

## ORIGINAL ARTICLE

## Length–mass allometries in amphibians

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### Abstract

Body mass is rarely recorded in amphibians, and other body measurements (e.g. snout to vent length, SVL) are generally collected instead. However, length measurements, when used as proxies of body mass in comparative analyses, are problematic if different taxa and morphotypes are included. We developed allometric relationships to derive body mass from SVL measurements. We fitted phylogenetic generalized least square models for frogs (Anura) and salamanders (Caudata) and for several families separately. We tested whether allometric relationships differed between species with different habitat preferences and between morphs in salamanders. Models were fitted with SVL–mass measurements for 88 frog and 42 salamander species. We assessed the predictive performance of the models by cross-validation. Overall, the models showed high explained variance and low forecasting errors. Models differed among semi-aquatic, terrestrial and arboreal frogs, and between paedomorphic and non-paedomorphic salamanders. Body mass estimates derived from our models allow for comparability of studies on multiple taxa and can be used for testing theories built upon evolutionary and ecological processes which are directly related to body mass.

**Key words:** Anura, body size, body weight, Caudata, SVL

### INTRODUCTION

Body mass is a fundamental parameter in ecology, as it is related to several key ecological features, such as species metabolic rates and energy intake (Gillooly *et al.* 2001; Brown *et al.* 2004), population abundance (Pe-

ters & Wassenberg 1983), dispersal distance (Jenkins *et al.* 2007; Hillman *et al.* 2014) and reproductive output (Blueweiss *et al.* 1978). Among vertebrates, body mass is commonly recorded in birds and mammals, whereas it is less often recorded in amphibians and reptiles (Meiri 2010; Feldman & Meiri 2013). In amphibians, body mass is highly variable within the same species, but can also vary in the same individual over short time frames. In fact, body mass in amphibians depends on the level of hydration of the animal, the physiological state, the content of the bladder and the cloaca, as well as the reproductive state in females (Dodd 2010). As a consequence, amphibians' body masses are rarely reported in ecological or taxonomic literature as compared to oth-

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er morphometric measurements. Among them, snout to vent length (SVL) is the most common measure of body size in amphibians (Dodd 2010; Vitt & Caldwell 2013). As a result, while SVL is available for many species, body mass data are sparse in the literature and only available for a minority of species.

Although SVL is undoubtedly preferable for many applications, information on body mass is necessary for others. For example, the average body mass of a species is needed to estimate the biomass of a population or of species assemblages (Watanabe *et al.* 2005; Gibbons *et al.* 2006; Deichmann *et al.* 2008; Williamson 2008). In many comparative analyses, SVL is used as a proxy for body mass; however, this presents conceptual and comparability issues. As an example, macroecological investigation has largely explored body mass variation along environmental clines in several taxa (Arnett & Gotelli 2003; Rodríguez *et al.* 2006; Olson *et al.* 2009); however, studies focused on amphibians have employed SVL measurements as a proxy of body mass (Ashton 2002; Diniz-Filho *et al.* 2004; Olalla-Tárraga & Rodríguez 2007; Adams & Church 2008; Cvetković *et al.* 2009; Ficetola *et al.* 2010; Guo & Lu 2016). This is conceptually wrong because the hypotheses proposed so far to explain the environmental clines in body size are based on mechanisms related to body mass, not length (e.g. Bergmann's rule is often explained by the heat conservation advantage of large body mass [Blackburn *et al.* 1999; Meiri & Dayan 2003]).

Similarly, macroevolutionary studies focusing on body mass have often employed mixed body size measurements for different taxa depending on data availability (Harmon *et al.* 2010), with unclear consequences for comparisons between taxa. In comparative conservation analyses body mass is often considered a proxy of extinction risk (Purvis *et al.* 2000; Cardillo *et al.* 2005). However, all comparative analyses on extinction risk in amphibians have employed SVL as a proxy of mass (Bielby *et al.* 2008, 2009; Cooper *et al.* 2008). This is problematic because SVL does not account for different body structures (Meiri 2010) and SVL and body mass probably scale at different rates in frogs (Anura), salamanders (Caudata) and caecilians (Gymnophiona), and between different morphotypes within these 3 taxonomic orders. In fact, morphotypes represent adaptations to environments imposing divergent selective forces (Vidal-García *et al.* 2014; Vidal-García & Keogh 2015), and morphological parameters often show distinct relationships (Guo & Lu 2016).

The development of length–mass allometric rela-

tionships for amphibians would contribute to overcome the abovementioned issues. However, while length–mass allometric relationships are available in scientific literature for a number of taxa (e.g. Silva 1998; Meiri 2010; Feldman & Meiri 2013), to our knowledge the only available allometric models for anurans and salamanders date back to the 1980s (Pough 1980). These are based on a limited number of species (Anura:  $n = 15$ ; Caudata:  $n = 16$ ), including multiple individuals for the same species while not controlling for phylogenetic autocorrelation. In addition, the raw data used for these relationships were never published; therefore, it is impossible to know the identity of the species underlying these relationships. Finally, allometric models that are meant to be used for predictions should be evaluated for prediction accuracy, yet this is rarely done.

