Maximum Growth Rate Does Not Determine Dinosaur Metabolism

Nathan P. Myhrvold
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Abstract

Many previous studies have used growth rates to determine dinosaur metabolism. These studies compared the allometric scaling of maximum growth rate (G_{max}) as a function of maximum body mass (M) for dinosaurs with the scaling for extant groups in order to classify dinosaur metabolism as endothermic, ectothermic, or something in between (mesothermic).

Kleiber's Law holds that basal metabolic rate $BMR = a\,M^b$. Previous studies have shown that, with reasonably high correlation, $G_{max} = c\,M^d$ with roughly similar exponents $0.6 < b, d < 0.9$, depending on the taxonomic group. It does not follow that G_{max} is related to BMR, however, because statistical correlation is not transitive. Prior studies used inappropriate regression variables that confounded this relationship by introducing a spurious correlation, which occurs because G_{max} has M as an explicit factor.

I show that when the correct variable (i.e., maximum mass-specific growth rate rather than G_{max}) is used in the regression, available data show no correlation between growth rate and BMR. Moreover, the practice of using regressions across dinosaur taxa as a means to classify all dinosaurs is not valid, for both statistical and biological reasons.

My reanalysis of previously published data sets in fact finds that the growth rates of dinosaur taxa overlap with those of both endothermic and ectothermic extant animals. I conclude that one cannot determine the metabolism of either dinosaur or extant animal species by using growth-rate studies alone.

Prior Work Built on "Case's Method"—A Method Case Rejected

Nearly all previous studies that use growth rates to analyze dinosaur metabolism use methods that build on pioneering work by Ted J. Case [1], which these later studies cite (fig. 1). Case's own papers make clear, however, that he did not believe that metabolism can be deduced from growth rates (fig. 2).

In fact, Case was troubled by the fact that empirically there seemed to be no universal law relating metabolic rate and body size—nor has one been found in the years since.

1978: Case [1]
2000: Erickson & Tumanova [2]
2001: Erickson, Rogers & Yerby [3]
2004: Erickson, Mackovicky et al. [4]
2009: Erickson, Rauhut et al. [5]
2014: Grady, Enquist et al. [6]
2014: Werner & Griebeler [7]

Figure 1. Ted Case's seminal 1978 paper examining growth rates of various species (*top left*) suggested possible connections between growth rate and metabolism, but concluded that the relationship was unreliable on both theoretical and empirical grounds (fig. 2). Nevertheless, many recent studies on the growth and metabolism of dinosaurs have built upon Case's method, on the faulty assumption that it has been proven to apply universally.

WHY, IN FACT, should growth rate and metabolic rate vary with body size at roughly the same rate? The answer is not at all obvious....

I conclude that an organism's growth rate is not solely determined by its metabolic rate, although the evolutionary achievement of endothermy seems to have resulted in lifting the physiological restraints upon growth rate enough to produce nearly a ten-fold increase over ectothermic growth rates.

—Ted J. Case, 1978 [1]

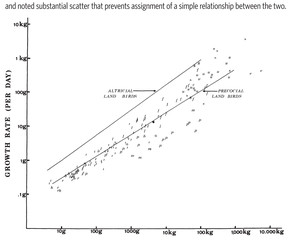

Figure 2. In his 1978 article, Case plotted growth rate versus body weight for species of many kinds and noted substantial scatter that prevents assignment of a simple relationship between the two.

FIG. 2. MAMMALIAN GROWTH AS A FUNCTION OF ADULT BODY WEIGHT AND COMPARED TO AVIAN GROWTH, AS IN FIG. 1

b, bats; i, insectivores; r, rodents; l, lagomorphs; f, finiped carnivores; s, pinniped carnivores; e, proboscideans; u, ungulates; p, primates; c, cetaceans; ★, edentates; m, marsupials; o, monotremes.

Statistical Problems

In studies that have claimed to find evidence for dinosaur mesothermy [6, 7], investigators regressed averages of G_{max} versus averages of M for polyphyletic groups of species. They found that the endothermic groups cluster separately from ectothermic groups on log-log charts; dinosaur groups occupied an intermediate position, which researchers interpreted as mesothermy.

However, my reanalysis of this approach and the underlying data sets has identified several serious statistical problems that call these conclusions into question [8, 9]. Four distinct kinds of statistical error are involved.

