On the use of log-transformation vs. nonlinear regression for analyzing biological power-laws

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Abstract

Power-law relationships are among the most well-studied functional relationships in biology. Recently the common practice of fitting power-laws using linear regression on log-transformed data (LR) has been criticized, calling into question the conclusions of hundreds of studies. It has been suggested that nonlinear regression (NLR) is preferable, but no rigorous comparison of these two methods has been conducted. Using Monte Carlo simulations we demonstrate that the error distribution determines which method performs better, with LR better characterizing data with multiplicative lognormal error and NLR better characterizing data with additive, homoscedastic, normal error. Analysis of 471 biological power-laws shows that both forms of error occur in nature. While previous analyses based on log-transformation appear to be generally valid, future analyses should choose methods based on a combination of biological plausibility and analysis of the error distribution. We provide detailed guidelines and associated computer code for doing so, including a model averaging approach for cases where the error structure is uncertain.

Keywords: power-law, allometry, log-transformation, nonlinear regression, model comparison, model averaging, parameter estimation

Introduction

Power-law relationships of the form $y = ax^b$ are one of the most common patterns in biology. They have been documented in a variety of different areas including the relationships between body size, physiological rates and life history traits (Brown *et al.* 2004), the scaling between body parts in morphology (Farlow *et al.* 1995), and the species-area relationship in biogeography (Martin & Goldenfeld 2006). These fitted relationships have been used to test the validity of biological theories (Brown *et al.* 2004), to infer the characteristics of extinct species (Farlow *et*

al. 1995), to assess the effect of evolutionary processes (Mortola & Limoges 2006), and to predict the consequence of habitat loss on biodiversity (Brooks *et al.* 2002).

Conventional analysis of power-law data uses the fact that log-transforming both sides of the equation yields a linear relationship, $\log(y)=\log(a)+b\log(x)$, allowing log-transformed data to be modeled using linear regression. However, it has been suggested that analysis on logarithmic scales is flawed and that instead, analysis should be carried out on the original scale of measurement using nonlinear regression (Fattorini 2007; Packard & Birchard 2008; Packard 2009; Caruso *et al.* 2010; Packard *et al.* 2010). If these claims are correct, the validity of decades of published research in ecology, evolution and physiology would be called into question.

One of the fundamental differences between linear regression on log-transformed data (hereafter, LR) and nonlinear regression on untransformed data (hereafter, NLR) lies in the assumptions about how stochasticity manifests in the model (Gingerich 2000, Kerkhoff & Enquist 2009). In NLR, it is assumed that the error term is normally distributed and additive on arithmetic scale (Bates & Watts 1988; Ritz & Streibig 2008):

$$y=ax^{b}+\varepsilon,\varepsilon \quad N(0,\sigma^{2}) \tag{1}$$

In contrast, LR assumes that error is normally distributed and additive on the logarithmic scale (Kerkhoff & Enquist 2009):

$$\log(y)=\log(a)+b\log(x)+\varepsilon,\varepsilon \quad N(0,\sigma^{2})$$

which corresponds to log-normally distributed, multiplicative error on the arithmetic scale:

$$y=ax^{b}e^{\varepsilon},\varepsilon \quad N(0,\sigma^{2}) \tag{2}$$

For a single dataset, both assumptions cannot be correct. Violation of statistical assumptions of

error can lead to biased point estimates as well as inaccurate confidence intervals (Bates & Watts 1988; see Figure 1 for an illustration).

Despite its importance in statistical model fitting, the issue of error distribution has been largely ignored in discussions about best practices for fitting power-laws to data. While both additive and multiplicative errors have been posited to occur in biological systems (Kerkhoff & Enquist 2009; Packard 2009; Cawley & Janacek 2010), to our knowledge there has been no systematic analysis that evaluates how NLR and LR estimation methods perform on different error structures, or what form the error structure actually takes in biological systems. This is surprising given the potential implications of these methodological issues for understanding biological systems and the strong arguments regarding appropriate methods being made in the literature (e.g., Packard 2009). Here we use Monte Carlo simulations to test the role of error structure on the performance of the two methods across empirical parameter space. For cases where the better model cannot be clearly determined, we develop an alternative estimation method based on model averaging. Based on these results, detailed guidelines for the analysis of biological power-laws, and computer code for their implementation, are provided.