In this study we developed allometric relationships in amphibians to derive body mass from SVL measurements. We fitted different models for frogs and salamanders, and tested whether the relationships were different among morphotypes (Moen *et al.* 2013, 2016) and between paedomorphic and non-paedomorphic species. We hypothesized that:

1. Allometric relationships between length and mass were different among species with different habitat preferences (Vidal-García & Keogh 2015), considering that gravity exerts a different effect on aquatic, terrestrial and arboreal species, and body mass is likely selected accordingly. Specifically, we predicted that at equal SVL arboreal frogs would be lighter than terrestrial and fossorial frogs, and terrestrial and fossorial frogs would, in turn, be lighter than aquatic frogs. Similarly, we predicted that at equal SVL terrestrial salamanders would be lighter than aquatic salamanders.

2. Paedomorphic species would display different relationships between length and mass than species undergoing a full development, as metamorphosis implies a major restructuring of the body's morphology, anatomy and physiology (Brown & Cai 2007).

We also fitted allometric models for all families having a sufficient sample size, to evaluate the heterogeneity of the length–mass relationship across the different lineages. Finally, we used cross-validation to assess the predictive abilities of our models, and, thus, to evaluate whether they can be successfully used to predict mass for species for which this parameter is not available.

## MATERIALS & METHODS

### Data collection

We searched the Web of Science database in August 2016 using the following search string: (body length OR body mass OR SVL OR length OR weight OR mass OR allometr\*) AND (amphibian OR anur\* OR caecilian OR urodel\* OR caudat\*). We saved the first 500 returned hits ordered by relevance. In addition, we opportunistically searched Google Scholar and Google using different combinations of the search terms “length,” “mass,” “SVL,” “weight,” “amphibian,” “Anura,” “frog,” “Gymnophiona,” “caecilian,” “Urodela,” “Caudata” and “salamander.” After removing duplicates, titles and abstracts were scanned by LS and AB for relevance. We recorded the mean, ranges and individual mass (g) and length (SVL, mm) data of adult male and female individuals, when possible, or for adults when there was no distinction between sexes. These data were extracted from tables or graphs using WebPlotDigitizer 3.1 Desktop (Rohatgi 2016). We recorded mass and SVL data reported together for the same animals. We supplemented the data found in publications with data collected in the field by one of the authors (GFF), and from several specialized websites (MVZ Herp Collection, AmphibiaWeb and CaliforniaHerps). For those species for which we only found SVL data we performed additional searches using the search string (species name) AND (SVL OR mass OR length OR weight). Besides morphometric measurements, we recorded information on the species’ ecology (habitat preference) and family. We categorized habitat as aquatic/semi-aquatic, fossorial/terrestrial and arboreal in frogs, and as terrestrial/fossorial and aquatic/semi-aquatic in salamanders. Insufficient data were found for caecilians and, therefore, we restricted our analyses to frogs and salamanders. In all our analyses we used one value of SVL and mass per species by taking an average from multiple individuals and studies weighted by sample size. All raw data collected are available in the supplementary materials of this manuscript (Suppl. Table S1).

## Analyses

Data were log<sub>10</sub>-transformed prior to the analyses to meet the assumptions of normality, linearity and homoscedasticity of regression models (Suppl. Appendix S1).

We first ran a linear regression between SVL and body mass and tested the residuals for Pagel’s  $\lambda$ . Pagel’s  $\lambda$  measures the phylogenetic autocorrelation, and ranges from 0 (no phylogenetic autocorrelation) to 1 (phylogenetic autocorrelation as expected under Brownian motion). Because Pagel’s  $\lambda$  was always significantly higher than zero (Anura:  $\lambda = 0.873$ ,  $P < 0.001$ ; Caudata:

$\lambda = 0.486$ ,  $P = 0.016$ ) we used a phylogenetic generalized least square model (PGLS) to develop the allometric models based on the phylogeny developed by Pyron (2014).

Amphibians often show sexual dimorphism for body size (Kupfer 2007). In principle, in sexually dimorphic species we should expect a difference in the allometric models for males and females only if the body shape changes between the 2 sexes (mass and SVL proportions remain constant). However, at a given SVL, females might be heavier because they carry eggs (or embryos). We evaluated this possibility in preliminary analyses (Appendix S2). As we did not observe differences between the 2 sexes, for the main analyses we pooled males and females. We only used averages that included both males and females. When individual data were available, we averaged the average mass for the 2 sexes to avoid sex-biased estimates due to differences in sample sizes.

