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REVIEW

# Complications with body-size correction in comparative biology: possible solutions and an appeal for new approaches

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## ABSTRACT

The magnitude of many kinds of biological traits relates strongly to body size. Therefore, a first step in comparative studies frequently involves correcting for effects of body size on the variation of a phenotypic trait, so that the effects of other biological and ecological factors can be clearly distinguished. However, commonly used traditional methods for making these body-size adjustments ignore or do not completely separate the causal interactive effects of body size and other factors on trait variation. Various intrinsic and extrinsic factors may affect not only the variation of a trait, but also its covariation with body size, thus making it difficult to remove completely the effect of body size in comparative studies. These complications are illustrated by several examples of how body size interacts with diverse developmental, physiological, behavioral and ecological factors to affect variation in metabolic rate both within and across species. Such causal interactions are revealed by significant effects of these factors on the body-mass scaling slope of metabolic rate. I discuss five possible major kinds of methods for removing body-size effects that attempt to overcome these complications, at least in part, but I hope that my Review will encourage the development of other, hopefully better methods for doing so.

**KEY WORDS: Allometric scaling, Body-size effects, Comparative biology, Interactive effects, Metabolic rate, Phenotypic trait variation**

## Introduction

The magnitude of many biological traits relates strongly to organismal size. Therefore, as a first step in attempting to understand variation of a trait, comparative biologists frequently estimate how that variation relates to body size. A next step that often follows is to remove the influence of body size, so that the effects of other biological and ecological factors on the variation of a specific phenotypic trait can be distinguished. Traditional methods for doing this include the ratio or division method (i.e. trait size is divided by body size), analysis of covariance (ANCOVA; see Glossary), residual analysis (see Glossary), partial correlation analysis (see Glossary), multiple regression analysis (see 'Regression' in Glossary, and principal component analysis (PCA) (see Glossary), among others (e.g. Gould, 1975; Smith, 1984a, 1984b; Reist, 1985, 1986; Packard and Boardman, 1987; Harvey and Pagel, 1991; Shea, 1995; Speakman, 2005b; Bushuev et al., 2018; Plavcan, 2018; Rogell et al., 2020; McNab, 2021; see also Supplementary Materials and Methods). Ratio analyses have been most criticized because they assume that the magnitude of a trait varies proportionately in a 1:1 way (i.e. are isometric; see Glossary) with body size, which is often not true (Bliss, 1936; Tanner, 1949; Gould, 1966; Katch, 1973; Packard and Boardman, 1988; 1999; Raubenheimer and Simpson, 1992; Nakagawa et al., 2017). Many traits vary disproportionately (i.e. are allometric; see Glossary) with body size, either increasing or decreasing in relative size as body size increases, and thus in these cases the ratio method does not completely remove the effect of body size. Other possible statistical or conceptual problems with various alternative methods, including those mentioned above, have also been scrutinized (e.g. Smith, 1984a; Reist, 1986; Freckleton, 2002; Barja, 2014; Rogell et al., 2020; see also Supplementary Materials and Methods), but the problem that I wish to address in this brief Review is that many traditional methods for body-size correction do not adequately separate the effects of body size from those of other biological and ecological factors on a specific phenotypic trait. Although it is well known that many traits covary with body size, it is less known or appreciated that these covariances are not fixed, but can vary considerably depending on context.

Allometric relationships between various traits and body size are often assumed to be constrained physically, developmentally or evolutionarily, thus making them relatively constant regardless of ecological conditions (e.g. McMahon and Bonner, 1983; Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004; Savage et al., 2004; Sibly et al., 2012; Voje et al., 2014; Houle et al., 2019). Furthermore, commonly used body-size correction methods, such as ANCOVA and residual analysis, assume that the slopes of relationships between trait size and body size (i.e. their scaling exponent; see Glossary) are constant among treatment groups. However, the assumption of invariant scaling slopes made by specific theoretical and statistical models of allometry (see Glossary; also see below) is violated if the scaling slopes between trait size and body size are significantly heterogenous among the groups being compared, i.e. if there are significant interactions between the effects of body size and that of the treatment factor on trait size. Note that although these interactive effects can be included in various statistical models (including ANCOVA; e.g. Johnson, 2016), this procedure does not by itself clearly isolate the effects of body size on trait size. Including interactive terms merely identifies a confounding covariance problem, rather than removing it so that a clear-cut body-size correction can be made.

My Review has two major purposes. First, I use examples of how various intrinsic and extrinsic factors affect the body-mass scaling slopes for metabolic rate to illustrate complications in clearly separating the relative effects of body size from those of other interacting factors on a trait. Second, I discuss five possible major kinds of methods for correcting for the effect of body size on trait variation even when there is significant covariance between this effect and that of the treatment factor being examined, or other relevant confounding factors. I hope that my Review not only gives readers an appreciation of the difficulties often involved in

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## Glossary

**Allometry**
Scaling analyses that involve proportional comparisons of the magnitude (variation) of a trait (structure or process) with the magnitude of other traits or the size of a whole living system (e.g. body size).

**Allometric**
When the relative magnitude of a trait increases or decreases as system size increases, and thus the scaling exponent≠1.

**Analysis of covariance**
Statistical comparisons of the mean magnitude of a variable (e.g. biological trait), corrected for the effect of a covarying variable or 'covariate' (e.g. body size), among multiple treatment groups.

**Isometric**
When the magnitude of a trait varies proportionately in a 1:1 way with system size, and thus the scaling exponent is 1.

**Partial correlation analysis**
A statistical method that calculates the numerical correlation between two variables (e.g. the magnitudes of a trait and a treatment factor) after removing the effect of other variables (e.g. body size).

**Path analysis**
A statistical method that calculates the numerical correlations among multiple variables portrayed as a branching chain of linked relationships.

**Regression**
Statistical analysis of how a dependent variable ($y$) relates quantitatively to an independent variable ($x$). Multiple regression includes multiple independent variables.

**Residual analysis**
Vertical deviations of data points from a least-squares regression line relating the magnitude of a trait to body size. These 'residuals' are used as relative estimates of trait size that are independent of body size.

**Principal component analysis**
A statistical method that represents multidimensional variation of data along two or more major orthogonal axes, called 'principal components'. In morphological studies, the first principal component is often regarded as representing variation related to overall system size. Other principal components are often considered to represent variation that is independent of overall system size.

**Scaling coefficient**
Antilog of the $Y$-intercept in a log-linear scaling regression. Sometimes called the 'normalization constant', as represented in an allometric power function.

**Scaling curvature coefficient**
The constant ($c$) of the quadratic term ($cx^2$) in a polynomial equation representing curvilinear scaling of the magnitude of a trait ($y$) versus body mass ($x$).

**Scaling elevation level**
The vertical position of a log-linear scaling relationship between trait size and body mass, estimated as the mass-specific trait size at the pivotal mid-point of the log body-mass range. Unlike the scaling coefficient, this parameter is not mathematically autocorrelated with the scaling exponent. Therefore, it permits biologically meaningful comparisons between the elevations and slopes of scaling relationships. The 'metabolic level' is a specific example of this parameter that has been used to characterize the elevations of metabolic scaling relationships.

**Scaling exponent**
Slope in a log-linear scaling regression.

**Size quotient**
The proportional relationship between the magnitude of a trait and body size. This can be represented by the scaling exponent when the scaling relationship is log-linear. As such, it represents a relative measure of trait size that is allometrically corrected for the effect of body size.

correcting for the effects of body size on various phenotypic traits, but also stimulates the development of new general approaches of body-size correction.

