



**University of
Zurich** ^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2012

Dichotomy of eutherian reproduction and metabolism

Müller, Dennis W H ; Codron, D ; Werner, J ; Fritz, J ; Hummel, J ; Griebeler, E M ; Clauss, Marcus

DOI: <https://doi.org/10.1111/j.1600-0706.2011.19505.x>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-53694>

Journal Article

Accepted Version

Originally published at:

Müller, Dennis W H; Codron, D; Werner, J; Fritz, J; Hummel, J; Griebeler, E M; Clauss, Marcus (2012). Dichotomy of eutherian reproduction and metabolism. *Oikos*, 121(1):102-115.

DOI: <https://doi.org/10.1111/j.1600-0706.2011.19505.x>

1 **Dichotomy of eutherian reproduction and metabolism**

2

3 **Dennis W. H. Müller¹, Daryl Codron¹, Jan Werner², Julia Fritz³, Jürgen Hummel⁴, Eva**

4 **Maria Griebeler², Marcus Clauss^{1*}**

5

6 ¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich,

7 Winterthurerstr. 260, 8057 Zurich, Switzerland

8 ²Institute of Zoology, Department of Ecology, Johannes Gutenberg-University of Mainz,

9 55099 Mainz, Germany

10 ³Chair of Animal Nutrition and Dietetics, Department of Veterinary Sciences,

11 Schönleutnerstraße 8, 85764 Oberschleißheim, Germany

12 ⁴Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn,

13 Germany

14

15 *to whom correspondence should be addressed (mclauss@vetclinics.uzh.ch)

16

16 **Abstract**

17 How anatomical, physiological and ecological (life history) features scale with body mass is a
18 fundamental question in biology. There is an ongoing debate in the scientific literature
19 whether allometric scaling follows a universal pattern that can be described in a single model,
20 or differs between groups. However, recently some analyses were published demonstrating a
21 change in scaling across the body mass range: brain-size allometry of mammals indicates that
22 scaling follows a curvilinear pattern in double-logarithmic space, and a quadratic pattern in
23 double-logarithmic space was found in one of the largest physiological datasets, on basal
24 metabolic rate (MR) in mammals. Here, we analysed a variety of independent datasets on
25 anatomical, physiological and ecological characteristics in mammals, birds and reptiles to
26 answer the question whether the quadratic scaling is a universal biological law, or a pattern
27 unique to mammals. The pattern was present in mammalian basal and field MR, brain size,
28 and reproduction parameters, but neither in other organ allometries in mammals, nor in the
29 scaling of MR in birds and reptiles. However, the curvature was better explained by separate
30 allometric scaling of three different mammalian reproduction strategies: marsupials, and
31 eutherian mammals with one and with many offspring. The two latter strategies are
32 distributed unequally over the body mass range in eutherian mammals. Our findings show that
33 a quadratic model, as well as a traditional allometric model with a universal scaling exponent
34 (such as 0.67 or 0.75), may be inappropriate in mammals as they are a result of different
35 scalings within these three reproductive groups. We propose that the observed distribution
36 pattern is the result of the eutherian mammal clade's uniquely pronounced dichotomy of
37 reproductive strategies.

38

39 **Keywords:** basal metabolic rate, field metabolic rate, life history, metabolic theory of
40 ecology, brain size, expensive tissue hypothesis

41

41 The traditional concept has metabolism (metabolic rate, MR) scale allometrically to body
42 mass (M) as a power function

$$43 \quad MR = a M^b. \quad (1)$$

44 This equation becomes linear when log-transformed

$$45 \quad \log(MR) = \log(a) + b \log(M). \quad (2)$$

46 In the framework of a ‘metabolic theory of ecology’, other life history traits are linked to the
47 allometry of MR (Lovegrove 2000, Dodds et al. 2001, Brown et al. 2004, Glazier 2005, White
48 and Seymour 2005). Predictions of equation (1) have therefore been used extensively to
49 describe scaling relationships in biology and ecology. The allometric scaling exponent b is
50 usually between 0.67 and 0.75 in mammals, and its biological meaning is at the core of a
51 long-standing debate.

52 An expanding view is that b is not constant but varies depending on the M range of the
53 dataset (Lovegrove 2000, Dodds et al. 2001, Glazier 2005, White and Seymour 2005) or on
54 the taxonomic composition of the sample (Hayssen and Lacy 1985, Sieg et al. 2009, White et
55 al. 2009, Capellini et al. 2010). Recently, several research groups have suggested that
56 mammal basal MR (BMR) is non-linearly linked to M in log-log plots (double-logarithmic
57 space), and can be better described by a quadratic function (Clarke et al. 2010, Isaac and
58 Carbone 2010, Kolokotronis et al. 2010); actually, a better fit of a quadratic function had
59 already been described by Hayssen and Lacy (1985) but had received little attention.
60 Curvature arises because the allometric exponent b varies as a function of M on a logarithmic
61 scale, thus

$$62 \quad b(M) = b_1 + b_2 \log(M). \quad (3)$$

63 Substituting $b(M)$ for b in equation (1)

$$64 \quad MR = a (M)^{(b_1+b_2(\log(M)))}, \quad (4)$$

65 and log-transformation gives the quadratic function

$$66 \quad \log(MR) = \log(a) + b_1 \log(M) + b_2 (\log(M))^2. \quad (5)$$

67 Equation (4) reflects that the exponent term changes systematically with M
68 (Kolokotronis et al. 2010). In this approach the magnitude of the parameter estimates for a
69 and b_1 (but not b_2) depend on the unit of M; however, the full exponent term $[b_1 + b_2 \log(M)]$
70 is constant for a given M independent of the unit of M, and increases in a consistent manner
71 with M (Fig. 1b in Kolokotronis et al. 2010).

72 In relaxing the assumption of a fixed allometric exponent, quadratic approaches to
73 metabolic scaling have the potential to unravel new trends in the evolution of life history
74 traits. A convenient interpretation of the quadratic scaling pattern is that, as mammals become
75 smaller or larger than some hypothetical M mid-point, they both increase their MR beyond
76 the general simple power allometry. Bats – which we will use repeatedly as an example here –
77 appear to be one exception (of several) to that pattern, with lower BMR than many mammals
78 of similar M (Fig. 1a).

79 However, the finding of such a quadratic scaling in mammalian BMR (Kolokotronis
80 et al. 2010), but apparently not in birds, reptiles or fish (Isaac and Carbone 2010), raises the
81 question whether quadratic scaling is (1) a universal principle, and (2) whether it is a
82 physiologically relevant characteristic of mammals or an empirical yet ambiguous
83 characteristic of the mammal MR dataset. The recent finding of a similar nonlinear scaling of
84 mammalian brain mass in logarithmic space (though with an opposite curvature; Albrecht et
85 al. 2010) supports the notion that quadratic scaling might be a universal characteristic at least
86 within mammals. Here, we explore various datasets on anatomical, physiological and
87 ecological characteristics of organisms for their scaling patterns, demonstrate quadratic
88 scaling in a variety of mammalian datasets, and offer an explanation why this scaling pattern
89 probably does not represent a universal law but is an artefact typical for certain mammal
90 datasets, because it reflects different reproductive strategies that are represented by species of
91 different body mass ranges.

92

93 **Methods**

94 We analysed datasets (see Table 1 for sources) for BMR in mammals, birds and reptiles, as
95 well as datasets for field MR (FMR) for these three clades, and independent datasets on
96 mammal characteristics that are functionally linked with MR. We analysed datasets on
97 mammal organ masses (brain, heart, liver, kidney, lung, digestive tract), breathing frequency,
98 alveolar lung surface area, heart rate, produced offspring mass per year and female, and the
99 maximum population growth rate (r_{\max}). However, a major limitation of several of these
100 mammalian datasets is that the sample size is distinctively lower than that of the BMR dataset
101 (see Table 1), and that overlap of species covered between the datasets is limited.

102 All mass data, including body mass (M), were transformed to a kg-basis. Metabolic
103 rates were expressed as kJ d^{-1} . Log-transformed data were first subjected to least-squares
104 regression analysis considering a linear function (equation 2) and a quadratic function
105 (equation 5) using the Non-linear Estimation procedures of STATISTICA V8.0 (Gauss-
106 Newton method, 1000 iterations) (Statsoft_Inc 2007). When the fitting procedure converged
107 on significant parameter estimates for functions (95% confidence limits for b , or b_1 and b_2
108 exclude zero), we compared goodness-of-fit using the small-sample Akaiques Information
109 Criterion (AIC_c) (Burnham and Anderson 2002). We calculated the ΔAIC_c for each model
110 ($AIC_c - \min(AIC_c)$), and followed the evaluation process suggested by Burnham and
111 Anderson (2002): ΔAIC_c scores less than 2 imply well-supported models, scores between 2
112 and 10 imply moderate support, and a score > 10 indicates a weakly-supported model relative
113 to the alternative. Note that, as stated in the discussion, we do not hypothesize that the
114 curvature is a real biologically meaningful effect, but an artefact produced by a dichotomy in
115 reproductive strategies across the body size range in eutherian mammals.

116 To test our prediction, we used only those datasets in which quadratic scaling yielded
117 a better fit than the linear scaling in mammals. We divided the eutherians into two groups:
118 species with ≤ 1.5 offspring per year (single offspring) and those with > 1.5 offspring per year

119 (multiple offspring), based on information on the number of offspring (per year) from the
120 dataset on reproductive characteristics. This classification was used to avoid discussions about
121 differences between altricial and precocial status of offspring, and to remain consistent within
122 the dataset without adding information from other sources. The general linear and quadratic
123 regressions of the log-transformed data were additionally compared (again using AIC_c) to
124 models of separate, or composite, linear regressions for marsupials/monotremes and
125 eutherians, and for marsupials/monotremes and eutherian species with ≤ 1.5 and > 1.5
126 offspring per year.

127 In order to control for the effect of common ancestors, the two-step analyses of
128 mammal datasets were repeated using the Phylogenetic Generalized Least-Squares (PGLS)
129 approach (Pagel 1999, Freckleton et al. 2002) in which a well-developed standard statistical
130 method was extended to enable the inclusion of interdependencies among species due to a
131 shared evolutionary history. Phylogenetic relationships among species were inferred from the
132 mammal tree given by Bininda-Emonds et al. (2007). They were adapted to each dataset by
133 removal of species not included in the respective dataset from the overall mammal tree. PGLS
134 analyses for linear and quadratic models were conducted using Pagel's "lambda" Correlation
135 Structure (corPagel) in R (version 2.11.2) applying the packages ape (phylogeny) and nlme
136 (fitting of linear and non-linear models using generalized least squares; functions gls and
137 gnls). Since to our knowledge PGLS analysis cannot be conducted for composite regression
138 models, goodness-of-fit of models via AIC values could not be assessed to the same extent for
139 the PGLS analyses. However, in order to assess whether PGLS analyses supported a difference
140 in slopes between our different reproductive groups, we also analysed a linear model with an
141 intercept term for the reproductive groups and an interaction term (reproductive groups and
142 body mass) (Kabat et al. 2008).

143 Datasets for mammal and bird BMR are sufficiently large for further interrogation, to
144 test the robusticity of the statistical analyses. In particular, we explored the sensitivity of each

145 test on the size of a sample and the distribution of M within it (see supplement). For example,
146 if the quadratic regressions are an artefact of some datasets, then the significance of the
147 parameters (especially b_2) and goodness-of-fit relative to linear regressions would decline
148 with a (1) smaller sample, (2) a smaller range of M or (3) a M distribution that does not
149 extend above or below a threshold required for detection of such curvature. Also, derivation
150 of the quadratic function requires that the allometric scaling exponent (b) is linearly related to
151 M on a logarithmic scale, a condition we explicitly test for in these procedures. These
152 explorations should indicate the likelihood of (1) detecting spurious quadratic fits, and (2)
153 detecting instances where M distributions are insufficient for a significant polynomial fit, e.g.
154 in smaller datasets. We used randomized resampling of subsets of data to explore this
155 sensitivity in both regression functions. From the two datasets, random subsamples of 10 %,
156 25 %, 50 %, and 75 % of the data were extracted, the significance of their parameters
157 checked, and goodness-of-fits compared. For each subset we performed 3×10^4 permutations.
158 Significance (p -value) was calculated as the number of occurrences of a satisfied condition
159 (e.g. parameter confidence intervals exclude 0, significance of regression, lowest AIC_c score)
160 divided by the number of permutations. Randomization was carried out using the PopTools
161 v3.0.6 Add-in package for MS-Excel (Hood 2008).

