ALLOMETRIC EXPONENTS SUPPORT A 3/4-POWER SCALING LAW

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Abstract. The relationship between metabolic rate and body mass follows a power function: $B \propto m^b$ where B is the basal metabolic rate, m is the species mass, and b is the allometric exponent. Older models based on a consideration of surface to volume ratios predict an exponent $b = 2/3$, whereas more recent models based on efficient transport and fractal design predict an exponent $b = 3/4$. We analyzed 22 published allometric exponents to address the following questions: (1) Is the published allometric exponent correlated with number of species, average mass, or range of mass in the study? (2) What is the mean and confidence interval for published exponents, and do they vary among taxa? (3) Given the published exponent data, what is the likelihood that $b = 2/3$ vs. 3/4? We found that published exponents were not correlated with sample size, average mass, or log(difference in mass). For mammals and birds, the allometric exponents were tightly clustered, with means of 0.72 and 0.73, respectively. The reptile data spanned a wider range but had a mean of 0.74. Likelihood analysis suggests that $b = 3/4$ is significantly more probable than $b = 2/3$. We built a linear regression simulation with experimental error in mass and showed that such measurement error systematically lowers estimates of the allometric exponent. Measurement error probably contributes to the observation that published allometric exponents often fall short of $b = 3/4$ as predicted by theoretical models.

Key words: allometric exponent; allometric scaling; basal metabolic rate; body mass; least-squares regression; likelihood; measurement error; meta-analysis.

INTRODUCTION

Allometric scaling equations of the form $B \propto m^b$ relate basal metabolic rate, B, and body mass, m, by an allometric exponent, b. Although metabolic scaling relationships have been recognized for decades (Kleiber 1932), controversy continues over the underlying value of the exponent and whether it is the same for all taxa (Koehl and Wolcott 2004). An older hypothesis, based on a consideration of surface area to volume ratios, predicts $b = 2/3$ (Rubner 1883, White and Seymour 2003). Several recent empirical studies (Enquist et al. 1998, Gillooly et al. 2001, Belgrano et al. 2002, West et al. 2002, Jun et al. 2003, Niklas et al. 2003, Savage et al. 2004) have concluded that $b = 3/4$. These studies support theoretical mechanisms of universal quarter-power scaling relationships based on fractal dimensions (West et al. 1999) and efficient space-filling energy transport (West et al. 1997). Building on the assumption that $b = 3/4$, the ''metabolic theory of ecology,'' developed by Brown et al. (2004), makes quarter-power scaling predictions at individual, population, and ecosystem levels.

However, other authors using alternative data sets and statistical methods have failed to find support for universal quarter-power scaling relationships. For example, in a re-analysis of five commonly cited bird and mammal data sets, Dodds et al. (2001) were unable to reject the hypothesis that b is 2/3. Bokma (2004) compiled intraspecific data on metabolic rates and body mass of 113 species of fish and found that the exponent was between 2/3 and 3/4. White and Seymour (2003) controlled for phylogenetic nonindependence by calculating mass and metabolism averages for mammalian orders and reported an exponent of 0.65, with a 95% confidence interval of 0.62–0.68. Heusner (1991) concluded that the allometric exponent for mammals is 2/3 but that different groups of species have different y intercepts in a log–log plot. However, West et al. (2002) analyzed a subset of species from Heusner's (1991) data, and found $b = 0.76 \pm 0.01$.

Most recent empirical studies of scaling relationships have proceeded piecemeal, with a small number of data sets assembled to test scaling patterns. Scaling exponents are typically estimated by least-squares regression of double log-transformed data, and the point estimate of the resulting exponent is compared to theoretical predictions. Alternatively, a 95% confidence is constructed and then inspected to see if it encompasses the theoretical value.

Enough studies have accumulated that it is timely to conduct a meta-analysis of published allometric scaling exponents (Horn 2004). We assembled data on 22 published exponents to address the following questions: (1) Is the published allometric exponent correlated with number of species, average mass, or range of mass in the study? (2) What is the mean and confidence interval for published exponents and do they vary among taxa?