### Complications with correcting for effects of body mass on metabolic rate

Traditional theory has assumed that the body-mass scaling of metabolic rate follows a universal 2/3 or 3/4 power law (Rubner, 1883; Kleiber, 1932; 1961; Hemmingsen, 1960; Savage et al., 2004; Brown et al., 2018; Burger et al., 2021). For example, the influential metabolic theory of ecology (MTE) has assumed that metabolic rate and the rates of various other biological and ecological processes supported by metabolism scale universally, or nearly so, with body mass according to a slope of 3/4 in log–log space (Brown et al., 2004), particularly in multicellular organisms with branching tubular resource-transport networks (West et al., 1997; Niklas, 2004; Savage et al., 2004; Banavar et al., 2010; DeLong et al., 2010). According to the MTE, taxonomic or environmental differences may affect the elevation of metabolic scaling relationships, but not their slope, which is fixed by 'engineering' constraints (McNab, 2012; p. 42) related to the rate-limiting geometry and physics of optimal resource transport to metabolizing cells throughout a three-dimensional body (West et al., 1997; Banavar et al., 2010).

Assuming a constant scaling slope (such as 3/4), it is relatively easy to remove the effect of body size on metabolic rate, at least statistically, in order to examine the effects of other factors. A method commonly used by animal scientists and proponents of the MTE has been to divide the rate of metabolism or other biological processes supported by metabolism by $M^b$ (the 'metabolic body size', or 'metabolically effective body weight', where $M$ is body mass and $b$ is the metabolic scaling slope with a value typically assumed to be 3/4 or nearly so: e.g. Brody and Procter, 1932; Brody, 1945; Kleiber, 1961; Thonney et al., 1976; Blaxter, 1989; Ultsch, 1995; Jørgensen et al., 1996; Brown et al., 2004; Sibly et al., 2012; although $b$=2/3 has also been used: e.g. Bliss, 1936; Nevill et al., 1992; Heymsfield et al., 2012). This ratio has then been compared to other factors, such as age (Kleiber, 1961), diet (Kleiber, 1961; Jørgensen et al., 1996), taxonomic group (Blaxter, 1989) and temperature (Brown et al., 2004; Sibly et al., 2012).

Another common method is to use residual analysis, where the residuals (deviations) of empirically observed values for metabolic rate in relation to a predictive log-linear regression against body mass are compared with various biological or ecological factors (e.g. McNab, 1986, 2002, 2012; Speakman, 2005a; De Magalhães et al., 2007; see also Supplementary Materials and Methods). This method, sometimes called the 'criterion of subtraction' (Gould, 1966; 1975; Smith, 1984a; 1984b; Anthony and Kay, 1993; Shea, 1995; Plavcan, 2018), examines how much a trait is relatively larger or smaller than that predicted by body size. Other methods such as ANCOVA, multiple regression and partial correlation analyses have also been used (e.g. Andrews and Pough, 1985; Harvey et al., 1991; Agosta et al., 2013; Naya et al., 2013; Dupoué et al., 2017; Hayes et al., 2018; Stark et al., 2020; Albuquerque and Garland, 2020).

However, complications arise if interactions occur between the effects of body size and that of other influential factors on metabolic rate. These interactions are indicated by significant effects of various intrinsic and extrinsic factors (singly or in combination) on the body-mass scaling slope for metabolic rate (many examples are reviewed in Glazier, 2005, 2010, 2014a, 2014b, 2018a; White and Kearney, 2013) or their body-size-dependent effect on the residuals of metabolic rate in relation to body mass (Naya et al., 2018). Furthermore, these factors may themselves have interactive effects (e.g. Glazier, 2018b, 2020a; Glazier et al., 2020b), as well as varying influences along different portions of a body-mass range, thus causing non-linear (curvilinear) scaling relationships (reviewed in Glazier, 2005, 2018a; also see next section).

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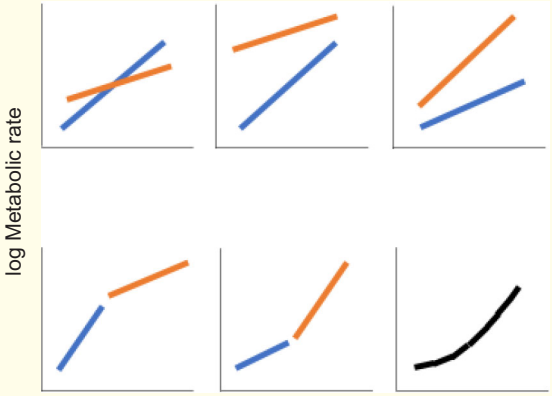
**Box 1. Schematic examples of how various intrinsic and extrinsic factors may affect the body-mass scaling slope for metabolic rate.**

These interactive effects are shown by different slopes of metabolic scaling relationships affected by different values of a specific factor (as shown by blue versus red lines), based on sources cited in the text. Each scaling comparison could be expanded to include more than two different scaling lines. Metabolic scaling relationships may also include more than two phase transitions (see e.g. Glazier, 2005; Gaitán-Espitia et al., 2013; Huang et al., 2020). Curvilinear relationships may be concave upwards (as shown here, following the pattern observed in mammals: e.g. Hayssen and Lacy, 1985; Kolokotrones et al., 2010) or concave downwards (as shown for plants: e.g. Mori et al., 2010).

**Intrinsic factors**
Taxonomic affiliation
Sex/genetic strain
Developmental stage
Physiological state
Body shape composition
Activity level
Mode of locomotion
Mode of thermoregulation




**Extrinsic factors**
Lifestyle
Diet and food supply
Habitat
Temperature
Oxygen supply
Water chemistry availability
Predators
Parasites
Other abiotic and biotic environmental factors

### How interactive effects between body size and various intrinsic and extrinsic factors complicate comparative analyses of variation in metabolic rate

Various intrinsic and extrinsic factors may cause the metabolic scaling exponent to vary in diverse ways (Box 1). They may cause situations where multiple body-mass scaling relationships criss-cross, or show increasing or decreasing scaling slopes with increasing vertical elevation of the line, or 'metabolic level' (see e.g. McNab, 1986, 2008, 2012; White et al., 2006; Glazier, 2008, 2010; Vaca and White, 2010; Glazier et al., 2011; Marsden et al., 2012; Pequeno et al., 2017; Rubalcaba et al., 2020). Or, they may cause discrete or continuous shifts in the scaling slope over different body-size intervals (see e.g. Glazier, 2005; Killen et al., 2007; Callier and Nijhout, 2012; Gaitán-Espitia et al., 2013; Glazier et al., 2015; Kolokotrones et al., 2010; Mori et al., 2010; Matoo et al., 2019; Huang et al., 2020). All these effects can confound body-size adjustments in comparative studies. If a specific factor causes the body-mass scaling lines to criss-cross, then that factor may be associated with relatively large magnitudes of a trait at small body sizes, but relatively small magnitudes at large body sizes, or vice versa. If a specific factor causes the scaling slope to decrease with increasing elevation of the line, then the effect of that factor on the relative magnitude of a trait will decrease with increasing body size. The opposite will occur if a specific factor causes the scaling slope to increase with increasing elevation of the line. If a specific factor causes shifts in the scaling slope with increasing body size, its effect on the magnitude of a trait will also be confounded with effects of body size.

Consider two hypothetical cases where a specific factor causes no change in the body-mass scaling slope for metabolic rate (Box 2A) versus a decrease in the slope with increasing metabolic level (Box 2B,C), as often observed for effects of increasing temperature on the scaling of resting metabolic rate in various ectothermic organisms (see e.g. Ivleva, 1980; Glazier, 2005, 2014b, 2020a; Killen et al., 2010; Carey and Sigwart, 2014; Fossen et al., 2019; Rubalcaba et al., 2020). In the first case, the factor in question tends to cause metabolic rate to be relatively high (blue circles) or low (red circles) with respect to the scaling line (see Box 2). Given that there is no change in slope, it is easy to factor out the effect of body mass by using standard statistical methods, including ANCOVA and residual analysis. However, in the second case, the factor causes a change in the body-mass scaling slope of metabolic rate, thus making it more difficult to factor out the effect of body mass. Body-size correction methods based on ANCOVA and residual analyses assume constancy of scaling slopes among treatment groups, and thus can no longer be used without modification. If one fits all the data by a single regression line, then it can be seen that the effect of the factor being considered increases with decreasing body mass. That is, at smaller body masses, sample points for each treatment group (as indicated by blue versus red circles) become increasingly divergent from the regression line (Box 2B). Observing a changing range of the minimum versus maximum deviation of sample points from a scaling line (either increasing or decreasing) with increasing body size, as often observed in scaling plots for various traits (e.g. mammalian metabolic rate, lifespan and gestation time; Martin et al., 2005; Müller et al., 2012; Clauss et al., 2014; Healy et al., 2014) may indicate that multiple scaling relationships related to specific factors may underly the pattern of data dispersion (also see the next two major sections of this Review). Therefore, one potential way to correct for this problem would be to fit separate regression lines to the sample points for each treatment group (Box 2C). Then the effect of body size could be factored out separately for each treatment group. However, this approach would not allow one to assess the effect of the factor in question on metabolic rate, because the two treatment groups are no longer being directly compared. So how can one adjust for the effect of body size and still assess the separate effect of a specific factor on metabolic rate or the magnitude of other traits of interest? Note that the hypothetical case shown in Box 2B,C is widely applicable (many examples of the metabolic scaling slope decreasing with increasing metabolic level,