162

163 **Results**

164 We found that a quadratic scaling provides a better fit to empirical data on BMR and FMR in
165 mammals (Fig. 1a,c; Tables 3 and 4), but not in reptiles (Fig. 1b,d; Table 2). When testing the
166 sensitivity of each test on the size of a sample and the distribution of M for mammalian basal
167 MR, we found that the significance of the polynomial term of the quadratic regression is only
168 evident when the M range is at least 4, possibly 5, orders of magnitude, and support for a
169 quadratic over a linear fit is reduced in smaller datasets, for example if the data do not include
170 species below 0.01 kg or above 1000 kg (results shown in Supplement). For birds, quadratic

171 scaling was not evident in the FMR dataset (Fig. 1d). For BMR, the quadratic scaling yielded
172 a significant regression for the entire avian dataset (Fig. 1b; Table 2); this effect was lost,
173 however, when smaller subsets were used for the analysis (see Supplement), indicating again
174 random significance of a quadratic fit.

175 For most mammalian anatomical and physiological datasets, no significant quadratic
176 scaling was found (see Supplement, Table S2). In contrast, brain size showed a negative
177 quadratic scaling (Fig. 2, Table 5), offspring mass showed a positive quadratic scaling (Fig. 3,
178 Table 6), and population growth rate (r_{\max}) again showed a negative quadratic scaling (Fig. 4,
179 Table 7). After controlling for phylogeny, the observed quadratic scaling was still significant
180 in BMR, FMR and brain mass, but not in offspring mass and r_{\max} (Tables 3-7).

181 When various approaches to explain the quadratic scaling by differences in simple
182 scaling patterns between the three reproductive mammal groups were tested with composite
183 linear regressions, solutions that considered marsupials and eutherians, and marsupials and
184 eutherians with single and multiple offspring separately, were always among the best-
185 supported models (Tables 3-7). The difference in AIC_c scores for quadratic compared with
186 best-supported composite linear models (i.e. ΔAIC_c) ranged from 11 to 833; for the field MR
187 data – the smallest dataset amongst those subjected to these tests – this difference barely
188 exceeded 2. Using PGLS, a composite approach cannot be assessed; however, a linear
189 approach with an interaction term for the reproductive groups was as supported as the
190 quadratic approach ($\Delta AIC_c < 2$) for BMR (Table 3), and was the best-supported model for
191 brain mass, offspring mass, and r_{\max} (Tables 5-7). With PGLS, the quadratic approach was the
192 best-supported model without alternative only for FMR (Table 4).

193 For BMR the analysis of raw data yielded significant differences in the scaling
194 exponent between the two eutherian groups (none of which differed significantly from the
195 marsupials). Eutherians with single offspring had a steeper allometric scaling at $M^{0.76}$ (95%CI
196 $^{0.74, 0.78}$) than eutherians with multiple offspring at $M^{0.69}$ (0.67, 0.71) (Table 3). The scaling of

197 offspring mass differed in the same direction, with $M^{0.80 (0.77, 0.83)}$ in eutherians with single
198 offspring and $M^{0.67 (0.62, 0.71)}$ in eutherians with multiple offspring (Table 6). Correspondingly,
199 the negative scaling of r_{\max} was steeper in eutherians with multiple offspring at $M^{-0.29 (-0.35, -$
200 $0.23)}$ than in eutherians with single offspring at $M^{-0.12 (-0.16, -0.09)}$ (Table 7). The scaling exponent
201 of brain mass did not differ significantly between the eutherian groups (overlapping 95% CI
202 from $M^{0.69}$ to $M^{0.72}$); however, the intercept (a) differed significantly between the groups, with
203 a higher level in eutherians with single offspring (Table 4) than in eutherians with multiple
204 offspring.

205

206 **Discussion**

207 The results indicate that some scaling occurs in mammals that can be described by the
208 quadratic model; depending on the dataset, this quadratic scaling is or is not significant after
209 correcting for the influence of phylogeny. The presence of quadratic scaling in both BMR and
210 FMR data supports the interpretation that this pattern is a true characteristic of mammals and
211 not a spurious finding of a particular dataset. However its absence in reptiles and birds (found
212 by Isaac and Carbone 2010 and corroborated by different datasets in this study) suggests that
213 this scaling pattern may not necessarily be universal. This, and the fact that quadratic scaling
214 was not evident in smaller subsets of the BMR data as detailed in the Supplement, indicates
215 that this scaling pattern might not be linked to a universal theory of resource distribution
216 networks (Savage et al. 2008, Kolokotronis et al. 2010). The repeated finding of quadratic
217 scaling indicates that fitting other than simple allometric equations to empirical data might be
218 a promising approach in comparative physiology. However, rather than just searching for an
219 equation with a higher fit, the choice of equations needs to be based on a theoretical
220 background. Because quadratic scaling does not appear to be universally supported in the
221 various datasets, being rejected either after controlling for phylogeny or when testing various
222 subsets of the data (see Supplement), assuming an effect of different scaling exponents (or

223 intercepts) for different functional groups is the most parsimonious approach. It appears that
224 quadratic scaling in these datasets – if it is detected – arises as an artefact of two different
225 simple scaling mechanisms that exist in varying predominance at different ranges of the M
226 spectrum of eutherians. Note that this is not only an effect of simply splitting the mammal
227 body size range in two distinct subunits: while the body mass range of eutherians with more
228 than one offspring is actually limited insofar as very large forms are excluded, the group of
229 eutherians with a single offspring comprises the full mammalian body size range (Fig. 1-4,
230 where bats are among those species included in the regression of eutherians with a single
231 offspring). This dichotomy may help explain why, when analysing mammal BMR data in
232 body size bins, there is little variation in the largest size classes but considerable variation in
233 the lower ones (Clarke et al. 2010) – where the two different reproductive modes coexist. For
234 these reasons, quadratic scaling should in our view be considered only as a tool for detecting
235 multiplicity in allometric exponents (or intercepts), but not necessarily for explaining overall
236 allometric relationships.

237 Morphological data (organ masses) and other physiological measurements did not
238 indicate a quadratic scaling. This could be attributed to their low sample size, but it should be
239 noted that low sample size did not prevent the general detection of a quadratic pattern in the
240 mammal field MR dataset. The only exception among the morphological measurements was
241 brain mass. The finding that brain mass shows a quadratic scaling pattern of opposite
242 curvature, i.e. with both very small and very large animals having lower brain masses than
243 predicted by a simple allometric regression, corroborates a recent identical finding by
244 Albrecht et al. (2010). The opposite direction of the curvature, and the difference in the
245 scaling pattern compared to that of the BMR or the offspring mass (with a difference in the
246 intercept a but not in the scaling exponent b), suggest that this general shape of brain mass
247 scaling cannot be explained by a direct link between brain mass and BMR. Actually, a variety
248 of strategies of both, the individual carrying a large brain or the mother producing the

249 offspring with a large brain, are currently considered important correlates of adult brain size,
250 with the level of BMR being just one among several parameters (Isler and van Schaik 2009,
251 Martin and Isler in press). Generally, there is a trade-off between the intensity of MR and the
252 time during which energy is invested in development (of brain tissue, for example) (Isler and
253 van Schaik 2009, Weisbecker and Goswami 2010, Martin and Isler in press).

254 The metabolic theory of ecology predicts a fundamental influence of MR on
255 ecological differences between species (Brown et al. 2004). Quadratic allometric scaling
256 might therefore be more evident in ecological than morphological parameters. In mammals,
257 reproductive strategies are closely linked to life history, for which large comparative datasets
258 are available (Duncan et al. 2007, Jones et al. 2009). The annual offspring mass per female
259 and the maximum population growth rate (a proxy for the number of surviving offspring) are
260 also better explained by a quadratic than by a simple power function in the raw data (Figs 3a
261 and 3b, Table 6 and 7). This means that for their respective M , very small and very large
262 mammals produce more offspring mass and more surviving offspring per unit time than
263 expected based on a simple allometric relationship (note that bats are again an exception, with
264 lower offspring mass than similar-sized small mammals - a possible adaptation to flight;
265 Hayssen and Kunz 1996). In particular, the similarity of the scaling exponents between BMR
266 and offspring mass in eutherians, and the reciprocal ranking of the BMR and the r_{\max} scaling
267 exponents, support some kind of functional link between BMR and these life history
268 parameters. On the other hand, the fact that curvature in the BMR dataset remained significant
269 when considering the evolutionary history of species, but not in the offspring mass or r_{\max}
270 datasets, could indicate that the two groups of characteristics are not as closely functionally
271 linked as proposed by metabolic theory. Alternatively, this could be the effect of differences
272 in the taxonomic composition of the datasets used, alone or in combination with the response
273 effect (e.g. offspring mass shows a dramatic dichotomy between eutherians and marsupials).
274 Further analyses are required to corroborate the link between BMR and life history.

275 In four of the five cases where quadratic scaling was detected in the raw data, a
276 combination of linear models taking into consideration the various mammalian reproduction
277 modes – marsupials, and eutherians with few and many offspring - provided a substantially
278 better fit to the data than a quadratic model (and indeed a linear model with universal scaling
279 exponent). Actually, there were different scaling relationships between the two reproductive
280 strategies in eutherians that combine to determine the shape of the overall relationship, but not
281 between each of the eutherian strategy and the marsupials. The difference in the scaling
282 exponent for BMR and offspring mass between single- and multiple-litter eutherians is
283 similar to those described for MR (Lovegrove 2000, Dodds et al. 2001, Glazier 2005, White
284 and Seymour 2005) between large and small mammals. A similar split of r_{\max} according to the
285 reproductive strategy (defined as the production of altricial or precocial offspring) was also
286 already described previously (Hennemann 1984); and again, a similar split is evident in data
287 on foetal growth between altricial and precocial mammals (Martin and MacLarnon 1985).

288 Further studies should aim at investigating scaling patterns for MR and other
289 morphological and physiological measurements not only on the basis of individual taxonomic
290 groups (such as e.g. by White et al. 2009), but on the basis of functional groups. Such an
291 approach allows to formulate hypotheses on the relationship of a functional adaptation and the
292 level of metabolism, and was widely used by McNab (2008, 2009), who concluded that BMR
293 in mammals and birds varied with natural diet, habitat, climate, the use of torpor, or the ability
294 to fly. Kolokotronis et al. (2010) found that even when all these factors were considered, a
295 quadratic scaling pattern still persisted in the mammal basal MR dataset. We propose this is
296 because the reproductive strategy – in terms of the number of offspring produced by
297 eutherians – was not among the factors they analysed. The fact that the reproductive strategy
298 was not included in previous studies must be considered a coincidence that should be
299 addressed in the future.

300 We conclude that the quadratic scaling inherent in various datasets confirms findings
301 that no common simple allometric scaling should be assumed as universal – neither for MR,
302 life history, nor morphophysiological measurements –, but indicates the existence of relevant
303 sub-groups that need to be investigated separately. We suggest that quadratic scaling in
304 metabolic rates is an artefact of different scaling laws in eutherian mammals with different
305 reproductive strategies, which are correlated to body size: the strategies to produce many
306 small offspring in many small (but no very large) species, or to produce few large offspring in
307 basically all large (and some small, including bats) species (Derrickson 1992). We propose
308 that the unique dichotomy of these strategies along the M gradient gives the eutherian MR
309 and life history curves their typical curvature shapes.

310 Our distinction of eutherians according to number of offspring somewhat resembles
311 the classification of precocial and altricial offspring. Martin and MacLarnon (1985) already
312 stated that the difference between precocial and altricial mammals was '*a particularly*
313 *convincing example of major allometric grade distinctions*'. However, there is an important
314 difference between classifying eutherians according to the precocial/altricial dichotomy and
315 the number of offspring produced. Bats represent one exceptional group of small mammals
316 (among several). Bat neonates are usually considered 'altricial'. Bats are, however, possibly
317 due to their adaptation to flight, limited in their number of offspring and might represent, so
318 to speak, allometric extrapolations to the low M range of the BMR, offspring mass and r_{\max}
319 patterns typical for large mammals that also only produce one offspring. This finding should
320 be corroborated in more detailed analyses; it could suggest that not only the precocial or
321 altricial state of the offspring itself, but more so its number may be an important physiological
322 characteristic between species.

323 Why is the strategy of having multiple offspring limited to the lower body size range?
324 Multiple offspring are mostly altricial, with few exceptions (Derrickson 1992); single
325 offspring are often precocial, with more exceptions. Simple reflections not correlated to

326 energetics could give ultimate explanations for why larger animals do not produce many
327 (altricial) offspring. For example, animals of large body size will have more difficulties in
328 hiding altricial young from potential predators; note that the largest altricial mammals are
329 mostly predators themselves that often use denning (bears) or cooperative breeding (other
330 carnivores). If such extrinsic or ecological factors were responsible for the observed pattern,
331 we would intuitively expect a scenario in which the production of multiple offspring is either
332 a) simply linked to the same offspring mass (and MR) with more but smaller
333 offspring, with identical slopes of the BMR or offspring mass scaling pattern
334 between eutherians of different litter size (Fig. 5a) or
335 b) linked to a consistently higher offspring mass (and MR) with parallel slopes
336 of the BMR or offspring mass scaling pattern between eutherians of different
337 litter size (Fig. 5b).

