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3 **Running title:** Length–mass allometries in amphibians

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5 **Length–mass allometries in amphibians**

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20

21 **Abstract**22 Body mass is rarely recorded in amphibians, and other body measurements (e.g. snout
23 to vent length, SVL) are generally collected instead. However, length measurements,
24 when used as proxies of body mass in comparative analyses, are problematic if different
25 taxa and morphotypes are included. We developed allometric relationships to derive
26 body mass from SVL measurements. We fitted phylogenetic generalized least square
27 models for frogs (Anura) and salamanders (Caudata) and for several families separately.
28 We tested whether allometric relationships differed between species with different

29 habitat preferences and between morphs in salamanders. Models were fitted with SVL–
30 mass measurements for 88 frog and 42 salamander species. We assessed the predictive
31 performance of the models by cross-validation. Overall, the models showed high
32 explained variance and low forecasting errors. Models differed among semi-aquatic,
33 terrestrial and arboreal frogs, and between paedomorphic and non-paedomorphic
34 salamanders. Body mass estimates derived from our models allow for comparability of
35 studies on multiple taxa and can be used for testing theories built upon evolutionary and
36 ecological processes which are directly related to body mass.

37

38 **Key words:** Anura, body length, body mass, body size, body weight, Caudata, frog,
39 salamander, snout to vent length

40

41 **INTRODUCTION**

42 Body mass is a fundamental parameter in ecology, as it is related to several key
43 ecological features, such as species metabolic rates and energy intake (Gillooly *et al.*
44 2001; Brown *et al.* 2004), population abundance (Peters & Wassenberg 1983), dispersal
45 distance (Jenkins *et al.* 2007; Hillman *et al.* 2014) and reproductive output (Blueweiss
46 *et al.*, 1978). Among vertebrates, body mass is commonly recorded in birds and
47 mammals, whereas it is less often recorded in amphibians and reptiles (Meiri 2010;
48 Feldman & Meiri 2013). In amphibians, body mass is highly variable within the same
49 species, but can also vary in the same individual over short time frames. In fact, body
50 mass in amphibians depends on the level of hydration of the animal, the physiological
51 state, the content of the bladder and the cloaca, as well as the reproductive state in
52 females (Dodd 2010). As a consequence, amphibians' body masses are rarely reported
53 in ecological or taxonomic literature as compared to other morphometric measurements.
54 Among them, snout to vent length (SVL) is the most common measure of body size in
55 amphibians (Dodd 2010; Vitt & Caldwell 2013). As a result, while SVL is available for
56 many species, body mass data are sparse in the literature and only available for a
57 minority of species.

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

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

86 The development of length–mass allometric relationships for amphibians would
87 contribute to overcome the abovementioned issues. However, while length–mass
88 allometric relationships are available in scientific literature for a number of taxa (e.g.
89 Silva 1998; Meiri 2010; Feldman & Meiri 2013), to our knowledge the only available

90 allometric models for anurans and salamanders date back to the 1980s (Pough 1980).
91 These are based on a limited number of species (Anura: $n = 15$; Caudata: $n = 16$),
92 including multiple individuals for the same species while not controlling for
93 phylogenetic autocorrelation. In addition, the raw data used for these relationships were
94 never published; therefore, it is impossible to know the identity of the species
95 underlying these relationships. Finally, allometric models that are meant to be used for
96 predictions should be evaluated for prediction accuracy, yet this is rarely done.

97 In this study we developed allometric relationships in amphibians to derive body
98 mass from SVL measurements. We fitted different models for frogs and salamanders,
99 and tested whether the relationships were different among morphotypes (Moen *et al.*
100 2013; Moen *et al.* 2016) and between paedomorphic and non-paedomorphic species.
101 We hypothesized that:

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

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

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

117

118 **METHODS**

119 **Data collection**

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

145

146 **Analyses**

147 Data were log₁₀-transformed prior to the analyses to meet the assumptions of
148 normality, linearity and homoscedasticity of regression models (Suppl. Appendix S1).
149 We first ran a linear regression between SVL and body mass and tested the residuals for
150 Pagel’s λ . Pagel’s λ measures the phylogenetic autocorrelation, and ranges from 0 (no