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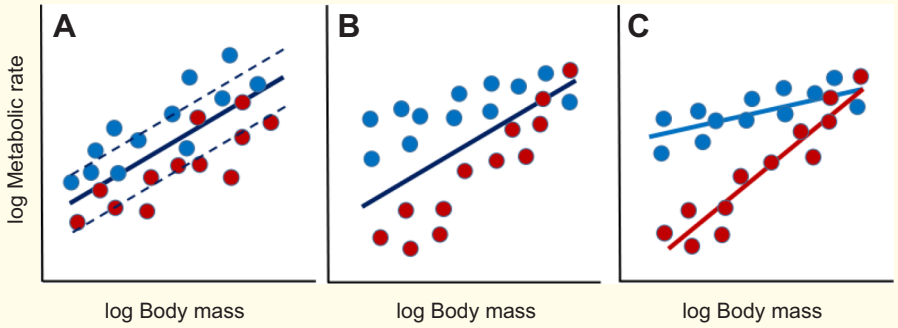
**Box 2. Hypothetical examples of how the residual variation of metabolic rate in relation to a body-mass scaling regression line may relate to two different values of a specific intrinsic or extrinsic factor.**

The sample points may refer to individuals, populations, species or higher taxa. The effect of the specific factor in question is indicated by blue versus red circles. For example, the blue and red circles could refer to high versus low values of a factor (e.g. activity level, resource availability or predation intensity), or to different diets, habitats or ecological lifestyles. (A) The factor affects metabolic rate independently of the effect of body mass. Therefore, the overall body-mass scaling slope (continuous line) and the slopes for sample points in each factor category (dashed lines) are not significantly different. (B) The effect of a factor on metabolic rate varies with body mass. In this example, the deviation of sample points from the overall body-mass scaling relationship increases as body size decreases (i.e. the metabolic rate of the sample points in the blue factor category become increasingly higher than that predicted by the scaling line, whereas it becomes increasingly lower for the sample points in the red factor category). (C) The scaling slope for metabolic rate in relation to body mass differs significantly between each factor category (blue and red sample points analysed separately).




in response to not only temperature, but also other intrinsic and extrinsic factors, have been described; see e.g. McNab, 1986; Glazier, 2005, 2010, 2014b; White et al., 2006; Killen et al., 2010; Hughes et al., 2011; Marsden et al., 2012; see also Fig. 1 discussed later in the section concerning the 'Contextual allometry' method). In addition, growing evidence indicates that other traits, such as life span, brain mass, stomach volume, genome size, and offspring size and number, show diverse body-mass scaling relationships that are related to various biological and ecological factors (see e.g. Hendriks and Mulder, 2008; Healy et al., 2014; Glazier, 2018a, 2021b; Griffen et al., 2018; Smaers et al., 2021). In the next section, I briefly discuss some possible methods that may help overcome this problem of interactive effects on trait variation, at least partially.

## Possible methods for correcting for the effect of body size when it is influenced by other intrinsic and extrinsic factors

Here I discuss five possible major kinds of methods, as summarized in Table 1. To avoid problems where variation in slopes occurs among comparative groups, some investigators (e.g. Reist, 1985, 1986) have recommended using the common within-groups scaling relationship for body-size correction (but see Bennett and Harvey, 1987). Others have used mixed-effects models that include random slopes to cope with variation in body-mass scaling slopes (e.g. Harrison et al., 2018; Sowersby et al., 2021). Although these models may improve the prediction of variation in the dependent variable, they do not solve the central problem addressed in this article, because they do not clearly separate the effect of body size from that of other specific causal factors on the magnitude of a trait. Therefore, these methods are not discussed further.

My focus is on statistical methods that adjust for effects of differences in body size on phenotypic trait variation, but other methods focused on patterns of genotypic (co)variation, such as artificial selection experiments (see Rogell et al., 2020) and quantitative genetic analyses of multiple traits (e.g. Careau et al., 2011; Videlier et al., 2021) should also be explored.

### 'Narrow allometry' (NA) method

The NA method requires that one makes comparisons only among organisms with an equivalent body mass or that occupy a narrow body-mass interval (Smith, 1980; 1984a). This approach is useful, but limited by its focus on only a narrow range of body sizes, and thus by reduced sample sizes and the associated power of statistical analyses. In addition, if a factor affects the mass-scaling slope for a trait, how that factor affects trait size may vary with the body-mass interval selected (e.g. Box 2B,C; and the previous section of this Review). Nevertheless, several investigators have used the NA method, at least with partial success, including Else and Hulbert (1981), Jungers (1988), Degen (1997), Sarmiento and Meldrum (2011), Turker (2011), Zotin and Ozernyuk (2014), Glazier and Paul (2017) and Plavcan (2018).

For example, Glazier and Paul (2017) compared the gill surface areas (GSA) of individuals with equivalent body mass among populations of a freshwater amphipod crustacean exposed to fish predators versus not. They showed that relatively large, mass-equivalent amphipods had significantly smaller GSA from spring habitats with versus without fish predators. However, no significant difference in GSA was found for relatively small, mass-equivalent amphipods. Glazier and Paul (2017) suggested that the mass-dependent difference in effect of fish predators on GSA (as shown by significant differences of the mass-scaling slopes for GSA between populations inhabiting springs with versus without fish) resulted from adaptive evolution in response to size-selective predation. This study clearly exemplifies my point that using the NA method to compare the effect of a factor on trait variation, independently of body size, may only be applicable to the narrow body-size interval selected. The same factor may have markedly different effects on trait variation, if other body-size intervals were chosen for analysis.

One partial remedy may be to use the Johnson–Neyman technique (Johnson and Neyman, 1936; Zerbe et al., 1982; White, 2003a; White and Kearney, 2014; Johnson, 2016) to determine the

