The need to scale for differences in body size and mass: an explanation of Kleiber's 0.75 mass exponent

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Nevill, Alan M. The need to scale for differences in body size and mass: an explanation of Kleiber's 0.75 mass exponent. *J. Appl. Physiol.* 77(6): 2870–2873, 1994.—When modeling intraspecific relationships between selected measurements (Y) for differences in body mass (m) using the allometric equation $Y = am^b$ (where a is a constant and b is the exponent parameter), various studies have reported exponents greater than the anticipated $^2/_3$, often closer to the exponent 0.75 identified by Kleiber. A possible explanation for these exponents is proposed based on the findings of Alexander et al. (*J. Zool. Lond.* 194: 539–552, 1981), who observed that, within a variety of species, larger mammals have a greater proportion of proximal leg muscle mass in relation to their body mass, $m^{1.1}$. If subjects that are used to record Y exhibit a similar disproportionate increase in muscle mass with body size, then the allometric equation is likely to identify both a contribution proportional to the subject's body mass and a contribution from the disproportionate increase in muscle mass within the group. These confounding influences in Y can be identified separately by incorporating a body size parameter as well as a mass component in the allometric equation. The factor "body size" can be introduced either by partitioning the sample into discrete subgroups according to body size or, in studies involving human subjects, by introducing height as a continuous covariate. In both studies reported involving human maximal exercise, these methods were able to identify a systematic increase in Y with body size, leaving the subject's body mass component, found to be proportional to $m^{2/3}$, independent of body size.

intraspecific allometric modeling; log-linear models; multiple regression

SELECTED PHYSIOLOGICAL measurements, such as maximum oxygen uptake (in l/min) and peak and mean power (in W), are known to vary with the subject's body size. In most studies (e.g., see Refs. 10, 13, 15, 16, 19, 21), the allometric equation has been used to model such relationships

$$Y = am^b\epsilon \qquad (1)$$

where Y, m, and ϵ represent the physiological measurement, body mass, and the error ratio term, respectively, since, after a log transformation, the parameters "log(a)" and "b" can be estimated conveniently by using linear regression. However, a number of authors (e.g., see Refs. 10, 18, 19) have explained why, other than for convenience, the log transformation of model *Eq. 1* is likely to be the most appropriate form to describe such relationships. When the variables Y and m are plotted against each other, the scores are likely to diverge as the variables Y and m increase. This feature in data, known as heteroscedasticity, contravenes an important assumption of linear regression, i.e., the error term should remain constant throughout the range of observations. Fortunately, this undesirable characteristic in data can be corrected by using a log transformation provided the errors diverge at a constant rate in relation to the mean of the dependent variable Y (18).

There has been some debate in the literature as to the numerical value of b when such intraspecific relationships are modeled. Astrand and Rodahl (3) argued that, to be independent of body size, maximum oxygen uptake (in l/min) should be proportional to body mass, $m^{2/3}$. The authors based their argument on theoretical and physiological grounds that one would anticipate b to be $^2/_3$, since human power output, per unit of time, is proportional to L^2 or body mass $m^{2/3}$, where L denotes a linear function of body size. Nevill et al. (19) were able to support this assertion not only for maximum oxygen uptake but also for peak and mean power. With the use of the allometric *Eq. 1*, the appropriate proportion of body mass, required to scale peak and mean power output to be independent of body size, was given by $m^{2/3}$. A similar result was obtained when peak power output of 81 subjects, recorded on a bicycle ergometer, was scaled for differences in lean leg volume (LLV; Ref. 20). Again, the appropriate proportion of LLV required to scale peak power output was given by $(LLV)^{0.63}$ (SE of b = 0.63; SE = 0.104), i.e., approximately proportional to the cross-sectional area of the leg muscle.