1 Choosing the wrong regression variables yields misleading results.

The maximum growth rate is obtained by using the equation $G_{max} = k\,M\,e^{-1}$, where k is a growth-rate parameter. M is an inappropriate choice of regression variable because it is a factor in this equation and is thus inextricably linked to G_{max}.

In fact, using M in the regression effectively applies a geometric shear transformation, which produces high correlation and low scatter as an artifact (fig. 1B). The inappropriate choice of regression variable thus confounds the analysis.

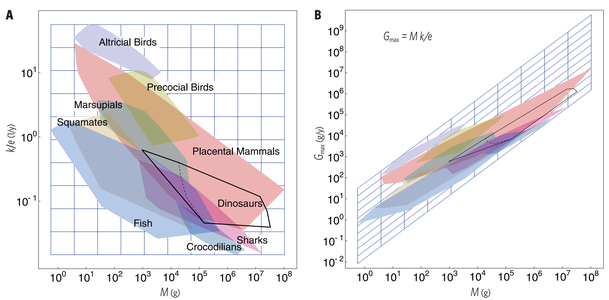

Figure 3. A convex hull surrounding data points published for several groups of animal species [1] seems to show that data sets for dinosaurs (*black outline*) overlap with several extant groups, whether plotted in terms of k/e (**A**) or in terms of G_{max} (**B**), where $G_{max} = M\,k/e$.

But the choice of M as a regression variable is inappropriate because regressing G_{max} versus M effectively adds an unnecessary shear transformation (*blue grid in* **B**) that artificially reduces scatter and inflates the apparent correlation. *Figure from ref. [8]*

2 Regression is not transitive.

Some prior studies assume implicitly that regression is transitive: i.e., that if it is valid to regress A on B and to regress B on C, then it must be valid to regress A on C as well. But this is demonstrably not the case, as is well known in statistics [10]. In the case of dinosaur data, results of regression analysis can differ greatly depending on the choice and order of the variables used (fig. 6).

3 Effects are not power laws.

Many studies of animal metabolism assume that growth rate varies with body mass as a simple power law in which a constant exponent applies to all organisms—or at least to all species within a broad taxonomic group. Researchers have mistakenly fit power-law functions to empirical measurements without checking whether other functional forms produce even better fits. In many cases, they do—and the best-fitting functions are complex curves such as cubics, not simple exponentials. It is a statistical error to fit data and claim a best fit has been found when only a subset of plausible functional forms have been tested.

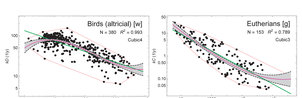

Figure 4. A reanalysis of growth and metabolic data presented by Werner and Griebeler [7] (*left*) and (B) by Grady *et al.* [6] (*right*) finds that the best fit for altricial birds, eutherians, and other groups is not a simple power law but instead a cubic or some other complex curve [9]. *Figures from ref. [9]*

4 The ecological fallacy: averages can mislead.

BMR and G_{max} are both properties of individual species; if they are correlated, then that should occur at the single-taxon level—it applies only to individual species. Performing regressions on averages taken across wide groups of biologically distinct species can produce highly misleading results when, as in the case of metabolism, characteristics are not actually shared among all members of the group. Such overgeneralization is an example of a famous problem in statistical inference known as the ecological fallacy [10].

Biological Problems

In addition to statistical issues, studies of dinosaur metabolism face substantial challenges imposed by fundamental constraints of biology. Three biological problems in particular undermine confidence in the prior conclusions about the metabolism of dinosaurs.

1 Metabolism cannot depend on the average of a polyphyletic group.

Basal metabolic rate (BMR) is a characteristic inherent to an individual species or taxon. The parameter has no valid meaning when estimated from an average of growth rates spanning broad taxonomic groups such as families or orders.

2 Growth rate can determine metabolism *only* at the level of species.

Animal species show a wide diversity of metabolic rates, and by definition this diversity cannot be "inherited" by a broad taxonomic group over millions of years of evolution—diversity *means* interspecies variation.

There exists no mechanism by which the metabolic rate of an extant species can reach back through time to inform, via some shared ancestor, the metabolic rate of a species on some other branch of the phylogenetic tree.