338 These patterns are both not consistent with the empirical data.

339 However, the similarity in scaling of MR and reproductive patterns also gives rise to
340 an ecophysiological, proximate explanation based on allometric scaling patterns. Given two
341 groups of animals with different levels of MR, we predict that the group with the higher MR
342 could outcompete the other because of its higher potential reproductive output (chapter 13 in
343 McNab 2002). The low M range, however, may offer animals with a comparatively low MR,
344 that produce less offspring mass, ample ecological niche space (with bats, as flyers, the
345 dramatic example; other blatant examples could be burrowing animals with their typically low
346 metabolism, (McNab 1966)). Thus, in the low M range, both reproductive strategies can occur
347 (Fig. 5c). Actually, the discussion about the differences between altricial and precocial
348 mammals appears to focus on the perceived ‘advantage’ of altricial species, for example in
349 terms of their higher potential for population growth, when compared to precocial mammals
350 *of similar size* (e.g. Hennemann 1984). Less attention has been drawn to the fact that the
351 different allometries of mammals with many and few offspring intersect at a certain M range,

352 and that above this intersection, mammals with few offspring will be at an advantage in terms
353 of MR, offspring mass, or population growth (Fig. 5c). In the high M range, where the
354 difference in MR between the reproductive strategies is reversed, animals with a single
355 offspring, and a steeper MR scaling, thus predominate. Niche space is less diverse for larger
356 animals, and animals with a reproductive strategy of multiple offspring, with their putatively
357 lower metabolism at high BM, therefore find no niches to support them in this M range (Fig.
358 5b). Evidently, the intersection should not be treated as a certain M point but as a range in
359 which some altricial mammals may adopt certain strategies, such as for example cooperative
360 breeding with or without breeding suppression (Creel and Creel 1991), to maintain high levels
361 of reproductive output.

362 These reflections raise the intriguing question why channelling resources to one single
363 offspring should allow a steeper scaling of MR than the production of multiple offspring. Is
364 this difference the effect of one physiological mechanism for all mammals, or a combination
365 of several different mechanisms, and why do these scaling relationships intersect at a certain
366 M range? Are scaling patterns within taxonomic and functional groups really best represented
367 by a linear (simple allometric) approach (regardless of differences in the scaling coefficient),
368 or do various scaling patterns coexist between such groups? Does the similarity in the scaling
369 of BMR and offspring mass reflect a causal relationship, or only the influence of a third
370 mechanism on both physiological measures? Do these scaling relationships differ in a relevant
371 way once body temperature effects are included in the analyses? All these questions clearly
372 warrant more detailed investigation. Whatever the reason for the difference in the scaling
373 patterns – these patterns also stimulate speculation about potential conceptual predominance
374 of large mammals over terrestrial birds and the only (many offspring-producing and
375 potentially endothermic) sauropsid group that reached equally large body sizes – the
376 dinosaurs.

377

378

Acknowledgements

379 We thank Barbara Schneider of the library of the Vetsuisse Faculty Zurich for her tireless
380 support in literature acquisition. This is contribution no. xx of the DFG Research Group 533
381 Biology of the Sauropod Dinosaurs: The Evolution of Gigantism.

382

References

- 384 Albrecht, G. H., Gelvin, B. R. and Miller, J. M. A. 2010. Complex curvilinear allometry of
385 brain size scaling in mammals. - *FASEB J.* 24: 642.
- 386 Andrews, R. M. and Pough, F. H. 1985. Metabolism of squamate reptiles: allometric and
387 ecological relationships. - *Physiol. Zool.* 58: 214-231.
- 388 Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D.,
389 Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. and Purvis, A. 2007. The delayed
390 rise of present-day mammals. - *Nature* 446: 507-512.
- 391 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. 2004. Towards a
392 metabolic theory of ecology. - *Ecology* 85: 1771-1789.
- 393 Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: A
394 practical information-theoretic approach. - Springer.
- 395 Capellini, I., Venditi, C. and Barton, R. A. 2010. Phylogeny and metabolic scaling in
396 mammals. - *Ecology* 91: 2783-2793.
- 397 Clarke, A., Rothery, P. and Isaac, N. J. B. 2010. Scaling of basal metabolic rate with body
398 mass and temperature in mammals. - *J. Anim. Ecol.* 79: 610-619.
- 399 Creel, S. R. and Creel, N. M. 1991. Energetics, reproductive suppression and obligate
400 communal breeding in carnivores. - *Behav. Ecol. Sociobiol.* 28: 263-270.
- 401 Crile, G. and Quiring, D. P. 1940. A record of the body weight and certain organ and gland
402 weights of 3690 animals. - *Ohio J. Sci.* 40: 219-259.
- 403 Derrickson, E. M. 1992. Comparative reproductive strategies of altricial and precocial
404 eutherian mammals. - *Funct. Ecol.* 6: 57-65.
- 405 Dodds, P. S., Rothman, D. H. and Weitz, J. S. 2001. Re-examination of the "3/4-law" of
406 metabolism. - *J. Theor. Biol.* 209: 9-27.
- 407 Duncan, R. P., Forsyth, D. M. and Hone, J. 2007. Testing the metabolic theory of ecology:
408 allometric scaling exponents in mammals. - *Ecology* 88: 324-333.
- 409 Fagan, W. F., Lynch, H. J. and Noon, B. R. 2010. Pitfalls and challenges of estimating
410 population growth rate from empirical data: consequences for allometric scaling relations.
411 - *Oikos* 119: 455-464.
- 412 Freckleton, R. P., Harvey, P. H. and Pagel, M. 2002. Phylogenetic analysis and comparative
413 data: a test and review of evidence. - *Am. Nat.* 160: 712-726.
- 414 Gehr, P., Mwangi, D. K., Amman, A., Maloiy, G. M. O., Taylor, C. R. and Weibel, E. R.
415 1981. Design of the mammalian respiratory system. V. Scaling morphometric pulmonary
416 diffusing capacity to body mass: wild and domestic mammals. - *Respir. Physiol.* 44: 61-
417 86.
- 418 Glazier, D. S. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific
419 scaling of metabolic rate in animals. - *Biol. Rev.* 80: 1-52.
- 420 Hayssen, V. and Kunz, T. H. 1996. Allometry of litter mass in bats: maternal size, wing
421 morphology, and phylogeny. - *J. Mammal.* 77: 476-490

422 Hayssen, V. and Lacy, R. C. 1985. Basal metabolic rates in mammals: taxonomic differences
423 in the allometry of BMR and body mass. - *Comp. Biochem. Physiol. A* 81: 741-754.
424 Hennemann, W. W. 1984. Intrinsic rates of natural increase of altricial and precocial
425 eutherian mammals: the potential price of precociality. - *Oikos* 43: 363-368.
426 Hood, G. M. 2008. PopTools v3.0.6. CSIRO Australia.
427 Isaac, N. J. B. and Carbone, C. 2010. Why are metabolic scaling exponents so controversial?
428 Quantifying variance and testing hypotheses. - *Ecol. Lett.* 13: 728-735.
429 Isler, K. and van Schaik, C. P. 2006. Metabolic costs of brain size evolution. - *Biol. Lett.* 2:
430 557-560.
431 Isler, K. and van Schaik, C. P. 2009. The expensive brain: a framework for explaining
432 evolutionary changes in brain size. - *J. Hum. Evol.* 57: 392-400.
433 Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D., Safi, K., Sechrest,
434 W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R.,
435 Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-
436 Emonds, O. R. P., Gittleman, J. L., Mace, G. M. and Purvis, A. 2009. PanTHERIA: a
437 species-level database of life history, ecology, and geography of extant and recently
438 extinct mammals. - *Ecology* 90: 2648 (Ecological Archives E090-184).
439 Kabat, A. P., Blackburn, T. M., McKechnie, A. E. and Butler, P. J. 2008. Phylogenetic
440 analysis of the allometric scaling of therapeutic regimes for birds. - *J. Zool.* 275: 359-367.
441 Kolokotronis, T., Savage, V. M., Deeds, E. J. and Fontana, W. 2010. Curvature in metabolic
442 scaling. - *Nature* 464: 753-756.
443 Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. - *Am. Nat.*
444 156: 201-219.
445 Mace, G. M., Harvey, P. H. and Clutton-Brock, T. H. 1981. Brain size and ecology in small
446 mammals. - *J. Zool.* 193: 333-354.
447 Martin, R. D. and Isler, K. in press. The maternal energy hypothesis of brain evolution: an
448 update. - In: Broadfield, D., Yuan, M., Toth, N. and Schick, K. (eds.), *The human brain*
449 *evolving: papers in honor of Ralph L. Holloway*. Stone Age Institute Press.
450 Martin, R. D. and MacLarnon, A. M. 1985. Gestation period, neonatal size and maternal
451 investment in placental mammals. - *Nature* 313: 220-223.
452 McNab, B. 1966. The metabolism of fossorial rodents: a study of convergence. - *Ecology* 47:
453 712-733.
454 McNab, B. K. 2002. *The physiological ecology of vertebrates. A view from energetics.* -
455 Cornell University Press.
456 McNab, B. K. 2008. An analysis of the factors that influence the level and scaling of
457 mammalian BMR. - *Comp. Biochem. Physiol. A* 151: 5-28.
458 McNab, B. K. 2009. Ecological factors affect the level and scaling of avian BMR. - *Comp.*
459 *Biochem. Physiol. A* 152: 22-45.
460 McNab, B. K. and Eisenberg, J. F. 1989. Brain size and its relation to the rate of metabolism
461 in mammals. - *Am. Nat.* 133: 157-167.
462 Mortolaa, J. P. and Lanthier, C. 2005. Breathing frequency in ruminants: a comparative
463 analysis with non-ruminant mammals. - *Respir. Physiol. Neurobiol.* 145: 265-277
464 Nagy, K. A., Girard, I. A. and Brown, T. K. 1999. Energetics of free-ranging mammals,
465 reptiles, and birds. - *Ann. Rev. Nutr.* 19: 247-277.
466 Noujaim, S. F., Lucca, E., Muñoz, V., Persaud, D., Berenfeld, O., Meijler, F. L. and Jalife, J.
467 2004. From mouse to whale - a universal scaling relation for the PR interval of the
468 electrocardiogram of mammals. - *Circulation* 110: 2802-2808.
469 Pagel, M. 1999. Inferring the historical patterns of biological evolution. - *Nature* 401: 877-
470 884.

471 Sacher, G. A. and Staffeldt, E. F. 1974. Relation of gestation time to brain weight for
472 placental mammals: implications for the theory of vertebrate growth. - *Am. Nat.* 108: 593-
473 615.

474 Savage, V. M., Deeds, E. J. and Fontana, W. 2008. Sizing up allometric scaling theory. -
475 *PLoS Comput. Biol.* 4: e1000171.

476 Savage, V. M. and West, G. B. 2007. A quantitative, theoretical framework for understanding
477 mammalian sleep. - *Proceedings of the National Academy of Science* 104: 1051-1056.

478 Sieg, A. E., O'Connor, M. P., McNair, J. N., Grant, B. W., Agosta, S. J. and Dunham, A. E.
479 2009. Mammalian metabolic allometry: do intraspecific variation, phylogeny, and
480 regression models matter? - *Am. Nat.* 174: 720-733.

481 Speakman, J. R. and Król, E. 2010. Maximal heat dissipation capacity and hyperthermia risk:
482 neglected key factors in the ecology of endotherms. - *J. Anim. Ecol.* 79: 726–746.

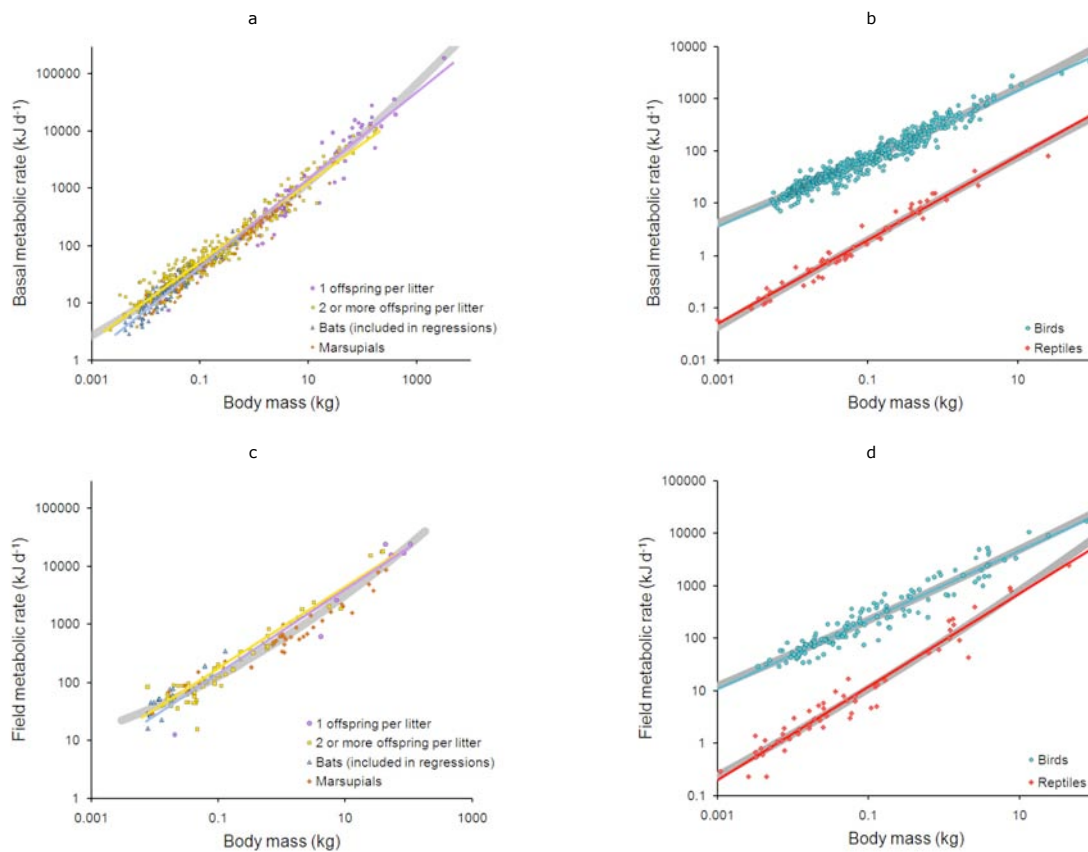
483 Statsoft_Inc. 2007. STATISTICA V8.0 (data analysis software system).

484 Weisbecker, V. and Goswami, A. 2010. Brain size, life history, and metabolism at the
485 marsupial/placental dichotomy. - *Proc. Nat. Acad. Sci.* 107: 16216-16221.

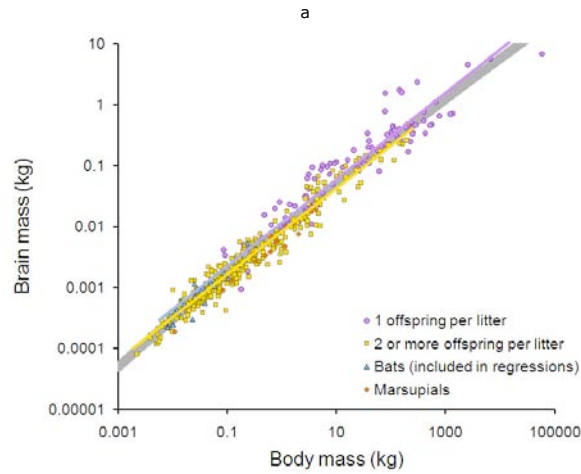
486 White, C. R., Blackburn, T. M. and Seymour, R. S. 2009. Phylogenetically informed analysis
487 of the allometry of mammalian basal metabolic rate supports neither geometric nor
488 quarter-power scaling. - *Evolution* 63: 2658-2667.

489 White, C. R. and Seymour, R. S. 2005. Allometric scaling of mammalian metabolism. - *J.*
490 *Exp. Biol.* 208: 1611-1619.

491
492
493

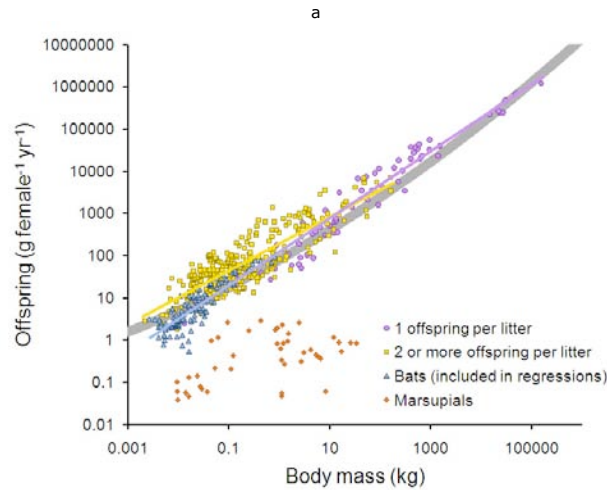


493
 494 **Figure 1** Relationship of body mass and basal metabolic rate in mammals of different
 495 reproductive strategies (a), birds and reptiles (b), and field metabolic rate in mammals of
 496 different reproductive strategies (c) and birds and reptiles (d). Linear regressions of the
 497 different reproductive groups (same colour as plots) as well as the curvature model for the
 498 whole dataset (grey shadow) are presented. For statistics, see Table 2, 3, and 4. Note that bats
 499 are included in the regression for eutherians with one offspring per litter.
 500



501
502
503
504
505
506

Figure 2 Relationship of body mass and brain mass in mammals of different reproductive strategies. Linear regressions of the different reproductive groups (same colour as plots) as well as the curvature model for the whole dataset (grey shadow) are presented. For statistics, see Table 5. Note that bats are included in the regression for eutherians with one offspring per litter.



508

509

510

511

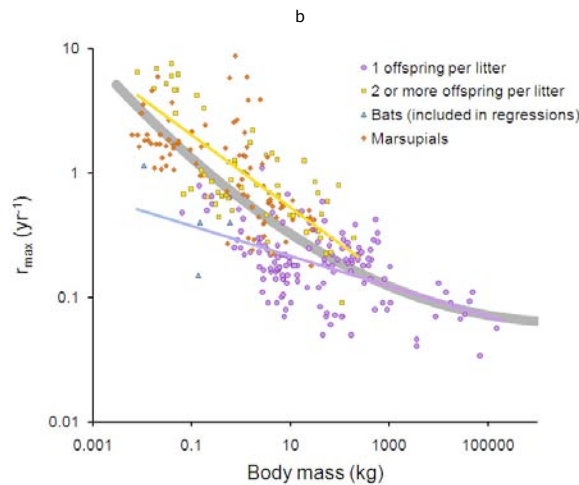
512

513

514

515

Figure 3 Relationship of body mass and mass of offspring per female and year in mammals of different reproductive strategies. Linear regressions of the different reproductive groups (same colour as plots) as well as the curvature model for the whole dataset (grey shadow) are presented. For statistics, see Table 6. Note that bats are included in the regression for eutherians with one offspring per litter.



516

517

518

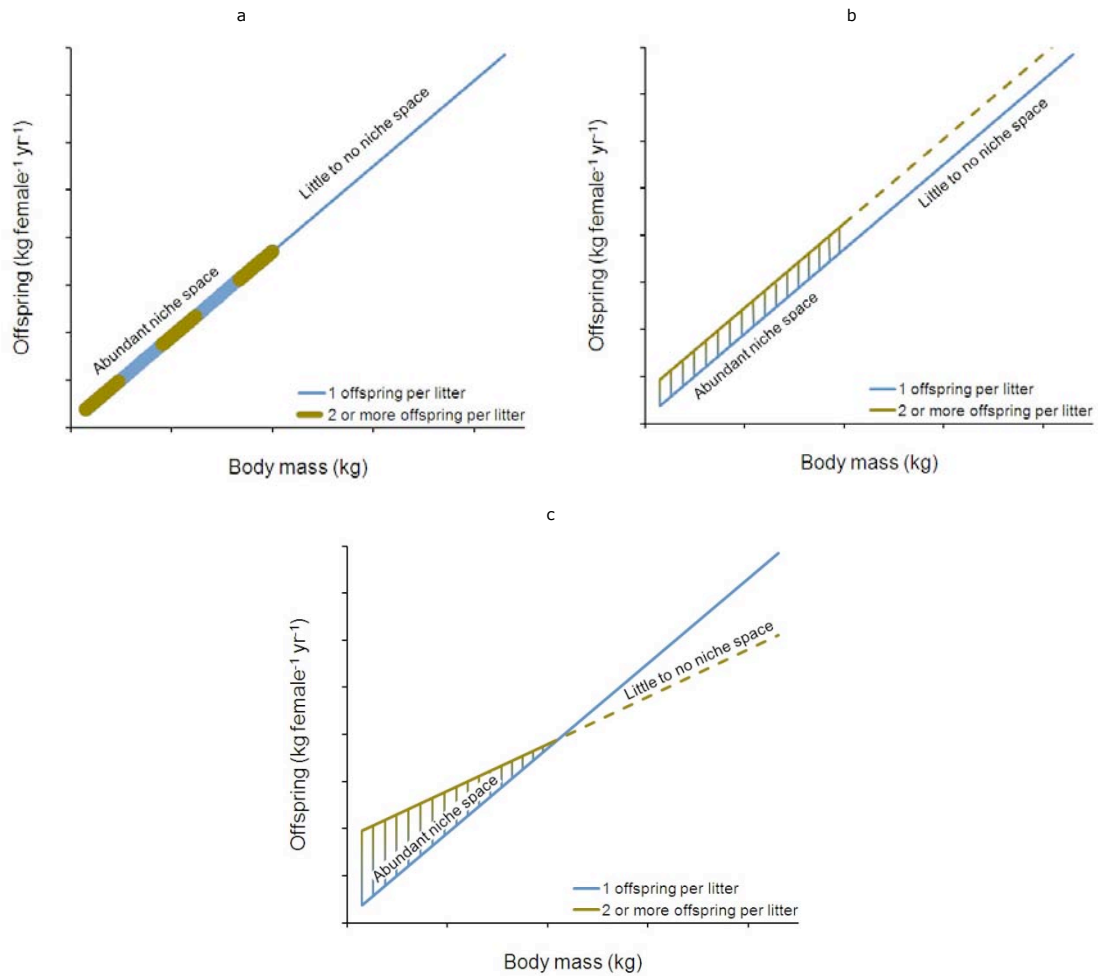
519

520

521

522

Figure 4 Relationship of body mass and r_{\max} per year in mammals of different reproductive strategies. Linear regressions of the different reproductive groups (same colour as plots) as well as the curvature model for the whole dataset (grey shadow) are presented. For statistics, see Table 7. Note that bats are included in the regression for eutherians with one offspring per litter.



523

524

525

526

527

528

529

530

531

532

Figure 5 Hypothetic models (a, b) and a model for the observed situation (c) of the relationship between body mass (M) and mass of offspring per year and female in eutherians of different reproductive strategies. Whereas in the small M range niche space is abundant and thus both reproductive strategies are present, niche space is less diverse for species in the high M range, and animals with a reproductive strategy of multiple offspring, with their putatively lower metabolism at high M , therefore find no niches.

Table 1. Datasets used for this study (n=number of species)

Trait	unit	Group	n	notes	Data source
Basal metabolic rate (BMR)	kJ d ⁻¹	Mammals	615		(McNab 2008)
		Birds	530		(McNab 2009)
		Reptiles	55	using only data for 20°C at rest	(Andrews and Pough 1985)
Field metabolic rate (FMR)	kJ d ⁻¹	Mammals	120	marine mammal data read from graph	(Speakman and Król 2010)
		Birds	130		
		Reptiles	55		(Nagy et al. 1999)
Heart mass			99		
Kidney mass			90		
Liver mass			93		(Crile and Quiring 1940)
Lung mass			93		
Gastrointestinal tract tissue mass	kg	Mammals	37		
Brain mass			450	using the respective older dataset if species occurred repeatedly in the total collection; correcting rodent data from Mace et al. (1981) by subtracting 0.59 g as described by Ister and van Schaik (2006)	(Crile and Quiring 1940, Sacher and Staffeldt 1974, Mace et al. 1981, McNab and Eisenberg 1989, Savage and West 2007)
Lung volume	ml	Mammals	33		(Gehr et al. 1981)
Lung alveolar surface area	m ²		33		
Breathing frequency	min ⁻¹	Mammals	56	excluding bovids as suggested by the authors	(Mortolaa and Lanthier 2005)
Heart rate			25		(Noujaim et al. 2004)
Offspring mass	kg female ⁻¹ yr ⁻¹	Mammals	521		(Jones et al. 2009)
Population growth rate (r _{max})	yr ⁻¹	Mammals	291	note that this dataset has been criticized recently by Fagan et al. (2010); note, however, that the shape of scaling in the data compilations of these authors (Fig. 2a and c of their paper) indicates a similar quadratic scaling	(Duncan et al. 2007)

534 Table 2. Comparison of linear (L) and quadratic (Q) regressions of basal (BMR) and field (FMR) metabolic rate in birds and reptiles.

	<i>n</i>	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	AIC _c	ΔAIC _c
BMR									
<i>Birds</i>									
Linear (<i>a+b₁M</i>)	530	2.4962	2.4778, 2.5147	0.6508	0.6370, 0.6647			-2235.01	3.70
Quadratic (<i>a+b₁M+b₂M²</i>)	530	2.4983	2.4799, 2.5168	0.6821	0.6530, 0.7112	0.0183	0.0033, 0.0333	-2238.71	0.00
<i>Reptiles</i>									
Linear (<i>a+b₁M</i>)	55	0.9029	0.8090, 0.9969	0.8010	0.7607, 0.8413			-	-
Quadratic (<i>a+b₁M+b₂M²</i>)	55	0.8415	0.7116, 0.9713	0.7163	0.5855, 0.8471	-0.0220	-0.0542, 0.0103	-	-
FMR									
<i>Birds</i>									
Linear (<i>a+b₁M</i>)	130	3.0091	2.9635, 3.0547	0.6582	0.6243, 0.6922			-	-
Quadratic (<i>a+b₁M+b₂M²</i>)	130	3.0029	2.9536, 3.0523	0.6719	0.6181, 0.7257	0.0109	-0.0222, 0.0439	-	-
<i>Reptiles</i>									
Linear (<i>a+b₁M</i>)	55	1.9571	1.8597, 2.0544	0.8879	0.8289, 0.9469			-	-
Quadratic (<i>a+b₁M+b₂M²</i>)	55	1.9441	1.8432, 2.0450	0.9320	0.8249, 1.0391	0.0254	-0.0261, 0.0768	-	-

AIC_c are only presented when both linear and quadratic model are significant

535
536

536 Table 3. Comparison of various models relating body mass (M, kg) to basal metabolic rate (kJ d⁻¹) in mammals (n=615) for raw data and under
 537 PGLS analyses. Best supported models are highlighted by grey shading.

Model	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	<i>b</i> ₃	95% CI	AIC _c	ΔAIC _c
Raw data										
Linear (<i>a</i> + <i>b</i> ₁ <i>M</i>)	2.3839	2.3685, 2.3992	0.7188	0.7069, 0.7307					-2217.18	59.44
Quadratic (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>M</i> ²)	2.3401	2.3211, 2.3590	0.7326	0.7205, 0.7446	0.0320	0.0233, 0.0406			-2265.79	10.83
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> ₁ <i>M</i>)	m 2.2856 e 2.3979	2.2465, 2.3246 2.3820, 2.4137	0.7214	0.7097, 0.7331					-2243.34	33.27
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e</i>} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m 2.2871 e 2.3976	2.2444, 2.3298 2.3815, 2.4137	m 0.7250 e 0.7211	0.6831, 0.7670 0.7089, 0.7333					-2241.36	35.26
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e,L=1</i>} <i>M</i> + <i>b</i> _{<i>e,L>1</i>} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m 2.2871 e 2.3863	2.2457, 2.3286 2.3703, 2.4023	m 0.7250 eL=1 0.7596 eL>1 0.6925	0.6843, 0.7658 0.7426, 0.7767 0.6776, 0.7074					-2276.62	0.00
Composite (<i>a</i> _{<i>e,L=1</i>} + <i>a</i> _{<i>e,L>1</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e,L=1</i>} <i>M</i> + <i>b</i> _{<i>e,L>1</i>} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m 2.2871 eL=1 2.3861 eL>1 2.3864	2.2456, 2.3286 2.3602, 2.4121 2.3660, 2.4068	m 0.7250 eL=1 0.7596 eL>1 0.6925	0.6843, 0.7658 0.7420, 0.7772 0.6762, 0.7088					-2274.58	2.04
Composite (<i>a</i> + <i>b</i> _{<i>e,L=1</i>} <i>M</i> + <i>b</i> _{<i>e,L>1</i>} <i>M</i>)	2.3743	2.3587, 2.3898	eL=1 0.7533 eL>1 0.6948	0.7361, 0.7706 0.6801, 0.7096					-2238.91	37.70
PGLS										
Linear (<i>a</i> + <i>b</i> ₁ <i>M</i>)	2.2480	2.0526, 2.4434	0.7312	0.7136, 0.7488					-819.04	7.20
Quadratic (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>M</i> ²)	2.2359	2.0452, 2.4266	0.7375	0.7197, 0.7553	0.0140	0.0050, 0.0230			-826.24	0.00
Linear with interaction (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>R</i> + <i>b</i> ₃ (<i>M</i> * <i>R</i>))	2.3822	2.0983, 2.4629	0.6557	0.6618, 0.7265	-0.0044	-0.0093, 0.0314	0.0193	0.0049, 0.0337	-824.46	1.78

538 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

539 Parameters *a*, *b*₁, *b*₂ correspond with function (2) and function (5), respectively, of the main text

540

540 Table 4. Comparison of various models relating body mass (M, kg) to field metabolic rate in mammals (n=120) for raw data and under PGLS
 541 analyses. Best supported models are highlighted by grey shading.

Model	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	<i>b</i> ₃	95% CI	AIC _c	ΔAIC _c
Raw data										
Linear ($a+b_1M$)	2.8220	2.7817, 2.8624	0.6698	0.6382, 0.7014					-383.62	16.17
Quadratic ($a+b_1M+b_2M^2$)	2.7456	2.6920, 2.7991	0.6976	0.6649, 0.7304	0.0564	0.0286, 0.0843			-396.98	2.81
Composite ($a_e+a_m+b_1M$)	m 2.7441 e 2.8699	2.6811, 2.8070 2.9205, 2.9193	0.6860	0.6538, 0.7182					-391.10	8.69
Composite ($a_e+a_m+b_eM+b_mM$)	m 2.7428 e 2.8929	2.6824, 2.8033 2.8435, 2.9423	m 0.5927 e 0.7146	0.5289, 0.6565 0.6793, 0.7499					-399.79	0.00
Composite ($a_e+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m 2.7428 e 2.9002	2.6825, 2.8031 2.8497, 2.9506	m 0.5927 eL=1 0.6957 eL>1 0.7348	0.5291, 0.6563 0.6503, 0.7411 0.6881, 0.7815					-399.38	0.41
Composite ($a_{e,L=1}+a_{e,L>1}+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m 2.7428 eL=1 2.9193 eL>1 2.8896	2.6824, 2.8033 2.8345, 3.0040 2.8265, 2.9527	m 0.5927 eL=1 0.7008 eL>1 0.7293	0.5289, 0.6565 0.6518, 0.7499 0.6784, 0.7801					-397.49	2.30
Composite ($a+b_{e,L=1}M+b_{e,L>1}M$)	2.8291	2.7864, 2.8718	eL=1 0.6551 eL>1 0.6859	0.6122, 0.6979 0.6413, 0.7306					-382.56	17.23
PGLS										
Linear ($a+b_1M$)	2.7604	2.4982, 3.0226	0.6966	0.6539, 0.7393					-68.61	3.59
Quadratic ($a+b_1M+b_2M^2$)	2.7199	2.4651, 2.9747	0.7119	0.6680, 0.7558	0.0396	0.0069, 0.0723			-72.20	0.00
Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$)	2.8807	2.6032, 3.1582	0.6848	0.5895, 0.7801	-0.0423	-0.1157, 0.0311	0.0073	-0.0331, 0.0476	-66.24	5.96

542 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

543 Parameters a , b_1 , b_2 correspond with function (2) and function (5), respectively, of the main text

544

544 Table 5. Comparison of various models relating body mass (M, kg) to brain mass (kg) in mammals (n=450) for raw data and under PGLS analyses.
 545 Best supported models are highlighted by grey shading.

Model	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	<i>b</i> ₃	95% CI	AIC _c	ΔAIC _c
Raw data										
Linear ($a+b_1M$)	-2.0388	-2.0580, -2.0195	0.7299	0.7158, 0.7440					-1434.66	38.63
Quadratic ($a+b_1M+b_2M^2$)	-2.0192	-2.0455, -1.9929	0.7344	0.7198, 0.7490	-0.0097	-0.0187, -0.0008			-1437.18	36.10
Composite ($a_e+a_m+b_1M$)	m e -2.1796 -2.0328	-2.2727, -2.0865 -2.0523, -2.0134	0.7301	0.7161, 0.7441					-1441.82	31.47
Composite ($a_e+a_m+b_eM+b_mM$)	m e -2.1716 -2.0329	-2.2718, -2.0713 -2.0524, -2.0134	m e 0.7633 0.7298	0.6098, 0.9168 0.7158, 0.7439					-1439.98	33.30
Composite ($a_e+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m e -2.1716 -2.0346	-2.2719, -2.0712 -2.0572, -2.0120	m eL=1 eL>1 0.7633 0.7322 0.7274	0.6097, 0.9170 0.7112, 0.7531 0.7058, 0.7489					-1438.01	35.27
Composite ($a_{e,L=1}+a_{e,L>1}+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m eL=1 eL>1 -2.1716 -1.9443 -2.0864	-2.2679, -2.0752 -1.9802, -1.9083 -2.1136, -2.0592	m eL=1 eL>1 0.7633 0.7117 0.7023	0.6157, 0.9109 0.6906, 0.7328 0.6802, 0.7245					-1473.28	0.00
Composite ($a+b_{e,L=1}M+b_{e,L>1}M$)	-2.0411	-2.0634, -2.0189	eL=1 eL>1 0.7332 0.7264	0.7121, 0.7543 0.7049, 0.7480					-1432.81	40.48
PGLS										
Linear ($a+b_1M$)	-2.1066	-2.3704, -1.8428	0.6330	0.6105, 0.6555					-464.14	10.10
Quadratic ($a+b_1M+b_2M^2$)	-2.0937	-2.3581, -1.8293	0.6360	0.6133, 0.6587	-0.0108	-0.0202, -0.0014			-467.21	7.03
Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$)	-2.1834	-2.4346, -1.9321	0.5675	0.5260, 0.6089	0.0283	-0.0003, 0.0568	0.0316	0.0138, 0.0495	-474.24	0.00

546 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

547 Parameters a , b_1 , b_2 correspond with function (2) and function (5), respectively, of the main text

548

549

549 Table 6. Comparison of various models relating body mass (M, kg) to offspring mass (kg female⁻¹ year⁻¹) mass in mammals (n=521) for raw data
 550 and under PGLS analyses. Best supported models are highlighted by grey shading.

Model	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	<i>b</i> ₃	95% CI	AIC _c	ΔAIC _c
Raw data										
Linear (<i>a</i> + <i>b</i> ₁ <i>M</i>)	1.9977	1.9240, 2.0714	0.6899	0.6406, 0.7392					-255.55	838.07
Quadratic (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>M</i> ²)	1.9110	1.8142, 2.0079	0.6711	0.6202, 0.7220	0.0336	0.0090, 0.0581			-260.74	832.88
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> ₁ <i>M</i>)	m -0.2060 e 2.2177	-0.3283, -0.0838 2.1775, 2.2578	0.7224	0.6967, 0.7482					-933.42	160.20
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e</i>} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m -0.3488 e 2.2330	-0.4679, -0.2297 2.1953, 2.2708	m 0.2625 e 0.7464	0.1542, 0.3708 0.7217, 0.7712					-1000.41	93.21
Composite (<i>a</i> _{<i>e</i>} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e</i>,<i>L</i>=1} <i>M</i> + <i>b</i> _{<i>e</i>,<i>L</i>>1} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m -0.3488 e 2.1793	-0.4603, -0.2372 2.1418, 2.2168	m 0.2625 eL=1 0.8127 eL>1 0.6157	0.1611, 0.3640 0.7850, 0.8404 0.5777, 0.6536					-1067.40	26.22
Composite (<i>a</i> _{<i>e</i>,<i>L</i>=1} + <i>a</i> _{<i>e</i>,<i>L</i>>1} + <i>a</i> _{<i>m</i>} + <i>b</i> _{<i>e</i>,<i>L</i>=1} <i>M</i> + <i>b</i> _{<i>e</i>,<i>L</i>>1} <i>M</i> + <i>b</i> _{<i>m</i>} <i>M</i>)	m -0.3488 eL=1 2.0783 eL>1 2.2774	-0.4575, -0.2401 2.0263, 2.1303 2.2261, 2.3286	m 0.2625 eL=1 0.8015 eL>1 0.6656	0.1637, 0.3614 0.7742, 0.8288 0.6244, 0.7069					-1093.62	0.00
Composite (<i>a</i> + <i>b</i> _{<i>e</i>,<i>L</i>=1} <i>M</i> + <i>b</i> _{<i>e</i>,<i>L</i>>1} <i>M</i>)	1.9574	1.8795, 2.0352	eL=1 0.7409 eL>1 0.5960	0.6815, 0.8003 0.5169, 0.6751					-262.31	831.31
PGLS										
Linear (<i>a</i> + <i>b</i> ₁ <i>M</i>)	2.0814	1.5873, 2.5755	0.7219	0.6825, 0.7613					148.47	4.49
Quadratic (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>M</i> ²)	2.0751	1.5814, 2.5688	0.7219	0.6825, 0.7613	0.0046	-0.0111, 0.0203			149.60	5.62
Linear with interaction (<i>a</i> + <i>b</i> ₁ <i>M</i> + <i>b</i> ₂ <i>R</i> + <i>b</i> ₃ (<i>M</i> * <i>R</i>))	-1.510	-2.1291, -1.0330	0.5806	0.5026, 0.6587	-0.0364	-0.0992, 0.0264	0.0340	0.0014, 0.0667	143.99	0.00

551 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

552 Parameters *a*, *b*₁, *b*₂ correspond with function (2) and function (5), respectively, of the main text

553

554 Table 7. Comparison of linear various models relating body mass (M, kg) to population growth rate (r_{\max}) in mammals (n=291) for raw data and
 555 under PGLS analysis. Best supported models are highlighted by grey shading.

Model	<i>a</i>	95% CI	<i>b</i> or <i>b</i> ₁	95% CI	<i>b</i> ₂	95% CI	<i>b</i> ₃	95% CI	AIC _c	ΔAIC _c
Raw data										
Linear ($a+b_1M$)	-0.1784	-0.2208, -0.1360	-0.2620	-0.2885, -0.2356					-634.08	129.49
Quadratic ($a+b_1M+b_2M^2$)	-0.2109	-0.2559, -0.1660	-0.3041	-0.3382, -0.2699	0.0234	0.0110, 0.0358			-645.62	117.96
Composite ($a_e+a_m+b_1M$)	m e -0.0428 -0.2662	-0.1111, 0.0255 -0.3203, -0.2121	-0.2312	-0.2596, -0.2029					-655.09	108.49
Composite ($a_e+a_m+b_eM+b_mM$)	m e -0.0391 -0.2631	-0.1098, 0.0317 -0.3194, -0.2067	m e -0.2196 -0.2342	-0.2829, -0.1562 -0.2659, -0.2024					-653.20	110.38
Composite ($a_e+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m e -0.0391 -0.2700	-0.1098, 0.0316 -0.3277, -0.2123	m eL=1 eL>1 -0.2196 -0.2266 -0.2701	-0.2829, -0.1562 -0.2612, -0.1920 -0.3429, -0.1972					-652.31	111.27
Composite ($a_{e,L=1}+a_{e,L>1}+a_m+b_{e,L=1}M+b_{e,L>1}M+b_mM$)	m eL=1 eL>1 -0.0391 -0.5460 0.0173	-0.0974, 0.0192 -0.6127, -0.4794 -0.0507, 0.0853	m eL=1 eL>1 -0.2196 -0.1219 -0.2925	-0.2718, -0.1673 -0.1554, -0.0883 -0.3527, -0.2324					-763.57	0.00
Composite ($a+b_{e,L=1}M+b_{e,L>1}M$)	eL=1 eL>1 -0.1879	-0.2369, -0.1390	eL=1 eL>1 -0.2539 -0.2803	-0.2876, -0.2202 -0.3341, -0.2266					-632.64	130.94
PGLS										
Linear ($a+b_1M$)	-0.1167	-0.5142, 0.2808	-0.2149	-0.2547, -0.1751					-89.23	34.59
Quadratic ($a+b_1M+b_2M^2$)	-0.1277	-0.5230, 0.2676	-0.2282	-0.2735, -0.1829	0.0089	-0.0060, 0.0238			-88.59	35.23
Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$)	0.2627	-0.0773, 0.6027	-0.3249	-0.4103, -0.2396	-0.1724	-0.2246, -0.1202	0.0581	0.0238, 0.0923	-123.82	0.00

556 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

557 Parameters a , b_1 , b_2 correspond with function (2) and function (5), respectively, of the main text

558

559 **Online supplement**

560

561 **Table S1.** Sensitivity of linear (L) and quadratic (Q) scaling to sample size, from regressions562 fitted to 3×10^4 random subsamples derived from the mammal and bird basal MR datasets.

Total n	% of dataset extracted	n per subsample	Model	Mean R^2	Mean AIC	$p(a)$	$p(b \text{ or } b_1)$	$p(b_2)$	$p(\text{best-fit})$
Mammals									
637	10	64	L	0.9576	-112.310	<0.0001	<0.0001		0.4988
			Q	0.9601	-112.851	<0.0001	<0.0001	0.4218	0.5012
	25	159	L	0.9577	-285.089	<0.0001	<0.0001		0.6077
			Q	0.9606	-287.871	<0.0001	<0.0001	0.0650	0.3923
	50	319	L	0.9578	-569.115	<0.0001	<0.0001		0.9994
			Q	0.9608	-579.596	<0.0001	<0.0001	0.0002	0.0006
	75	478	L	0.9578	-854.634	<0.0001	<0.0001		
			Q	0.9609	-871.320	<0.0001	<0.0001	<0.0001	<0.0001
Birds									
530	10	53	L	0.9405	-109.481	<0.0001	<0.0001		0.0952
			Q	0.9403	-107.878	<0.0001	<0.0001	0.8585	0.9048
	25	133	L	0.9411	-277.165	<0.0001	<0.0001		0.1718
			Q	0.9414	-275.973	<0.0001	<0.0001	0.7579	0.8282
	50	265	L	0.9413	-556.608	<0.0001	<0.0001		0.2674
			Q	0.9417	-555.990	<0.0001	<0.0001	0.6258	0.7326
	75	398	L	0.9414	-836.061	<0.0001	<0.0001		0.3749
			Q	0.9418	-835.938	<0.0001	<0.0001	0.4183	0.6251

This table shows that a linear allometric fit and its parameters remain significant irrespective of the size and M range of the sample, but the parameter b_2 of a quadratic fit becomes less significant at smaller sample sizes. Accordingly, in smaller datasets, the relative strength of quadratic over linear models is likely to be lost, even in cases where b_2 retains its significance.

Birds are an extreme example: in the whole dataset, a quadratic function provides a slightly better fit compared with a linear function, but this preference rapidly subsides, as does the significance of the polynomial term, in smaller data subsets.

These results suggest that sample size may influence statistical power, particularly of quadratic regressions, when comparing linear with non-linear scaling in allometry. We demonstrate below that these effects of sample size are, however, not entirely an effect of reduced statistical power, but are more likely influenced by the range of M included in a dataset.

563

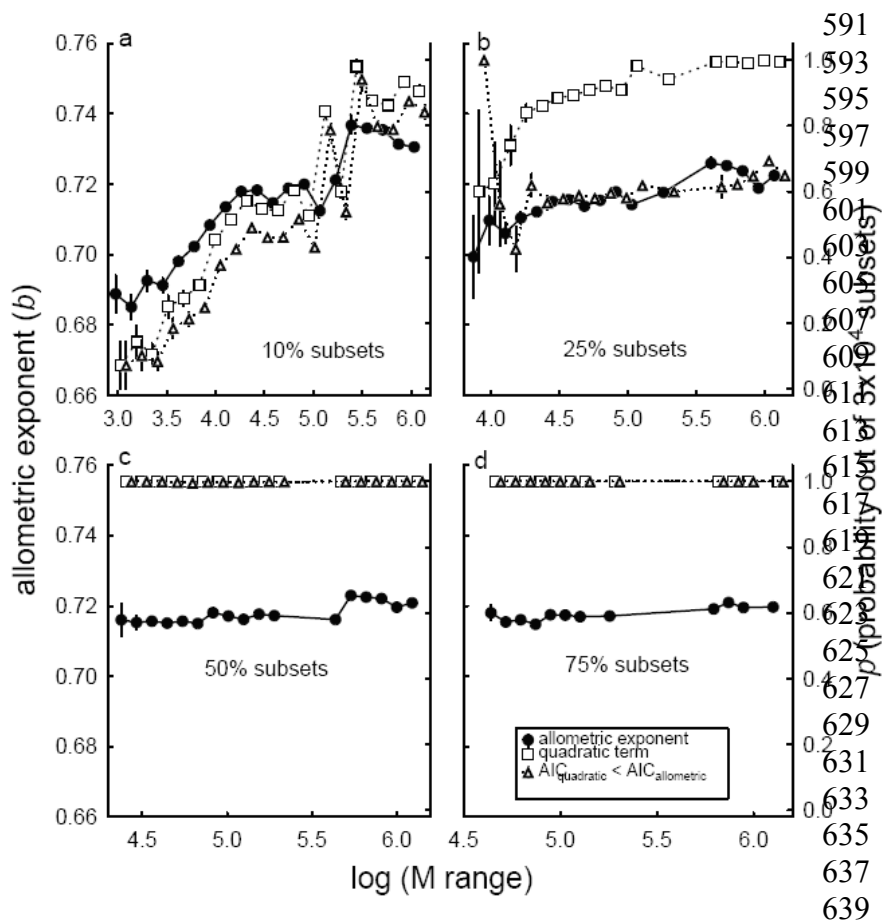
563 The figures below show the influence of body mass (M) distributions on linear and quadratic
564 fits. M distributions were manipulated in the mammal (Part 1) and bird (Part 2) basal MR
565 datasets by random resampling. We explore the effect of M range and mean M, and of the
566 minimum and maximum M point included in a dataset, on three statistics related to a
567 comparison of linear (L) with quadratic (Q) scaling: significance of the allometric exponent
568 (b), significance of the polynomial term (b_2), and the evidence to support a better fit of Q to L
569 (lower AIC score for Q). The mean \pm 1 standard error for each of these statistics, derived
570 from 3×10^4 permutations, are shown.

571
572 In both datasets, the parameters a , b and b_1 for the respective equations were consistently
573 significant, but the polynomial term b_2 was not. In mammals, a linear increase of b_1 with M
574 on a logarithmic scale is evident (Fig. S1.2a), and is a condition supporting that any curvature
575 in allometry solves to a quadratic polynomial (equations 3-5 in the main text). However,
576 significance of the polynomial term is only evident when the M range is at least 4, possibly 5,
577 orders of magnitude (Fig. S1.1b), and this condition may be missing in smaller datasets.
578 Similarly, whereas the polynomial term and quadratic fit is unanimously favored for mammal
579 BMR in larger datasets, this support is reduced in smaller datasets, for example if the data do
580 not include species below $\log(M) \approx -2.0$ (i.e. 0.01 kg, or 10 g; Fig. S1.3a), or excludes species
581 above $\log(M) \approx 3.0$ (i.e. 1000 kg; Fig. S1.4a). In summary, larger datasets are likely to
582 include a wide range of M, from where quadratic scaling would be evident, but in datasets
583 excluding species < 0.01 kg and/or > 1000 kg, quadratic scaling is unlikely to be detected.
584 This indicates that quadratic scaling is an artefact of changes in allometry at the extreme ends
585 of the M range. For birds, similar rules for the detection of quadratic scaling could be found:
586 simply, scaling appears to be linear except in the entire dataset, strongly indicating a spurious
587 result for the significance of a quadratic fit.