A number of studies (e.g., see Refs. 5, 12, 14, 16, 22, 23) have reported estimated exponents greater than $^2/_3$, often closer to the b = 0.75 proposed by Kleiber (12), although McNab (16) restricts the 0.75 exponent to the larger mammal species with $m > 300$ g. McMahon (14) offered an explanation for these findings based on a model of elastic similarity. Heusner (8) argued that the exponent b = 0.75 was a statistical artifact caused by attempting to fit the same allometric model (*Eq. 1*) to data obtained from a number of different species. Subsequently, Feldman and McMahon (7) offered a mathematical explanation to justify the use of both these exponents when basal energy metabolism among animals of different sizes is described. However, Heusner still concludes that "to date there is no biologically satisfactory theoretical explanation of the 0.75 power of mass."

A POSSIBLE EXPLANATION FOR KLEIBER'S 0.75 MASS EXPONENT

A number of the studies that report mass exponents greater than $b = 2/3$ involve human subjects still undergoing growth or development. There is evidence to suggest that as children grow into adults their leg volume increases in a greater proportion to their body mass, $m^{1.1}$ (17). Indeed, within a variety of species (mammals) ranging from the shrew *Sorex* to the elephant *Loxodonta,* the proximal leg muscle mass was found to have a greater proportion of muscle mass to body mass in the larger mammals, $m^{1.1}$ (1).

If the subjects on which the physiological measurements of Y were obtained include individuals with a wide range of different body sizes, then the subjects will possibly have an increasing proportion of leg muscle mass in relation to their body mass. Hence, when one attempts to model the dependent variable Y for differences in body mass, the allometric *Eq. 1* will be unable to separate the contribution that reflects the increasing proportion of muscle mass within the group from the contribution of a subject's available body mass. For example, when recording measurements involving human maximal exercise, such as maximum oxygen uptake and peak and mean power, the contribution from a subject's available muscle mass, presumably proportional to $m^{2/3}$, is likely to be inflated by the increasing proportions of muscle mass among the range of different body sizes within the group, presumably proportional to $m^{1.1}$, assuming the proximal leg muscles are making a major contribution to the subjects' measurement of performance (Y)

$$Y = a_1(a_2 m^{2/3})^{1.1} = a_3 m^{0.74}$$

This argument is similar to the algebraic solution proposed by Calder (6) when offering a mathematical "explanation" for the parameter $b = 0.75$, where the author's "other factor" would be the subjects' disproportionate increase in leg muscle mass.

However, if the subjects are exhibiting this disproportionate increase in muscle mass, an important assumption associated with fitting the allometric model (*Eq. 1*) will have been violated, i.e., the proportion of muscle mass is common (homogeneous) to all subjects within the group.

ASSUMPTIONS ASSOCIATED WITH THE ALLOMETRIC EQUATION

When the allometric *Eq. 1* is fitted to data by use of log-linear regression, an important assumption associated with the model is that the parameters a and b "represent" all the subjects within the sample; e.g., if the subjects are randomly divided into two groups and separate allometric models are then fitted, there should be no significant difference between the two groups' fitted parameters a and b (this is the principle adopted to cross-validate a regression model). If there are any known factors within the sample that may systematically influence the physiological variable Y, such as age, gender, or body size, these factors must be incorporated into the allometric model to prevent distortion of the parameters a and b.

Thus, when Nevill et al. (19) modeled the maximum oxygen uptake of a group of recreationally active subjects (n = 179 men, n = 129 women) for differences in body mass, it was essential that, initially, the modeling process allowed the parameters a and b to be fitted separately for both the men and women. However, no statistically significant differences were found between the exponent parameters (0.63 and 0.72, respectively), but a significant difference was found between the constant multipliers (0.29 and 0.15, respectively). Hence, when these data were remodeled to allow for separate constant multipliers but a common exponent parameter, the following allometric equations (the parsimonious solution) were obtained: men, $Y = 0.244m^{0.67}$; women, $Y = 0.183m^{0.67}$ (R^2 = 79.1, SE of b = 0.67, SE = 0.050). If the gender differences in maximum oxygen uptake had been ignored, the fitted allometric model common for both men and women would have been $Y = 0.025m^{1.18}$ (R^2 = 55.6, SE of b = 1.18, SE = 0.060). The solution is physiologically implausible, providing an inexplicable exponent, b = 1.18, together with a smaller constant multiplier that fails to represent either the men or the women.