We used the primary habitat preference as a categorical fixed factor, to account for differences among morphotypes. However, the sample size of some categories was small and the distinction between aquatic and semi-aquatic, and terrestrial and fossorial species is often unclear. Therefore, we clumped aquatic with semi-aquatic species, and terrestrial with fossorial species in the same categories (semi-aquatic and terrestrial, respectively). In addition, we used pedomorphosis as an additional categorical fixed factor to distinguish between morphs in salamanders. We ran 4 PGLS models for frogs and 7 for salamanders, for a total of 11 models (i.e. 2 sets of candidate models). For both frogs and salamanders, the first model included only SVL as predictor; the second included SVL and habitat, the third included SVL and an interactive term for habitat, and the fourth included SVL and an additive and an interactive term for habitat. For salamanders, we also considered an additive, an interaction only, and an additive and interaction model with the category paedomorphic (Table 1). The 2 models with the interaction terms were considered as we can expect that the difference between morphotypes increases/decreases with SVL.

For each order, models were ranked using the AIC corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Models were compared using Akaike weights ( $\omega$ ), indicating the relative weight of evidence of competitive models. Models were considered unequivocally supported if  $\omega > 0.9$ . If no model showed unequivocal support, we used model averaging, which produced model parameters that take into account the

uncertainty detected by the model selection procedure (Burnham & Anderson 2002). The average model was calculated by taking the average of models' coefficients weighted by the models' Akaike weights, and assuming a weight of zero for the models in which a given variable was not included. We also calculated the relative importance of variables, by summing the weights of all models including that variable. Then for each family having  $N \geq 5$ , we ran a separate allometric model including only SVL as a predictor because species belonging to the same family generally have the same habitat preferences (see Suppl. Table S1). Because in the Ambystomatidae family measurements for the Axolotl (*Ambystoma mexicanum*) were particularly influential on the slope, we ran an additional model excluding the Axolotl.

We used a 5-fold cross-validation to test the accuracy of the allometric models by splitting the dataset into training (random 80% of the data) and testing datasets (remnant 20% of the data), where the former was used to fit the model, and the latter to validate it. For each validation we calculated 2 forecasting error estimates: the root mean square error (RMSE) and the mean absolute percentage error (MAPE). The RMSE is a scale-dependent measure, in which the errors are squared before

the average. Therefore, the RMSE penalizes more large errors and it is more sensitive to outliers than MAPE. Conversely, MAPE is scale-independent and provides an intuitive measure for interpretation (Hyndman 2006). The cross-validation procedure was repeated 10 times and the forecasting errors averaged. For the allometric models for each family, we used a jackknife cross-validation instead by removing 1 observation at a time. This was necessary as the sample size of some families did not allow for conducting a 5-fold cross-validation.

Our main analyses were limited to species for which paired measurements of body mass and SVL were available from the same individuals. However, in interspecific allometric models on traits and taxa for which a limited amount of data are available, it is not unusual to derive data for the dependent and the independent variables from separate sources to increase sample size and taxonomic coverage (Gittleman & Harvey 1982; Pagel & Harvey 1988; Swihart *et al.* 1988; White & Seymour 2003; Hendriks *et al.* 2009; Santini *et al.* 2013). Therefore, we repeated the analyses presented in the main text using a larger dataset that also included mass–length measurements collected from different sources for species for which paired measurements were not available, and compared the results with those in the main text (Suppl. Appendix S3).

All analyses were conducted in R 3.0.3 (R Core Team 2016) using the packages “ape” (Paradis *et al.* 2004), “caper” (Orme 2013) and “phytools” (Revell 2012).

**Table 1** Phylogenetic generalized least square model selection results ordered by AICc

Taxon	Formula	AICc	$\Delta$ AICc	$\omega$	Df
Anura	$M \sim SVL:H$	-129.201	0	0.532	4
	$M \sim SVL+H$	-128.216	0.985	0.325	4
	$M \sim SVL*H$	-126.567	2.634	0.142	6
	$M \sim SVL$	-116.141	13.060	0.001	2
Caudata	$M \sim SVL*P$	-25.831	0	0.925	4
	$M \sim SVL:P$	-20.304	5.527	0.058	3
	$M \sim SVL+P$	-16.672	9.159	0.009	3
	$M \sim SVL*H$	-14.000	11.831	0.002	4
	$M \sim SVL:H$	-13.311	12.520	0.002	3
	$M \sim SVL$	-13.217	12.614	0.002	2
	$M \sim SVL+H$	-12.504	13.327	0.001	3

AICc, Akaike information criterion corrected for small sample sizes;  $\Delta$ AICc, difference in AICc from the most supported model;  $\omega$ , Akaike weights; df, degrees of freedom; H, habitat preference; M, mass; P, paedomorphic; SVL, snout-to-vent length; :, interaction term; \*, additive and interaction term.

## RESULTS

Data were gathered from 207 different sources including peer-reviewed articles, PhD and MSc theses, and specialized websites (see Suppl. Table S1). We found body mass data on 190 frog species and 88 salamander species, but for 111 and 49 species only paired SVL measurements calculated on the same individuals were available. Because not all species in our datasets were included in the phylogeny, we excluded from the analyses 23 species of frogs and 3 species of salamanders. The final dataset included 88 species of frogs and 46 species of salamanders. Frog species ranged between 15.99 and 262-mm SVL and 0.32 and 1907-g body mass, whereas salamanders ranged between 23.99 and 542-mm SVL and 0.23 and 912.7-g body mass.

