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Statistical models for jointly analyzing multiple allometries

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HIGHLIGHTS

- Statistical model is developed for jointly analyzing multiple allometries.
- It is suitable for multiple biological traits with same property or comparability.
- It takes into account the correlations among multiple traits.
- It facilitates statistical and genetic analysis for multiple allometries.
- Two examples are used to illustrate the joint analysis for multiple allometries.

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ABSTRACT

As the reciprocal of simple allometry equation, power allometry equation can also be used to define allometry scaling but the scaling exponent has an opposite meaning to that of simple allometry equation. Based on this observation, a joint static allometry scaling model of entire body size on multiple partial body size is established, which can not only simultaneously evaluate allometry scaling of multiple partial body sizes, but also take into account the correlations among multiple partial body sizes, facilitating subsequent statistical inference and practice. Since ontogenetic allometry may be time-dependent, ontogenetic allometry is estimated by jointly analyzing changes of entire and multiple partial body sizes as growth time using multivariate stepwise analysis. Joint analysis of allometry scaling is suitable for multiple biological traits and functions with same property or comparability, which is illustrated by two examples.

1. Introduction

Allometry scaling, generally expressed as a power function, describes how morphological traits of organisms change with body size. Since the introduction of allometry scaling equation by Huxley (1932) a number of attempts have been made by biologists to justify the broad dependence of physiological, morphological, developmental, anatomic, life-historical, ecological as well as evolutional factors on body size (Calder, 1984; Enquist and Niklas, 2002; Kleiber, 1932; Niklas, 1994, 2006; Peters, 1983; West and Brown, 2005). Among diverse allometry scaling relationships, the most important and fundamental one is that metabolic rate scales to the three-quarters power of the mass of animals or plants, also known as Kleiber's law (Kleiber, 1932).

Around Kleiber's law, many biological and biochemical assumptions and models are developed, in hopes of explaining power-allometry scaling relationships between metabolic rate and body size. These models include fractal-like distribution network models (West et al., 1997, 1999a, 1999b), efficient transportation network model (Banavar et al., 1999), multi-causes model (Darveau et al., 2002), minimal overall entropy production model (Andresen et al., 2002), constructal theory (Bejan, 2000), cell model (Kozlowski et al., 2003) and energy consumption model (Makarieva et al., 2003).They offer theoretical perspectives on various possible ways to achieve

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maximum efficiency in biology under natural selection, ranging from the heat transfer, fluid mechanics, bio-energetics, statistical thermodynamics to physiology. Many observations, however, do not support the universal applicability of Kleiber's law, since power exponents vary with different factors (Price et al., 2007), such as temperature, physiological state, individual size and availability of environmental resource. As a result, the power exponent of three quarter may be explained as the average across species (Kozlowski et al., 2003), and the improvement of existing models are required for accurate interpretation of allometry scaling in biology.

Actually, there are the three terms of allometries available to describe scaling relationships between different organ parts: static allometry, ontogenetic allometry and evolutionary allometry (Cheverud, 1982; Klingenberg and Zimmermann, 1992; Stern and Emlen, 1999). Static allometry represents the relative growth between two different traits or functions in adult or at a particular developmental stage. Ontogenetic allometry refers to the growth trajectory of one trait relative to the other in ontogeny. Evolutionary allometry is the relative size between traits across species. In practice, static and ontogenetic allometries are evaluated by fitting the power function and growth trajectories, while evolutionary allometry can be estimated with the same methods as those for static and ontogenetic allometries. To investigate allometry scaling among multiple organ parts, separate parameter estimations and multiple comparisons between them are usually required. In this study, a joint analysis for allometry scaling is proposed to simultaneously estimate scaling exponents of multiple organ parts in terms of static and ontogenetic allometries.