Error Distribution Determines the Best Method for Fitting Power-Laws

Previous arguments regarding the performance of different methods have typically been based on empirical data (but see Hui *et al.* 2010), despite the fact that the true data generating mechanism is generally unknown. As such, previous studies provide little insight into the best methodological approach. Monte Carlo simulation, where data are simulated from known distributions, allows for a direct comparison between statistically estimated parameters and their true values. Here we implement the Monte Carlo approach based on parameterizations from empirical datasets so that our results will be valid for the range of empirically observed

parameter values. Results from these empirically motivated simulations were consistent with standard Monte Carlo simulations based on hypothetical parameterizations (see Appendix A).

We compiled 471 datasets published between 2004 and 2008 in the fields of ecology and evolution where significant power-law relationships were reported. The selected datasets were either morphological or physiological allometries between organismal traits (for details of data selection and the full list of datasets, see Appendix B). To generate the parameters for simulations each empirical dataset was assumed to have: 1) a multiplicative log-normal error structure, and a, b, and σ were estimated with LR (with σ estimated as the standard deviation of the residuals); and 2) an additive normal error structure, and the parameters were estimated with NLR. For each dataset, 10^5 independent simulations were carried out using the estimated parameters under the assumption of each error structure. Each simulated dataset was analyzed with both LR and NLR, and the performance of the two methods was compared to determine which method had the better point estimation of a and b, as well as more accurate confidence interval (CI) coverage measured by the percentage of simulations where the true parameter value falls within the estimated 95% CI. Only 239 datasets generated valid simulations under the assumption of additive error (see Appendix C for technical details on the procedure of the simulations). All simulations and analyses were carried out using R version 2.9.1 (R Development Core Team 2009). The “nlrwr” package (Ritz & Streibig 2008) was used to compute asymptotic CIs for NLR.

Our simulations confirm the importance of correctly identifying the error distribution when fitting statistical models. Among 471 empirical datasets LR outperformed NLR under the assumption of multiplicative error in all of the datasets (100%) for a and 427 datasets (90.7%) for b. Similarly, NLR outperformed LR under the assumption of additive error in 196 datasets

(82.0%) for *a*, and 238 datasets (99.6%) for *b* (out of n = 239 valid parameterizations). The method with the appropriate error assumption also had excellent confidence interval (CI) coverage, whereas CI coverage for the inappropriate method was highly variable, reaching levels as low as 0.2 (Figure 2).

Error Forms Observed in Nature

Given the critical nature of the error distribution in determining the appropriate method for analyzing power-law data, it is necessary to understand the form of the error distribution in nature. Previous papers have argued for both normal error (Packard 2009) and log-normal error (Kerkhoff & Enquist 2009), but no systematic analysis of biological power-laws has been conducted.

Taking a likelihood approach to compare the appropriateness of the two error forms for the 471 empirical datasets described above, we used Akaike's information criterion (AIC), which measures the goodness of fit of a statistical model by incorporating both the likelihood of the model and a penalty for extra parameters (Burnham & Anderson 2002). For each of the 471 empirical datasets, we computed likelihoods and the values of AICc (a second order variant of AIC that corrects for small sample size; see Burnham & Anderson 2002) for both the LR and NLR based models. We compared the AICc values by following the conventional rule that if $|\Delta AICc|$ (the magnitude of the difference between the two values of AICc) is less than 2, the two models have relatively equal support and cannot be distinguished from each other; otherwise, the model with the lower AICc is considered to have better data support (Burnham & Anderson 2002). Since AICc for the LR model is based on the likelihood from a log-normal distribution conditioned on untransformed data, such comparison does not violate the assumption of identical response variable in AIC-based model selection (Burnham & Anderson 2002, Section 2.11.3).

Consistent with previous suggestions that multiplicative error is biologically more realistic (Gingerich 2000; Kerkhoff & Enquist 2009; Cawley & Janacek 2010), our likelihood analysis of 471 allometric datasets shows that log-normal error distributions are substantially more common than normal error distributions, with 68.6% of relationships being better characterized by log-normal error, 16.6% by normal error, and 14.8% having uncertain error structure.