151 phylogenetic autocorrelation) to 1 (phylogenetic autocorrelation as expected under
152 Brownian motion). Because Pagel's λ was always significantly higher than zero (Anura:
153 $\lambda = 0.873$, $P < 0.001$; Caudata: $\lambda = 0.486$, $P = 0.016$) we used a phylogenetic
154 generalized least square model (PGLS) to develop the allometric models based on the
155 phylogeny developed by Pyron (2014).

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

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

181 For each order, models were ranked using the AIC corrected for small sample
182 sizes (AICc) (Burnham & Anderson 2002). Models were compared using Akaike

183 weights (ω), indicating the relative weight of evidence of competitive models. Models
184 were considered unequivocally supported if $\omega > 0.9$. If no model showed unequivocal
185 support, we used model averaging, which produced model parameters that take into
186 account the uncertainty detected by the model selection procedure (Burnham &
187 Anderson 2002). The average model was calculated by taking the average of models'
188 coefficients weighted by the models' Akaike weights, and assuming a weight of zero for
189 the models in which a given variable was not included. We also calculated the relative
190 importance of variables, by summing the weights of all models including that variable.
191 Then for each family having $N \geq 5$, we ran a separate allometric model including only
192 SVL as a predictor because species belonging to the same family generally have the
193 same habitat preferences (see Suppl. Table S1). Because in the Ambystomatidae family
194 measurements for the Axolotl (*Ambystoma mexicanum*) were particularly influential on
195 the slope, we ran an additional model excluding the Axolotl.

196 We used a 5-fold cross-validation to test the accuracy of the allometric models
197 by splitting the dataset into training (random 80% of the data) and testing datasets
198 (remnant 20% of the data), where the former was used to fit the model, and the latter to
199 validate it. For each validation we calculated 2 forecasting error estimates: the root
200 mean square error (RMSE) and the mean absolute percentage error (MAPE). The
201 RMSE is a scale-dependent measure, in which the errors are squared before the average.
202 Therefore, the RMSE penalizes more large errors and it is more sensitive to outliers
203 than MAPE. Conversely, MAPE is scale-independent and provides an intuitive measure
204 for interpretation (Hyndman 2006). The cross-validation procedure was repeated 10
205 times and the forecasting errors averaged. For the allometric models for each family, we
206 used a jackknife cross-validation instead by removing 1 observation at a time. This was
207 necessary as the sample size of some families did not allow for conducting a 5-fold
208 cross-validation.

209 Our main analyses were limited to species for which paired measurements of
210 body mass and SVL were available from the same individuals. However, in
211 interspecific allometric models on traits and taxa for which a limited amount of data are
212 available, it is not unusual to derive data for the dependent and the independent
213 variables from separate sources to increase sample size and taxonomic coverage
214 (Gittleman & Harvey 1982; Pagel & Harvey 1988; Swihart *et al.* 1988; White &

215 Seymour 2003; Hendriks *et al.* 2009; Santini *et al.* 2013). Therefore, we repeated the
216 analyses presented in the main text using a larger dataset that also included mass–length
217 measurements collected from different sources for species for which paired
218 measurements were not available, and compared the results with those in the main text
219 (Suppl. Appendix S3).

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

222

223 **RESULTS**

224 Data were gathered from 207 different sources including peer-reviewed articles, PhD
225 and MSc theses, and specialized websites (see Suppl. Table S1). We found body mass
226 data on 190 frog species and 88 salamander species, but for 111 and 49 species only
227 paired SVL measurements calculated on the same individuals were available. Because
228 not all species in our datasets were included in the phylogeny, we excluded from the
229 analyses 23 species of frogs and 3 species of salamanders. The final dataset included 88
230 species of frogs and 46 species of salamanders. Frog species ranged between 15.99 and
231 262-mm SVL and 0.32 and 1907-g body mass, whereas salamanders ranged between
232 23.99 and 542-mm SVL and 0.23 and 912.7-g body mass.