In frogs, the best AICc model suggested an interactive effect between habitat and SVL, but no model was unequivocally supported ( $\omega > 0.9$ ) so we averaged all models weighting by Akaike  $\omega$  (Table 1). In the aver-

age model, the slope of the length–mass relationship was steeper for semi-aquatic and terrestrial species than for arboreal species, partly supporting our first prediction (Fig. 1). The importance of habitat as an additive or interactive term was not very high (Table 2), yet the average model that accounts for the weight of evidence of the models suggests different estimates (Table 3).

In salamanders, we found 1 highly supported model that included an additive and an interaction term with the factor “paedomorphic” (Fig. 1, Table 1), in accordance with our second prediction. Paedomorphic animals displayed a less steep relationship, indicating longer and lighter bodies. The variance explained by the

**Table 2** Variable importance estimate based on Akaike weights

Taxon	Variable	Importance
Anura	SVL	1.000
	Habitat (interaction)	0.674
	Habitat (additive)	0.467
Caudata	SVL	1.000
	Paedomorphic (interactive)	0.983
	Paedomorphic (additive)	0.934
	Habitat (additive)	0.003
	Habitat (interaction)	0.004

SVL, snout-to-vent length.

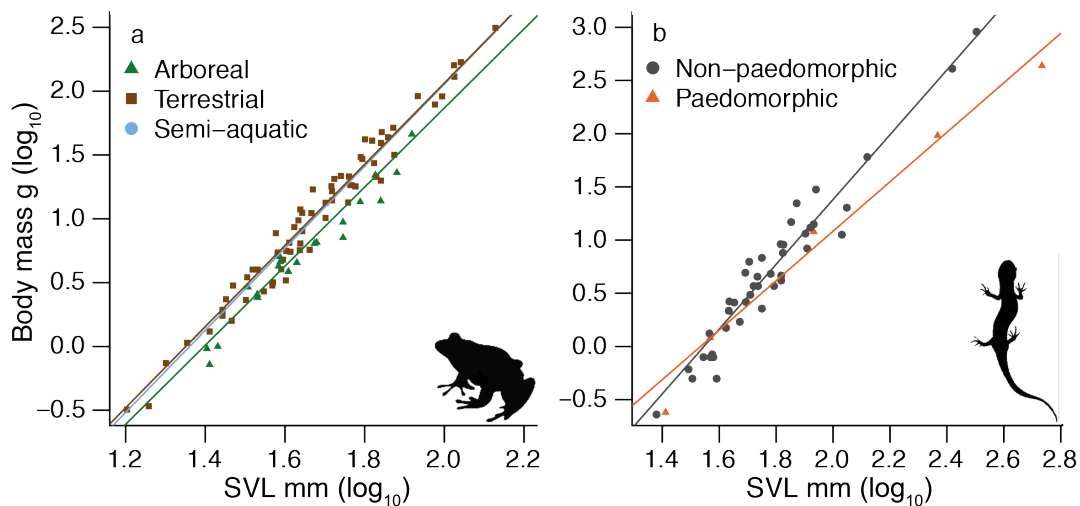
models was high (adjusted  $R^2 > 0.9$ ; Table 3). The models on frogs showed good predictive performances with RMSE ranging between 0.12 and 0.15 and MAPE ranging between 17.97% and 31.01%. The supported model on salamanders had lower predictive performances with RMSE = 0.28 and MAPE = 44.79% (Table 3). Complete model outputs are presented in Supplementary Table S7.

We ran allometric models for 5 Anura and 3 Caudata families (Table 3 and Table S7; Fig. 2). The slopes for the individual families differed slightly from the models at the order level, yet the differences were not significant. The intercepts of the relationships between families were similar with the exception of true toads (Bufonidae), which were systematically heavier. These models performed better than the models at the order level in terms of forecasting errors and explained variance (Table 3).

Although the sample size of the dataset including unpaired mass–length measurements was almost twice as large as the dataset including only paired measurements, the resulting models had lower explained variance and predictive performances (Appendix S3).

## DISCUSSION

Snout to vent length is the most frequently available morphometric measure reported for amphibians (Dodd 2010; Vitt & Caldwell 2013), yet body mass (although variable between populations and within individuals

