CI = confidence interval.

Group	n	Intercept			Slope			R <sup>2</sup>	P
		Intercept	SE	95% CI	Slope	SE	95% CI		
<i>Liolaemus</i>	29	-4.678	0.209	-5.107, -4.248	3.097	0.117	2.857, 3.337	0.96	<<0.0001
<i>Phymaturus</i>	7	-5.040	1.323	-8.441, -1.638	3.323	0.675	1.588, 5.058	0.83	<0.01
Tropicuridae	32	-4.216	0.418	-5.069, -3.360	2.846	0.220	2.396, 3.295	0.85	-
Legged lizards	866	-4.804	0.043	-4.888, -4.720	3.088	0.022	3.045, 3.132	0.96	-

ard group. A comparison of models with and without the offset term tested whether the observed common slope deviated significantly from Meiri's slope. Finally, we asked whether the regression lines from the two lizard groups compared differed in intercept, by testing the main effect of data source. Using this procedure we compared allometric regressions of *Liolaemus* against Tropicuridae, *Liolaemus* against legged lizards, *Phymaturus* against Tropicuridae, and *Phymaturus* against legged lizards. All statistical analyses were performed using R version 2.9.1 (R Development Core Team, 2008).

## RESULTS

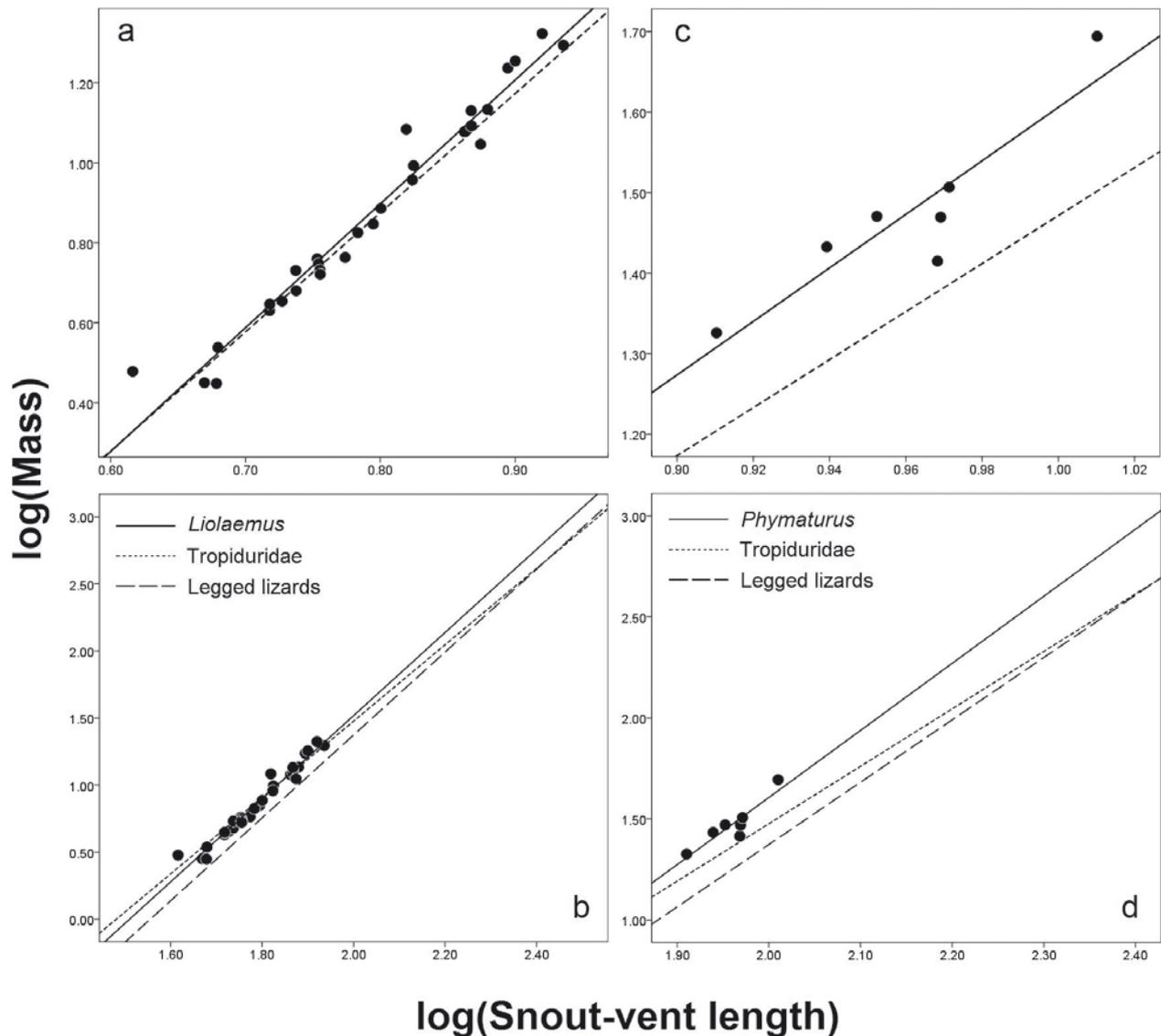
Our analyses reveal that body mass in *Liolaemus* and *Phymaturus* lizards is more accurately predicted by the clade-specific allometric equation derived for Tropicuridae by Meiri, while the remaining two equations, for lizards in general (Pough) and for legged lizards (Meiri), consistently failed to accurately predict mass from SVL in both Liolaemidae lineages (Tables 2 and 3; Fig. 1). Comparisons of slopes showed that the slopes calculated from both *Liolaemus* and *Phymaturus* mass-on-length linear regressions ("common slopes" in Table 3) do not differ from the slopes of any of the three allometric equations presented by Pough and Meiri (Table 3). Forcing each of the regressions to have slopes equal to Meiri's equations showed that these established slopes are suitable predic-

