Growth and Allometry in Modern Morphometrics: Review

Modern Morfometride Büyüme ve Allometri

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ABSTRACT In traditional shape analysis, linear distance, angles and ratios of measurements are used in multivariate statistical analyses. The challenge in any analysis of growth is to extend quantitative description and to explore aspects of the biology of a given organism, such as the genetic basis of morphogenesis, the phylogenetic underpinnings of developmental patterns, or the role of hormones, teratogens, dietary elements, and other environmental variables on the growth process. It is important to define the growth process with mathematical equations that include biologically meaningful parameters. Size has several different meanings such as length, area, volume, and even the linear combinations of different measured quantities. However, in statistical shape analysis, size is obtained by a specific approach, which provides the geometrical information of an object. Allometry theory was developed as a result of shape variations that occur with the growth of an organism's different parts or organs at different rates. As the idea of size and shape has been one of the most controversial subjects in traditional morphometrics, allometry (relationship between size and shape) plays an important role in the development of statistical shape analysis. The quantities used in traditional morphometrics for size are highly correlated with shape. Thus, many different methods have been proposed for size correction. However, because of disagreement regarding relevant methods of size correction, researchers have investigated different methods for the analysis of shape data. Today, new geometrical morphometric approaches are being used extensively to explore and model growth and allometry.

Key Words: Allometry; growth models, statistical shape analysis

ÖZET Geleneksel şekil analizinde, doğrusal uzaklık, açı ve oran ölçümleri çok değişkenli istatistiksel analizlerde kullanılmaktadır. Büyümenin analiz edilmesinde karşılaşılan zorluklar, verilen bir organizmanın biyolojisinin nicel olarak tanımı vermek ve organizmanın biyolojisinin morfogenezinin genetik temelleri, gelişimsel örneklerin filogenetik destekleyicileri veya hormonların, teratojenlerin, diyet öğelerinin ve diğer çevresel değişkenlerin büyüme süreci üzerindeki rolü gibi yönlerini araştırmaktır. Büyüme sürecinin, biyolojik olarak anlamlı olan parametreleri içeren matematiksel eşitlikler ile tanımlanması oldukça önemlidir. Büyük kavramının uzunluk, alan, hacim ve hatta ölçülen farklı niceliklerin doğrusal kombinasyonları gibi çeşitli farklı anlamları bulunmaktadır. Ancak istatistiksel şekil analizinde büyüklük, nesnenin geometrik bilgisinin elde edilmesini sağlayan özel bir yaklaşım ile elde edilmektedir. Allometri teorisi, bir organizmanın farklı bölge veya organlarının farklı oranlarda büyümesiyle meydana gelen şekil değişkenliklerinin sonucu olarak geliştirilmiştir. Büyüklük ve şekil kavramları geleneksel morfometride tartışmaya açık konular olduklarından, allometri (büyüklük ve şekil arasındaki ilişki), istatistiksel şekil analizinin gelişmesinde oldukça önemli bir rol oynamıştır. Geleneksel morfometride büyüklük için kullanılan niceliklerin, şekil ile yüksek derede ilişkili oldukları görülmüştür. Bu nedenle, büyüklük düzeltmesi için pek çok yöntem önerilmiştir. Ancak, büyüklük düzeltmesi için önerilen yöntemler üzerine olan uyuşmazlık nedeniyle araştırmacılar şekil verilerinin analizi için farklı yöntemler araştırmışlardır. Günümüzde bu yeni geometrik morfometrik yaklaşımlar büyüme ve allometriyi araştırmak ve modellemek için yaygın olarak kullanılmaktadır.