Model Averaging: An Alternative Approach When Error Form Is Uncertain

Monte Carlo simulations show that if the underlying error structure is known then the model assuming the appropriate error form (i.e., NLR with normal error, and LR with log-normal error) will perform well for estimating both the parameters of the power-law and the CIs of those parameters. However, the underlying error form of real datasets is not known and our likelihood analysis shows that identification of the error form will not be clear-cut in all empirical datasets; in part because the error form in real datasets may be more complex than assumed by the two standard methods. Even in our simulation models where one distinct error structure has been specified, likelihood tests sometimes failed to identify the correct error structure. For over half of the parameterizations (50.7% when error was assumed to be log-normal and 71.1% when error was assumed to be normal), error structure was either miscategorized or deemed uncertain by likelihood tests in more than 10% of the simulated datasets.

When two or more models with appreciably different parameter estimates have similar support, model averaging provides a way to incorporate information from multiple models so that more stable inference can be made based on the weighted average of the entire set (Burnham & Anderson 2002; Link & Barker 2006). The most common weighting strategies are AIC weight (Burnham & Anderson 2002) and BIC weight (Link & Barker 2006). In our analysis we adopted

AIC weight (see Appendix C for the detailed procedure). Based on point estimates and CIs, we assessed whether the weighted model was able to accurately capture the underlying relationship under the assumption of the two error structures, i.e. whether it indicated the correct error structure if one existed. R package "boot" was used to construct CIs for the weighted average model (Davidson & Hinkley 1997; Canty & Ripley 2009).

Comparison of relative bias among LR, NLR and weighted average models shows that the weighted model closely resembles the model with the appropriate error assumption in both point estimation and CI coverage (Figure 2) regardless of error structure. Thus the weighted average model can provide an indication of the appropriate error distribution.

General Guidelines for the Analysis of Biological Power-laws

For future analysis of power-law relationships, we recommend the application of the following three-step procedure to correctly identify and apply the appropriate method:

1. Determine the appropriate error structure by either biological reasoning (e.g., Kerkhoff & Enquist 2009, Cawley & Janacek 2010) or likelihood analysis. The relative likelihood of the two error structures can be compared with AICc or other similar measures. To compute AICc, first fit the two models using NLR and LR respectively and estimate the parameters a, b, and σ^2 for each model. Then calculate the likelihood that the data are generated from a normal distribution with additive error

$$L_{norm} = \prod_{i=1}^{n} \left(\frac{1}{\sqrt{2\pi\,\sigma_{NLR}^2}} \exp\left(\frac{-\left(y_i - a_{NLR}\, x_i^{b_{NLR}} \right)^2}{2\sigma_{NLR}^2} \right) \right),$$

and the likelihood that the data are generated from a log-normal distribution with multiplicative

error

$$L_{logn}=\prod_{i=1}^{n}\left(\frac{1}{y_i\sqrt{2\pi\,\sigma_{LR}^2}}\exp\left(\frac{-\left(\log\left(y_i\right)-\log\left(a_{LR}x_i^{b_{LR}}\right)\right)^2}{2\,\sigma_{LR}^2}\right)\right),$$

where *n* is sample size. AICc for each model can then be computed as

$AICc=2\mathrm{k}-2\log\left(L\right)+\frac{2\mathrm{k}\left(k+1\right)}{n-k-1}$, where *k* is the number of parameters (3 in both models) and *L* is the corresponding likelihood (Burnham & Anderson 2002).

2a. If the assumption of normal error is favored compared to log-normal error for either biological or statistical reasons (i.e., $AICc_{norm} - AICc_{logn} < -2$), proceed with the results obtained from NLR.

2b. If the assumption of log-normal error is favored compared to normal error (i.e., $AICc_{norm} - AICc_{logn} > 2$), proceed with the results obtained from LR.