tors of the relationship between body mass and body length ("slope comparisons" in Table 3). In contrast, our intercept comparisons revealed different results. The intercept obtained from *Liolaemus* data significantly differs from the intercepts derived for lizards in general (Pough) and for legged lizards (Meiri), while no differences were found with Meiri's intercept obtained for Tropicuridae (Table 3). Hence, this latter equation is a powerful predictor of mass in *Liolaemus*, in contrast with the former two (although our equation is still a better predictor). Comparisons with *Phymaturus* revealed relatively similar results (Table 3). The intercept calculated for these lizards strongly differed from lizards in general and from legged lizards, as observed in *Liolaemus*. However, we also found statistically significant differences with the intercept of Tropicuridae, although the significance value ( $P=0.049$ ) falls in the borderline between significant and non-significant differences (Table 3). In all four cases where Liolaemidae intercepts strongly differ from intercepts obtained in Pough's and in one of Meiri's equations (i.e. *Liolaemus* and *Phymaturus* vs lizards in general, and vs legged lizards), our analyses reveal that Liolaemidae body masses predicted from a given SVL were underestimated (Table 3; Fig. 1). However, the masses of *Phymaturus* lizards were underestimated to a greater extent than those of *Liolaemus* (Fig. 1).

Additionally, inspections of the plots in Figure 1 show that the accuracy of equations derived in this study for

**Table 3.** Comparative analyses for slopes and intercepts of allometric equations derived for *Liolaemus* and *Phymaturus* in this study and the allometric equation proposed by Pough (1981) for lizards in general and those for Tropicuridae and legged lizards (which both contain *Liolaemus* and *Phymaturus*) presented by Meiri (2010). Raw SVL data for comparisons with Pough's equation in centimetres, and in millimetres for comparisons with Meiri's equations.

Comparison	Common slope		Slope comparisons		Intercept comparisons	
	F (df)	P	F (df)	P	F (df)	P
<i>Liolaemus</i> vs Pough's eq	1.006	0.32	-	-	4.91	0.03
<i>Phymaturus</i> vs Pough's eq	0.26	0.62	-	-	41.77	<0.001
<i>Liolaemus</i> vs Tropicuridae	0.69 (1,57)	0.41	0.31 (1,58)	0.58	0.17 (1,59)	0.68
<i>Phymaturus</i> vs Tropicuridae	0.07 (1,35)	0.79	0.001(1,36)	0.98	4.12 (1,37)	0.049
<i>Liolaemus</i> vs legged	0.001 (1,891)	0.98	0.0003 (1,892)	0.99	18.67 (1,893)	<0.0001
<i>Phymaturus</i> vs legged	0.01 (1,869)	0.92	0.0003 (1,870)	0.99	11.16 (1,871)	<0.001



**Fig. 1.** Best-fit line allometric relationships from regressions of *Liolaemus* (solid line) against Pough's equation (dashed line) for lizards (a), and against Meiri's equations for Tropiduridae and legged lizards (b), and regressions of *Phymaturus* (solid line) against Pough's equation (dashed line) (c), and Meiri's equations (d). Raw SVL data for comparisons with Pough's equation in centimetres, and in millimetres for comparisons with Meiri's equations. See text and Tables 2 and 3 for quantitative results.