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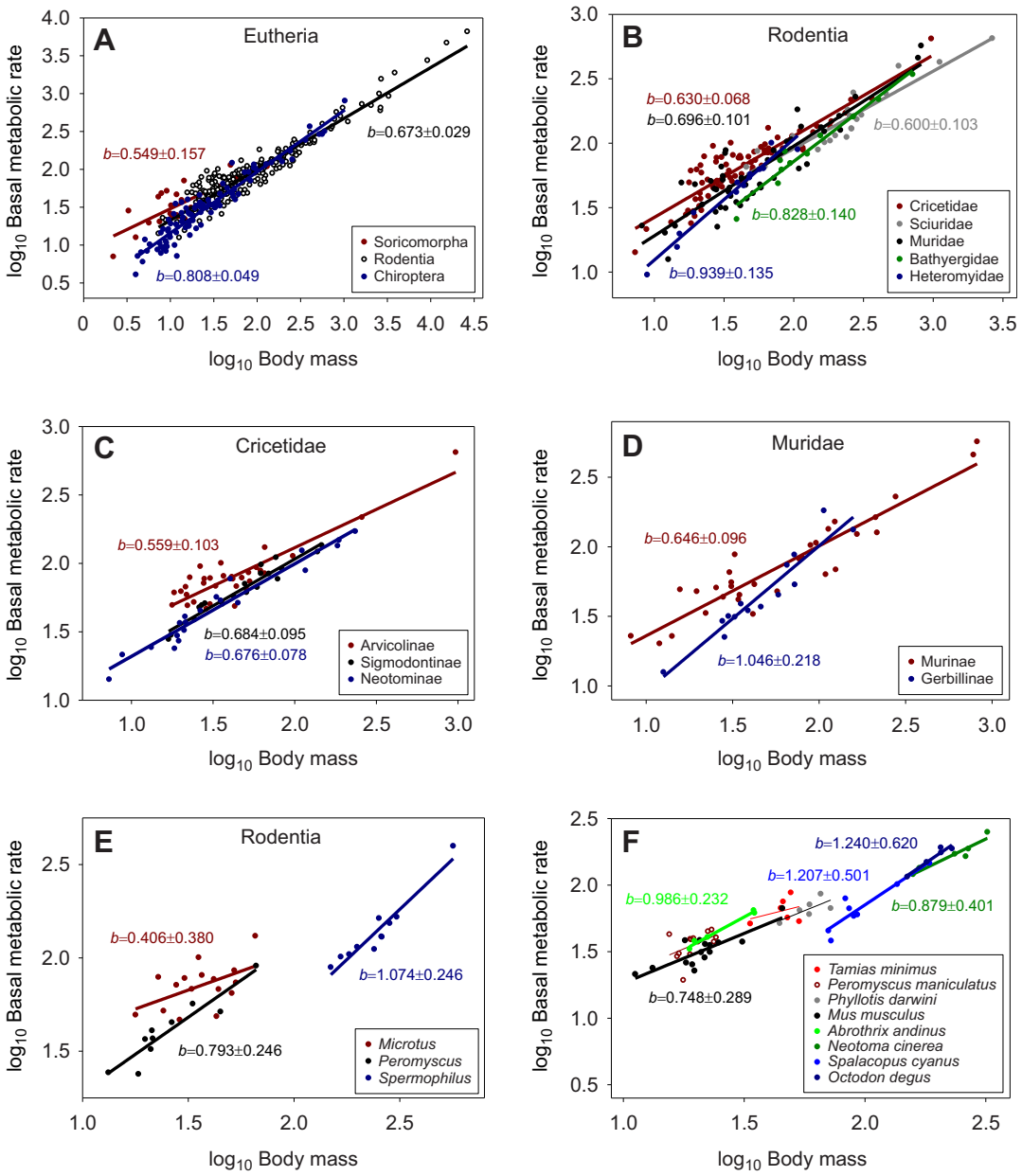


**Fig. 1. Relationships between $\log_{10}$ basal metabolic rate (ml $O_2$ $h^{-1}$) and $\log_{10}$ wet body mass (g) of various taxa of small eutherian mammals.** The small mammal taxa were selected because of their relatively large sample sizes and to avoid complications with different scaling relationships observed between small and large mammals (see e.g. Hayssen and Lacy, 1985; Glazier, 2005; Clarke et al., 2010; Kolokotrones et al., 2010). Only species data accepted by Genoud et al. (2018) were used (means calculated for species with multiple measurements). Scaling exponents (*b*) ±95% confidence intervals, many of which are significantly different, are indicated (see also Table S2). Least squares regression equations and statistics are presented in Table S1. (A) Scaling relationships for the three most species-rich eutherian orders are shown. (B) Scaling relationships for five rodent families with sample sizes ≥10. (C) Scaling relationships for three cricetid subfamilies with sample sizes ≥10. (D) Scaling relationships for two murid subfamilies with sample sizes ≥10. (E) Scaling relationships for three rodent genera with sample sizes ≥10. (F) Scaling relationships for eight rodent species with sample sizes ≥5. Thick regression lines indicate significant relationships, whereas thin lines indicate non-significant relationships. Only scaling exponents for significant regression lines are indicated.

body-size interval over which a factor has a significant effect on a trait. This method allows one to extend the use of ANCOVA to cases where the size-scaling slopes for the compared focal groups differ significantly (see e.g. White, 2003a, 2003b; Hölker, 2006; Glazier and Deptola, 2011; Polymeropoulos et al., 2017). For example, Glazier and Deptola (2011) were able to delineate the body-size interval within which habitat effects had a significant effect on amphipod eye size, despite the fact that the size-scaling slope for eye size varied significantly among populations in habitats with versus without fish predators.

However, further complications may arise if multiple factors have interactive effects on how a trait varies with body size. For example, Glazier et al. (2020b) have shown that changes in fish predation regime reverse the effect of ambient temperature on the body-mass scaling slope of metabolic rate in a freshwater amphipod. Therefore, when comparing individuals or species of equivalent body size, the effect of one factor on a trait may change when a second factor is considered.

Therefore, the NA method has only narrow applicability, and only offers a partial solution to the problem of removing the effect of

**Table 1. Possible methods of correcting, at least partially, for the effect of body size on a phenotypic trait when this effect interacts with the effects of other intrinsic and extrinsic factors**

| Method | Brief description | References |
|---|---|---|
| Narrow allometry | The NA method compares the effect of an intrinsic or extrinsic factor on a phenotypic trait among organisms with similar body sizes | Smith (1980, 1984a) |
| Contextual allometry | The CA method adjusts effect of body size on a phenotypic trait only for individuals, populations or species sharing a common taxonomic affiliation, developmental state, ecological lifestyle or similar effects of other specific intrinsic or extrinsic factors. One can compare the residuals from each context-dependent regression line to an intrinsic or extrinsic factor of interest that is different from the factor already framing the CA analysis. Alternatively, an ANCOVA can be carried out on the data used for each context-dependent scaling relationship. Or one can compare the magnitudes of traits among various distinct groups by dividing them by $M^b$, where $M$ is body mass and $b$ is the scaling slope specific to each group | Thonney et al. (1976), McNab (1988), Harvey and Pagel (1991); present study |
| Adjusted allometry | The AA method corrects for the effect of one or more specific intrinsic or extrinsic factors on the body-mass scaling of a trait. One can compare the residuals from the adjusted scaling regression line to various intrinsic and extrinsic factors not involved in the allometric adjustment | Reich et al. (2006); McNab (2008, 2009, 2012); Huang et al. (2020); present study |
| Multiple factor allometry | MFA methods include multiple regression and path analysis. These methods quantify the relative effects of body size and other intrinsic and extrinsic factors on a phenotypic trait, and their interactions. The variance of a dependent trait can be partitioned among independent variables, whose covariance can also be assessed in multiple regression analyses | Multiple sources including Shipley (2000); Freckleton (2002); von Hardenberg and Gonzalez-Voyer (2013); van der Bijl (2018) |
| Synthetic allometry | The SA method compares the body-mass scaling slopes and elevations for various phenotypic traits. For log-linear scaling relationships, the scaling slope ($b$) is size independent or 'scale invariant' (i.e. it is the same regardless of body-size interval). Therefore, comparisons based on body-mass scaling slopes offer another way to factor out the effect of body size. Instead of analysing how a factor affects the magnitude of a trait *per se*, one analyses how it affects the proportional relationship between the magnitude of a trait and body size, i.e. the trait's 'size quotient'. In addition, the scaling intercept ($\log a$) or 'elevation level' $L$ (where $L$ is the mass-specific value of a trait at the midpoint of a log–log scaling relationship) may be compared among scaling relationships (see text for further details) | Multiple sources including Adolph (1949); Lindstedt and Calder (1981); Stahl (1962); Western (1979); Lavigne (1982); Peters (1983); Calder (1984); Brown et al. (2004); Glazier (2010, 2020b); Hatton et al. (2019); Glazier et al. (2020a); present study |

body size on trait variation when that effect interacts with the effects of other factors of focal interest. Other methods that encompass broad (rather than narrow) body-size intervals are considered next.