2c. If neither model is favored for either statistical (i.e., $|AICc_{norm} - AICc_{logn}| \leq 2$) or biological reasons, model averaging should be adopted. The point estimates for *a* and *b* in the mixed model are then weighted average of the corresponding point estimates from the two original models. The AICc weights of the two models are computed as

$$w_i=C\cdot\exp\left(\frac{-AICC_c-min\left(AICc_{norm},AICc_{logn}\right)}{2}\right)$$

where C is a normalizing constant so that w_{norm} and w_{logn} sum to 1. CIs for *a* and *b* can be

186 generated by bootstrapping for datasets of sufficient size (Efron & Tibshirani 1994).

187 3. Assess the validity of underlying statistical assumptions with diagnostic plots or tests
188 (e.g., Packard & Birchard 2008, Cawley & Janacek 2010), a step that has often been overlooked
189 in the analyses of biological power-laws. While it is rare that all assumptions are fully satisfied
190 by empirical datasets, major violations indicate the inappropriateness of the model and potential
191 invalidity of the results.

192 Computer code that implements these recommendations is available in Appendix D.

193 **Implications for Previous Studies**

194 For decades LR has been the conventional approach in the analysis of biological
195 power-laws. If the current proposition to replace LR with NLR (e.g., Packard 2009, Packard *et*
196 *al.* 2010) were generally legitimate, the conclusions from large numbers of allometric studies
197 would be called into question. However, our likelihood analysis with 471 empirical datasets
198 spanning ecology, evolution and physiology shows that log-normal error consistently provides
199 superior fits to normal error distribution. This implies that the majority of previous allometric
200 studies in these fields are generally valid and contradicts the recent argument that LR is
201 inherently flawed and should be replaced by NLR (e.g., Packard 2009; Packard *et al.* 2010). As
202 our Monte Carlo simulation studies show, the application of NLR to such datasets may lead to
203 biased parameter estimates and potentially erroneous inferences.

204 The implications of these results for real biological patterns can be seen by applying the
205 guidelines described in the previous section to arbitrate two debates regarding the exponents of
206 morphological and physiological power-laws. The first example addresses whether or not the
207 scaling of mammalian metabolic rate as a function of body size is consistent with the canonical
208 0.75 scaling exponent predicted by metabolic theory (Brown *et al.* 2004). Savage et al. (2004)

analyzed a large compilation of mammalian basal metabolic rates using LR and found that the empirical data supported the predicted form of the relationship (b_{LR} = 0.74, $CI_{0.95}$ = (0.71, 0.76); see Figure 3a). However, reanalyzing the same data using NLR resulted in different parameter estimates and confidence intervals (b_{NLR} = 0.91, $CI_{0.95}$ = (0.88, 0.94)), which suggested that the 0.75 exponent should be rejected as a reasonable description of the data (Packard & Birchard 2008). A quantitative analysis of the error structure in this dataset shows that the assumption of multiplicative log-normal error is strongly supported compared to additive normal error ($AICc_{norm} - AICc_{logn}$= 306) with no major violations of the assumptions. This suggests that the data are consistent with the theoretical exponent.

Another example of how this approach can provide clear guidance when LR and NLR yield different results is the scaling relationship between eye size and brain mass. Burton (2006) analyzed this relationship in *fissiped Carnivora* using LR and argued that because the exponent did not differ significantly from one (b_{LR} = 0.87, $CI_{0.95}$ = (0.55, 1.19)) that eye size is determined (at least in part) by a simple limitation on the amount of space available in the head. A reanalysis of this data using NLR suggested that bears were outliers and that excluding this taxon the exponent was steeper than the hypothesized value of one (b_{NLR} = 1.42, $CI_{0.95}$ = (1.13, 1.70); Packard 2009). However, both the identification of outliers and the use of nonlinear regression were controversial (Kerkhoff & Enquist 2009). Likelihood analysis demonstrates that the assumption of log-normal error is more strongly supported regardless of whether the bears are included ($AICc_{norm} - AICc_{logn}$= 35.9) or not ($AICc_{norm} - AICc_{logn}$= 7.88), and the assumptions of normality and heteroscedasticity are not strongly violated in either case. Therefore since LR yields confidence intervals that include one even when the bears are excluded (b_{LR} = 1.24, $CI_{0.95}$ = (0.96, 1.53); see Figure 3b), the proposed isometric relationship is supported by the data.