233 In frogs, the best AICc model suggested an interactive effect between habitat
234 and SVL, but no model was unequivocally supported ($\omega > 0.9$) so we averaged all
235 models weighting by Akaike ω (Table 1). In the average model, the slope of the length–
236 mass relationship was steeper for semi-aquatic and terrestrial species than for arboreal
237 species, partly supporting our first prediction (Fig. 1). The importance of habitat as an
238 additive or interactive term was not very high (Table 2), yet the average model that
239 accounts for the weight of evidence of the models suggests different estimates (Table
240 3).

241 In salamanders, we found 1 highly supported model that included an additive
242 and an interaction term with the factor “paedomorphic” (Fig. 1, Table 1), in accordance
243 with our second prediction. Paedomorphic animals displayed a less steep relationship,
244 indicating longer and lighter bodies. The variance explained by the models was high
245 (adjusted $R^2 > 0.9$; Table 3). The models on frogs showed good predictive performances
246 with RMSE ranging between 0.12 and 0.15 and MAPE ranging between 17.97 and

247 31.01%. The supported model on salamanders had lower predictive performances with
248 RMSE = 0.28 and MAPE = 44.79% (Table 3). Complete model outputs are presented in
249 Supplementary Table S7.

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

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

261

262 **DISCUSSION**

263 Snout to vent length is the most frequently available morphometric measure reported for
264 amphibians (Dodd 2010; Vitt & Caldwell 2013), yet body mass (although variable
265 between populations and within individuals [Dodd 2010]) is necessary for some
266 applications (Watanabe *et al.* 2005; Gibbons *et al.* 2006). In this work we developed
267 allometric relationships that can be used for estimating body mass from SVL
268 measurements. The allometric models performed well both in terms of explained
269 variance and forecasting errors, and can, therefore, provide reliable predictions for
270 species for which average body mass measurements are unavailable. Our allometric
271 model for frogs provides predictions comparable to those derived from the model in
272 Pough (1980). Specifically, the model developed by Pough (1980) provides similar
273 predictions to our model on arboreal species at small SVLs, and similar to our model on
274 semi-aquatic and terrestrial at larger SVLs (Suppl. Fig. S5). In contrast, Pough's model
275 for salamanders provides different results, consistently underestimating the mass of
276 non-paedomorphic species, and overestimating the mass of paedomorphic species with
277 SVL > 63 mm while underestimating the mass of larger paedomorphic species (Suppl.
278 Fig. S5).

279 Two main hypotheses (so-called similarity hypotheses) describe how anatomical
280 structures would be affected by increasing body size (Schmidt-Nielsen 1984). The
281 geometric similarity hypothesis predicts body length to scale with body mass to the
282 power of 0.33, whereas the elastic similarity hypothesis predicts body length to scale
283 with body mass to the power of 0.25. Our results seem to support the geometric
284 similarity hypothesis better, but do not strictly conform to that, and are in line with
285 previous length–mass allometries in vertebrates that generally range between 0.25 and
286 0.32 (Green 2001).

287 As expected, the relationship between SVL and body mass is somehow
288 heterogeneous among frogs with different habitat preferences (Moen *et al.* 2013, 2016),
289 with arboreal species being lighter than terrestrial and semi-aquatic species at a given
290 SVL. Furthermore, body mass increases more rapidly with increasing SVL for
291 terrestrial and semi-aquatic species, suggesting that for arboreal frogs limiting body
292 mass is particularly important in larger species. These differences result in body mass
293 estimates that vary by a factor of approximately 1.35–1.85 between arboreal and both
294 semi-aquatic and terrestrial species (for an SVL range of 16–158 mm). Conversely,
295 contrary to our predictions, we found only a slight difference between terrestrial and
296 semi-aquatic species. In frogs, body length and body mass are key determinants of
297 locomotor performance: longer body length is often associated with longer legs, and
298 heavier body generally determines higher muscle mass and acceleration (Wassersug &
299 Sperry, 1977; Ficetola & De Bernardi 2006). Overall, larger and heavier frogs tend to
300 have better locomotor performance, and heavy body mass is not disadvantageous, even
301 when taking into account leg length (Emerson 1978; Semlitsch *et al.* 1999; Ficetola &
302 De Bernardi 2006). However, arboreal frogs often move on small branches, which may
303 deform substantially under heavy loads (Astley *et al.* 2015). Therefore, a limited body
304 mass likely improves the possibility of movement in the tree canopy. Furthermore, after
305 hopping, arboreal frogs often land by attaching with toes to small branches. Forces
306 acting on toes at landing may be up to 14 times the mass of the animal (Bijma *et al.*
307 2016), and this might additionally impose limits to body mass. Conversely, these are
308 probably less important for terrestrial and semi-aquatic frogs.