#### 'Contextual allometry' (CA) method

The CA method corrects for body-size effects by using referential scaling analyses in separate and distinct contexts, such as in different taxa, developmental stages, physiological states, or environmental conditions (see Table 1; Box 2C). For example, separate ANCOVA or residual analyses could be based on the body-mass scaling of a trait for each contextual group. The effects of other causal factors on trait variation, independent of body mass, could then be more clearly discerned. However, the CA method is not as straightforward if the causal factor in question was also used to establish the separate contextual scaling relationships. For example, if separate body-mass scaling relationships are established for high and low temperature groups, then the effect of temperature on size-independent trait variation is no longer easily assessed (unless the CA method is combined with another method, e.g. the SA method: see Summary of methods below). However, the effects of other factors (e.g. taxonomic affiliation, activity level, etc.) on size-independent trait variation could be assessed. One possible way around this problem is to divide the magnitude of a focal trait by $M^b$, where $b$ is context dependent (following Thonney et al., 1976), before assessing the effect of the factor used in delineating the contextual scaling relationships, or the effect of any other factor. However, this method commingles a variety of body-size-related effects, without showing how the effect of a factor on a trait may vary with body size. This problem could lead to misleading predictions regarding the effects of a factor on a trait for individuals, populations or species within specific body-size intervals.

Although a step in the right direction, the CA method may be limited in various ways. First, if only subsets of data are used for each contextual scaling analysis, then relatively small sample sizes may weaken the rigor of the body-correction analysis (see Genoud et al., 2018). Second, it is not always clear what kind of contextual partitioning should be selected for carrying out the CA method in specific cases. Data visualization may help with this decision. Third, the level of contextualization that should be used is not clear-cut. For example, what taxonomic level should be considered appropriate for making body-size corrections? Consider that the body-mass scaling of metabolic rate varies considerably among orders, families, subfamilies and even genera and species of eutherian mammals (Fig. 1; see also Thonney et al., 1976; Hayssen and Lacy, 1985; Glazier, 2005; Kozłowski and Konarzewski, 2005; Duncan et al., 2007; Clarke et al., 2010). Fourth, multiple causal factors (some undetected) may interact with the effect of body size on the variation of a trait. As already mentioned, one causal factor may even reverse how another factor interacts with the effect of body size. Therefore, results of analyses using the CA method should be considered conditional: they are valid only within the contexts considered. The CA method may not always provide a clear-cut or fail-safe way of factoring out the effect of body size on a focal trait.

### 'Adjusted allometry' (AA) method

The AA method focuses on correcting for interactive effects between a causal factor and body size. This method (or class of methods) 'adjusts' for the effect that a specific intrinsic or extrinsic factor has on the body-mass scaling of a trait. Phylogenetically informed methods (e.g. phylogenetic regression and independent contrasts) adjust for the effects of evolutionary relatedness among species (e.g. Harvey and Pagel, 1991; Garland and Ives, 2000; Garland et al., 2005; Rezende and Diniz-Filho, 2012; Smaers and Rohlf, 2016). Other examples of adjusting for the effects of intrinsic factors include metabolic scaling analyses in plants that adjust for nitrogen or water content (indicators of metabolically active mass) (e.g. Reich et al., 2006; Huang et al., 2020). These kinds of body-composition adjustments result in relatively uniform, isometric scaling patterns, thus eliminating the diversity of scaling seen for whole body mass, which includes various size-dependent proportions of metabolically inert mass (non-living tissues). Using the AA method to correct for body-composition effects (inert versus metabolically active tissues) may be applied widely across the tree of life (e.g. Spaargaren, 1994; Heymsfield et al., 2012; Huang et al., 2020).

Another kind of AA method adjusts for the effect of extrinsic factors on the body-mass scaling of a trait. For example, McNab (2008, 2009, 2012, 2021) has shown how metabolic scaling relationships for birds and mammals change significantly when adjusted for effects of various extrinsic factors such as climate, habitat, insularity and elevation, as well as intrinsic factors such as torpor use, type of reproduction, flight ability and food habits. These scaling relationships explain significantly more of the variation in metabolic rate than do those based on body mass alone.

Many researchers have added independent variables other than body mass to the basic allometric equation to increase its ability to predict trait variation. For decades, many investigators have included additive or multiplicative factors, such as temperature, salinity, ration size and activity level, in metabolic scaling relationships (e.g. Newell and Roy, 1973; Elliott, 1976; Robinson et al., 1983; Andrews and Pough, 1985; Gillooly et al., 2001; Brown et al., 2004; and other references cited in Glazier, 2014a). In most cases, these equations assume that these added factors do not interact with body size in causing trait variation, but interactive terms may be included (e.g. Newell and Roy, 1973; Xie and Sun, 1990; Ohlberger et al., 2012).

The AA method increases the biological and ecological realism of body-size corrections, but clearly depends on the kinds of intrinsic and extrinsic factors that are considered. Furthermore, if significant interactive effects are identified, then the effect of body size on trait variation has not been completely isolated from that of other interactive factors.

### 'Multiple factor allometry' (MFA) method

The MFA method, including multiple regression and path analyses, quantifies the effects of multiple factors, including body size and their interactive effects, on the magnitude of a trait. In these analyses, the effect of body size is not only divorced from that of other factors, but also the relative contribution of each to trait variation is assessed. Freckleton (2002) has recommended multiple regression analysis over ANCOVA and residual analysis when correlations exist between the independent variables, including body size and specific treatment factors (but see Rogell et al., 2020). The use of multiple regression and partial regression coefficients to delineate the relative effect of body size and other causal factors on trait variation has become popular in recent years (e.g. Martin and Palumbi, 1993; Agosta et al., 2013; Dupoué et al., 2017; Hayes et al., 2018; Stark et al., 2020; Albuquerque and Garland, 2020; Sowersby et al., 2021). Path analysis (see Glossary), an extension of multiple regression, has also been increasingly used to partition the relative contributions of various factors to trait variation and to identify chains of effects (e.g. Boyce et al., 2020; Zhang et al., 2021). Therefore, the MFA method is useful for body-size correction in the context of a network of causal factors, but conclusions derived using it depend on the kinds of factors that are considered. However, note that although multiple regression and path analysis can include interactive effects between various independent variables, including body size (Jaccard and Turrisi, 2003; Sowersby et al., 2021), doing so merely identifies the problem I address, rather than resolving it (i.e. the effect of body size on trait variation has not been clearly isolated). Multiple regression and path analyses also assume normal distribution of residuals, and that effects of causal factors on trait variation are additive and linear (Shipley, 2000; Mitchell, 2001; Streiner, 2005). Recently, phylogenetically informed versions of path analysis have become available (von Hardenberg and Gonzalez-Voyer, 2013; van der Bijl, 2018).

### 'Synthetic allometry' (SA) method

The SA method compares scaling parameters (e.g. slopes and elevations) for specific traits. In a log–log linear regression, the scaling slope ($b$) is constant, regardless of body-size interval. Therefore, the scaling slope can be used as a size-independent parameter to explore inter-relationships among traits and various causal factors. Instead of analysing how a factor affects the magnitude of a trait *per se*, one analyses how it affects the proportional relationship between the magnitude of a trait and body size, herein called the 'size quotient' (see Glossary).

Other scaling parameters, such as the intercept (log $a$) and 'scaling elevation level' ($L$) (see Glossary), defined as the mass-specific value of a trait at the pivotal midpoint of a log–log regression (following the concept of 'metabolic level' used in studies of body-mass scaling relationships of metabolic rate by Glazier, 2009, 2010, 2020b and Killen et al., 2010; see Glossary) may also be compared to specific causal factors. The antilog of the intercept in a log–log plot ($a$) is standardized to 1-unit mass, but its use is complicated by mathematical autocorrelation with the slope ($b$) (see Gould, 1966; Peters, 1983; McNab, 1988; Glazier, 2009, 2010, 2020b; Niklas and Hammond, 2019). By contrast, although $L$ is not autocorrelated with $b$, it depends on the midpoint body mass at which it is estimated (Glazier, 2009; 2010; 2020b). Comparison of $L$ among scaling relationships is most useful when their midpoint masses are most similar. Under these conditions, body mass is largely controlled, but only at the midpoint body masses. If the slopes of multiple scaling relationships differ, comparisons of trait size within body-size intervals outside the midpoint of each body-size range will still be subject to varying body-size effects (see also Boxes 1 and 2).