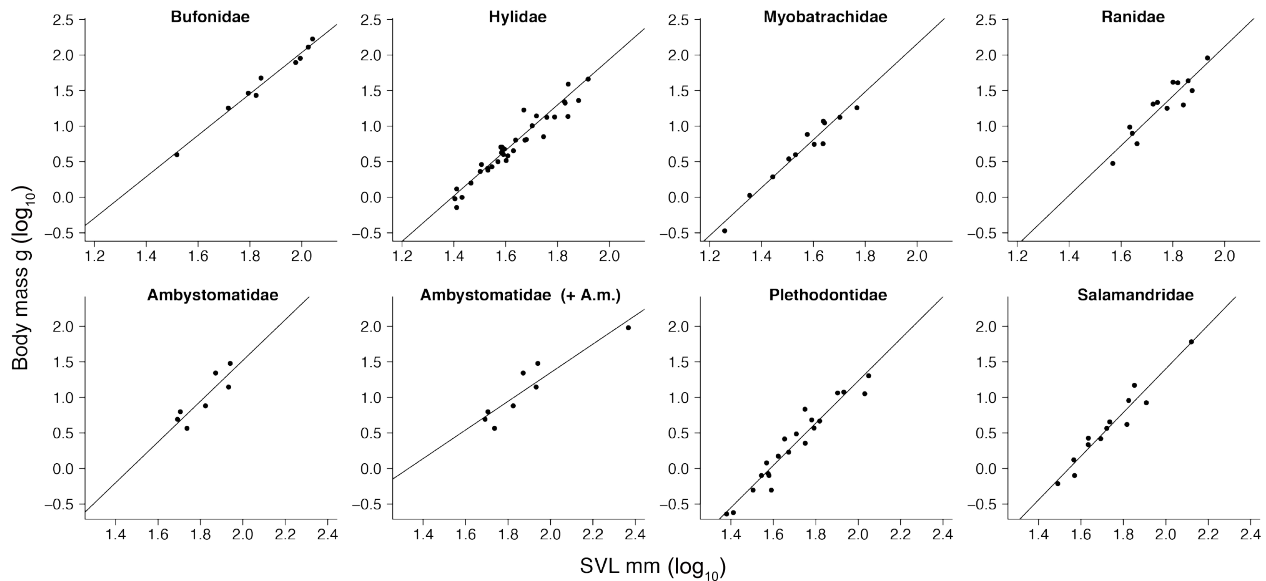


**Figure 1** Relationships between snout-to-vent length (SVL) and body mass for frogs (a) and salamanders (b).

**Table 3** Power laws for predicting body mass (g) from SVL (mm) for anurans, caudates and families with  $N \geq 5$ 

Taxon	Formula	Power law	Adjusted $R^2$	$n$	RMSE	MAPE
Anura	<i>Average model</i>	<i>A</i> : $10^{-4.328} \times SVL^{3.098}$ <i>SA</i> : $10^{-4.375} \times SVL^{3.215}$ <i>T</i> : $10^{-4.298} \times SVL^{3.181}$	0.949–0.966	88	0.119–0.150	17.969–31.010
Bufonidae	<i>M~SVL</i>	$10^{-3.791(\pm 0.275)} \times SVL^{2.914(\pm 0.148)}$	0.980	9	0.081	5.731
Hylidae	<i>M~SVL</i>	$10^{-4.462(\pm 0.236)} \times SVL^{3.201(\pm 0.141)}$	0.938	35	0.207	18.856
Myobatrachidae	<i>M~SVL</i>	$10^{-4.586(\pm 0.357)} \times SVL^{3.372(\pm 0.228)}$	0.952	12	0.128	13.206
Ranidae	<i>M~SVL</i>	$10^{-4.862(\pm 0.749)} \times SVL^{3.492(\pm 0.425)}$	0.847	13	0.179	12.100
Caudata	<i>M~SVL*P</i>	<i>nP</i> : $10^{-4.709(\pm 0.255)} \times SVL^{3.045(\pm 0.134)}$ <i>P</i> : $10^{-3.567(\pm 0.361)} \times SVL^{2.325(\pm 0.246)}$	0.940	46	0.278	44.792
Ambystomatidae	<i>M~SVL</i>	$10^{-4.215(\pm 1.265)} \times SVL^{2.867(\pm 0.696)}$	0.727	7	0.199	19.070
Ambystomatidae (+A.m.)	<i>M~SVL</i>	$10^{-2.677(\pm 0.629)} \times SVL^{2.012(\pm 0.332)}$	0.836	8	0.836	11.178
Plethodontidae	<i>M~SVL</i>	$10^{-4.706(\pm 0.322)} \times SVL^{2.968(\pm 0.189)}$	0.925	21	0.184	19.331
Salamandridae	<i>M~SVL</i>	$10^{-4.744(\pm 0.414)} \times SVL^{3.073(\pm 0.237)}$	0.933	13	0.176	26.382

All models' coefficients, associated standard errors and statistical significance are presented in Supplementary Table S7. A, arboreal; adj $R^2$ , adjusted  $R^2$ ; H, habitat preference; MAPE, mean absolute percentage error;  $n$ , sample size; P, paedomorphic; RMSE, root mean square error; SA, semi-aquatic and aquatic; SVL, snout-to-vent length; T, terrestrial.

**Figure 2** Relationships between snout-to-vent length (SVL) and body mass for families with  $N \geq 5$ . + A.m., dataset including the axolotl (*Ambystoma mexicanum*).