309 Contrary to our predictions, the allometric models for salamanders were not
310 different between terrestrial and semi-aquatic species. As predicted, however,

311 paedomorphic species exhibited lower slopes than non-paedomorphic species. This
312 difference is likely associated with the restructuring of body morphology and anatomy
313 taking place during metamorphosis (Brown & Cai 2007). Nonetheless, caution on the
314 interpretation of this difference is needed as the number of paedomorphic species in our
315 sample was low. A comparison between metamorphosed and paedomorphic adults in
316 species with facultative pedomorphosis could shed light on these differences.

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

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

335 Although our models showed consistently high predictive performance, the
336 accuracy and the generality of the allometric relationships is limited by sample size,
337 especially in salamanders. For example, more complex models also including habitat
338 might have been selected for salamanders if a sufficient sample size was provided.
339 Similarly, within frogs, the three supported models suggest that both the intercepts and
340 the slopes differ between semi-aquatic, terrestrial and arboreal species but, due to the
341 limited sample size, the most complex model was not supported (additive and
342 interactive term for habitat). Therefore, although our models show good predictive

343 performances, additional data on body mass for frogs and salamanders would contribute
344 to develop even better allometric models, and, more importantly, to increase the number
345 of families and species for which family-specific and species-specific models can be
346 fitted (Deichmann *et al.* 2008). All data used for the modeling are available in the
347 supplementary materials of this paper, providing a good basis for further data collection
348 and studies on amphibians' morphometric measurements and their intra-specific
349 variability.

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

364

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369

370 **REFERENCES**

- 371 Adams DC, Church JO (2008). Amphibians do not follow Bergmann's rule. *Evolution*
372 (N. Y). **62**, 413–20.
- 373 Arnett AE, Gotelli NJ (2003). Bergmann's rule in larval ant lions: Testing the starvation
374 resistance hypothesis. *Ecological Entomology* **28**, 645–50.

- 375 Ashton KG (2002). Do amphibian follow Bergmann's rule? *Canadian Journal of*
376 *Zoology* **80**, 708–16.
- 377 Astley HC, Haruta A, Roberts TJ (2015). Robust jumping performance and elastic
378 energy recovery from compliant perches in tree frogs. *Journal of Experimental*
379 *Biology* **218**, 3360–63.
- 380 Bielby J, Cardillo M, Cooper N, Purvis A (2009). Modelling extinction risk in
381 multispecies data sets: Phylogenetically independent contrasts versus decision
382 trees. *Biodiversity and Conservation* **19**, 113–27.
- 383 Bielby J, Cooper N, Cunningham AA, Garner TWJ, Purvis A (2008). Predicting
384 susceptibility to future declines in the world's frogs. *Conservative Letters* **1**, 82–
385 90.
- 386 Bijma NN, Gorb SN, Kleinteich T (2016). Landing on branches in the frog
387 *Trachycephalus resinifictrix* (Anura: Hylidae). *Journal of Comparative*
388 *Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* **202**,
389 267–76.
- 390 Blackburn TM, Gaston KJ, Loder N (1999). Geographic gradients in body size: A
391 clarification of Bergmann's rule. *Diversity and Distribution* **5**, 165–74.
- 392 Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978). Relationships
393 between body size and some life history parameters. *Oecologia* **37**, 257–72.
- 394 Brown DD, Cai L (2007). Amphibian metamorphosis. *Development Biology* **306**, 20–
395 33.
- 396 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004). Toward a metabolic
397 theory of ecology. *Ecology* **85**, 1771–89.
- 398 Burnham KP, Anderson DR (2002). *Model Selection and Multimodel Inference: A*
399 *Practical Information-Theoretic Approach*. Springer, New York.
- 400 Cardillo M, Mace GM, Jones KE *et al.* (2005). Multiple causes of high extinction risk
401 in large mammal species. *Science* **309**, 1239–41.
- 402 Cooper N, Bielby J, Thomas GH, Purvis A (2008). Macroecology and extinction risk
403 correlates of frogs. *Global Ecology and Biogeography* **17**, 211–21.
- 404 Cvetković D, Tomašević N, Ficetola GF, Crnobrnja-Isailović J, Miaud C (2009).
405 Bergmann's rule in amphibians: Combining demographic and ecological
406 parameters to explain body size variation among populations in the common toad