Commonality of body-mass scaling slope (e.g. $b \approx 3/4$) has been used to support the view that the rates of various biological processes, such as metabolism, growth, maturation, reproduction and aging, are mechanistically linked (e.g. Brody, 1945; Fenchel, 1974; Peters, 1983; Blaxter, 1989; Brown et al., 2004; Sibly et al., 2012). Peters (1983) discussed the parallelism of scaling slopes of various 'biochemical and physiological processes' as evidence that they are supported by metabolism (p. 40). He described this 'allometric parallelism', also called 'allometric symmetry' (Calder, 1984) or 'symmorphic allometry' (Glazier et al., 2020a), as

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illustrating the principle of similitude (Thompson, 1942) or similarity (Kleiber, 1961). Other examples of allometric parallelism, involving similar scaling slopes among the rates or durations of various biological processes, are provided by Adolph (1949), Stahl (1962), Western (1979), Lindstedt and Calder (1981) and Lavigne (1982), among others.

Even more interesting and revealing are cases where scaling slopes (size quotients) are not fixed, but vary in related ways for multiple traits. Some examples (involving positive or negative associations) include the scaling slopes for offspring size and number among various taxa of animals and plants (Hendriks and Mulder, 2008; Glazier, 2018a), basal metabolic rate and genome size among orders of birds and mammals (Kozłowski et al., 2003), resting metabolic rate and longevity among classes of vertebrates (Glazier, 2010), resting metabolic rate and diving duration in ectothermic versus endothermic animals (Glazier, 2010; Verberk et al., 2020), rate of metabolism or excretion and body surface area among pelagic invertebrates (Hirst et al., 2014; 2017; Glazier et al., 2015; Tan et al., 2019), resting metabolic rate, ingestion rate, growth rate and gill surface area among populations of a freshwater amphipod from spring habitats with versus without fish predators (Glazier et al., 2011; 2020a; Glazier and Paul, 2017), and basal metabolic rate and longevity among three orders of small eutherian mammals (Fig. 2B). Other examples are cited in Glazier (2010) and the Supplementary Materials and Methods.

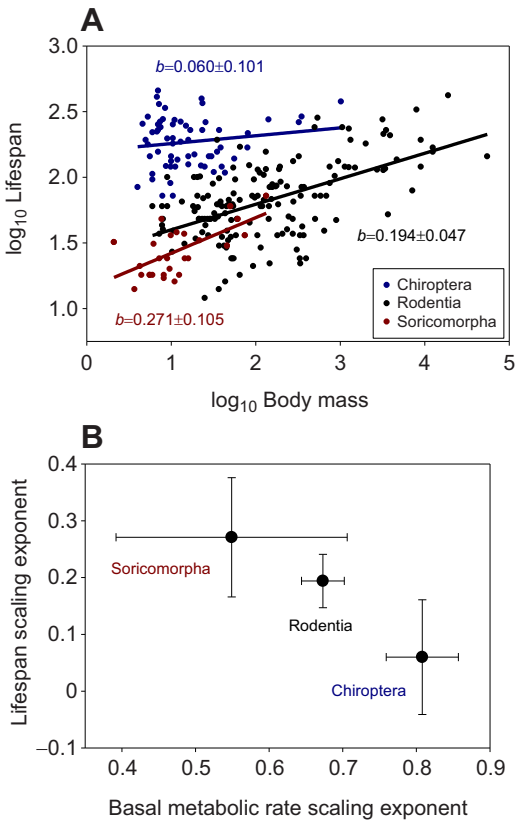


**Fig. 2. Comparisons of the body-mass scaling of maximum lifespan and basal metabolic rate of three orders of small eutherian mammals.** (A) Relationships between $\log_{10}$ lifespan (months) and $\log_{10}$ wet body mass (g). Scaling exponents (*b*) ±95% confidence intervals are indicated. Least squares regression equations and statistics are given in Table S1. Data from Wilkinson and South (2002) and Ernest (2003). (B) Comparison of body-mass scaling exponents (±95% confidence intervals) for life span with those for basal metabolic rate (values from Fig. 1A). Note the negative correlation between these exponents, as predicted by metabolic theory.

Of course, the SA method assumes that scaling relationships are log-linear. However, even non-linear or curvilinear scaling patterns may be compared. Polyphasic scaling patterns may be compared by focusing on the scaling parameters of specific linear segments. For example, the scaling slope for metabolic rate shows ontogenetic shifts in various aquatic invertebrates that parallel changes in the slope for body surface area, as estimated by Euclidean geometry (Glazier et al., 2015). In addition, curvilinear relationships may be compared according to their overall pattern of curvature [as indexed by the coefficient $c$ of the quadratic term ($cx^2$) in a polynomial equation, herein called the 'scaling curvature coefficient'; see Glossary]. For example, the concave upward scaling of basal metabolic rate in mammals is paralleled by similar concave upward scaling of maternal energy intake during lactation (Douhard et al., 2016), ingestion rate, offspring biomass production, population growth rate and locomotor costs (Bueno and López-Urrutia, 2014) (all with positive curvature coefficients), but concave downward scaling of longevity (Bueno and López-Urrutia, 2014) (showing a negative curvature coefficient). Similarly, in crustaceans, the concave downward body-mass scaling of egg mass ($c$=−0.079) is the mirror image of the concave upward scaling of number of eggs per clutch ($c$=+0.095), as would be expected from a trade-off between egg size and number (Glazier, 2018a).

Comparisons of the intercepts or elevations of scaling relationships may also be revealing. For example, Fenchel (1974) showed how the elevation of the scaling relationship for the intrinsic rate of population growth of different groups of unicellular and multicellular organisms relates positively to that for metabolic rate, thus suggesting a mechanistic link between these traits. Among various taxa of animals and plants, the elevation of the scaling relationship for offspring mass tends to correlate negatively with that for offspring number in a clutch (Hendriks and Mulder, 2008). In addition, Glazier (2010) reported a significant negative correlation between the scaling coefficients ($a$) (see Glossary) for maximum longevity and resting metabolic rate among classes of vertebrates. This finding supports the classical 'rate of living theory' (Rubner, 1908; Pearl, 1928), unlike residual analyses (see e.g. Speakman, 2005a, 2005b; De Magalhães et al., 2007; Glazier, 2015).

The SA method provides an alternative (complementary) method to commonly used residual analyses. Residual analysis focuses on how specific causal factors relate to deviations of trait values of individuals, populations or species from an overall body-mass scaling relationship. By contrast, the SA method focuses on how specific factors relate to the size dependence of a trait, as revealed by the slopes or elevations of various scaling relationships in different biological or ecological contexts. Both of these methods (and others) may be needed to understand fully how particular factors affect specific phenotypic traits, independently of body size. However, although the SA method may be useful, it is limited by the availability of sufficient data to construct multiple scaling relationships suitable for rigorous statistical comparisons of scaling parameters.

### Summary of methods

I have briefly discussed five possible major kinds of methods for removing the effect of body size on trait variation when that effect interacts with the effects of other causal factors (see also Table 1). These methods focus on different aspects of this commonly encountered problem. The NA method controls for body size, by

restricting the body-size range examined. The CA method controls for how a trait relates to body size in specific biological or ecological contexts. The AA method controls for interactive effects between body size and other specific causal factors. The MFA method controls for and partitions multiple effects of body size and other factors (independent variables). The SA method controls for body size at the level of whole size-scaling relationships. No method is a panacea. Each has merits and demerits. Note that simply including an interaction term in a statistical model is not a sufficient remedy because this procedure merely identifies a covariance between the effects of body size and a treatment factor, rather than clearly separating their effects.

