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Allometric Scaling in the Dentition of Primates and Insectivores

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Introduction

Size is probably the single most important determinant of body architecture, physiology, ecology, life history, and social organization in mammals. Morphological characteristics associated with each of these broadly defined aspects of structure and function can profitably be studied in relation to size, and none can be fully understood without considering size. Here we outline the relationship of tooth size to body size in frugivorous and folivorous primates. For comparison we shall also consider the relationship of tooth size to body size in insectivorous mammals.

Why study tooth size in relation to body size? There are at least three distinct ways that the relationship of tooth size to body size is important:

1. *Functional inference.* Physiological requirements of animals change in predictable ways as body size changes, and one way to study the functional significance of a characteristic like tooth size is to examine how it changes in relation to body size and coordinated physiological changes.

2. *Baseline comparison.* A clear understanding of the common or general relationship of tooth size to body size permits one to identify outliers that require different and special functional explanation.

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3. *Prediction of body mass.* Body size is a powerful predictor of diet and other life history parameters in living primates and other mammals, and tooth size can be used to estimate body size in fossils, providing access to a more complete reconstruction of the biology of extinct species than would otherwise be possible.

Geometry and Metabolism

Organisms are commonly described in terms of lengths, areas, and volumes. Taken singly or together, length, area, and volume (or weight) are the measures of size. These simple elements of different dimension are interrelated in complex geometric ways. Length can be measured in any one or a combination of two or three independent orthogonal directions. Two lengths are necessary to define an area, and three are required to define a volume. Change in one length affects both area and volume, and leads to a change of shape. In fact, any change in any single measure of size (length, area, or volume) leads to a change in shape. Shape remains constant only when all lengths are changed by equal proportions (not equal amounts), and even here areas and volumes change disproportionately.

As an example, imagine a morphological transformation preserving shape. This change will be *isometric,* requiring all linear dimensions to change by a constant proportion. If one length, say height, doubles, what are the consequences for breadth and depth? These too must double, as shown in Fig. 1. What about surface area? Surface area will not only double but, being of greater dimension, surface area will increase as doubling raised to the power of two. Volume will increase as doubling raised to the power of three. These powers and proportions hold no matter how complex the shape involved.

We can write a series of equations describing the relationships of length, area, and volume under the constraint of isometry, when shape is preserved:

$$\text{length } Y_1 = b_1(\text{length } X)^{1.0} \tag{1}$$

$$\text{area } Y_2 = b_2(\text{length } X)^{2.0} \tag{2}$$

$$\text{volume } Y_3 = b_3(\text{length } X)^{3.0} \tag{3}$$

where b_i is a constant of proportionality and the exponents k_i equal to 1.0, 2.0, and 3.0 are associated with length, area, and volume, respectively.

One additional comparison is important here, comparison of a volume to an area. Considering that length $X = [(\text{area } Y_2)/b_2]^{1/2}$ [Eq. (2)] and that length $X = [(\text{volume } Y_3)/b_3]^{1/3}$ [Eq. (3)], then

$$\frac{\text{volume } Y_3}{b_3} = \left(\frac{\text{area } Y_2}{b_2}\right)^{3/2}$$

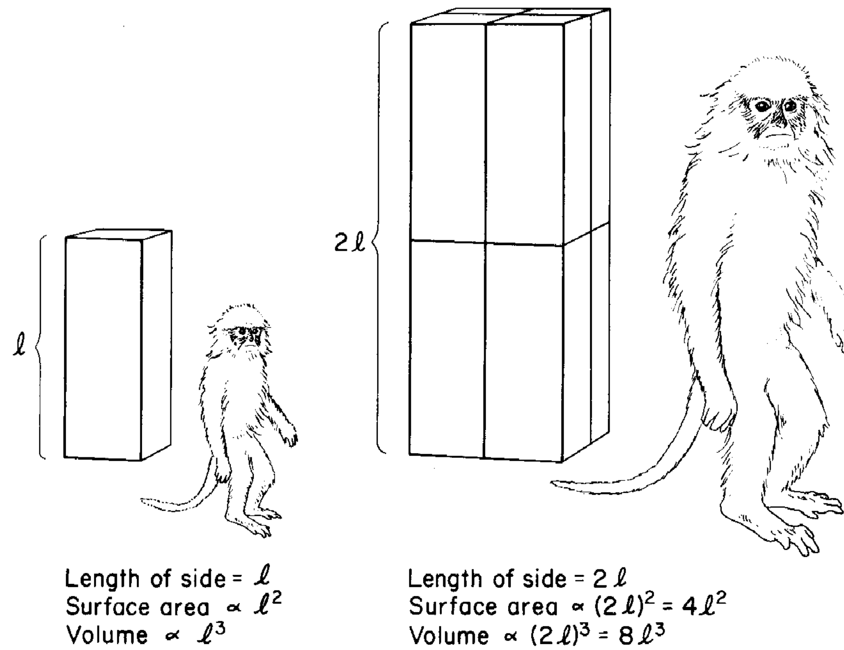

Fig. 1. Isometric transformation of simple or complex figures. Doubling all lengths l in figures at left leads to disproportionate increases in surface area and volume (or weight) in figures at right. To maintain shape at different sizes, all lengths must be changed by the same proportion, and area and volume will necessarily change as the second and third powers of this proportion.