Parallel examples where datasets with normal or undetermined error structures suffer from methodological problems are rarer in the literature due to the prevalence of the log-normal error distribution observed in nature. Nonetheless, reanalysis of the original data is warranted in cases where there is reason to suspect that an additive normal error structure or an undetermined error structure is more realistic.

Complexities

Apart from making inferences about the parameters, power functions are also frequently used to make predictions for new observations, which is particularly important in paleontology and conservation biology. For LR, it should be noted that although the parameter estimates are unbiased when the error is log-normal and multiplicative (Ferguson 1986), the model predicts log(y), and the predicted value of y obtained by anti-log transformation is biased on arithmetic scale (Hayes & Shonkwiler 2006). Measures should be taken to correct for this bias if predictions are to be made from log-transformed power functions (Hayes & Shonkwiler 2006).

One class of commonly observed biological power-law relationships not included in this study is the scaling relationship between species richness and attributes of the habitat (e.g., area, resource availability, distance to mainland, etc.). The most widely studied of these relationships is the species-area relationship (SAR). SARs are of fundamental importance in conservation biology where they are used for making predictions regarding the effect of habitat loss on biodiversity (Brooks *et al.* 2002) as well as the identification of hotspots (Veech 2000). It has been shown that inference related to the SAR varies with the method used for fitting the data (Fattorini 2007). One often overlooked characteristic of SARs is that the response variable, species richness, is a discrete count, which in principle cannot be accommodated by either LR or NLR because both assume a continuous data distribution (which is why this type of data was not

included in our empirical analyses). The existence of discrete error structure in some biological power-laws highlights the fact that additive normal error and multiplicative log-normal error are often not the only options that should be considered when analyzing error distributions. O'Hara and Kotze (2010) showed that ignorance of the error characteristics can lead to failure of the statistical analysis. Our understanding of the validity of previous studies of SARs and other relationships that potentially violate the distributional assumptions of LR and NLR would be enhanced by a systematic comparison between methods that accommodate their statistical and biological properties and currently applied methods such as NLR and LR.

Conclusions

Power functions are one of the most broadly studied relationships in biological systems. The current debate surrounding the methodology used in their analysis has generated considerable confusion in the field. As a result the conclusions of previous studies have been called into question and the progress of new analyses has been hampered. Our study provides a clear answer to the current controversy surrounding the appropriate methodology for analyzing allometric data. Neither linear regression on log-transformed data nor standard nonlinear regression is inherently superior for fitting power-laws to data. Which method performs better depends on the distribution of the error. For most allometric datasets like those we studied, the error is distributed such that log-transformed linear regression will produce more accurate parameter estimates and confidence intervals. As a result, most published results are likely valid. However, the methodology chosen for future analyses of power-laws in ecology and evolution should be based on explicit analyses (both statistical and biological) of the underlying error structure. We recommend that likelihood comparisons be applied to assess the error structure of the dataset. In cases where the error is approximately multiplicative lognormal, the log-transformed linear

regression should be used, while nonlinear regression on untransformed data should be applied to those datasets with additive normal error. For datasets with an indeterminate error structure, we recommend using model averaging to calculate the weighted average of the parameter estimates. As in all statistical analyses, the assumptions of the chosen model should be carefully evaluated.

