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The difficulty with correlations: Energy expenditure and brain mass in bats

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ABSTRACT

Brain mass has been suggested to determine a mammal's energy expenditure. This potential dependence is examined in 48 species of bats. A correlation between characters may be direct or derived from shared correlations with intervening factors without a direct interaction. Basal rate of metabolism in these bats increases with brain mass: large brains are more expensive than small brains, and both brain mass and basal rate increase with body mass. Basal rate and brain mass also correlate with food habits in bats. Mass-independent basal rate weakly correlates with mass-independent brain mass, the correlation only accounting for 12% of the variation in basal rate, which disappears when the combined effects of body mass and food habits are deleted. The correlation between basal rate and brain mass seen in this and other studies usually accounts for $<$ 10% of the variation in basal rate and often $<$ 4%, even when statistically significant, a minimalist explanation for the level the basal rate. This correlation probably reflects the intermediacy of secondary factors, as occurred with food habits in bats. Most biological correlations are complicated and must be examined in detail before assurance can be given as to their bases.

1. Introduction

Scientific inquiries often start with an observation that some aspect of nature correlates with another. A temptation is to conclude that the correlation describes a fundamental relationship dictating an operation in nature. However, many correlations mask complex factor interactions. A correlation may reflect the impact of other correlations and not a direct interaction among the elements of the observed correlation. This is not to deny the importance of correlations, but they must be treated with caution because of their potential complexity. Correlations may not be as determinative as they might appear.

As an example of the complexity of correlations, the basal rate of metabolism of mammals (BMR) correlates with body mass, which led to the concept that the rate of metabolism correlates with mass in the form of a power function (Kleiber, 1932; Benedict, 1938; Brody, 1945), a view that continues (Glazier, 2005; McNab, 2008). Brain mass also correlates with body mass as a power function, as has been shown by many authors, including Eisenberg and Wilson (1978), Mace et al. (1981), Hofman (1983), McNab and Eisenberg (1989), Aiello and Wells (2002), Pitnick et al. (2005), and Smaers et al. (2012). The justification for these correlations is that the amount of active tissue increases with body mass, which leads to the increase in energy expenditure. These correlations led several authors to suggest that a fundamental relationship exists between a mammal's energy expenditure and brain mass beyond the influence of body mass (Martin, 1981; Aiello and Wheeler, 1995; Leonard and Robertson, 2005; McGuire and Ratcliffe, 2010) such that brain mass determines basal rate.

An increase in energy expenditure with brain mass is not unique but a pattern that applies to all organs. However, all species of a given mass do not necessarily have the same rate of metabolism or same brain mass. A direct functional relationship therefore may exist between energy expenditure and brain mass if the mass-independent residual variation in energy expenditure correlates with the mass-independent variation in brain mass.

The apparent correlation between basal rate and brain mass may also occur through the intermediacy of factors other than body mass. For example, brain mass correlates with food habits (Hutcheon et al., 2002; Jones and MacLarnon, 2004; Safi et al., 2005; Safi and Dechmann, 2005; Rojas et al., 2013), as does basal rate (McNab, 1969, 2003b, 2008). Food habits, then, can associate BMR with brain mass. Body composition also influences BMR. Wang et al. (2001) examined the extent to which they could reconstruct Kleiber's mass law for mammalian basal rates (i.e., BMR [kcal/d] $= 70 \cdot m^{0.75}$, where m is body mass in kg) by summing the products of tissue and organ masses with their appropriate mass-specific rates of metabolism. The attempt came quite close: BMR (kcal/d) $= 67 \cdot \text{kg}^{0.76}$, although it obviously did not

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include expenditures associated with the intact body, as in the costs of respiration, circulation, and thermoregulation. A modification of body composition therefore can modify BMR, which might be the basis for a mass-independent correlation of basal rate with brain mass.

Various techniques have been used to determine whether basal rate depends on variation in brain mass. Some have used a scaling analysis (Hofman, 1983; Armstrong, 1983), but the correlation shown could not be isolated from a mutual correlation with mass. Another approach, a phylogenetic analysis, was used in many studies, including Mace et al. (1981), Jones and MacLarnon (2004), Schoenemann (2004), Safi et al. (2005), Isler (2011), and Rojas et al. (2013). Rojas et al., however, doubted the value of using phylogeny for the analysis of the ecological correlates of brain mass because the phylogenetic signal was inadequate.

The use of phylogenetic analyses is inappropriate when analyzing the quantitative variation in physiological performances (McNab, 2003b, 2012, 2015) because these analyses combine two separate questions. The evolution of brain mass is a phylogenetic question, whereas the relationship between BMR and brain mass is a physiological question, that is, of brain performance. A particular character state does not always have the same effect because its performance is often modified by conditions in the environment. Phylogeny does not determine the performance of a character state, but it describes their occurrence.