REPORTS

(3) Given the published exponent data, what is the likelihood that $b = 2/3$ vs. $3/4$? Although sample size (= number of species in study) is not expected to have any systematic effects on the average of published allometric exponents, small sample size may contribute to variation in published exponents among studies, which might mask an underlying constant value. If allometric exponents vary systematically with body size or range of body sizes measured, they should not be modeled as a simple constant, and the argument for a universal allometric constant would be weakened. By constructing a confidence interval around point estimates for different taxonomic groups, we can evaluate the competing hypotheses that $b = 2/3$ vs. $b = 3/4$. This is a more general approach than any single study that examines whether the confidence interval for a single allometric relationship brackets hypothesized values of $b = 2/3$ or $b = 3/4$. Further, by using a likelihood analysis, we can compare the relative probability of the two competing hypotheses, given the data.

METHODS

Meta-analysis

We conducted a meta-analysis of 22 published allometric exponents relating basal metabolic rate and body mass ($n = 11$ mammal data sets, $n = 4$ bird data sets, $n = 4$ reptile data sets, $n = 1$ insect data set, and $n = 2$ mammal and bird data sets). We used published exponents, at least 17 of which were based on least-squares regression of $\log_{10}$–$\log_{10}$ transformed data; raw data were not re-analyzed. Published values and citations are summarized in the Appendix. Some publications in our analysis reported exponents for multiple groups of species. When the species formed mutually exclusive data sets (e.g., passerine and non-passerine birds in Lasiewski and Dawson [1967]), we used the exponent for each data set in our analysis. When the species did not form mutually exclusive data sets (e.g., Galvao et al. 1965, Bartles 1982) we used only the most inclusive data set. In this way, we included each species only once for each publication. Studies that corrected for temperature using either the Q_{10} principle or Boltzmann constant were excluded.

Using least-squares linear regression (Model I), we tested for correlations between the calculated allometric exponents and sample size, average body size, and range of body sizes. Sample size was the number of species, not the number of individuals, included in the study. Because we did not have complete mass data in all studies, we calculated average body size as the midpoint of the high and low mass. Range of body size was quantified as the $\log_{10}$ difference between the largest and smallest species in the analysis. Because the variance in estimated exponents was greater for small sample sizes, we also tested for correlations between the calculated allometric exponents and average body

size and range of body size using least squares regression weighted by sample size.

Meta-analysis assumes that the data from published studies are independent samples (Scheiner and Gurevitch 2001). Two sorts of nonindependence are present in the published allometric exponents. First, as Bokma (2004) and White and Seymour (2003) have emphasized, there is phylogenetic nonindependence because the species within a study exhibit varying levels of phylogenetic relatedness. The second kind of nonindependence arises because data on the same species are sometimes used in multiple studies. To control for the latter, we used an independent contrast analysis (Harvey and Pagel 1991). We paired studies analyzing related taxa, but sharing none in common (e.g., marsupials and other mammals). Each study was included in only one pair; when multiple combinations including a particular study were possible, a pair was chosen randomly. The absolute value of the difference in the allometric exponent was then regressed against the absolute value of the difference in sample size. Although this pair wise procedure reduces the sample size, it ensures that the comparisons are independent and do not share species. This analysis was repeated for midpoint of mass and range of mass.

Likelihood analysis

Likelihood analysis was used to assess the relative probability of different hypotheses given the data. We calculated the likelihood of allometric exponents ranging from 0.60 to 0.85. Based on the results of a Kolmogorov-Smirnov test, in our analysis we assumed that the published exponents were normally distributed. Because likelihood is proportional to the probability of a particular parameter estimate, the likelihood ratio can be interpreted as a ratio of probabilities (Hilborn and Mangel 1997). We found the maximum likelihood estimate (MLE) as well as the likelihood ratio of $b = 3/4$ to $b = 2/3$ for all data as well as for subsets of mammal, bird, and reptile data sets. All calculations were done in R (R Development Core Team 2004).

Simulation model

One of the key assumptions of Model I regression is that the x variable is measured without error (Sokal and Rohlf 1995). If measurement error is present, slope estimates of the model may be biased. We built a simulation model in R version 1.9.1 (2004) to quantify the effects of measurement error in biasing the slope estimates of linear regression. We used a sample size of 400 (about typical for the mammal studies in the Appendix) and an evenly spaced sample of body sizes from 1 to 4000 kg, encompassing four orders of magnitude. We assumed that the true underlying model is

$$Y_i = m_i^{3/4}.$$

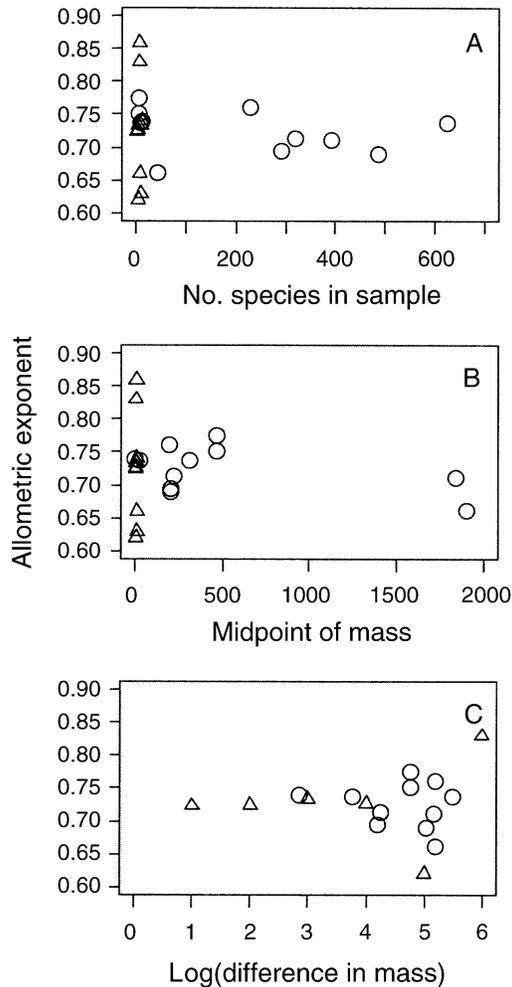In other words, we assumed that the true exponent b

FIG. 1. Estimates of allometric exponent as a function of (A) number of species, (B) midpoint of masses, and (C) range of masses expressed as log(difference in mass) in each data set. Circles are mammal data sets; triangles represent all other taxonomic groups. Data are from the Appendix.

was 3/4, and that all of the variation in metabolic rate Y could be attributed to variation in body mass m. Next, we introduced random measurement error X into the following model:

$$Y_i = (m_i + X_i)^b$$

where

$$X_i = Km_iZ$$

$$Z \sim N(0,1).$$

K is a constant that represents the proportion measurement error of body mass m_i and Z is a standard normal random variable with a mean of 0.0 and a variance of 1.0. Thus, the true x value for each observation is altered by a constant K percentage measurement error.

Finally, we took logarithms of the x and y variables, fit a standard linear regression, and estimated the exponent. For each level of K, we repeated the simulation 100 times and calculated the average exponent, the true 95% confidence interval and the estimated parametric confidence interval. Increasing values of K reveal the effect of measurement error on slope estimates.

RESULTS

For these 22 studies, the allometric exponent did not vary consistently with sample size ($P = 0.6491$; Fig. 1a), midpoint of mass ($P = 0.5781$; Fig. 1b), or range of body size ($P = 0.5792$; Fig. 1c). When we weighted by sample size in our regression, there was also no correlation between the allometric exponent and midpoint of mass ($P = 0.565$), or range of body size ($P = 0.649$). The independent contrast analysis revealed no statistically significant relationship between the difference in the allometric exponent and the difference in sample size ($P = 0.2371$), the difference in midpoint of mass ($P = 0.8827$), or the difference in range of mass ($P = 0.1441$).