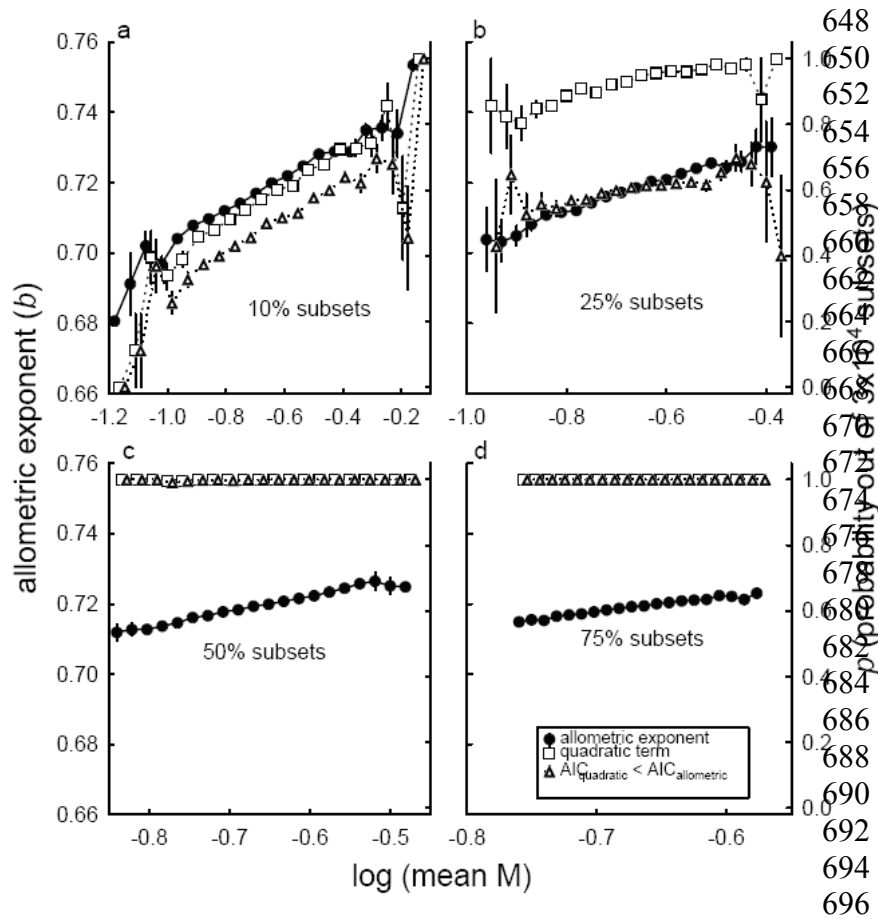
588

588 **Supplementary figures Part 1: Mammal BMR**

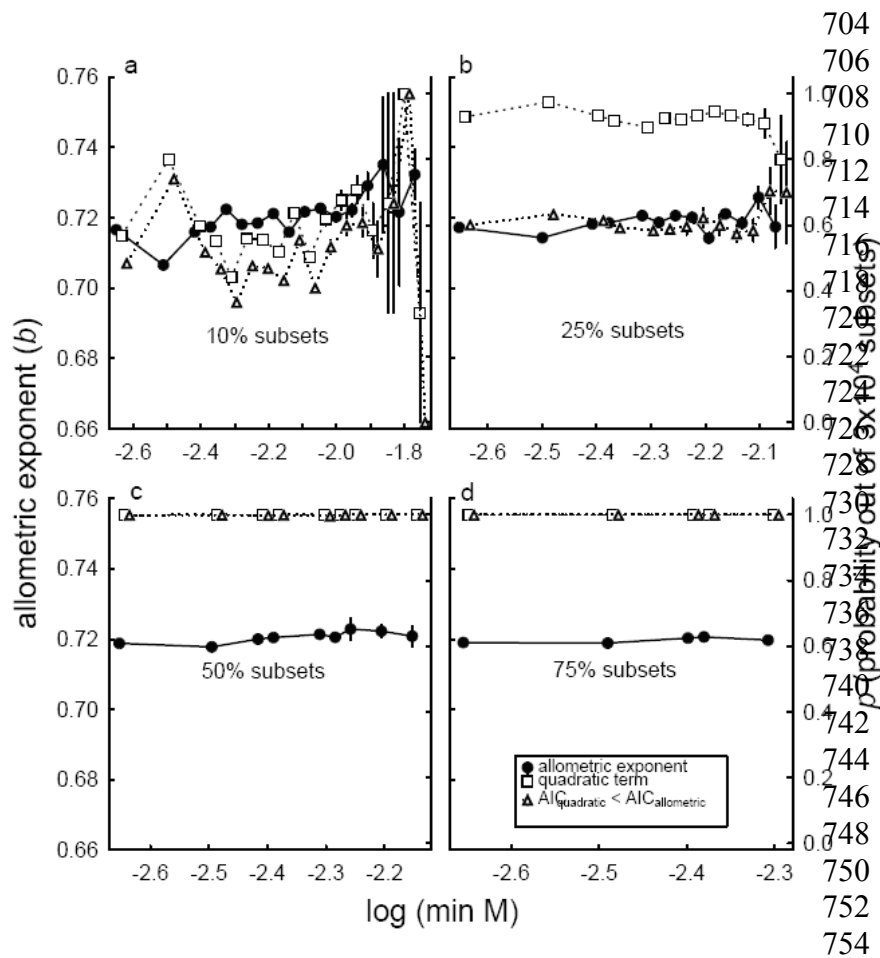
589



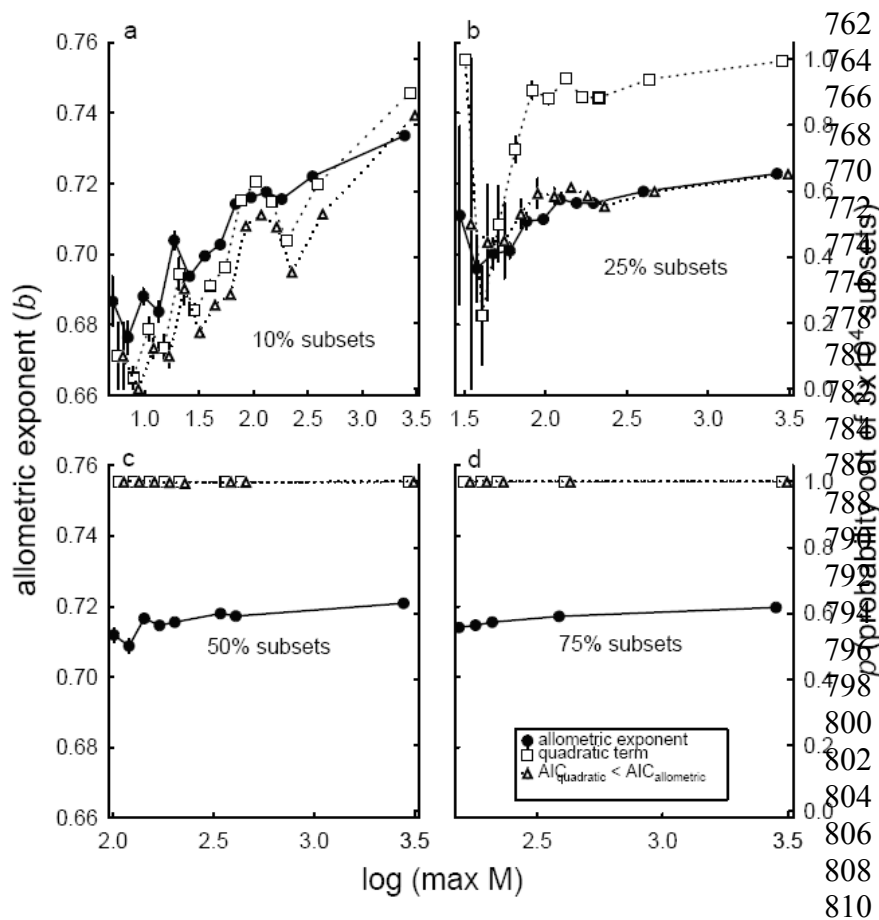
640 **Fig. S1.1.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 641 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 642 function provides a better-fit to log-transformed data than the linear function (probability of
 643 lower AIC score in the former) (open triangles), to increases in the range of body mass (M ,
 644 kg) included in the data (maximum – minimum M). M ranges were manipulated by random
 645 subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4
 646 permutations.
 647



697 **Fig. S1.2.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 698 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 699 function provides a better-fit to log-transformed data than the linear function (probability of
 700 lower AIC score in the former) (open triangles), to increases in the mean body mass (M , kg)
 701 included in the data. M ranges were manipulated by random subsamples representing 10 %
 702 (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.
 703



755 **Fig. S1.3.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 756 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 757 function provides a better-fit to log-transformed data than the linear function (probability of
 758 lower AIC score in the former) (open triangles), to increases in the minimum body mass (M ,
 759 kg) included in the data. M ranges were manipulated by random subsamples representing 10
 760 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.
 761

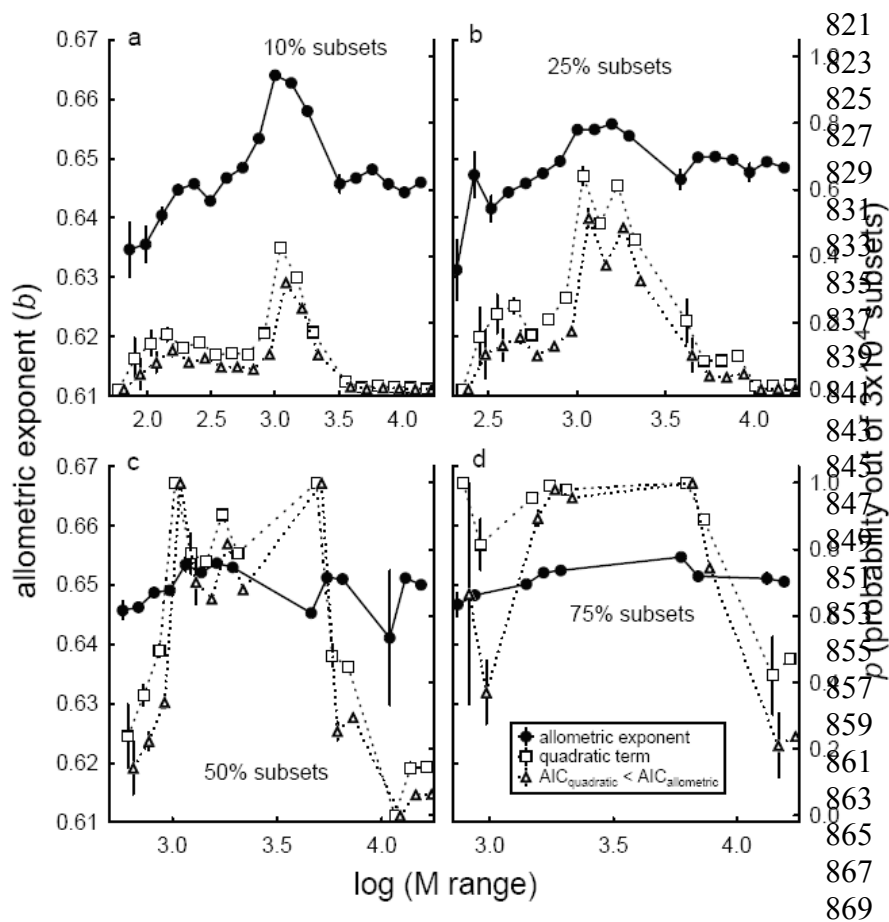


811 **Fig. S1.4.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 812 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 813 function provides a better-fit to log-transformed data than the linear function (probability of
 814 lower AIC score in the former) (open triangles), to increases in the maximum body mass (M ,
 815 kg) included in the data. M ranges were manipulated by random subsamples representing 10
 816 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.