McNab and Eisenberg (1989) compared mass-independent measures of brain mass and BMR in 174 species of mammals. These measures were ratios of the measured rates to the rates expected at the same mass from the appropriate scaling relationship. The residual variation in BMR did not correlate with the residual variation in brain mass ($P = 0.11$; $r^2 = 0.015$). This analysis was criticized because the brain mass data were derived from Mace et al. (1981), who apparently added 0.59 g to brain masses (Isler and van Schaik, 2006). This addition would have affected the size of the brains, not their residual variation, and therefore does not disqualify the analysis. Martin (1989) criticized this approach for using 'improper' statistics, without indicating the 'proper' statistics.

The use of ratios to examine the impact of correlations has been criticized for ignoring the complexities of factor interactions, multifactorial regressions being more accurate (Freckleton, 2002). That view is appropriate in complex interactions. Then ratios based on multifactorial regressions should be used as the standard for performance, as will occur here.

Another complication is that all correlations show residual variation, an estimate of which is $1 - r^2$, r^2 being the correlation coefficient. A large r^2 indicates a small variation beyond the correlation. But residual variation may hide clues to unidentified complications in a correlation. A large r^2, therefore, does not indicate a complete understanding of the basis of a correlation, especially at the species level (BKM in prep.).

The goal of this analysis is to reexamine whether the residual variation in basal rate reflects the residual variation of brain mass in mammals. This opportunity appeared with discovering measurements of brain mass in 256 species of bats, 48 of which have estimates of their basal rates available. Insectivorous bats constitute the majority of species in the sample, but they are not committed to inflexible endothermy and therefore cannot be included in this analysis because of the inability to define BMR.

2. Data and methods

We summarize (Table 1) data on the brain mass and their associated body masses obtained from a catalogue at Michigan State University (http://www.brainatlas.msu.edu/databases/stephan/stephan.xls). For the same species we report data on the basal rate of metabolism and body masses associated with these measurements (McNab, 2008). With few exceptions, body mass in a species is similar in the two studies.

Statistical analyses were based on ANCOVA via JMP, first to examine whether a relationship exists between BMR and brain mass. Then the relationships between basal rate and body mass and between brain size and body mass are described, both of which take the form of a power function. The residual variation in BMR is calculated by dividing the measured rate of each species with that at its mass calculated from the rate/mass eq. A similar calculation was made for brain mass relative to the brain/mass equation. These two ratios, expressed as a percent of the values "expected" from mass, represent the mass-independent residual variations in brain mass and BMR, which can be examined to determine whether they correlate under the assumption that they are the only variables.

ANCOVA then brings food habits into the power functions of both BMR and brain mass. These equations permit analyses to correct BMR and brain mass for the influence of food habits and body mass by dividing the measured BMRs with the rates derived from the equation that incorporates food habits and mass. This permits the measured BMR to be expressed as a percent of the value expected from the multifactorial equation. A similar calculation is made for brain mass. Then these fruit and mass independent values can be compared to determine whether BMR and brain mass correlate with each other when food habits and body mass have been deleated. The potential influence of family affiliation is also examined, by bringing the eight families to which the bats belong into an ANCOVA analysis.

3. Results

Basal rate of metabolism (mLO_2/h) directly correlates with brain mass (g) ($P < 0.0001$; Fig. 1):

$$BMR = 50\ brain^{1.00},\ r^2 = 0.961. \tag{1}$$

Log_{10} BMR correlates with log_{10} body mass ($p \leq 0.0001$; Fig. 2); $r^2 = 0.949$:

$$BMR = 2.92\ m^{0.757},\ r^2 = 0.946. \tag{2}$$

To extend this analysis, another factor, food habits, was inserted into Eq. (2). Food habits, broken into six categories (Table 1), correlated with log_{10} BMR ($P = 0.036$), but the BMR associated with each food habit was not statistically distinct. This means that the individual categories of food habits, as classified, have no distinctive effect on basal rate, which does not justify their separation. Food habits coalesce into two statistically significant groups in three ways: the combination of insects, omnivory, and carnivory vs other foods ($P = 0.0010$), insects and blood vs other foods ($P = 0.0057$), and insects vs other foods ($P = 0.028$). However, blood and omnivory are food habits limited in this sample to one family, the Phyllostomidae, and carnivory to three families, which means that food habits cannot be separated from family affiliation ($P < 0.0001$). Low basal rates in insectivorous bats have been widely seen (McNab, 1969, 2003b; Bonaccorso and McNab, 2003), which is why the insect/other food division is chosen, as well as because of the distinctive impact of insects in all three food-habit divisions.

Food habits, now defined by the insect/other food category is a significant correlate of basal rate ($P = 0.028$), which when combined with log_{10} mass ($P < 0.0001$), accounted for 95.4% of the variation in log_{10} BMR:

$$BMR = 3.08\ (F)\ m^{0.727 \pm 0.028},\ r^2 = 0.941, \tag{3}$$

where the dimensionless coefficient F for food habits equals 0.83 in insectivorous species and 1.00 in other species, i.e., insectivorous species have basal rates that average 83% of species with other food habits. The other divisions of food lead to equations that are nearly identical to Eq. (3).

Brain mass in these bats is similarly determined. It principally varies with body mass. Log_{10} brain mass correlates with log_{10} body mass ($P \leq 0.0001$; Fig. 3): $r^2 = 0.968$. Then: