# ALLOMETRIC STUDIES IN MAMMALIAN METABOLISM

C.R. WHITE

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*Abstract*

Terrestrial mammals span a size range of ~6 orders of magnitude from 2 g shrews to 4000 kg elephants. The consequences of these size differences are well known: the 4000 kg elephant lives longer than the 2 g shrew, for example, but the shrew's heart beats faster than the elephant's, and 1 g of shrew uses considerably more energy per unit time than 1 g of elephant. This thesis examines the effect of body mass ($M$) on a range of physiological variables and the nature of the residual variation about these relationships (i.e. variation not accounted for by body mass) both within and between species.

1. The relationship between mammalian basal metabolic rate (BMR) and body mass ($M$) has been the subject of regular investigation for over a century. The scaling exponent (b, where BMR = a $M^{b}$) remains a point of contention and arguments for and against geometric ($b = 2/3$) and quarter-power ($b = 3/4$) scaling continue to be made and rebutted in the literature. Here a new analysis of the allometry of mammalian BMR that accounts for variation associated with body temperature, digestive state and phylogeny finds no support for a metabolic scaling exponent of 3/4. Data encompassing five orders of magnitude variation in $M$ and featuring 619 species from 19 mammalian orders show that BMR $\propto M^{2/3}$.

2. BMR is a useful measurement only if if the strictly defined conditions required for its measurement are adhered to. If variation associated with body temperature and digestive state is removed, the BMRs of eutherians and marsupials do not differ and no significant allometric exponent heterogeneity remains between orders. Of the 19 orders considered here, only Chiroptera and Dasyuromorphia have significantly different BMRs after eliminating body mass effects. The usefulness of BMR as a general measurement is supported by the observation that, after the removal of body mass effects, the residuals of BMR are significantly correlated with the residuals for a variety of physiological and ecological variables, including maximum metabolic rate, field metabolic rate, resting heart rate, litter size, and population density.

3. Mammalian BMR is one of the most widely measured physiological metrics, with the nature and causes of the interspecific relationship between $M$ and BMR continuing to be investigated and debated. However, analysis of interspecific data both neglects considerable intraspecific variation and averages out the variation on which natural selection acts. This chapter assesses intraspecific variation in a range of physiological variables including BMR in the murid rodent, *Notomys alexis*. Most variables were significantly repeatable, suggesting that individual measurements were reliable. Mean values were similar to values predicted by allometry, but variation between individuals was considerable and in many cases approached 50% of that observed between species. A number of variables were significantly correlated, and the implications of these correlations are discussed.

4. The low BMR of fossorial mammals has been suggested either to compensate for the enormous energetic demands of subterranean foraging ("cost of burrowing hypothesis") or to prevent overheating in closed burrow systems ("thermal stress hypothesis"). These hypotheses are examined by comparing fossorial (subterranean foraging) and semi-fossorial (surface foraging) burrowing mammals. In support of the thermal stress hypothesis, the BMRs of mesic fossorial and semi-fossorial mammals can not be reliably distinguished, nor can the BMRs of large (> 77 g) arid fossorial and semi-fossorial

mammals. However, in support of the cost of burrowing hypothesis, small (< 77 g) arid fossorial species have significantly lower BMRs than semi-fossorial species of similar size. The greatly reduced BMR of small arid fossorial species may compensate for the enormous energetic demands of subterranean foraging in an environment where resources are sparse and widely distributed.

5. The allometric relationship between body mass and burrow cross-sectional area for burrowing animals holds across greater than six orders of magnitude variation in body mass. Only birds that construct relatively large burrows, and vermiform animals that construct relatively narrow burrows, are separated from the remaining burrowing species. No difference is found between the cross-sectional area of burrows constructed by fossorial and semi-fossorial mammals, although solitary fossorial mammals do construct significantly larger nest chambers than semi-fossorial and colonial fossorial mammals. These large nest chambers probably provide a better thermally insulated microenvironment and offset the thermoregulatory problems faced by these animals, which are characterised by low, labile body temperatures and poor thermoregulatory ability.

6. How many species covering what range of body masses are required to arrive at a reasonable estimate of the relationship between BMR and *M*? To answer this question, 4600 artificial species are generated based on the variation in BMR and *M* observed in extant mammals. Randomly selected subsets of the artificial species are examined to determine if calculation of a single 'true' allometric scaling exponent is currently possible. This analysis shows that 75 species spanning five orders of magnitude variation in body mass are sufficient to accurately determine the relationship between BMR and *M*.

7. Much of the interest in the relationship between BMR and *M* stems from the debate surrounding the value of the scaling exponent (b, where BMR $\propto M^{b}$) with the relative merits of 2/3 and 3/4 exponents having now been debated for almost seven decades. Recent evidence suggests that phylogenetically informed (PI) comparative analyses are unable to resolve the debate because the value of the exponent depends on the evolutionary tree and the regression model used in the analysis. This chapter approaches the problem from a different perspective using randomly generated evolutionary trees and a homogenous selection of randomly generated 'artificial species' together with a literature compilation of PI and conventional scaling exponent estimates. It shows that although exponents estimated with PI and conventional regression methods can differ substantially, PI methods do not systematically bias exponent determination, suggesting that comparative analyses will remain a useful tool for resolving the debate.

8. Allometric data for different groups are most often compared using analysis of covariance (ANCOVA), a statistical procedure that compares treatment means (groups) after accounting for and removing their relationship with a covariate (often body mass). A requirement of ANCOVA is that the relationship with the covariate is uniform across groups, i.e. the regression slopes must be identical. This chapter describes a procedure (the Johnson-Neyman technique) that is applied following a finding of significantly heterogeneous regression slopes and allows for identification of the range of x-values at which there is a significant difference between groups. This allows potentially valuable information to be gleaned from data that might otherwise have been overlooked because of statistical limitations.