*Liolaemus* and *Phymaturus* (shown in Table 2) to predict mass appears not to be affected by variation in SVL, as there is no clear tendency for increasing residual  $\log_e(\text{body mass})$  magnitude with increasing  $\log_e(\text{SVL})$  (Fig. 1).

## DISCUSSION

We have investigated the predictive power of known allometric equations derived to estimate body mass in lizards from SVL (Pough, 1980; Meiri, 2010). As far as we know, Pough's equation was until recently the only allometric equation for mass predictions in these organisms, and for about three decades has largely been assumed to serve as a reliable analytical instrument in lizard ecological and evolutionary research, as implicitly suggested by studies

that have employed it before tests have been performed (see discussions in Meiri, 2010). Meiri's (2010) recent study showed that the considerable extent of body shape variation among lizards is unlikely to be precisely captured by general equations (e.g. one for lizards in general), and that more clade-specific predictions might deliver better predictive performance. Our study, where allometric equations were derived for *Liolaemus* and *Phymaturus* lizards (Liolaemidae) from real data, support the view that more clade-specific equations are better alternatives. Our results revealed that body masses in *Liolaemus* were precisely predicted only by the more clade-specific equation derived for Tropiduridae lizards by Meiri (2010), while the more general equations for lizards in general (Pough, 1980) and legged lizards (Meiri, 2010) failed to

obtain mass measures consistent with real data. Likewise, comparisons with *Phymaturus* showed that general equations substantially fail to predict masses. Yet, although we found a borderline statistically significant difference between the intercepts of *Phymaturus* and Tropicuridae (Table 3), we argue that this difference might not reflect a serious predictive inaccuracy of Meiri's equation, but an artefact of our relatively limited *Phymaturus* data. However, our equation for *Phymaturus* remains a better alternative than the equation for Tropicuridae. Therefore, these results collectively suggest that family-level equations (i.e. for Tropicuridae in this case) might provide sufficient predictive power, and that genus-specific equations might not always be required (although we suggest that genus-specific equations should be used whenever possible; e.g. Fig 1).

Evolutionary change is a multivariate process that involves the adaptive response to selection of several phenotypic traits simultaneously (Lande, 1979; Roff, 1997). Since body size is a complex polygenic trait (Falconer & Mackay, 1996; Barsh et al., 2000), its different components are likely to follow different adaptive trajectories during the course of evolution. Therefore, the potential asymmetric responses of the different dimensions of body size (e.g. length and mass) are expected to result in the expression of different patterns of allometric variation among species, which are expressed in diverse patterns of body shape. As predicted above, one of the major limitations of general allometric equations for mass predictions is their lack of ability to capture this body shape variation among different components of body size, which may substantially restrict their predictive power (Meiri, 2010). Given that the two lizard radiations analysed here, *Liolaemus* and *Phymaturus*, exhibit important variation in their body shape (Cei, 1986), we expected to find that the performance of more general equations was limited when attempting to predict their body masses from SVL, as supported by our analyses.