The NA method controls the effect of body size by focusing on only a narrow range of body sizes, and thereby side-steps potential problems involving interactions between the effect of body and that of other causal factors. Therefore, results using this method may depend on the body-size interval chosen. By contrast, the CA, AA, MFA and SA methods consider the entire range of body sizes for which data are available, and include additional relevant biological or ecological factors, as well. Although the NA, CA, AA and MFA methods factor out effects of body size at the level of individual data points, the SA method factors out body size at the level of whole scaling relationships. However, each of these methods depends on the causal factors (independent variables) that are included for analysis. Conclusions may change depending on the factors that are considered. In addition, potentially influential factors may have been missed, a general problem for comparative biological studies (cf. Harvey and Pagel, 1991). To arrive at robust conclusions, multiple methods of body-size correction should be employed.

Combining methods may also be useful. For example, it may be profitable to combine the CA and SA methods. First, one could calculate multiple body-mass scaling relationships for specific traits in different biological or ecological contexts. Second, one could then examine whether the scaling parameters of the relationships for these different traits covary among the contextual groups that have been identified. For example, one could calculate scaling relationships for separate taxa and then examine whether the scaling slopes (size quotients) for various traits covary among these taxa. For heuristic purposes, I have done this for three major taxa of small eutherian mammals (Fig. 1A and Fig. 2). As can be seen, the scaling slopes for basal metabolic rate and maximal lifespan not only differ significantly among these taxa, but also covary negatively among them (Fig. 2B), thus suggesting a mechanistic link, as predicted by metabolic theory (e.g. Rubner, 1908; Pearl, 1928; Western, 1979; Western and Ssemakula, 1982; Peters, 1983; Rollo, 1995; Brown et al., 2004). As another example, Glazier et al. (2020a) have shown that resting metabolic rate, growth rate, gill surface area and inferred ingestion rate show body-mass scaling slopes that are all substantially lower in a parallel way in populations of the freshwater amphipod *Gammarus minus* Say 1818 from spring habitats with versus without fish predators. This 'symmorphic allometry' suggests that size-selective fish predation has favored concerted evolutionary changes in multiple traits that transcend effects of body size.

## Perspectives and conclusions

I hope that I have made clear in my Review that controlling for the effect of body size on trait variation is complicated. The classic 'criterion of subtraction' is not a precise 'surgical instrument', because the effect of body size on a specific trait may itself depend on the effects of various other associated intrinsic and extrinsic causal factors. Therefore, conclusions derived using it and other methods of size correction must be considered contingent on the biological or ecological context of the analysis performed. Much attention has been given to using phylogenetic approaches when carrying out comparative analyses, including those involving corrections for effects of body size (Garland and Ives, 2000; Smaers and Rohlf, 2016). However, trait variation is influenced by not only evolutionary ancestry, but also present-day ecological conditions (Westoby et al., 1995; McNab, 2002). Species may have not only different degrees of evolutionary relatedness, but also different degrees of ecological relatedness that may affect how specific traits relate to body size, and thus the body-size correction methods used. This is true even if the ecological effects do not involve the ecological factor that is being examined. Therefore, I recommend that body-size correction in comparative analyses should be not only 'phylogenetically informed', but also 'ecologically informed' (see also Glazier, 2014a).

For example, McNab (1988, 2008, 2009, 2012) has noted that body-mass scaling relationships for metabolic rate may depend not only on the taxonomic groups included, but also the biological and ecological characteristics of the species analysed. Therefore, he has recommended analysing metabolic scaling within 'ecologically and physiologically uniform sets of species' (McNab, 1988, p. 25: essentially the CA method), or by adjusting metabolic scaling relationships to the effects of various biological or ecological factors (McNab, 2008; 2009; 2012: essentially the AA method). The classic 3/4-power law of metabolic scaling was originally based on a relatively homogenous sample of domesticated birds and mammals (Kleiber, 1932; 1961), which helps explain why this purported law often does not apply to more heterogenous samples. In my opinion, ecologically informed analyses could advance comparative biological studies just as much as phylogenetically informed analyses have done. As McNab (1988) has remarked, 'The contamination of [metabolic] scaling by secondary ecological and physiological factors will probably apply to other scaling functions' (p. 48). In some cases, ecological factors may affect body-mass scaling relationships even more than phylogenetic factors (e.g. McNab, 1988; Bushuev et al., 2018).

Further complications arise when scaling relationships are curvilinear or exhibit heterogeneous variation of sample points along the body-mass axis. ANCOVA and multiple regression analyses (MFA method) assume that body-mass scaling relationships are linear (but see Packard, 2018). Although residual analyses can be based on curvilinear polynomial regressions, they are problematic when the effect of the treatment factor covaries with that for body size. They are also problematic when the range of variation of sample points depends on body size. For example, the range of residual variation may increase or decrease with increasing body mass (Box 2). This may even be seen for log-linear scaling relationships, even though logarithmic transformation helps to reduce heteroscedastic variation (see e.g. Kerkhoff and Enquist, 2009; Glazier, 2021a). For example, litter size, lifespan and gestation time are much more variable among small versus large mammals (see e.g. Eisenberg, 1981; Speakman, 2005a; De Magalhães et al., 2007; Turbill et al., 2011; Müller et al., 2012; Clauss et al., 2014; Healy et al., 2014; Lemaître et al., 2014; Szekely et al., 2015). One possible way to deal with these situations is to examine whether the expanded range of residual variation at the low or high end of the body-mass range is due to variation in the scaling slopes for different taxa or ecological groups making up the overall species sample (i.e. by using the CA method). This indeed seems to be the case for mammalian lifespan. The divergent scaling of three speciose orders of small eutherian mammals (Fig. 2A) helps explain

why the residual variation of lifespan increases towards the lower end of the body-mass range. Alternatively, one can explain the triangular variation in lifespan by separating out specific ecological or locomotor lifestyles. For example, significant differences in the scaling slopes and elevations for lifespan between volant and terrestrial mammals helps explain the relatively broad variation of lifespan at small body sizes (see Healy et al., 2014; Szekely et al., 2015; Fig. 2A). Omitting flying mammals (bats) helps to homogenize the residual variation in lifespan along the body-mass scaling axis (Austad and Fischer, 1991).

My Review has assumed that it is both possible and worthwhile to remove the effect of body size on trait variation, even when that effect interacts with the effects of other causal factors. However, this assumption may be questioned. First, one might argue about whether the effect of body size should be removed at all, because in the process some or all of the effects of causal factors that are related to body size may be removed (see e.g. Smith, 1984a; Rollo, 1995; Jeschke and Kokko, 2009; Barja, 2014; White and Kearney, 2014; Rogell et al., 2020). Body size covaries with so many factors that removing its effect precisely and completely, independently of the effect of other associated factors, may be impossible. Second, one might argue that body size is not a truly independent variable that constrains the variation of other traits, but that it has co-evolved with other traits (e.g. Rollo, 1995; Witting, 2017; White et al., 2019; Kozłowski et al., 2020; Rogell et al., 2020).

Nevertheless, I would argue that attempting to control for trait variation that relates to differences in body size is still worthwhile, even if only partial controls that are context dependent can be achieved. Controlling variation is a hallmark of scientific methodology, especially with regard to causal analyses. Although space limits prevent me from discussing relevant philosophical issues, I contend that dissecting out the effects of various factors, even if incomplete, can improve the understanding of complex living systems. Science is a stepwise, potentially endless process, which nevertheless requires one to make a first step, however imperfect, to initiate the investigation of a particular problem. Not all aspects of a complex scientific problem can be solved in one step.

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**Table S1. Least squares regression equations and statistics for relationships between $\log_{10}$ basal metabolic rate (BMR: mL O2 $h^{-1}$) or $\log_{10}$ life span (LS: months) and $\log_{10}$ wet body mass (M: g) of various taxa of small eutherian mammals depicted in Figures 1 and 2.**

| Taxon | Regression equation | r | N | P |
|---|---|---|---|---|
| **EUTHERIAN ORDERS** | | | | |
| Soricomorpha | BMR = 0.549 (M) + 0.931 | 0.812 | 26 | <0.00001 |
| | LM = 0.271 (M) + 1.150 | 0.688 | 33 | 0.00001 |
| Rodentia | BMR = 0.673 (M) + 0.654 | 0.952 | 218 | <0.00001 |
| | LM = 0.194 (M) + 1.406 | 0.548 | 157 | <0.00001 |
| Chiroptera | BMR = 0.808 (M) + 0.351 | 0.959 | 95 | <0.00001 |
| | LM = 0.060 (M) + 2.197 | 0.149 | 64 | 0.240 |
| **RODENT FAMILIES** | | | | |
| Cricetidae | BMR = 0.630 (M) + 0.794 | 0.904 | 78 | <0.00001 |
| Sciuridae | BMR = 0.600 (M) + 0.759 | 0.935 | 23 | <0.00001 |
| Muridae | BMR = 0.696 (M) + 0.586 | 0.898 | 48 | <0.00001 |
| Bathyergidae | BMR = 0.828 (M) + 0.203 | 0.976 | 11 | <0.00001 |
| Heteromyidae | BMR = 0.939 (M) + 0.154 | 0.977 | 13 | <0.00001 |
| **CRICETID SUBFAMILIES** | | | | |
| Arvicolinae | BMR = 0.559 (M) + 0.996 | 0.896 | 32 | <0.00001 |
| Sigmodontinae | BMR = 0.684 (M) + 0.664 | 0.965 | 19 | <0.00001 |
| Neotominae | BMR = 0.676 (M) + 0.644 | 0.974 | 20 | <0.00001 |
| **MURID SUBFAMILIES** | | | | |
| Murinae | BMR = 0.646 (M) + 0.714 | 0.931 | 31 | <0.00001 |
| Gerbillinae | BMR = 1.046 (M) - 0.084 | 0.949 | 14 | <0.00001 |
| **RODENT GENERA** | | | | |
| *Microtus* | BMR = 0.406 (M) + 1.219 | 0.522 | 16 | 0.038 |
| *Peromyscus* | BMR = 0.793 (M) + 0.492 | 0.935 | 10 | 0.00007 |
| *Spermophilus* | BMR = 1.074 (M) - 0.425 | 0.957 | 11 | <0.00001 |
| **RODENT SPECIES** | | | | |
| *Tamias minimus* | BMR = 0.456 (M) + 1.051 | 0.346 | 6 | 0.502 |
| *Peromyscus maniculatus* | BMR = 0.768 (M) + 0.561 | 0.463 | 13 | 0.111 |
| *Phyllotis darwini* | BMR = 0.734 (M) + 0.523 | 0.724 | 6 | 0.104 |
| *Mus musculus* | BMR = 0.748 (M) + 0.515 | 0.840 | 15 | 0.00009 |
| *Abrothrix andinus* | BMR = 0.986 (M) + 0.281 | 0.992 | 5 | 0.00088 |
| *Neotoma cinerea* | BMR = 0.879 (M) + 0.150 | 0.950 | 6 | 0.0037 |
| *Spalacopus cyanus* | BMR = 1.207 (M) - 0.563 | 0.923 | 8 | 0.0011 |
| *Octodon degus* | BMR = 1.240 (M) - 0.625 | 0.965 | 5 | 0.0079 |

**Table S2. Scaling exponents (± 95% confidence intervals) for relationships between $log_{10}$ basal metabolic rate (BMR: mL O2 $h^{-1}$) or $log_{10}$ life span (LS: months) and $log_{10}$ wet body mass (M: g) of various taxa of small eutherian mammals depicted in Figures 1 and 2.**

| Taxon | Variables | Exponent (*b*) | ±95% CI |
|---|---|---|---|
| **EUTHERIAN ORDERS** | | | |
| Soricomorpha | BMR vs. M | 0.549 | 0.157 |
| | LM vs. M | 0.271 | 0.105 |
| Rodentia | BMR vs. M | 0.673 | 0.029 |
| | LM vs. M | 0.194 | 0.047 |
| Chiroptera | BMR vs. M | 0.808 | 0.049 |
| | LM vs. M | 0.60 | 0.101 |
| **RODENT FAMILIES** | | | |
| Cricetidae | BMR vs. M | 0.630 | 0.068 |
| Sciuridae | BMR vs. M | 0.600 | 0.103 |
| Muridae | BMR vs. M | 0.696 | 0.101 |
| Bathyergidae | BMR vs. M | 0.828 | 0.140 |
| Heteromyidae | BMR vs. M | 0.939 | 0.135 |
| **CRICETID SUBFAMILIES** | | | |
| Arvicolinae | BMR vs. M | 0.559 | 0.103 |
| Sigmodontinae | BMR vs. M | 0.684 | 0.095 |
| Neotominae | BMR vs. M | 0.676 | 0.078 |
| **MURID SUBFAMILIES** | | | |
| Murinae | BMR vs. M | 0.646 | 0.096 |
| Gerbillinae | BMR vs. M | 1.046 | 0.218 |
| **RODENT GENERA** | | | |
| *Microtus* | BMR vs. M | 0.406 | 0.380 |
| *Peromyscus* | BMR vs. M | 0.793 | 0.246 |
| *Spermophilus* | BMR vs. M | 1.074 | 0.246 |
| **RODENT SPECIES** | | | |
| *Tamias minimus* | BMR vs. M | 0.456 | 1.717 |
| *Peromyscus maniculatus* | BMR vs. M | 0.768 | 0.977 |
| *Phyllotis darwini* | BMR vs. M | 0.734 | 0.971 |
| *Mus musculus* | BMR vs. M | 0.748 | 0.289 |
| *Abrothrix andinus* | BMR vs. M | 0.986 | 0.232 |
| *Neotoma cinerea* | BMR vs. M | 0.879 | 0.401 |
| *Spalacopus cyanus* | BMR vs. M | 1.207 | 0.501 |
| *Octodon degus* | BMR vs. M | 1.240 | 0.620 |

# Supplementary Materials and Methods

## ADDITIONAL SELECTED REFERENCES regarding body-size correction and scrutiny of methods used to do so

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## EXAMPLES OF COVARIANCE AMONG SCALING SLOPES OF DIFFERENT TRAITS

Animals:

Negative correlation between scaling slopes for basal metabolic rate and genome size among orders of birds and mammals (Kozłowski et al., 2003)

Negative correlation between scaling slopes for resting metabolic rate and longevity among classes of vertebrates (Glazier, 2010)

Positive correlations among scaling slopes for resting metabolic rate, ingestion rate, growth rate and gill surface area among populations of a freshwater amphipod from spring habitats with vs. without fish predators (Glazier et al., 2011, 2020; Glazier and Paul, 2017)

Positive correlation between scaling slopes for resting metabolic rate and offspring mass in mammals (Müller et al., 2012)

Positive correlation between scaling slopes for rates of feeding and respiration in pelagic animals (Kiørboe and Hirst, 2014)

Positive correlation between scaling slopes for cold-induced metabolic rate and thermal conductance in birds and mammals (Calder, 1981; Glazier, 2018b)

Positive correlation between scaling slopes for rate of metabolism or excretion and body surface area among pelagic invertebrates (Hirst et al., 2014, 2017; Glazier et al., 2015; Tan et al., 2019)

Negative correlation between scaling slopes for resting metabolic rate and diving duration in ectothermic vs. endothermic animals (Glazier, 2010; Verberk et al., 2020)

Resting metabolic rate and cell size in carabid beetles (Schramm et al., 2021)

Positive correlation between scaling slopes for metabolic rate and gill surface area in fishes (Scheuffele et al., 2021)

Phytoplankton and plants:

Negative correlation between scaling slopes for carbon-fixation rate and abundance of phytoplankton (Huete-Ortega et al., 2012)

Negative correlation between scaling slopes for photosynthetic leaf mass and population density (Deng et al., 2008)

Correlations between scaling slopes for morphological traits of plant leaves (Price and Weitz, 2012)

Prokaryotes, protists, plants and animals:

Positive correlation between scaling slopes for metabolic rate and population growth rate among prokaryotes, protists and multicellular eukaryotes (DeLong et al., 2010)

Negative correlation between scaling slopes for offspring size and number among various taxa of animals and plants (Hendriks and Mulder, 2008; Glazier, 2018a)

Other examples are cited in Glazier (2010).

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