Anahtar Kelimeler: Allometri; büyüme modelleri, istatistiksel şekil analizi

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Many studies in medicine are related to the examination of the geometrical properties of an organ or organism. In these studies, statistical analysis consists of the quantitative or qualitative measuring of given values; recently, a given organ or organism's appearance or shape has been used as the input data for the development of imaging techniques.[1] Two-group comparison, asymmetry, growth and allometry studies are examples of the most used statistical shape analysis applications.[2-4]

Statistical shape analysis involves methods where geometrical information is obtained from given objects. Morphometric researches are frequently used in comparison of biological structures.[5] In traditional shape analysis methods, traditional or classical techniques include among others, principal component analysis, principal coordinate analysis, factor analysis, discriminant analysis, and multivariate analysis of variance, have been applied largely to measurement or distance data.[6] In 1926, Pearson studied a "coefficient of racial likeness," which is a measure of resemblance of the two races or groups based on length measurements between landmarks on skulls.[7] In the 1960s and 1970s, biometricians began using multivariate statistical methods to describe patterns of shape variation within and among groups. The multivariate statistical analysis approaches that are applied to sets of morphological variables are now referred as traditional morphometry or multivariate morphometry.[8]

Because size and shape have been controversial subjects in traditional morphometrics, allometry (the relationship between size and shape) plays an important role in the development of statistical shape analysis. While linear distance measurements are highly correlated with size, many different methods have been proposed for size correction.[9] However, because the proposed methods provide different results, there is disagreement regarding the relevant methods for size correction. Because of these challenges, researchers have investigated different methods for the analysis of shape data. Concurrent with these advances, David Kendall and other statisticians developed a rigorous statistical theory for shape analysis that made the combined use of multivariate statistical methods and methods for the direct visualization in biological form possible.[8]

Shape theory brought statistical analysis to geometry in the sense of Klein, who by the end of the 19th century defined the geometry of an object as those properties which are invariant to certain transformations in a given space.[10] Bookstein's, Kendall's and Goodall's and works brought together the fields of geometry, biology, and statistics and created new methods for analyzing shapes.[9, 11, 12] One of these methods is known as landmark based geometric morphometrics.[13] So that, rather than working with measurements obtained from organisms, it became possible to work with the geometric objects themselves, by taking coordinates of the landmarks as shape variables.

Many common medical and biological studies relate to how an organ or organism's shape is affected by disease, how shape is related to covariates (e.g., sex, age or environmental conditions), the comparison of shapes, how to discriminate and classify using shape, how to describe shape variability, how an organ or organism's shape changes during growth, and how shape is related to size.[14]

The form of an organism is determined by its rate of growth in various directions.[15] Change in form is intuitively thought of as the result of a combination of change in size and change in shape. A great deal of effort has been aimed at developing ways to separate these intertwined components, but such attempts often remove biologically important information from the analysis.[16]

Growth involves changes in the weight, height or other growth features of a biological structure within specific time duration. This change generally is explained by growth curve models. The shape of growth curves can show differences based on the species of the organism, environmental conditions and the structure of the feature being measured.[17]

Allometry theory was developed as a result of shape variations that occur with the growth of an organism's different parts or organs at different rates.

Allometry is based upon a principle first described by Galilei in the 1630s regarding the finding that the proportions of an organism must change as the organism grows.[18] In 1917 Thompson mentioned that there is no simple and direct relation between the size of the body and its organs; in his book that he analyzed biological processes in their mathematical and physical aspects.[15] Huxley stated that, if x be the magnitude of the animal (as measured by some standard linear measurement, or by its weight minus the weight of the organ) and y be the magnitude of the differentially-growing organ, then the relation between them is $y=bx^k$, where b and k are constants. [19] These traditional methods used in allometry consisted of fitting linear and non-linear regression equations to size measurements.

A new allometry description arose from geometric morphometry. In this new approach, allometry is defined broadly as the study of size and its consequences, and also as an association between shape and size.[20, 21] The Procrustes method, which is one of the statistical shape analysis methods, allows the calculation of size and shape as independent vectors. The Procrustes method defines size and shape as multivariate concepts, which avoids the statistical bias created by ratios.[22] Hence, allometry calculated with independent size and shape vectors will provide different results from classical allometry, which is calculated with dependent size and shape variables. Thus, it is not possible to perform bivariate regression with shape as a dependent variable and size as an independent variable because shape data are obtained as multivariate variables. Instead, a multivariate regression model could be used to demonstrate the relationship. Today, these new approaches, coupled with geometrical morphometrics, are being used extensively to explore and model growth and allometry.[23, 24, 25]