For mammals and birds, published allometric exponents were clustered around a narrow range of values (Fig. 2). For birds, the average of four allometric exponents was 0.73, with a 95% parametric confidence interval of 0.72 to 0.73. For mammals (including marsupials), the average of 11 allometric exponents was 0.72, with a 95% confidence interval of 0.70 to 0.75. In contrast to the mammalian and avian results, the published exponents for reptiles were highly variable. Although the average exponent for four studies was 0.74, the confidence interval was from 0.55 to 0.93.

The Kolmogorov-Smirnov test indicated that the data were normally distributed ($D = 0.732$, quantiles: 2.5%, 0.710; 50%, 0.733; 95%, 0.748). The likelihood ratios ($b = 3/4$: $b = 2/3$) were 16 074 for all species, 105 for mammals, 7.08 for birds, and 2.20 for reptiles.

Our simulation model demonstrated that, as measurement error increased, the least-squares estimate of the slope was biased downward (Fig. 3). For example, with a measurement error of 10%, the estimated slope decreased from 0.750 to 0.743, and the 95% confidence
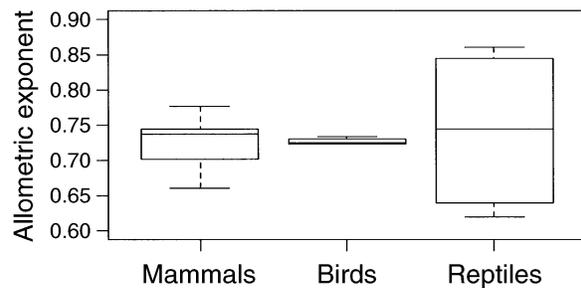

FIG. 2. Allometric exponent for mammals (including marsupials), birds, and reptiles. The center line is the median, and the box includes the middle two quartiles. The horizontal lines encompass the range of the data.
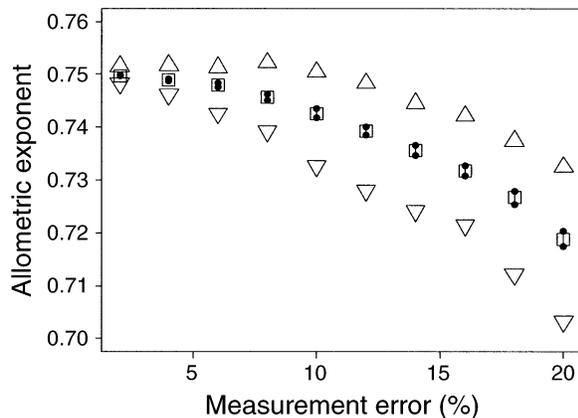
FIG. 3. Estimated allometric exponents as a function of random measurement error in body mass. Random measurement error was added to each mass observation before log transformation and calculation of the least-squares slope. The boxes represent the mean of 100 trials at each level of measurement error. The dots represent the limits of the true 95% confidence intervals, calculated from the 100 simulated slopes. The triangles represent the estimated 95% parametric confidence intervals.

interval encompassed 0.742 to 0.743. When the measurement error was increased to 20%, the estimate dropped to 0.719, with a 95% confidence interval of 0.717 to 0.720.

Discussion

Because the allometric exponent was not correlated with sample size, midpoint of mass, or range of body size, we conclude that reported values are not simply statistical artifacts that reflect the sampling details of the study. Of course, large samples always increase the precision of the estimate, so the plot of allometric exponents versus sample size (Fig. 1a) shows a familiar funnel shape (Underwood 1997). Specifically, studies with a sample size of fewer than 100 species span a larger range than studies with a sample size greater than 100. There is also no evidence that the allometric exponent varies systematically with the average body size or range of body sizes, which suggests that the exponent can be appropriately modeled as a constant.