2. Model

2.1. Static allometry

Following Huxley (1932), Huxley's "Simple equation of allometry" is of the form:

$$x = a' y^{b'} \tag{1}$$

where y and x are the entire and partial body size, respectively, a' is a normalization constant and b' is the scaling exponent. Furthermore, b' can be denoted as the ratio of relative growth rates between partial and entire body sizes:

$$b' = \frac{ydx}{xdy} = \frac{dx}{xdt} \Big/ \frac{dy}{ydt} \tag{2}$$

Let

$$b = \frac{xdy}{ydx} = \frac{dy}{ydt} \Big/ \frac{dx}{xdt} \tag{3}$$

Apparently, b also reflects the allometry scaling between partial and entire body sizes, but it has an opposite meaning against b'. Since Eq. (3) is equivalent to:

$$dy/dx = b\, y/x \tag{4}$$

by solving this differential equation, a new equation of allometry scaling can be established as:

$$y = ax^b \tag{5}$$

To investigate allometry scaling of m partial body sizes to entire body size, a joint system of differential equations can be formed on the basis of Eq. (4):

$$\begin{cases} \partial y/\partial x_1 = \beta_1 y/x_1 \\ \partial y/\partial x_2 = \beta_2 y/x_2 \\ \quad \cdots \\ \partial y/\partial x_m = \beta_m y/x_m \end{cases}, \tag{6}$$

where $\partial y/\partial x_i = \beta_i y/x_i$ $(i = 1, 2, \ldots, m)$ holds when fixing all the independent variables except for x_i. The solution for this system of equations takes the form:

$$y = \beta_0 x_1^{\beta_1} x_2^{\beta_2} \ \cdots \ x_m^{\beta m} \tag{7}$$

where β_i is partial scaling exponent of the ith partial body size to entire body size.

We define Eq. (7) as joint allometry scaling model, whose form is exactly of the same as the Cobb–Douglas function (Cobb and Douglas, 1928). This joint allometry scaling model can not only simultaneously estimate the scaling exponents of multiple partial body sizes to entire body size, but also take into account the correlations among the m partial body sizes, facilitating subsequent statistical analysis, such as statistical comparisons of allometry scaling between different partial body sizes and genetic analysis for allometry scaling of multiple partial body sizes to entire body size, among others.

2.2. Ontogenetic allometry

After the partial and entire body sizes are observed at given time points, the static scaling exponents at different ontogenetic stages or growth points can be estimated according to the corresponding static allometry scaling model. The scaling exponents may be different due to ontogenetic stages or growth points, so ontogenetic allometry scaling can be characterized by fitting changes of these scaling exponents with growth time. In practice, however, only a limited number of individuals are observed at a given time point and such a small sample is not enough to obtain a reliable estimate of scaling exponent at each time point. In this case, we can first establish the functions of partial and entire body sizes on growth time by using multivariate analysis, and then estimate the ontogenetic scaling exponents $\beta(t)$ by:

$$\beta(t) = x(t)dy(t)/y(t)dx(t) \tag{8}$$

where $x(t)$ and $y(t)$ is the functions of partial and entire body sizes on growth time, respectively.

3. Examples

3.1. Static allometry scaling of carcass traits in beef cattle

During the period of slaughter, living weight and fourteen slaughtering and carcass traits are collected on 1029 individuals. According to Institutional Meat Purchase Specifications (IMPS) for Fresh Beef guidelines, the live weight (y) is measured before slaughter after fasting 24 h; Carcass weight (x_1) is done after slaughter and bloodletting by eliminating the hide, head, feet, tail, entrails and gut fill; Net weight of beef (x_2) is that of carcass after removing the bones, ligaments and breast; The high quality beef (x_3) includes tenderloin, striploin, ribeye and high rib. The weight of bones (x_4) is that of whole bones besides head, tail and feet. The cowhide (x_9) does not include the parts of head and tail. The red offal (x_6), pizzle (x_7), oxtail (x_8), white offal (x_{10}), mesentery and omentum (x_{11}), leaf fat (x_{12}), kidney (x_{13}) and diaphragm (x_{14}) are collected by removing the surrounding fat and contents. Among that, the red offal (x_6) includes heart, liver and lung; the white offal (x_{10}) consists of stomach and intestinal. The intramuscular fat (x_5) is obtained from the sample of ribeye muscle.

The animals are randomly sampled from commercial populations of seven breeds in beef cattle. They are fed with three kinds of feedstuffs and slaughtered from 13 to 22 months old. In order to investigate the effect of breeds, feedstuff and months old of slaughter, we separately analyze the original and modified datasets. In the modified dataset, every trait is adjusted for breed, feedstuff and month old of slaughter.