407 *Bufo bufo*. *Journal Zoological Systematics and Evolutionary Research* **47**, 171–80.

408 Deichmann JL, Duellman WE, Bruce Williamson G (2008). Predicting biomass from
409 snout–vent length in new world frogs. *Journal of Herpetology* **42**, 238–45.

410 Diniz-Filho JAF, Bini LM, Bastos RP *et al.* (2004). Anurans from a local assemblage in
411 central Brazil: Linking local processes with macroecological patterns. *Brazilian*
412 *Journal of Biology* **64**, 41–52.

413 Dodd CK (2010). *Amphibian Ecology and Conservation. A Handbook of Techniques*.
414 Oxford University Press, Oxford.

415 Emerson SB (1978). Allometry and jumping in frogs: Helping the twain to meet.
416 *Evolution (N. Y.)* **32**, 551–64.

417 Feldman A, Meiri S (2013). Length–mass allometry in snakes. *Biological Journal of the*
418 *Linnean Society* **108**, 161–72.

419 Ficetola GF, De Bernardi F (2006). Trade-off between larval development rate and
420 post-metamorphic traits in the frog *Rana latastei*. *Evolutionary Ecology* **20**, 143–
421 58.

422 Ficetola GF, Scali S, Denoël M *et al.* (2010). Ecogeographical variation of body size in
423 the newt *Triturus carnifex*: Comparing the hypotheses using an information-
424 theoretic approach. *Global Ecology and Biogeography* **19**, 485–95.

425 Gibbons JW, Winne CT, Scott DE *et al.* (2006). Remarkable amphibian biomass and
426 abundance in an isolated wetland: Implications for wetland conservation.
427 *Conservative Biology* **20**, 1457–65.

428 Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001). Effects of size and
429 temperature on metabolic rate. *Science* **293**, 2248–51.

430 Gittleman JL, Harvey PH (1982). Carnivore home-range size, metabolic needs and
431 ecology. *Behavioral Ecology Sociobiology* **10**, 57–63.

432 Green AJ (2001). Mass/length residuals: Measures of body condition or generators of
433 spurious results? *Ecology* **82**, 1473–83.

434 Guo C, Lu X (2016). Lifestyle-based approaches provide insights into body size
435 variation across environmental gradients in anurans. *Evolutionary Biology* **43**,
436 208–14.

437 Harmon LJ, Losos JB, Jonathan Davies T *et al.* (2010). Early bursts of body size and
438 shape evolution are rare in comparative data. *Evolution (N. Y.)* **64**, 2385–96.

439 Hendriks AJ, Willers, BJC, Lenders HJR, Leuven RSEW (2009). Towards a coherent
440 allometric framework for individual home ranges, key population patches and
441 geographic ranges. *Ecography (Cop.)* **32**, 929–42.

442 Hillman SS, Drewes RC, Hedrick MS, Hancock TV (2014). Physiological vagility:
443 Correlations with dispersal and population genetic structure of amphibians.
444 *Physiological and Biochemical Zoology* **87**, 105–12.