[Dodd 2010]) is necessary for some applications (Watanabe *et al.* 2005; Gibbons *et al.* 2006). In this work we developed allometric relationships that can be used for estimating body mass from SVL measurements. The al-

lometric models performed well both in terms of explained variance and forecasting errors, and can, therefore, provide reliable predictions for species for which average body mass measurements are unavailable. Our allo-

metric model for frogs provides predictions comparable to those derived from the model in Pough (1980). Specifically, the model developed by Pough (1980) provides similar predictions to our model on arboreal species at small SVLs, and similar to our model on semi-aquatic and terrestrial at larger SVLs (Fig. S5). In contrast, Pough's model for salamanders provides different results, consistently underestimating the mass of non-paedomorphic species, and overestimating the mass of paedomorphic species with SVL > 63 mm while underestimating the mass of larger paedomorphic species (Fig. S5).

Two main hypotheses (so-called similarity hypotheses) describe how anatomical structures would be affected by increasing body size (Schmidt-Nielsen 1984). The geometric similarity hypothesis predicts body length to scale with body mass to the power of 0.33, whereas the elastic similarity hypothesis predicts body length to scale with body mass to the power of 0.25. Our results seem to support the geometric similarity hypothesis better, but do not strictly conform to that, and are in line with previous length–mass allometries in vertebrates that generally range between 0.25 and 0.32 (Green 2001).

As expected, the relationship between SVL and body mass is somehow heterogeneous among frogs with different habitat preferences (Moen *et al.* 2013, 2016), with arboreal species being lighter than terrestrial and semi-aquatic species at a given SVL. Furthermore, body mass increases more rapidly with increasing SVL for terrestrial and semi-aquatic species, suggesting that for arboreal frogs limiting body mass is particularly important in larger species. These differences result in body mass estimates that vary by a factor of approximately 1.35–1.85 between arboreal and both semi-aquatic and terrestrial species (for an SVL range of 16–158 mm). Conversely, contrary to our predictions, we found only a slight difference between terrestrial and semi-aquatic species. In frogs, body length and body mass are key determinants of locomotor performance: longer body length is often associated with longer legs, and heavier body generally determines higher muscle mass and acceleration (Wassersug & Sperry, 1977; Ficetola & De Bernardi 2006). Overall, larger and heavier frogs tend to have better locomotor performance, and heavy body mass is not disadvantageous, even when taking into account leg length (Emerson 1978; Semlitsch *et al.* 1999; Ficetola & De Bernardi 2006). However, arboreal frogs often move on small branches, which may deform substantially under heavy loads (Astley *et al.* 2015). There-

fore, a limited body mass likely improves the possibility of movement in the tree canopy. Furthermore, after hopping, arboreal frogs often land by attaching with toes to small branches. Forces acting on toes at landing may be up to 14 times the mass of the animal (Bijma *et al.* 2016), and this might additionally impose limits to body mass. Conversely, these are probably less important for terrestrial and semi-aquatic frogs.

Contrary to our predictions, the allometric models for salamanders were not different between terrestrial and semi-aquatic species. As predicted, however, paedomorphic species exhibited lower slopes than non-paedomorphic species. This difference is likely associated with the restructuring of body morphology and anatomy taking place during metamorphosis (Brown & Cai 2007). Nonetheless, caution on the interpretation of this difference is needed as the number of paedomorphic species in our sample was low. A comparison between metamorphosed and paedomorphic adults in species with facultative pedomorphosis could shed light on these differences.

The allometric models for the individual families showed different coefficients, and generally better predictive performances, than models fitted across all families. Consequently, allometric relationships for families are preferable for predictions when possible. An exception is given by the Pelobatidae family (spade-foot toads), for which the predictive power was lower than that of models including all families. This is probably because Pelobatidae in our dataset had a very limited range of SVL variation (SVL range: 49–74 mm) that hampers obtaining relationships with high determination coefficients and predictive value.

The dataset supplemented with unpaired length–mass measurements allowed us to use information on a larger number of species and families, but increased the error associated with the models (Appendix S3). In fact, amphibians show strong intraspecific variation in body size, with differences among individuals within populations, and among populations within the species (Morrison & Hero 2003; Adams & Church 2008; Cvetković *et al.* 2009; Ficetola *et al.* 2010; Guo & Lu 2016). The better performance of the model based exclusively on paired measurements suggests that when analyzing macroecological relationships among morphological traits with high intraspecific variability, it is better to improve data quality at the expense of quantity.

Although our models showed consistently high predictive performance, the accuracy and the generality of the allometric relationships is limited by sample size,

especially in salamanders. For example, more complex models also including habitat might have been selected for salamanders if a sufficient sample size was provided. Similarly, within frogs, the three supported models suggest that both the intercepts and the slopes differ between semi-aquatic, terrestrial and arboreal species, however, due to the limited sample size, the most complex model was not supported (additive and interactive term for habitat). Therefore, although our models show good predictive performances, additional data on body mass for frogs and salamanders would contribute to develop even better allometric models, and, more importantly, to increase the number of families and species for which family-specific and species-specific models can be fitted (Deichmann *et al.* 2008). All data used for the modeling are available in the supplementary materials of this paper, providing a good basis for further data collection and studies on amphibians' morphometric measurements and their intra-specific variability.