Another important influencing factor on variables, such as maximum oxygen uptake, is age (3). Indeed, when modeling the estimated maximum oxygen uptake results taken from the Allied Dunbar National Fitness Survey (2), Nevill and Holder (18) incorporated the age decline as a continuous negative exponential term in the allometric equation

$$Y = am^b \exp[c(\text{age})]\epsilon$$

The parameters a, b, and c were initially fitted separately for men (n = 852) and women (n = 880), who were further subdivided according to those who had, or had not, recorded at least one incidence of vigorous exercise during the 4 wk before the exercise test. After careful modeling by using the statistical package GLIM (4), the parsimonious solution retained just a single parameter for the body mass exponent b for all four groups. Not only was the single exponent parameter the most physiologically plausible solution, but the estimated value of $b = 0.67$ (R^2 = 74.1, SE = 0.025) agrees precisely with the anticipated $b = 2/3$ (3, 19). If, on the other hand, the age term had been excluded from the allometric model when maximum oxygen uptake was predicted, the resulting mass exponent would have been significantly reduced, b = 0.60 (R^2 = 65.3, SE = 0.029).

Hence, there is a clear need to extend the role of the parameter a in the allometric *Eq. 1* to incorporate all known factors that systematically influence the dependent variable Y

$$Y = a(Z)m^b\epsilon \qquad (2)$$

where $a(Z)$ can be either a discrete (e.g., gender) or continuous (e.g., age) function as described above. If, as suggested in A POSSIBLE EXPLANATION FOR KLEIBER'S 0.75 MASS EXPONENT, the group of subjects exhibits an increase in the proportion of muscle mass with body size, it will be necessary to incorporate a factor of body size as a function $a(Z)$ in allometric *Eq. 2*. This can be done in one of two different ways.

CONTROLLING FOR BODY SIZE AS WELL AS BODY MASS

One method of controlling for body size would be to partition the subjects into discrete subgroups according to their body size (using body mass as the criterion) and fitting separate a constants to each subgroup. This would create groups of similar body size that would be relatively (approximately) homogeneous in muscular development. If the proportion of muscle mass is systematically increasing with body size, then the constant multiplier a will reflect the increases in body size, leaving the contribution of body mass independent of the developmental increase in muscle mass.

An alternative method for studies involving human subjects would be to control for body size statistically by introducing height as a continuous covariate $a(Z)$ in *Eq. 2*. The effect of introducing height as a covariate is equivalent to investigating the effect of m on the dependent variable Y, having simultaneously removed the effect of differences in the subjects' heights. Because height or stature will accurately reflect body size, this method of controlling for body size will be at least as successful as the alternative discrete (but nevertheless approximate) method described above. Once again, if the proportion of muscle mass is steadily increasing, the continuous variable height will be able to reflect this rising trend.

These methods are illustrated in the following two examples involving human maximal exercise taken from previously reported studies where mass exponents were greater than $b = {}^2/_3$.

Example 1: body size used as a discrete factor in the allometric equation. When Nevill et al. (19) modeled the maximum oxygen uptake separately for men and women, the allometric equation for women was given by $Y = 0.15m^{0.72}$. If the elevated $b = 0.72$ ($R^2 = 44.3$, SE = 0.071) in the model is due to the increase in proportion of muscle mass with body size, such an effect can be controlled for by subdividing the female subjects into discrete groups according to their mass (e.g., above or below the median body mass) and fitting separate a constants to each subgroup in *Eq. 2*. When this was done, the following allometric equations were obtained: below median, $Y = 0.187m^{0.66}$; above median, $Y = 0.194m^{0.66}$ ($R^2 = 45.7$, SE of $b = 0.66$, SE = 0.077). The difference between the constant multipliers (0.186 vs. 0.194) was not quite significant ($P = 0.07$).