445 Hyndman R (2006). Another look at forecast-accuracy metrics for intermittent demand.
446 *Foresight: The International Journal of Applied Forecasting* **4**, 43–6.

447 Jenkins DG, Brescacin CR, Duxbury CV *et al.* (2007). Does size matter for dispersal
448 distance? *Global Ecology and Biogeography* **16**, 415–25.

449 Kupfer A (2007). Sexual size dimorphism in amphibians: An overview. In: Fairbairn
450 DJ, Blanckenhorn WU, Székely T, eds. *Sex, Size and Gender Roles: Evolutionary*
451 *Studies of Sexual Size Dimorphism*. Oxford University Press, Oxford, pp. 50–59.

452 Meiri S (2010). Length–weight allometries in lizards. *Journal of Zoology* **281**, 218–26.

453 Meiri S, Dayan T. (2003). On the validity of Bergmann’s rule. *Journal of Biogeography*
454 **30**, 331–51.

455 Moen DS, Irschick DJ, Wiens JJ (2013). Evolutionary conservatism and convergence
456 both lead to striking similarity in ecology, morphology and performance across
457 continents in frogs. *Proceedings of the Royal Society B: Biological Sciences* **280**,
458 20132156.

459 Moen DS, Morlon H, Wiens JJ (2016). Testing convergence versus history:
460 Convergence dominates phenotypic evolution for over 150 million years in frogs.
461 *Systematic Biology* **65**, 146–60.

462 Olalla-Tárraga MA, Rodríguez MA (2007). Energy and interspecific body size patterns
463 of amphibian faunas in Europe and North America: Anurans follow Bergmann’s
464 rule, urodeles its converse. *Global Ecology and Biogeography* **16**, 606–17.

465 Olson VA, Davies RG, Orme DL *et al.* (2009). Global biogeography and ecology of
466 body size in birds. *Ecology Letters* **12**, 249–59.

467 Orme D (2013). The caper package: Comparative analysis of phylogenetics and
468 evolution in R. *R Package Version 0.5*, **2**, 1–36.

469 Pagel MD, Harvey PH (1988). The taxon-level problem in evolution of mammalian
470 brain size: facts and artifacts. *The American Naturalist* **132**, 344–59.

471 Paradis E, Claude J, Strimmer K. (2004). APE: Analyses of phylogenetics and evolution
472 in R language. *Bioinformatics* **20**, 289–90.

473 Peters RH, Wassenberg K (1983). The effect of body size on animal abundance.
474 *Oecologia* **60**, 89–96.

475 Pough FH (1980). Advantages of ectothermy for tetrapods. *The American Naturalist*
476 **115**, 92–112.

477 Purvis A, Agapow PM, Gittleman JL, Mace GM (2000). Nonrandom extinction and the
478 loss of evolutionary history. *Science* **288**, 328–30.

479 Pyron RA (2014). Biogeographic analysis reveals ancient continental vicariance and
480 recent oceanic dispersal in amphibians. *Systematic Biology* **63**, 779–97.

481 R Core Team (2016). R: A language and environment for statistical computing. R
482 Foundation for Statistical Computing, Vienna, Austria. Available from URL:
483 <http://www.R-project.org/>.

484 Revell LJ (2012). Phytools: An R package for phylogenetic comparative biology (and
485 other things). *Methods in Ecology and Evolution* **3**, 217–23.

486 Rodríguez MA López-Sañudo, IL, Hawkins BA (2006). The geographic distribution of
487 mammal body size in Europe. *Global Ecology Biogeography* **15**, 173–81.

488 Rohatgi A (2016). WebPlotDigitizer – Extract data from plots, images, and maps. v.
489 3.12. Available at: (<http://aohatgi.info/WebPlotDigitizer>)
490

491 Santini L, Di Marco M, Visconti P, Daniele B, Luigi B, Rondinini C (2013). Ecological
492 correlates of dispersal distance in terrestrial mammals. *Hystrix, the Italian Journal*
493 *of Mammalogy* **24**, 181–6.