Do these analyses support the idea of a universal allometric exponent? Not for poikilotherms; although the average exponent was 0.74, the range of published values was 0.62 to 0.86, with a 95% confidence interval from 0.55 to 0.93. All of the reptile analyses were based on small sample sizes (<100 species), which certainly contributed to the broad confidence interval. Moreover, because the body temperature of poikilotherms is not regulated internally (Randall et al. 1997), measures of metabolic rate may be sensitive to experimental conditions.

For homeotherms, the published exponents show a more impressive clustering of values close to 0.75, the predicted 3/4 scaling law (Fig. 2). As in Bokma's

(2004) analysis of fish, the actual confidence interval for birds does not encompass 0.75, and just barely does so for mammals. Standard frequentist analysis suggests that the true exponent lies somewhere between 2/3 and 3/4, with a mean exponent of 0.72, and a normal distribution of deviations. However, the likelihood ratio analysis suggests that $b = 3/4$ is 16 074 times more likely than $b = 2/3$ for all species. Although the likelihood ratios were less extreme, there was also strong support within taxonomic groups for the hypothesis that $b = 3/4$.

Several biological and statistical forces may cause the measured exponents to be less than the predicted value of $b = 3/4$. Most data sets in our study contained more small-bodied mammal species than large-bodied species. Small mammals tend to have basal metabolic rates slightly higher than those predicted by $b = 3/4$ (Savage et al. 2004), which would tend to decrease the estimated exponent. An exponent slightly less than $b = 3/4$ is also consistent with the prediction of West et al.'s (1997) arterial design model, which is slightly curvilinear at small body masses.

There are also statistical reasons why published exponents may be less than $b = 3/4$. Most of the published exponents were estimated with standard Model I least-squares regression, which assumes that measurements of the x variable (body mass) do not contain measurement error. In addition to measurement imprecision, transcription error (Savage et al. 2004), and variability caused by small sample sizes, there may be systematic variation in reported body mass due to differences in genetics, geographic distribution, age, and nutritional status within or among populations (Pagel and Harvey 1988). McNab (1988) noted that mammalian body mass varies by 12–15% of the mean in addition to being seasonally variable. In a complete review of the primate literature, Smith and Jungers (1997) calculated the co-efficient of variation (cv = sd/mean × 100) for 19 primate species to be 12.5, with a range of 4.3–19.5. In the context of a regression analysis, all of this variation represents "measurement error" because it causes the reported body mass to be different from the true mean body mass of a species.

Even modest measurement error biases slope estimates downward, but never upward (Fig. 3), which perhaps explains the fact that published slopes seem to be slightly lower than the theoretical prediction of $b = 3/4$. For now, there are no competing hypotheses in the neighborhood of $b = 0.70$, and measurement error seems the most parsimonious explanation for discrepancy between observed and predicted allometric constants for homeotherms.

In summary, our meta-analysis revealed no consistent effects of sample size, body size, or range of body sizes on measured allometric exponents. Published exponents are highly variable for poikilotherm studies based on small sample sizes, but cluster tightly for homeotherms at values that are slightly lower than the

predicted exponent of 3/4. However, likelihood analysis provides strong support for $b = 3/4$ over $b = 2/3$. Deviations from the predicted 3/4 exponent may be partly explained by measurement error in the predictor variable (body mass), which always biases least-squares slope estimates downward. Small sample size also introduces considerable variability in measured exponents. Taken at face value, these results collectively lend support to the idea of a universal metabolic constant (Brown et al. 2004).

Nevertheless, there is no getting around the problem in meta-analysis that some of these data sets were presented in papers precisely because they provided support for certain theoretical models. Additionally, the results of a meta-analysis are sensitive both to which studies are included, and which subsets of data are used in those studies. As additional empirical data accumulate in the literature, it will be worthwhile to repeat the meta-analysis we have reported here to see if the patterns are sustained.

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APPENDIX

A summary of data used in the meta-analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E086-109-A1.

REPORTS