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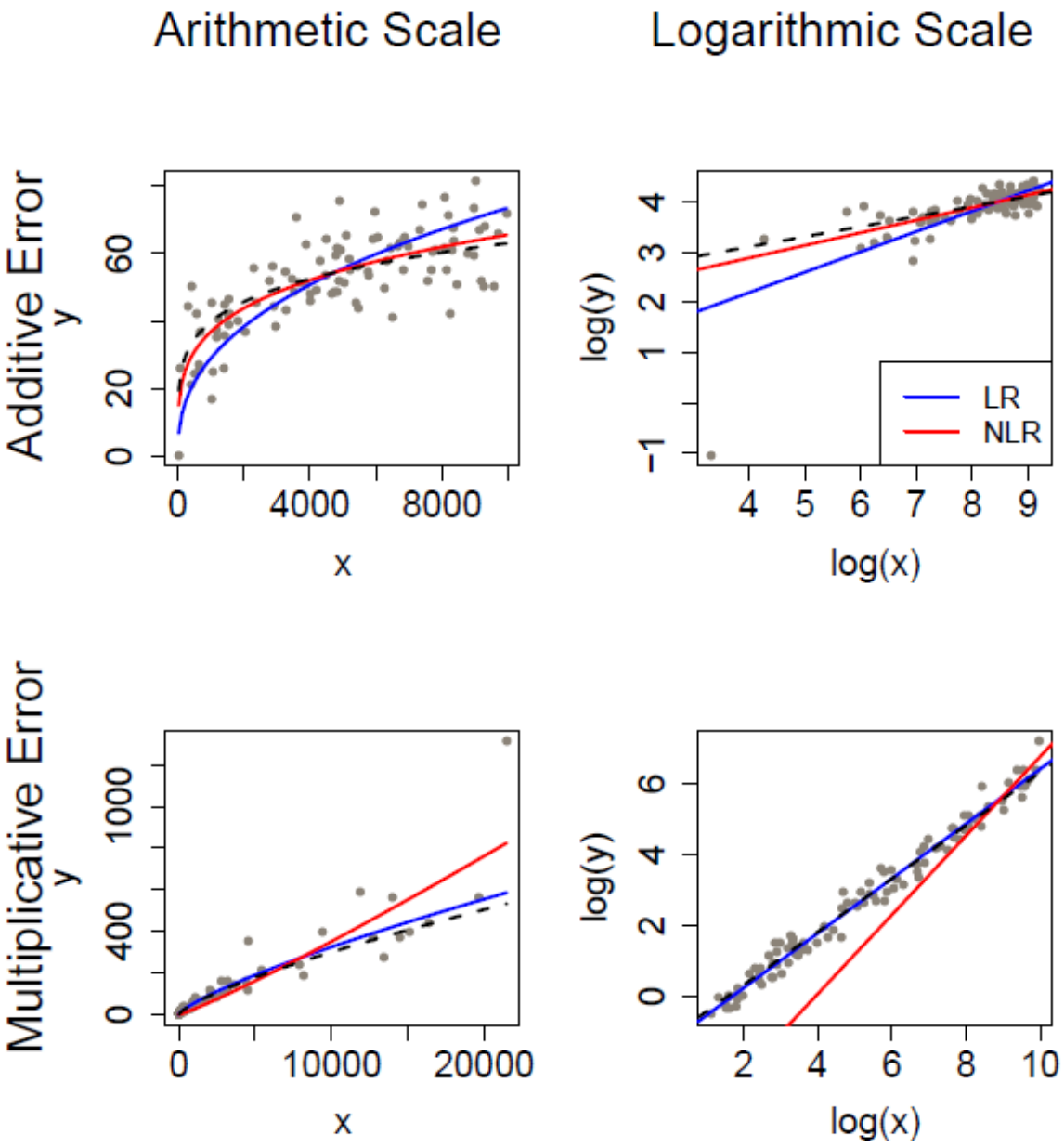
Figure 1. An illustration of additive normal error and multiplicative log-normal error displayed on both arithmetic and logarithmic scales, and how the underlying relationships can be distorted by the application of inappropriate methods. For additive error, x was generated from a uniform distribution ranging from 10 to 10000, y was generated using Eqn.1 with $a = 10$, $b = 0.2$, $\sigma = 10$. For multiplicative error, x was generated from a log-uniform distribution ranging from 1 to 10 on the logarithmic scale, y was generated using Eqn.2 with $a = 0.3$, $b = 0.75$, $\sigma = 0.3$. The dashed curves correspond to the true underlying relationships.

Figure 2. Comparison of bias in point estimation and CI coverage among LR, NLR and AICc-weighted average models in simulations with parameters estimated from 471 empirical datasets for multiplicative error structure and 239 empirical datasets for additive error structure. Relative bias (mean estimate/true value) is depicted because a spans a wide range across empirical datasets. For point estimation, each curve represents the relative frequency distribution of relative bias. An appropriate method peaks at 0 (on logarithmic scale) with small dispersion, while an inappropriate method shows a wide range of relative bias. For CI coverage, the horizontal dashed line represents the nominal 0.95 level. Note that point estimates were generated based on 10^5 simulated datasets, while CIs were based on 400 additional simulated datasets due to computational limitation. CI results are only shown for b.