Variation in overall body shape across these Liolaemidae lizards seems to result primarily from differences in allometric relationships among body size dimensions (i.e. mass and length of the body trunk), as the extent of variation in other parts of the body (e.g. limb proportions) does not exhibit dramatic interspecific divergence. Indeed, research on ecomorphological adaptations among several *Liolaemus* species has repeatedly revealed remarkable similarities in the proportion of traits involved in locomotor performance (Jaksic et al., 1980; Schulte et al., 2004; Pincheira-Donoso et al., 2009). However, this is not the norm for lizards in general. The extent of variation in other parts of the body, such as heads, limbs or tails, is enormous among the thousands of known lizard species (Pianka & Vitt, 2003; Losos, 2009; Meiri, 2010). Some experimental field studies have even shown that episodes of differential natural selection on conspecific lizard populations may result in strikingly rapid modifications in parts of these body shape components (e.g. Losos et al., 2004). Therefore, body shape variation is a major feature of diversity at all levels of phylogenetic hierarchy. This global scenario suggests that the formulation of one single equation aimed at predicting body mass

from a linear measure of size among lizards in general (even if legless lineages are excluded) is an inappropriate approach. Indeed, it might reasonably be argued that no single equation would be able to capture the dynamic variation in body shape observed among different lizard lineages. A potential, yet complex, alternative may rely on the establishment of different equations fitted to specific lizard lineages. However, as shown by our results, the degree of specificity of these clade-specific formulas might, in some cases, need to reach the level of genus, as closely related clades (such as *Liolaemus* and *Phymaturus*) may often differ in their body plans.

### Body mass versus body length: debating the best variable

The use of body mass is often regarded as a better proxy for body size than its counterpart linear measure SVL (Calder, 1984; Hedges, 1985), as this size dimension implicitly captures variation in body shape. This means that a given number of lizards showing identical SVL values will be unlikely to show identical body mass values, and hence, mass expresses a more diverse array of body size variation than SVL, ultimately reflecting the real variation in body size within a population or lineage. Consequently, the advantage of body mass over SVL relies on its ability to incorporate additional dimensions of body size variation with each value of SVL. An unavoidable question is, therefore, why a body mass measure that fails to capture variation in body shape (in this case, the mass values calculated by equations such as Pough's equation, which assigns the same mass to lizards of identical SVL) is more desirable than SVL, if both reflect exactly the same magnitude of body size variation? Effectively, given that Pough's, Meiri's and our equations predict one single mass value from one single SVL value, the extent of variation expressed by this predicted body mass and SVL are identical. Therefore, the quantitative benefits provided by real measurements of body mass are lacking from body mass values derived from SVL, and hence, under several circumstances there are no general advantages of these predicted masses over SVL when exploring ecological and evolutionary problems involving body size. Nevertheless, for some primary areas of research the use of body mass would offer substantial benefits over measures of body length. For example, the study of macroecological processes among major clades (e.g. vertebrate classes) would require the use of standard surrogates for body size (Meiri, 2010). Since linear measures of size in these organisms are highly heterogeneous, a unique, comparable, mass variable would be desirable to investigate these problems appropriately, and hence, the use of equations to predict body mass would be an ideal approach.

On the other hand, SVL offers several important advantages even over actual measures of body mass (some of which are also true for proxies of body length in general). First, body mass experiences considerable size-independent fluctuations caused by the amount of food consumed at a given time, by environmental seasonality, and by reproductive status (Huey et al., 2001). In contrast, SVL is free from these effects – although it is worth pointing out that it has been reported that individual adults of Gala-

pagos marine iguanas, *Amblyrhynchus cristatus*, shrink in body length in response to El Niño events (Wikelski & Thom, 2000). Second, while SVL can be measured in any single available lizard, body mass should only be recorded from individuals with full tails. Since a substantial proportion of individuals in lizard populations may show cut-off or regenerated tails (Pianka & Vitt, 2003), this represents a serious limitation to collecting mass data, which can even result in analytical bias if individuals of a given size are more likely to lose their tails (e.g. size-related exposure to predators). Also, although body length is only slightly altered with preservation (Roughgarden, 1995), body mass can be dramatically distorted by the use of preservation liquids or after using individuals for studies involving the removal of body parts (e.g. stomachs for trophic research). Indeed, countless ecological and evolutionary studies involving lizard body size routinely rely on the use of SVL measured from preserved specimens (e.g. Losos et al., 2003; Espinoza et al., 2004; Wiens et al., 2006; Pincheira-Donoso et al., 2008).

In conclusion, our results suggest that allometric equations should be used cautiously as they might wrongly estimate the real body mass of lizards, especially when different clades are involved, even if they are closely related (as in the two radiations studied here). In addition, the use of body masses obtained from linear measures of size is mainly justified when conducting integrative analyses on different lineages in which body length is measured using heterogeneous criteria (e.g. total length in fish and snakes, wing and tarsus length in birds, and SVL in lizards). However, this returns the discussion to the need mentioned above to formulate different, clade-specific equations for different lineages, where an initial step would be the empirical test of the other body mass estimation equations proposed for other ectotherms by Pough (1980).

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## REFERENCES

- Andersson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.
- Barsh, G.S., Farooqi, I.S. & O’Rahilly, S. (2000). Genetics of body-weight regulation. *Nature* 404, 644–651.
- Bell, G. (2008). *Selection. The Mechanism of Evolution*. Oxford: Oxford University Press.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Calder, W.A. (1984). *Size, Function and Life History*. Cambridge, Massachusetts: Harvard University Press.
- Cei, J.M. (1986). *Reptiles del Centro, Centro-Oeste y Sur de la Argentina. Herpetofauna de las Zonas Áridas y Semiáridas*. Torino: Museo Regionale di Scienze Naturali di Torino.
- Crawley, M.J. (2007). *The R Book*. Sussex: John Wiley & Sons.
- Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. & Schulte, J.A. (2005). The importance of phylogenetic scale in tests of Bergmann’s and Rapoport’s rules: lessons from a clade of South American lizards. *Journal of Evolutionary Biology* 18, 1559–1574.
- Díaz-Gómez, J.M. (2009). Historical biogeography of *Phymaturus* (Iguania: Liolaemidae) from Andean and Patagonian South America. *Zoologica Scripta* 38, 1–7.
- Espinoza, R.E., Wiens, J.J. & Tracy, C.R. (2004). Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences, USA* 101, 16819–16824.
- Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T. (2007). *Sex, Size & Gender Roles. Evolutionary Studies of Sexual Size Dimorphism*. Oxford: Oxford University Press.
- Falconer, D.S. & Mackay, T.F.C. (1996). *Introduction to Quantitative Genetics*. London: Prentice Hall.
- Fox, S.F. & Shipman, P.A. (2003) Social behavior at high and low elevations: environmental release and phylogenetic effects in *Liolaemus*. In *Lizard Social Behavior*, 310–355. Fox, S.F., McCoy, J.K. & Baird, T.A. (eds). Baltimore & London: Johns Hopkins University Press.
- Greer, A.E. & Wadsworth, L. (2003). Body shape in skinks: the relationship between relative hind limb length and relative snout–vent length. *Journal of Herpetology* 37, 554–559.
- Harvey, P.H. & Pagel, M.D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hedges, S.B. (1985). The influence of size and phylogeny on life history variation in reptiles: a response to Stearns. *American Naturalist* 126, 258–260.
- Huey, R.B., Pianka, E.R. & Schoener, T.W. (1983). *Lizard Ecology. Studies of a Model Organism*. Massachusetts: Harvard University Press.
- Huey, R.B., Pianka, E.R. & Vitt, L.J. (2001). How often do lizards “run on empty”? *Ecology* 82, 1–7.
- Ibargüengoytía, N.R., Acosta, J.C., Boretto, J.M., Villavicencio, H.J., Marinero, J.A. & Krenz, J.D. (2008). Field thermal biology in *Phymaturus* lizards: comparisons from the Andes to the Patagonian steppe in Argentina. *Journal of Arid Environments* 72, 1620–1630.
- Ibargüengoytía, N.R. & Cussac, V.E. (2002). Body temperatures of two viviparous *Liolaemus* lizard species, in Patagonian rain forest and steppe. *Herpetological Journal* 12, 131–134.
- Jaksic, F.M., Núñez, H. & Ojeda, F.P. (1980). Body proportions, microhabitat selection, and adaptive radiation of *Liolaemus* lizards in central Chile. *Oecologia* 45, 178–181.
- Labra, A., Pianaar, J. & Hansen, T.F. (2009). Evolution of thermal

- physiology in *Liolaemus* lizards: adaptation, phylogenetic inertia, and niche tracking. *American Naturalist* 174, 204–220.
- Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33, 402–416.
- Losos, J.B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44, 1189–1203.
- Losos, J.B. (2009). *Lizards in an Evolutionary Tree. Ecology and Adaptive Radiation of Anoles*. California: University of California Press.
- Losos, J.B., Butler, M. & Schoener, T.W. (2003). Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards. In *Lizard Social Behavior*, 356–380. Fox, S.F., McCoy, J.K. & Baird, T.A. (eds). Baltimore and London: Johns Hopkins University Press.
- Losos, J.B., Schoener, T.W. & Spiller, D.A. (2004). Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* 432, 505–508.
- Meiri, S. (2008). Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography* 17, 724–734.
- Meiri, S. (2010). Length–weight allometries in lizards. *Journal of Zoology* 281, 218–226.
- Miles, D.B. & Ricklefs, R.E. (1984). The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* 65, 1629–1640.
- Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Pianka, E.R. & Vitt, L.J. (2003). *Lizards. Windows to the Evolution of Diversity*. California: University of California Press.
- Pincheira-Donoso, D., Hodgson, D.J., Stipala, J. & Tregenza, T. (2009). A phylogenetic analysis of sex-specific evolution of ecological morphology in *Liolaemus* lizards. *Ecological Research* 24, 1223–1231.
- Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T. (2008a). The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology* 8, 68.
- Pincheira-Donoso, D., Scolaro, J.A. & Sura, P. (2008b). A monographic catalogue on the systematics and phylogeny of the South American iguanian lizard family Liolaemidae (Squamata, Iguania). *Zootaxa* 1800, 1–85.
- Pincheira-Donoso, D., Tregenza, T. & Hodgson, D.J. (2007). Body size evolution in South American *Liolaemus* lizards of the *boulengeri* clade: a contrasting reassessment. *Journal of Evolutionary Biology* 20, 2067–2071.
- Pough, F.H. (1980). The advantages of ectothermy for tetrapods. *American Naturalist* 115, 92–112.
- Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., Savitzky, A.H. & Wells, K.D. (2004). *Herpetology*. New Jersey: Pearson, Prentice Hall.
- R Development Core Team. (2008). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Reilly, S.M., McBrayer, L.B. & Miles, D.B. (2007). *Lizard Ecology*. Cambridge: Cambridge University Press.
- Roff, D.A. (1997). *Evolutionary Quantitative Genetics*. New York: Chapman & Hall.
- Roff, D.A. (2001). *Life History Evolution*. Sunderland: Sinauer Associates.
- Roughgarden, J. (1995). *Anolis Lizards of the Caribbean. Ecology, Evolution, and Plate Tectonics*. Oxford: Oxford University Press.
- Schulte, J.A., Losos, J.B., Cruz, F.B. & Núñez, H. (2004). The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae: Liolaemini). *Journal of Evolutionary Biology* 17, 408–420.
- Schulte, J.A., Macey, J.R., Espinoza, R.E. & Larson, A. (2000). Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biological Journal of the Linnean Society* 69, 75–102.
- Scolaro, J.A. (2005). *Reptiles Patagónicos Sur. Una Guía de Campo*. Trelew: Editorial Universidad Nacional de la Patagonia.
- Scolaro, J.A., Ibagüengoytia, N.R. & Pincheira-Donoso, D. (2008). When starvation challenges the tradition of niche conservatism: on a new species of the saxicolous genus *Phymaturus* from Patagonia Argentina with pseudoarborescent foraging behaviour (Iguania, Liolaeminae). *Zootaxa* 1786, 48–60.
- Scolaro, J.A. & Pincheira-Donoso, D. (2010). Lizards at the end of the world: two new species of *Phymaturus* of the *patagonicus* clade (Squamata, Liolaemidae) revealed in southern Patagonia of Argentina. *Zootaxa* 2393, 17–32.
- Shine, R. (2005). Life-history evolution in reptiles. *Annual Reviews of Ecology, Evolution and Systematics* 36, 23–46.
- Wiens, J.J., Brandley, M.C. & Reeder, T.W. (2006). Why does a trait evolve multiple times within a clade? Repeated evolution of snake-like body form in squamate reptiles. *Evolution* 60, 123–141.
- Wikelski, M. (2005). Evolution of body size in Galapagos marine iguanas. *Proceedings of the Royal Society of London, Biological Sciences* 272, 1985–1993.
- Wikelski, M. & Thom, C. (2000). Marine iguanas shrink to survive El Niño. *Nature* 403, 37–38.
- Zar, J. H. (2009). *Biostatistical Analysis*. New Jersey: Pearson International.

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