Example 2: height used as a continuous factor in the allometric equation. When modeling the power output results recorded on a maximum 30-s arm cycling test for a group of 20 javelin throwers of ranging abilities and body sizes, Kabitsis and Nevill (11) found the allometric relationship between power output (in W) and body mass (in kg) to be $Y = 14.88m^{0.76}$ ($R^2 = 48.6$, SE of $b = 0.76$, SE = 0.184). Again, if the elevated exponent parameter $b = 0.76$ in the model is due to the increase in proportion of muscle mass with body size, such differences can be separated from the body mass term by introducing height as a second predictor in the allometric *Eq. 2*, i.e., by allowing the continuous power function $a(Z) = a(\text{height})^c$ to reflect any increase in muscular development with body size. When log(height) was included in the multiple log-linear regression model to predict the power output Y, the resulting allometric equation was $Y = 2.27(\text{height}^{0.44})m^{0.66}$ ($R^2 = 49.4$, SE of $b = 0.66$, SE = 0.26). The contribution of the height parameter was not significant ($P > 0.05$).

DISCUSSION AND SUMMARY

When the intraspecific relationship between various physiological measurements for differences in body mass is modeled by using the allometric equation $Y = am^b$, a number of studies have reported mass exponents of approximately $b = 0.75$. An explanation is proposed on the basis of the work of Alexander et al. (1), who found that within a range of different species larger mammals have a greater proportion of proximal leg muscle mass in relation to their body mass, $m^{1.1}$. If a similar type of muscular development is present within the group of subjects from which Y measurements were obtained, then the fitted allometric equation will reflect both a contribution from the individual's muscle mass, together with the contribution due to the group's increase in proportion of muscle mass with body size. Theoretically, the combined effect on variables, such as maximum oxygen uptake in humans, could produce a body mass exponent of approximately $b = 0.74$.

These confounding influences in data can be partitioned or separated by scaling the measurements of Y by using both body size and body mass. Either by partitioning the sample into discrete subgroups according to body size or, in the case of human subjects, by introducing height as a continuous covariate in the allometric equation, any increase in proportion of muscle mass will be explained or controlled, leaving the contribution of body mass independent of body size.

The "discrete" method of controlling the effects of body size is precisely the same technique proposed by Heusner (8) to explain the "statistical artifact $b = 0.75$" between different species. However, on the basis of the studies presented here, where the fitted mass exponents are greater than $b = {}^2/_3$, there would also appear to be a need to divide the subjects according to body size within such groups (or species).

In both examples presented involving human maximal exercise, the independent contribution of body mass was very close to the anticipated $m^{2/3}$, leaving evidence of a systematic increase in both the discrete and continuous factors of body size, $a(Z)$, on the dependent variable Y. These findings, together with the results from two further studies (17, 23) where the above methods have been applied, support the proposition that the larger subjects will make a greater contribution to the dependent variable Y in relation to their body mass, implying a greater proportion of muscle mass. Combining the results from all four studies in a meta-analysis, methods described in Fisher (7a), the positive contribution of the body size component $a(Z)$ was significant ($P < 0.01$).

The evidence presented here is based on the assumption that the physiological measurements Y will be influenced, to a large extent, by the amount of available muscle mass, e.g., maximum oxygen uptake and peak and mean power. At present, the difficulty of estimating the muscle mass of subjects often precludes scaling using

this quantity. As improved techniques for measuring muscle mass become available, this line of investigation should be pursued. On the other hand, because muscle accounts for <25% of standard energy metabolism (in humans), some caution should be exercised before extending these arguments to other measurements, such as basal metabolic rate. Measurements that do not involve activity or exercise may not be influenced in quite the same way by the likely disproportionate increase in muscle mass within the groups or species. Nevertheless, when standard energy metabolism is modeled, any systematic increase in the proportion of muscle mass within a species will still contribute to an inflated estimate of the mass exponent b that can be satisfactorily explained by incorporating a function of body size as described in CONTROLLING FOR BODY SIZE AS WELL AS BODY MASS.

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