The high predictive power of our models suggests that they can be used in macroevolutionary and macroecological analyses that require information on species body mass, especially when these data are not available for some species, or the available values do not seem to be representative of the species as coming from a few individuals. Predictions from our models allow estimating body masses that are comparable between frogs and salamanders, and between different morphotypes in frogs. Our models would clearly be inappropriate for predictions on single individuals, because body weight in a specific period strongly depends on the body condition of the animal. Nevertheless, they will provide a good approximation of the average mass of a species, provided that representative averages of the species SVL are available. In conclusion, our models can contribute to uniform conservation, macroecological and macroevolutionary analyses by employing a single measurement of body size that increases comparability among taxa and is more directly related to the underlying ecological processes for which it is used as a proxy.

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## REFERENCES

Adams DC, Church JO (2008). Amphibians do not fol-

- low Bergmann's rule. *Evolution (N. Y.)* **62**, 413–20.
- Arnett AE, Gotelli NJ (2003). Bergmann's rule in larval ant lions: Testing the starvation resistance hypothesis. *Ecological Entomology* **28**, 645–50.
- Ashton KG (2002). Do amphibian follow Bergmann's rule? *Canadian Journal of Zoology* **80**, 708–16.
- Astley HC, Haruta A, Roberts TJ (2015). Robust jumping performance and elastic energy recovery from compliant perches in tree frogs. *Journal of Experimental Biology* **218**, 3360–63.
- Bielby J, Cardillo M, Cooper N, Purvis A (2009). Modelling extinction risk in multispecies data sets: Phylogenetically independent contrasts versus decision trees. *Biodiversity and Conservation* **19**, 113–27.
- Bielby J, Cooper N, Cunningham AA, Garner TWJ, Purvis A (2008). Predicting susceptibility to future declines in the world's frogs. *Conservative Letters* **1**, 82–90.
- Bijma NN, Gorb SN, Kleinteich T (2016). Landing on branches in the frog *Trachycephalus resinifictrix* (Anura: Hylidae). *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* **202**, 267–76.
- Blackburn TM, Gaston KJ, Loder N (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distribution* **5**, 165–74.
- Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978). Relationships between body size and some life history parameters. *Oecologia* **37**, 257–72.
- Brown DD, Cai L (2007). Amphibian metamorphosis. *Development Biology* **306**, 20–33.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771–89.
- Burnham KP, Anderson DR (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Cardillo M, Mace GM, Jones KE *et al.* (2005). Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–41.
- Cooper N, Bielby J, Thomas GH, Purvis A (2008). Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* **17**, 211–21.
- Cvetković D, Tomašević N, Ficetola GF, Crnobrnja-Isailović J, Miaud C (2009). Bergmann's rule in amphibians: Combining demographic and ecological parameters to explain body size variation among populations in the common toad *Bufo bufo*. *Journal Zoo-*



- logical Systematics and Evolutionary Research* **47**, 171–80.
- Deichmann JL, Duellman WE, Bruce Williamson G (2008). Predicting biomass from snout–vent length in new world frogs. *Journal of Herpetology* **42**, 238–45.
- Diniz-Filho JAF, Bini LM, Bastos RP *et al.* (2004). Anurans from a local assemblage in central Brazil: Linking local processes with macroecological patterns. *Brazilian Journal of Biology* **64**, 41–52.
- Dodd CK (2010). *Amphibian Ecology and Conservation. A Handbook of Techniques*. Oxford University Press, Oxford.
- Emerson SB (1978). Allometry and jumping in frogs: Helping the twain to meet. *Evolution (N. Y.)* **32**, 551–64.
- Feldman A, Meiri S (2013). Length–mass allometry in snakes. *Biological Journal of the Linnean Society* **108**, 161–72.
- Ficetola GF, De Bernardi F (2006). Trade-off between larval development rate and post-metamorphic traits in the frog *Rana latastei*. *Evolutionary Ecology* **20**, 143–58.
- Ficetola GF, Scali S, Denoël M *et al.* (2010). Ecogeographical variation of body size in the newt *Triturus carnifex*: Comparing the hypotheses using an information-theoretic approach. *Global Ecology and Biogeography* **19**, 485–95.
- Gibbons JW, Winne CT, Scott DE *et al.* (2006). Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. *Conservative Biology* **20**, 1457–65.
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001). Effects of size and temperature on metabolic rate. *Science* **293**, 2248–51.
- Gittleman JL, Harvey PH (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology Sociobiology* **10**, 57–63.
- Green AJ (2001). Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology* **82**, 1473–83.
- Guo C, Lu X (2016). Lifestyle-based approaches provide insights into body size variation across environmental gradients in anurans. *Evolutionary Biology* **43**, 208–14.
- Harmon LJ, Losos JB, Jonathan Davies T *et al.* (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution (N. Y.)* **64**, 2385–96.
- Hendriks AJ, Willers, BJC, Lenders HJR, Leuven RSEW (2009). Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography (Cop.)* **32**, 929–42.
- Hillman SS, Drewes RC, Hedrick MS, Hancock TV (2014). Physiological vagility: Correlations with dispersal and population genetic structure of amphibians. *Physiological and Biochemical Zoology* **87**, 105–12.
- Hyndman R (2006). Another look at forecast-accuracy metrics for intermittent demand. *Foresight: The International Journal of Applied Forecasting* **4**, 43–6.
- Jenkins DG, Brescacin CR, Duxbury CV *et al.* (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography* **16**, 415–25.
- Kupfer A (2007). Sexual size dimorphism in amphibians: An overview. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford University Press, Oxford, pp. 50–59.
- Meiri S (2010). Length–weight allometries in lizards. *Journal of Zoology* **281**, 218–26.
- Meiri S, Dayan T (2003). On the validity of Bergmann’s rule. *Journal of Biogeography* **30**, 331–51.
- Moen DS, Irschick DJ, Wiens JJ (2013). Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology and performance across continents in frogs. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20132156.
- Moen DS, Morlon H, Wiens JJ (2016). Testing convergence versus history: Convergence dominates phenotypic evolution for over 150 million years in frogs. *Systematic Biology* **65**, 146–60.
- Olalla-Tárraga MA, Rodríguez MA (2007). Energy and interspecific body size patterns of amphibian faunas in Europe and North America: Anurans follow Bergmann’s rule, urodeles its converse. *Global Ecology and Biogeography* **16**, 606–17.
- Olson VA, Davies RG, Orme DL *et al.* (2009). Global biogeography and ecology of body size in birds. *Ecology Letters* **12**, 249–59.
- Orme D (2013). The caper package: Comparative analysis of phylogenetics and evolution in R. *R Package Version 0.5*, **2**, 1–36.
- Pagel MD, Harvey PH (1988). The taxon-level problem in evolution of mammalian brain size: facts and artifacts. *The American Naturalist* **132**, 344–59.
- Paradis E, Claude J, Strimmer K. (2004). APE: Analyses