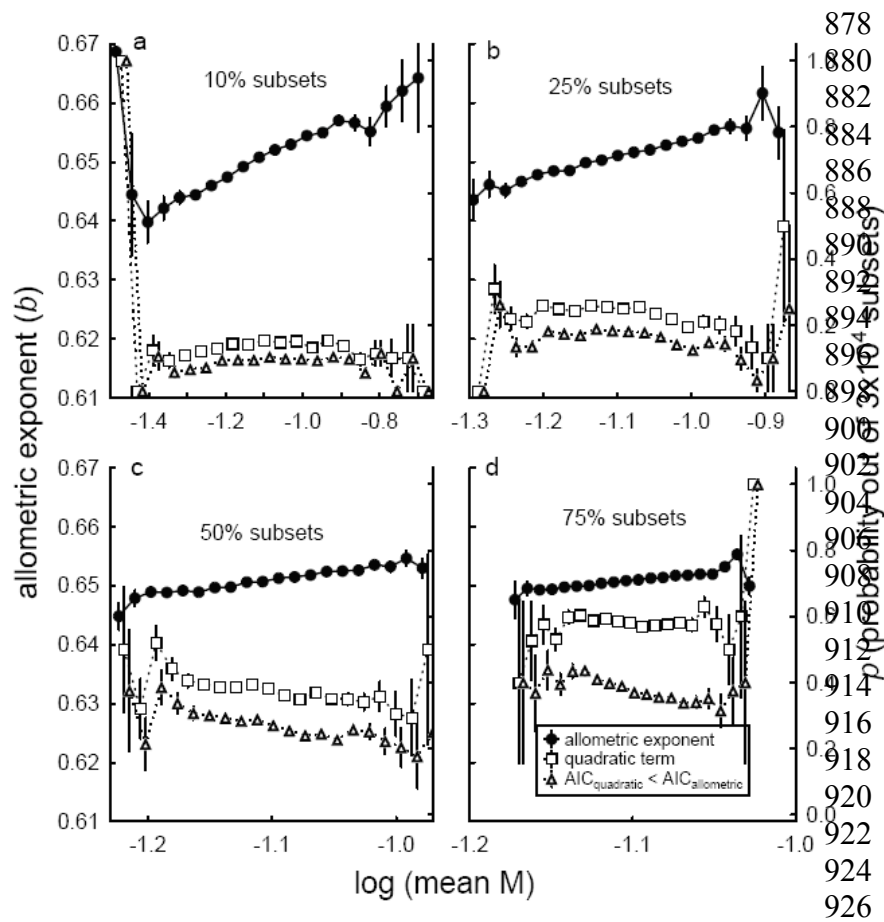
817
818

818 **Supplementary figures Part 2: Bird BMR**

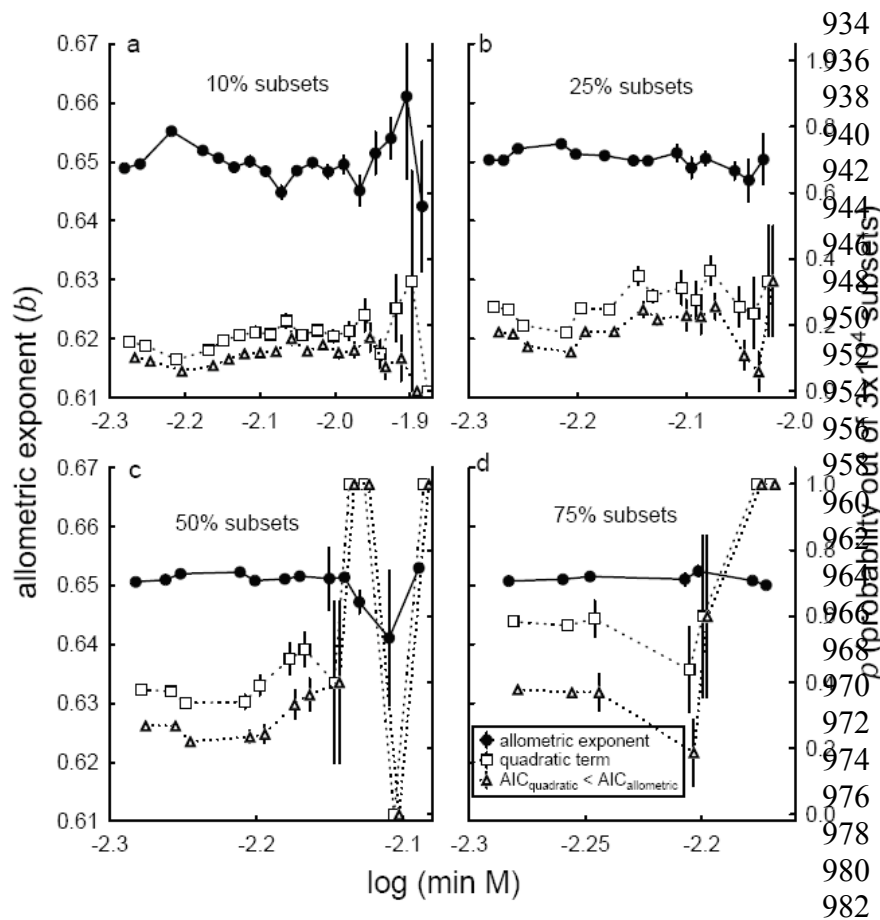
819



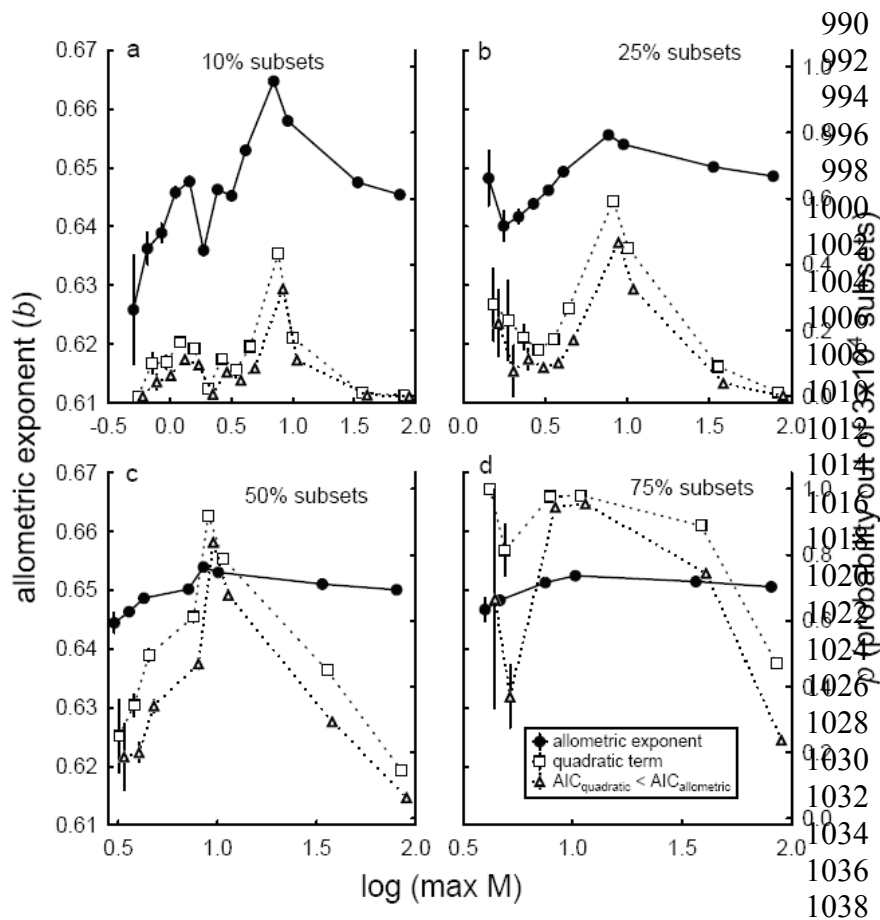
870 **Fig. S2.1.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 871 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 872 function provides a better-fit to log-transformed data than the linear function (probability of
 873 lower AIC score in the former) (open triangles), to increases in the range of body mass (M ,
 874 kg) included in the data (maximum – minimum M). M ranges were manipulated by random
 875 subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4
 876 permutations.
 877



927 **Fig. S2.2.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 928 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 929 function provides a better-fit to log-transformed data than the linear function (probability of
 930 lower AIC score in the former) (open triangles), to increases in the mean body mass (M , kg)
 931 included in the data. M ranges were manipulated by random subsamples representing 10 %
 932 (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.
 933



983 **Fig. S2.3.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 984 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 985 function provides a better-fit to log-transformed data than the linear function (probability of
 986 lower AIC score in the former) (open triangles), to increases in the minimum body mass (M ,
 987 kg) included in the data. M ranges were manipulated by random subsamples representing 10
 988 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.
 989



1039 **Fig. S2.4.** Response of i) the simple allometric exponent b (solid circles); ii) probability of a
 1040 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
 1041 function provides a better-fit to log-transformed data than the linear function (probability of
 1042 lower AIC score in the former) (open triangles), to increases in the maximum body mass (M ,
 1043 kg) included in the data. M ranges were manipulated by random subsamples representing 10
 1044 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with 3×10^4 permutations.
 1045

1046 Table S2a. Comparison of linear (L) and quadratic (Q) regressions for raw data of anatomical and physiological traits on body mass (kg) in
 1047 mammals. All variables were log-transformed prior to analysis. Note that the quadratic term was not significant in any case.
 1048

Trait	Shape	<i>n</i>	<i>a</i>	-95% CI	+95% CI	<i>b</i> or <i>b</i> ₁	-95% CI	+95% CI	<i>b</i> ₂	-95% CI	+95% % CI
Organ mass											
Heart	L	82	-2.2123	-2.2575	-2.1671	0.9754	0.9454	1.0055			
	Q	82	-2.2175	-2.2648	-2.1703	0.9624	0.9171	1.0076	0.0076	-0.0121	0.0274
Kidney	L	74	-2.1452	-2.1918	-2.0987	0.8686	0.8381	0.8990			
	Q	74	-2.1473	-2.1969	-2.0978	0.8641	0.8182	0.9099	0.0027	-0.0175	0.0228
Liver	L	76	-1.4902	-1.5306	-1.4498	0.8998	0.8733	0.9263			
	Q	76	-1.4889	-1.5317	-1.4461	0.9026	0.8628	0.9424	-0.0017	-0.0192	0.0159
Lung	L	76	-1.9663	-2.0292	-1.9034	1.0141	0.9724	1.0559			
	Q	76	-1.9843	-2.0496	-1.9189	0.9730	0.9113	1.0347	0.0242	-0.0028	0.0511
GIT	L	32	-1.0855	-1.2114	-0.9596	1.0150	0.9457	1.0843			
	Q	32	-1.0863	-1.2201	-0.9524	1.0133	0.8986	1.1280	0.0009	-0.0439	0.0456
Respiratory and circulation											
Lung volume	L	32	1.6668	1.6195	1.7141	1.0549	1.0273	1.0825			
	Q	32	1.7025	1.6299	1.7750	1.0587	1.0307	1.0866	-0.0125	-0.0320	0.0069
Lung alvolar surface	L	32	0.5363	0.4844	0.5882	0.9358	0.9055	0.9661			
	Q	32	0.4940	0.4148	0.5732	0.9313	0.9008	0.9618	0.0149	-0.0064	0.0362
Breathing frequency	L	53	1.7410	1.6614	1.8206	-0.2379	-0.2793	-0.1965			
	Q	53	1.7326	1.6489	1.8164	-0.2560	-0.3237	-0.1883	0.0091	-0.0178	0.0360
Heart rate	L	23	2.3466	2.2945	2.3987	-0.2034	-0.2305	-0.1764			
	Q	23	2.3513	2.2955	2.4072	-0.1944	-0.2376	-0.1511	-0.0041	-0.0190	0.0109

1049 Parameters *a*, *b*₁, *b*₂ correspond with function (2) and function (5), respectively, of the main text
 1050

1050 Table S2b. Comparison of linear (L) and quadratic (Q) regressions for Phylogenetic Generalized Least-Squares of anatomical and physiological
 1051 traits on body mass (kg) in mammals. All variables were log-transformed prior to analysis. Note that the quadratic term was not significant in any
 1052 case.
 1053

Trait	Shape	<i>a</i>	-95% CI	+95 % CI	<i>b</i> or <i>b</i> ₁	-95% CI	+95 % CI	<i>b</i> ₂	-95% CI	+95 % CI
Organ mass										
Heart	L	-2.2454	-2.3881	-2.1027	0.9465	0.9120	0.9810			
	Q	-2.2488	-2.3921	-2.1055	0.9377	0.8854	0.9900	0.0047	-0.0159	0.0253
Kidney	L	-2.1508	-2.2941	-2.0075	0.8749	0.8414	0.9084			
	Q	-2.1594	-2.3021	-2.0167	0.8561	0.8055	0.9067	0.0098	-0.0102	0.0298
Liver	L	-1.4631	-1.5558	-1.3704	0.8941	0.8659	0.9223			
	Q	-1.4734	-1.5671	-1.3797	0.8696	0.8269	0.9123	0.0132	-0.0040	0.0304
Lung	L	-1.9589	-2.0728	-1.8450	1.0024	0.9544	1.0504			
	Q	-1.9625	-2.0142	-1.9108	0.9764	0.9058	1.0470	0.0215	-0.0083	0.0513
GIT	L	-0.9959	-1.1400	-0.8518	0.9803	0.9070	1.0536			
	Q	-0.9937	-1.3396	-0.6478	1.2211	1.1719	1.2703	-0.0454	-0.0932	0.0024
Respiratory and circulation										
Lung volume	L	1.6513	1.5468	1.7558	1.0114	0.9687	1.0541			
	Q	1.6691	1.5568	1.7814	1.0188	0.9729	1.0647	-0.0080	-0.0270	0.0110
Lung alvolar surface	L	0.5086	0.3761	0.6411	0.9174	0.8666	0.9682			
	Q	0.4732	0.3291	0.6173	0.9032	0.8495	0.9569	0.0159	-0.0049	0.0367
Breathing frequency	L	1.7532	1.6658	1.8406	-0.2414	-0.2845	-0.1983			
	Q	1.7406	1.6783	1.8029	-0.2557	-0.3116	-0.1998	0.0099	-0.0146	0.0344
Heart rate	L	2.3541	2.2831	2.4251	-0.2087	-0.2381	-0.1793			
	Q	2.3671	2.3485	2.3857	-0.1834	-0.2057	-0.1611	-0.0083	-0.0187	0.0021

1054 Parameters *a*, *b*₁, *b*₂ correspond with function (2) and function (5), respectively, of the main text
 1055
 1056

1057
1058
1059