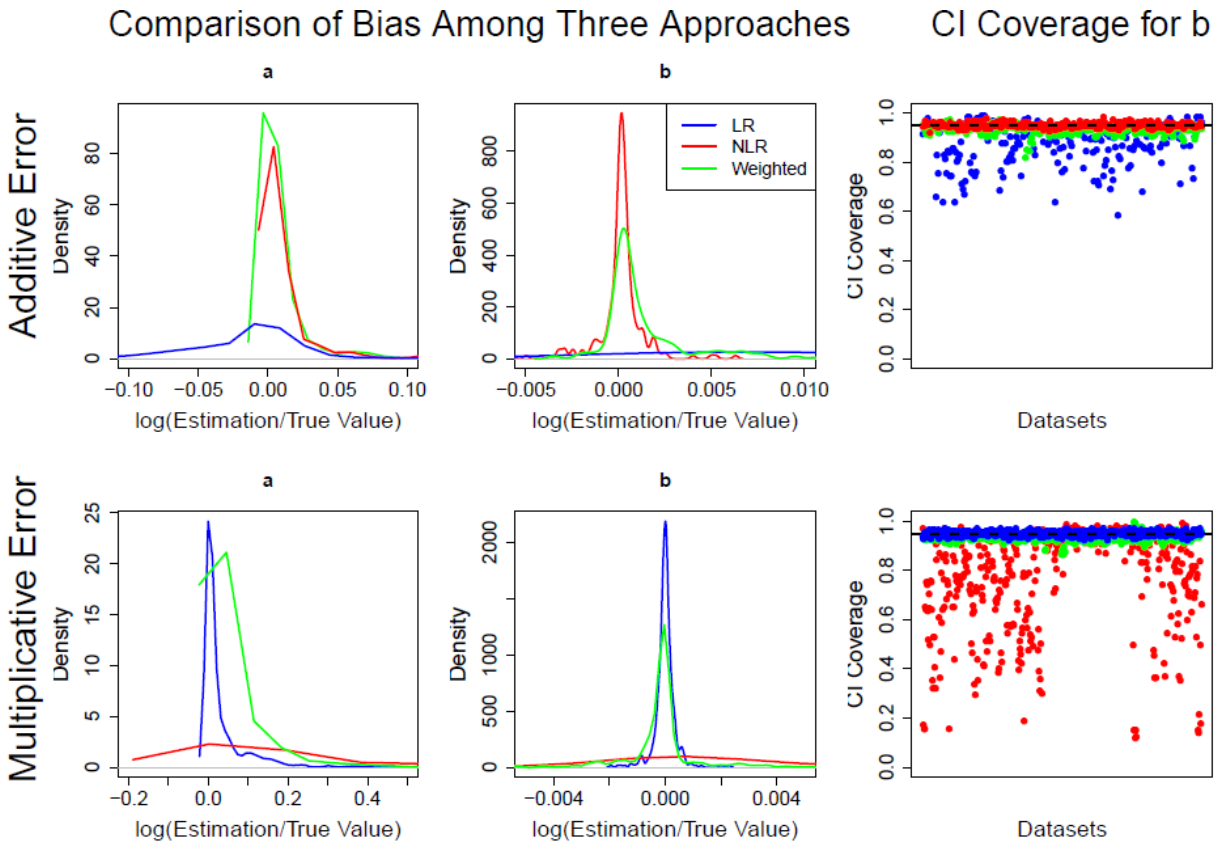
Figure 3. Examples of biological power-law relationships where an analysis of the error structure of the data can be used to arbitrate debates regarding the form of the underlying relationship. a. Basal metabolic rate – body mass relationship from Savage *et al*. (2004), reanalyzed in Packard & Birchard (2008); b. eye size – brain mass relationship from Burton (2006), analyzed in Packard (2009). See text for details.