GROWTH

The challenge in any analysis of growth is to extend quantitative description and to explore aspects of the biology of a given organism, such as the genetic basis of morphogenesis, the phylogenetic underpinnings of developmental patterns, or the role of hormones, teratogens, dietary elements, and other environmental variables on the growth process.[26] It is important to define the growth process with mathematical equations that include biologically meaningful parameters; indeed, a living organism's growth process can be expressed mathematically.[27] In growth studies data can be consist of longitudinal or cross-sectional. In cross-sectional data, only once measurement is taken from any individual in a specific point in time. Longitudinal data consist of repeated measurements on the same subject at different time points. Both types of data have limitations and advantages depending upon the research question.[26]

The growth features of living structures can become non-linear over time, and linear models may not accurately explain growth. In addition, the growth of living organisms usually reaches an asymptote over time. Non-linear growth models can provide better predictions for such data sets.[17] Many different algorithms are used in non-linear regression analysis, such as the Levenberg-Marquardt, Gauss-Newton and Newton-Raphson algorithms.[28, 29] A general non-linear regression model can be written as

$$Y_i = f(X_i;\theta) + \varepsilon_i \quad i = 1, \ldots, n \tag{1}$$

In equation 1, θ is the parameter vector which is going to be predicted, ε_i are independent and identically distributed error terms with 0 mean and σ^2 variance.[30] These models are suitable for cross-sectional data where a single size measurement is obtained from each individual. The parameters that are used in the growth curves (α, β, κ, δ, and γ) have some biological meanings. α refers to the final size and corresponds to the maximum asymptote point of the curve. β represents the size at the onset and corresponds to the minimum asymptote point of the curve. κ shows the growth rate, and γ is the inflection point of the curve. δ is the second inflection point, which is found in the Richards model.[27]

In the regression models, the independent variable (X) is time (age or duration) and the dependent variable (Y) is size. Non-linear models that are commonly used in growth studies include exponential model, monomolecular model, Gom-

TABLE 1: Commonly used growth models.

Three parameter logistic model	$f(x) = \frac{\alpha}{1+\beta e^{-\kappa x}}$
Four parameter logistic model	$f(x) = \gamma + \frac{\alpha-\gamma}{1+\beta e^{-\kappa x}}$
Gompertz model	$f(x) = \alpha e^{\left\{-e^{-\kappa(x-\gamma)}\right\}}$
Richards model	$f(x) = \alpha[1+(\delta-1)e^{-\kappa(x-\gamma)}]^{\frac{1}{1-\delta}}$
Monomoleculer model	$f(x) = \alpha\left(1-e^{-\kappa(x-\gamma)}\right)$

pertz model, logistic models and Richards model (Table 1).[28, 31]

ALLOMETRY

To obtain the shape of an object, translation, scale and rotational effects must be removed from that object. If only translation and rotational effects are removed from an object, the size information of the object remains. Size-and-shape (or, form) represents geometrical information that is retained when location and rotational effects are filtered from an object.[14]

One type of statistical shape analysis is allometry, where the relationship between size and shape is investigated. The concept of allometry has several different meanings, and multiple methodological approaches are available for analysis. The concept of allometry has developed over time, and there are currently two major conceptual frameworks of allometry: Huxley-Jolicoeur and Gould-Mosimann.[32]

HUXLEY-JOLICOEUR

In 1924 Huxley stated that the best method of detecting and analyzing heterogonic growth-rate was by plotting the percentage size of the part in question against the absolute size of some dimension of the whole body.[33] The term "heterogonic growth" was used by Pezard in1918 to refer growth that is special or conditioned. This term remained the commonest expression for individual relative growth until the introduction of "allometry" in 1935.[34]

In this framework, allometry consists of the pattern of conversation among parts, and organismal shape is defined informally as the relative part sizes.[33] In traditional allometry, by measuring the size of any part of the body as a dependent variable, and the size of another part or whole of the body as an independent variable, bivariate regression analysis can be applied. If one considers t as time, x as a single measurement (e.g., the length of a bone) and y as another single measurement (e.g., the width of the same bone), then the growth rate of x (increase in length per time) can be given as dx/dt. Similarly, the growth rate of y can be given as dy/dt. The relative growth rates are proportional.[35, 36]

$$\frac{dy/dt}{y} = k\frac{dx/dt}{x} \qquad (2)$$

From equation-2 the simple allometry equation proposed by Huxley[19] has been obtained as follow:

$$y = bx^k \qquad (3)$$

By calculating ln(y) as a dependent variable and ln(x) as an independent variable, the estimates of constant b and regression coefficient k can be obtained by bivariate regression analysis.

$$\ln(y) = b + k\ln(x) + e \qquad (4)$$

If $k>1$, y is called positively allometric with respect to x, and the ratio y/x will increase through the growth period. Conversely, there is negative allometry if $k<1$, and the value of y/x will decrease with growth. If $k=1$, the traits are isometric, and only the absolute sizes of x and y change during growth because the ratio between x and y is constant (i.e., $x/y=b$). As long as the ratio of the specific growth rates of the two traits (k) is constant, the resulting allometric plot will be linear on a log-log scale.[32] In 1963 Jolicoeur proposed to use the first principal component of the covariance matrix of logarithms for the multivariate generalization of the allometry equation.[37]

GOULD-MOSIMANN

The concept of allometry has developed with geometric morphometry. Gould stated that the allometry should be defined broadly as the study of size and its consequences, not narrowly as the application of power functions to the data of growth.[21] He can be seen as the person who most aptly recapitulated and renewed the subject.[34] Mosimann defined size and shape variables in a general form from geometric considerations and Mosimann provided a mathematical framework for the analysis of size and shape based on geometric similarity.[20] With this revision, allometry is an association between shape and size, whereas isometry is their stochastic independence. [32]

Size has several different meanings such as length, area, volume, and even the linear combinations of different measured quantities. However, in statistical shape analysis, size is obtained by a specific approach, which provides the geometrical information of an object.

An important feature of size in statistical shape analysis is that it is independent from shape. This feature is not relevant for the other size features (e.g., length, area and volume). It is important to obtain a size measure that is independent from shape to determine whether the changes in size affect the shape of a given object.

The most commonly used size measure in statistical shape analysis is the centroid size which can be given as follow:[14]

$$S(X) = \|CX\| = \sqrt{\sum_{i=1}^{k}\sum_{j=1}^{m}(X_{ij} - \overline{X}_j)^2}\ ,\ X \in R^{km} \qquad (5)$$

In equation 5, X_{kxm} is the k ×m configuration matrix (Cartesian coordinates of k landmarks in m real dimensions) of an object with k landmarks in m dimensions, $\overline{X}_j = \frac{1}{k}\sum_{i=1}^{k} X_{ij}$ and $\|X\| = \sqrt{\mathrm{trace}(X'X)}$ is the Euclidean norm and C is the centering matrix which can be given as:

$$C = I_k - \frac{1}{k} 1_k 1_k{}' \qquad (6)$$

In equation 6, I_k is the k x k identity matrix and l_k is the k x l vector of ones. Centroid size is the only variable that does not correlate with shape in the absence of allometry. This independence from shape is one of the primary reasons why centroid size is often used. The other reason is that centroid size is crucial role for defining the metric for the distance between two shapes.[35]

The Procrustes method, which is one of the statistical shape analysis methods, allows for the calculation of size and shape as independent vectors. The Procrustes method defines size and shape as multivariate concepts, which avoids statistical biases created by ratios.[22] Shape can be regressed on centroid size using multivariate regression in which "shape" is the dependent variable and "centroid size" (or its logarithm) is the independent variable. Shape variables can be Procrustes coordinates, can be partial warp scores or principal component scores, which are obtained after performing principal component analysis to Procrustes coordinates.[35, 36]

Allometric analyses can be defined at three levels, according to the source of variation. Klingenberg have classified these levels of allometry as static, evolutionary and ontogenetic allometry. Static allometry deals with individuals at a single developmental stage. Ontogenetic allometry is the covariation among traits across ontogenetic stages of a given species. Evolutionary (or phylogenetic) allometry is the covariation in the phylogenetic changes of morphometric traits. [32]

STATISTICAL METHODS IN ALLOMETRY

In traditional morphometry, allometry is the covariation pattern among different body parts. With geometrical morphometry, the definition of allometry is revised to reflect the relationship between shape and size. To apply this theory to shape, it must be extended to the multivariate case because shape is multidimensional.[16, 35, 36] The multivariate linear regression model can be given as:

$$\mathbf{Y}_{n\times p} = \mathbf{X}_{n\times q}\boldsymbol{\beta}_{q\times p} + \boldsymbol{\varepsilon}_{n\times p} \quad , \quad \boldsymbol{\varepsilon} \sim N(0, \Sigma \otimes I_n) \qquad (7)$$

In this model, it is assumed that **Y** and ε have normal distributions. If n is taken as the number of individuals, p the number of dependent variables in the model, k the number of independent variables in the model, and q=k+1, the model can be written as below: [38]

$$\begin{bmatrix} Y_{11} & Y_{12} & \cdots & Y_{1p} \\ Y_{21} & Y_{22} & \cdots & Y_{2p} \\ \vdots & \vdots & \ddots & \vdots \\ Y_{n1} & Y_{n2} & \cdots & Y_{np} \end{bmatrix}_{n\times p} = \begin{bmatrix} X_{10} & X_{11} & \cdots & X_{1k} \\ X_{20} & X_{21} & \cdots & X_{2k} \\ \vdots & \vdots & \ddots & \vdots \\ X_{n0} & X_{n1} & \cdots & X_{nk} \end{bmatrix}_{n\times q} \begin{bmatrix} \beta_{01} & \beta_{02} & \cdots & \beta_{0p} \\ \beta_{11} & \beta_{12} & \cdots & \beta_{1p} \\ \vdots & \vdots & \ddots & \vdots \\ \beta_{k1} & \beta_{k2} & \cdots & \beta_{kp} \end{bmatrix}_{q\times p} + \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} & \cdots & \varepsilon_{1p} \\ \varepsilon_{21} & \varepsilon_{22} & \cdots & \varepsilon_{2p} \\ \vdots & \vdots & \ddots & \vdots \\ \varepsilon_{n1} & \varepsilon_{n2} & \cdots & \varepsilon_{np} \end{bmatrix}_{n\times p} \quad (8)$$

There are some assumptions involved with multivariate regression analysis (For these assumptions see: [39]).

To regress shape on an independent (scalar) variable, we regress p shape variables on the 1 independent variable (centroid size). Then the linear model for the regression of that vector on a scalar is: [35]

$$[Y_1 \ Y_2 \ \ldots \ Y_p] = [\beta_{01} \ \beta_{02} \ \ldots \ \beta_{0p}] + [\beta_{11} \ \beta_{12} \ \ldots \ \beta_{1p}]x + [\varepsilon_1 \ \varepsilon_2 \ \ldots \ \varepsilon_P] \quad (9)$$

Here, $[Y_1 \ Y_2 \ldots Y_p]$ is the vector of shape variables, $[\beta_{01} \ \beta_{02} \ldots \beta_{0P}]$ is the vector of constant terms, $[\beta_{11} \ \beta_{12} \ldots \beta_{1p}]$ is the vector of regression coefficients and $[\varepsilon_1 \ \varepsilon_2 \ldots \varepsilon_p]$ is the vector of residuals.

CONCLUSIONS

With the developments in the technology for medical and biological studies, various methods have been proposed for analyzing a given organ's or organism's forms by recording geometrical locations of specific landmarks. One potential method is to investigate the effects of environmental factors and diseases on the organs or organisms in terms of growth and allometry. Statistical shape analysis, a modern geometric morphometric method, plays an important role in such investigations.

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