3 The metabolic theory of ecology is not supported by empirical data.

The metabolic theory of ecology, widely applied in these studies, assumes that a simple power law, such as $BMR = a\,M^b$, relates metabolism to maximum body mass. But the value of the exponent b used in published studies varies considerably; it is now clear that no single value applies universally.

Moreover, when empirical data for BMR and M are plotted on a semilog chart, often the result is a complex curve, not the straight line that a power law should produce (fig. 4).

Results

A reanalysis of the data on dinosaur growth and mass previously used to support claims of mesothermy [6, 7] finds that, when the errors mentioned above are corrected, no meaningful correlation exists between G_{max} and M (fig. 5). Other researchers have similarly concluded that body mass and metabolism are unrelated [11].

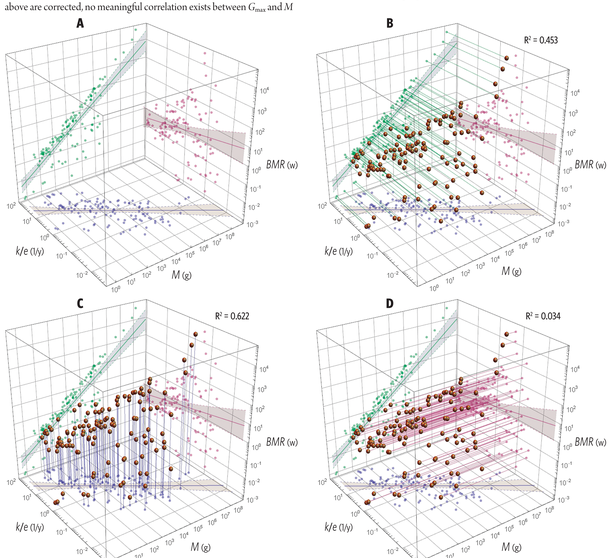

Figure 5. Correlation is nontransitive among growth rate (k/e), metabolic rate (BMR), and maximum mass (M). The dramatic differences in results that occur when one performs pairwise regression of these variables is illustrated here. The correlations are moderately strong for BMR versus M (**B**) and k/e versus M (**C**), but there is little correlation between BMR and k/e (**D**). *Figure from ref. [8]*

Moreover, a comparison of the growth rates obtained from these data sets reveals a pronounced degree of overlap among dinosaurs and other animals groups in both the endothermic and ectothermic metabolic categories (fig. 6). This result challenges the idea that dinosaurs exhibited a metabolic mode distinct from extant species.

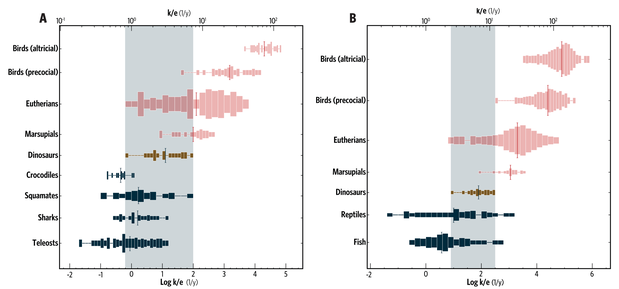

Figure 6. Large groups of taxa do not divide cleanly into metabolic groups by growth rate. These histograms of mass-adjusted growth rates assume a fixed exponent of ¼ for data sets from (**A**) ref [1] and (**B**) ref [6]. Mean values for each group are indicated by capped bars. Shaded bands highlight the growth rates that overlap among extant endotherms and ectotherms. *Figure from ref. [4]*

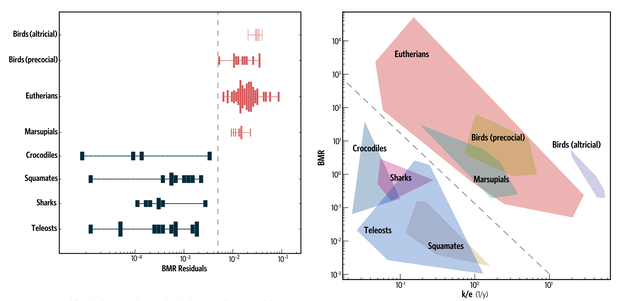

Figure 7. BMR acts differently than G_{max} in that it can be cleanly separated between endothermic groups (*blue in left chart, below dashed line in right chart*) and exothermic groups. *Figure from ref. [4]*

References and Acknowledgements

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