377 Figure 1.



378

379 Figure 2.



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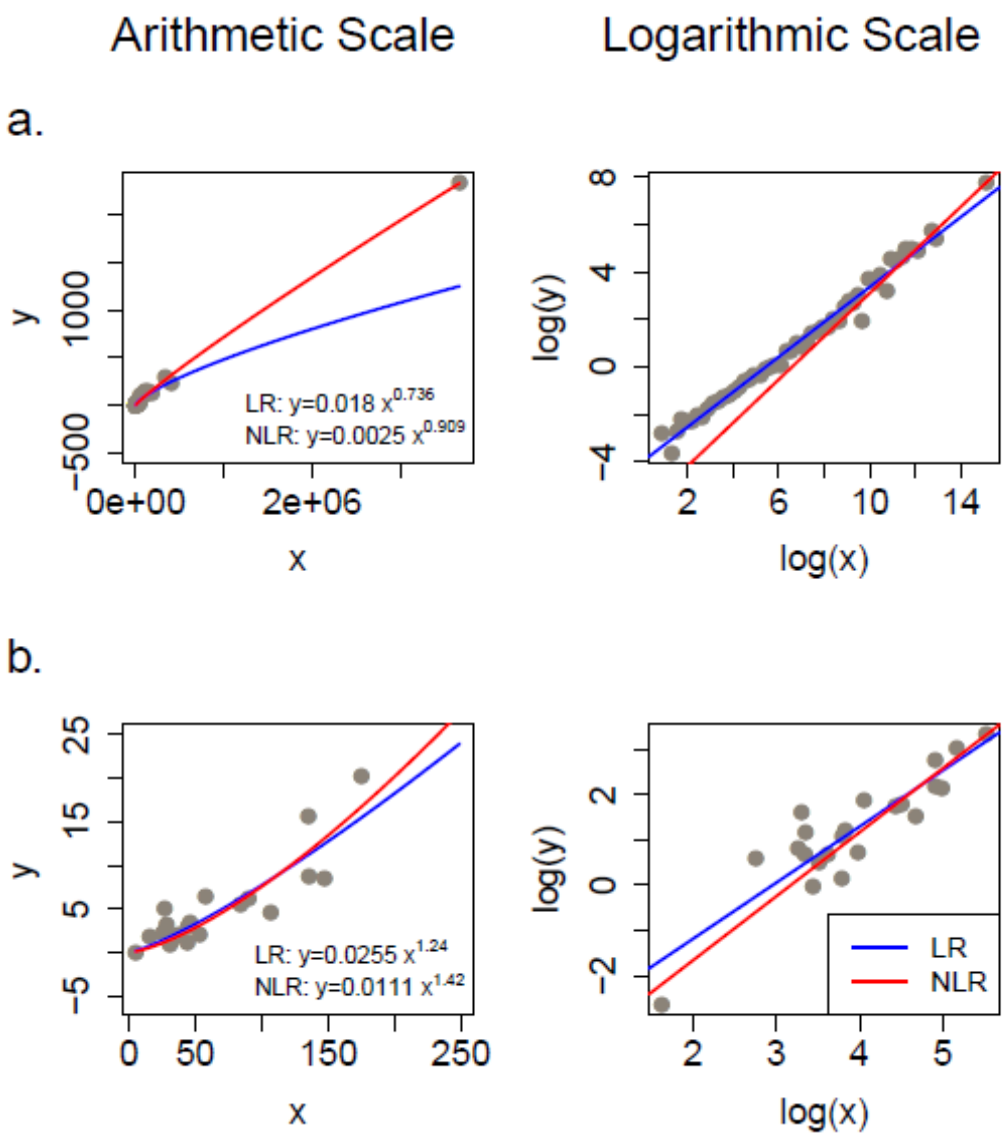
381 Figure 3.


Arithmetic Scale
Logarithmic Scale
a.
y
x
LR: y=0.018 x^0.736
NLR: y=0.0025 x^0.909
log(y)
log(x)
b.
y
x
LR: y=0.0255 x^1.24
NLR: y=0.0111 x^1.42
log(y)
log(x)
LR
NLR