- of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–90.
- Peters RH, Wassenberg K (1983). The effect of body size on animal abundance. *Oecologia* **60**, 89–96.
- Pough FH (1980). Advantages of ectothermy for tetrapods. *The American Naturalist* **115**, 92–112.
- Purvis A, Agapow PM, Gittleman JL, Mace GM (2000). Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328–30.
- Pyron RA (2014). Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Systematic Biology* **63**, 779–97.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from URL: <http://www.R-project.org/>.
- Revell LJ (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–23.
- Rodríguez MA, López-Sañudo IL, Hawkins BA (2006). The geographic distribution of mammal body size in Europe. *Global Ecology Biogeography* **15**, 173–81.
- Rohatgi A (2016). WebPlotDigitizer – Extract data from plots, images, and maps. v. 3.12. Available from URL: <http://arohatgi.info/WebPlotDigitizer>
- Santini L, Di Marco M, Visconti P, Daniele B, Luigi B, Rondinini C (2013). Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix, the Italian Journal of Mammalogy* **24**, 181–6.
- Schmidt-Nielsen K (1984). *Scaling: Why is Animal Size So Important?* Cambridge University Press, Cambridge.
- Semlitsch D, Pickle J, Parris MJ, Sage RD (1999). Jumping performance and short-term repeatability of newly metamorphosed hybrid and parental leopard frogs (*Rana sphenocephala* and *Rana blairi*). *Canadian Journal of Zoology* **77**, 748–54.
- Silva M (1998). Allometric scaling of body length: Elastic or geometric similarity in mammalian design. *Journal of Mammalogy* **79**, 20–32.
- Swihart RK, Slade NA, Bergstrom BJ, Swihart RK, Bergstrom BJ (1988). Relating body size to the rate of home range use in mammals. *Ecology* **69**, 393–9.
- Vidal-García M, Byrne PG, Roberts JD, Keogh JS (2014). The role of phylogeny and ecology in shaping morphology in 21 genera and 127 species of Australo-Papuan myobatrachid frogs. *Journal of Evolutionary Biology* **27**, 181–92.
- Vidal-García M, Keogh JS (2015). Convergent evolution across the Australian continent: Ecotype diversification drives morphological convergence in two distantly related clades of Australian frogs. *Journal of Evolutionary Biology* **28**, 2136–51.
- Vitt LJ, Caldwell JP (2013). *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Academic Press, USA.
- Wassersug R, Sperry D (1977). The relationships of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). *Ecology* **58**, 830–39.
- Watanabe S, Nakanishi N, Izawa M (2005). Seasonal abundance in the floor-dwelling frog fauna on Iriomote Island of the Ryukyu Archipelago, Japan. *Journal of Tropical Ecology* **21**, 85–91.
- White CR, Seymour RS (2003). Mammalian basal metabolic rate is proportional to body mass  $2/3$ . *PNAS* **100**, 4046–9.

## SUPPLEMENTARY MATERIALS

**Appendix S1** Variable transformation and parametric assumptions

**Appendix S2** Allometric models for males and females separately

**Appendix S3** Allometric models including both paired and unpaired measurements

**Appendix S4** Additional information on the models presented in the main text

**Appendix S5** Comparison with previous allometric models on amphibians

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