and

$$\text{volume } Y_3 = \frac{b_3}{(b_2)^{3/2}} \left(\text{area } Y_2\right)^{3/2}$$

Consequently

$$\text{volume } Y_3 \propto (\text{area } Y_2)^{1.5} \quad (4)$$

Using a similar series of steps, but solving for area, one has

$$\text{area } Y_2 \propto (\text{volume } Y_3)^{0.67} \quad (5)$$

The exponents (or their inverses) 1.0, 2.0 (0.5), 3.0 (0.33), and 1.5 (0.67) are the powers associated with isometric or "geometric" scaling, preserving shape while the relationships of length, area, and volume are altered.

Nonisometric changes, involving changes in shape, are termed *allometric.* While there is a finite number of isometric relationships, allometry includes an infinite number of possibilities. For our purposes, only one allometric change is important. This is the allometry of heat production (basal metabolism) in eutherian mammals relative to body mass, which has been determined empirically to involve an allometric exponent k of 0.75 (Kleiber, 1932; Schmidt-Nielsen, 1975). Note that this metabolic exponent of 0.75 differs from all of the geometric exponents and their inverses discussed above. If, in examining tooth crown area in relation to body mass, we can distinguish a scaling coefficient of 0.75 from 0.67, then we might suspect that crown area is somehow responding to requirements of metabolism and not simply changing isometrically.

Methods

Quantitative study of size and shape requires careful consideration of the nature of the problem to be solved, and appropriate choices of variables to be compared, models of underlying relationship, and curve fitting techniques.

Choice of Variables

Body mass is usually used as a baseline in the study of primate body architecture, locomotion, substrate preference, ecology, faunal structure, home range size, life history, social organization, sexual dimorphism, and other parameters, but this is not invariably the case. Choice of a body size standard is often dictated by the standard employed in other studies to which comparison will be made. Occasionally it may be necessary to repeat allometric analyses with different body size standards to make them comparable to a diverse range of related studies. It is sometimes best to study the allometry of body architecture in relation to body length or limb length rather than body mass. Cranial allometry in a series of fossil species, for example, might best be studied relative to one or more cranial dimensions rather than body mass because body mass cannot be measured directly in fossil species. However, comparison with modern species for which body mass is known might make it advantageous to use predicted body mass in the fossils as a baseline. The choice of a body size standard must be appropriate for the overall objectives of any given study.

Choice of a measure or measures of tooth size also affects the results in studying tooth size allometry. Hylander (1975) used maxillary incisor breadth as a measure of tooth size in studying functional differences in the anterior dentition of folivorous and frugivorous cercopithecoids. Kay (1975*b*) measured total crown length and other detailed morphological characteristics of lower second molars to relate functional features of molar structure to diet in primates. Gould (1975) measured the sum of maxillary postcanine crown areas in studying the relationship of tooth size to metabolism and/or environmental grain. Each of these measures of tooth size is appropriate for a specific study, yet none can be regarded as representative for all possible problems of allometric scaling one might encounter.

Tooth crown area (crown length multiplied by width) is often used as a measure of tooth size, but crown area does not necessarily scale like crown same dimension. Power functions, as general models, include comparisons of quantities of the same dimension as a special case. Finally, as we shall show in the following analysis, power functions often fit actual data significantly better than do simple linear models.

Curve Fitting Techniques

In the Introduction we discussed three distinct objectives of a study of tooth size in relation to body size. The first two of these objectives, functional inference and baseline comparison, require quantification of the structural relationship of tooth size to body size. Error is inherent in both variables and, given some degree of correlation between variables, the principal or major axis best describes the slope or scaling relationship of the variables. The third objective, prediction of body size from tooth size, requires a different approach. Here tooth size is assumed to be known and error is inherent in only one variable, predicted body size. Least squares regression is explicitly designed for prediction problems, minimizing error in the dependent variable. Regression of body size on tooth size is appropriate in determining equations for predicting body size from tooth size.

Slopes calculated by regression are systematically lower than those calculated as principal or major axes, with the difference in calculated slopes increasing as the correlation between variables decreases. If regression is used to analyze structural relationship, the value of slopes (and allometric coefficients) will be systematically underestimated. The choice of methods for estimating slopes makes a difference, and this choice should be made with the differing objectives of analyzing structure versus making predictions clearly in mind.

Tooth Size and Body Size in Primates

Our objectives in studying primate tooth size scaling in relation to body size are several. We are interested to know whether the sizes of individual teeth, or upper and lower cheek teeth considered as a unit, scale isometrically or allometrically. This question is considered in relationship to the more specific problem of geometric versus metabolic scaling of tooth size. Second, we want to know the uniformity of tooth size–body size scaling in primates and to identify outliers that do not fit baseline scaling as defined by the majority of primate species. Finally, we want to know how to use tooth size to predict body size.

Metabolic scaling is defined in terms of body mass, and for this and other reasons we have used body weight or mass as our criterion of body size. Tooth size is measured as crown area—crown length multiplied by width—to avoid