494 Schmidt-Nielsen K (1984). *Scaling: Why is Animal Size So Important?* Cambridge
495 University Press, Cambridge.

496 Semlitsch D, Pickle J, Parris MJ, Sage RD (1999). Jumping performance and short-term
497 repeatability of newly metamorphosed hybrid and parental leopard frogs (*Rana*
498 *sphenocephala* and *Rana blairi*). *Canadian Journal of Zoology* **77**, 748–54.

499 Silva M (1998). Allometric scaling of body length: Elastic or geometric similarity in
500 mammalian design. *Journal of Mammalogy* **79**, 20–32.

501 Swihart RK, Slade NA, Bergstrom BJ, Swihart RK, Bergstrom BJ (1988). Relating
502 body size to the rate of home range use in mammals. *Ecology* **69**, 393–9.

503 Vidal-García M, Byrne PG, Roberts JD, Keogh JS (2014). The role of phylogeny and

504 ecology in shaping morphology in 21 genera and 127 species of Australo-Papuan
505 myobatrachid frogs. *Journal of Evolutionary Biology* **27**, 181–92.

506 Vidal-García M, Keogh JS (2015). Convergent evolution across the Australian
507 continent: Ecotype diversification drives morphological convergence in two
508 distantly related clades of Australian frogs. *Journal of Evolutionary Biology* **28**,
509 2136–51.

510 Vitt LJ, Caldwell JP (2013). *Herpetology: An Introductory Biology of Amphibians and*
511 *Reptiles*. Academic Press, USA.

512 Wassersug R, Sperry D (1977). The relationships of locomotion to differential predation
513 on *Pseudacris triseriata* (Anura: Hylidae). *Ecology* **58**, 830–39.

514 Watanabe S, Nakanishi N, Izawa M (2005). Seasonal abundance in the floor-dwelling
515 frog fauna on Iriomote Island of the Ryukyu Archipelago, Japan. *Journal of*
516 *Tropical Ecology* **21**, 85–91.

517 White CR, Seymour RS (2003). Mammalian basal metabolic rate is proportional to
518 body mass $2/3$. *Proceedings of the National Academy of Science U S A* **100**, 4046–
519 9.

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521 **Supplementary Materials**

522 **Supplementary Appendix S1** Variable transformation and parametric assumptions

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

524 **Supplementary Appendix S3** Allometric models including both paired and unpaired
525 measurements

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

528 **Supplementary Appendix S5** Comparison with previous allometric models on
529 amphibians

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

AICc, Akaike information criterion corrected for small sample sizes; Δ AICc,

Taxon	Formula	AICc	Δ AICc	ω	Df	difference in AICc from the most supported model;
Anura	$M \sim SVL:H$	-129.201	0	0.532	4	ω , Akaike weights;
	$M \sim SVL+H$	-128.216	0.985	0.325	4	df, degrees of
	$M \sim SVL*H$	-126.567	2.634	0.142	6	freedom; H, habitat
	$M \sim SVL$	-116.141	13.060	0.001	2	preference; M,
Caudata	$M \sim SVL*P$	-25.831	0	0.925	4	mass; P,
	$M \sim SVL:P$	-20.304	5.527	0.058	3	paedomorphic;
	$M \sim SVL+P$	-16.672	9.159	0.009	3	SVL, snout-to-vent
	$M \sim SVL*H$	-14.000	11.831	0.002	4	length; :,
	$M \sim SVL:H$	-13.311	12.520	0.002	3	interaction term; *,
	$M \sim SVL$	-13.217	12.614	0.002	2	additive and
	$M \sim SVL+H$	-12.504	13.327	0.001	3	

interaction term.

Table 2 Variable importance estimate based on Akaike weights

SVL, snout-to-vent length.

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

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

All models' coefficients, associated standard errors and statistical significance are presented in Supplementary Table S7. A, arboreal; $\text{adj}R^2$, 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 legends

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

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*).