Stochastic Ontogenetic Allometry: The Statistical Dynamics of Relative Growth

Anthony Papadopoulos*

Department of Biological Sciences, Texas Tech University, Lubbock, Texas, United States of America

Abstract

Background: In the absence of stochasticity, allometric growth throughout ontogeny is axiomatically described by the logarithm-transformed power-law model, $\theta_t = \log_a b + k\,\phi_t$, where $\theta_t \equiv \theta(t)$ and $\phi_t \equiv \phi(t)$ are the logarithmic sizes of two traits at any given time t. Realistically, however, stochasticity is an inherent property of ontogenetic allometry. Due to the inherent stochasticity in both θ_t and ϕ_t, the ontogenetic allometry coefficients, $\log_a b$ and k, can vary with t and have intricate temporal distributions that are governed by the central and mixed moments of the random ontogenetic growth functions, θ_t and ϕ_t. Unfortunately, there is no probabilistic model for analyzing these informative ontogenetic statistical moments.

Methodology/Principal Findings: This study treats θ_t and ϕ_t as correlated stochastic processes to formulate the exact probabilistic version of each of the ontogenetic allometry coefficients. In particular, the statistical dynamics of relative growth is addressed by analyzing the allometric growth factors that affect the temporal distribution of the probabilistic version of the relative growth rate, $k \equiv D_t(u\langle\Omega_t\rangle)/D_t(v\langle\Omega_t\rangle)$, where $\langle\Omega_t\rangle$ is the expected value of the ratio of stochastic θ_t to stochastic ϕ_t, and $u\langle\Omega_t\rangle$ and $v\langle\Omega_t\rangle$ are the numerator and the denominator of $\langle\Omega_t\rangle$, respectively. These allometric growth factors, which provide important insight into ontogenetic allometry but appear only when stochasticity is introduced, describe the central and mixed moments of θ_t and ϕ_t as differentiable real-valued functions of t.

Conclusions/Significance: Failure to account for the inherent stochasticity in both θ_t and ϕ_t leads not only to the miscalculation of k, but also to the omission of all of the informative ontogenetic statistical moments that affect the size of traits and the timing and rate of development of traits. Furthermore, even though the stochastic process θ_t and the stochastic process ϕ_t are linearly related, k can vary with t.

Competing Interests: The author has declared that no competing interests exist.

* E-mail: anthony.papadopoulos@ttu.edu

Introduction

The most notable contributor to the mathematical analysis of allometry is J. S. Huxley, who in 1924 published a seminal paper in which he proposed that the power-law function (f) be used to describe allometric growth [1]:

$$y = f(x; b,k) = bx^k,$$

where y is the size of a trait, x is the size of another trait, and b and k are useful descriptors of allometric growth [1,2]. Since then, numerous papers that support $f(x; b,k)$ as a model for allometric growth have been published. One paper, in particular, shows that f is an axiomatic functional form of allometry [3]. In theory, this suggests that the composite model $f(x(t); b,k)$, in which extrinsic time t is treated explicitly, yields an exact correspondence between $y_t \equiv y(t)$ and $x_t \equiv x(t)$, assuming that there is no stochasticity in $f(x_t; b,k)$ [4]:

$$y_t = f(x_t; b,k) = bx_t^k,$$

where y_t and x_t are the sizes of two ontogenetically related traits at any given t [4]. In reality, however, y_t and x_t are inherently correlated stochastic processes, which are correlated random variables that depend on the deterministic variable t. It is not known with certainty the value of y_t and the value of x_t until after their measurements have taken place. Thus, $f(x_t; b,k)$ is exact, but unrealistic, only as a deterministic model. Subsequently, when the relationship between the realizations of stochastic y_t and the realizations of stochastic x_t is described by f, the probabilistic version of either b or k is not always constant with t. In fact, as this paper will show, the statistical moments of the random ontogenetic growth function for y_t and for x_t affect the temporal distribution of both b and k. This phenomenon has significant implications with regard to organismal form and function. And so the objectives of this study are to first incorporate stochasticity into $f(x_t; b,k)$ by treating y_t and x_t as correlated stochastic processes, thereby formulating an exact probabilistic model for allometric growth that applies throughout the ontogeny of any organism, and then to analyze the ontogenetic statistical moments that specifically govern the temporal distribution of k.

Unlike b, k is an important descriptor of relative growth [1,5–7]. In ontogenetic studies of allometry, k is the coefficient of interest because it describes the specific growth rate of y_t relative to the specific growth rate of x_t [1,5–7]. Thus, the dimensionless ontogenetic allometry coefficient, k, is commonly referred to as the relative growth rate. Since allometric growth is inherently a stochastic process, k must be defined via stochastic analysis; but before this is done, it is necessary to first discuss important mathematical concepts, definitions, and notations used throughout this paper.

Definitions and notations

Suppose $\mathcal{S}$ is a probability space on which the stochastic process $\theta_t \equiv \theta(t)$ is defined. If $\langle \theta_t \rangle$ is the expected value (also known as the first statistical moment or the probability average) of θ_t, then the nth central moment of θ_t is $\langle \tilde{\theta}_t^n \rangle = \langle\langle^n \theta_t \rangle\rangle$, where $\tilde{\theta}_t = \theta_t - \langle \theta_t \rangle$, $\langle \tilde{\theta}_t^0 \rangle = \langle\langle^0 \theta_t \rangle\rangle = 1$ at every $t \in [0, +\infty)$, and $\langle \tilde{\theta}_t \rangle = \langle\langle^1 \theta_t \rangle\rangle = 0$ at every $t \in [0, +\infty)$. Now suppose $\phi_t \equiv \phi(t)$ is another stochastic process defined on the probability space $\mathcal{S}$. Then the probability covariance between θ_t and ϕ_t is $\langle \tilde{\theta}_t \tilde{\phi}_t \rangle = \langle\langle \theta_t, \phi_t \rangle\rangle$; an obvious extension to this relation is the important identity $\langle \theta_t \phi_t \rangle = \langle\langle \theta_t, \phi_t \rangle\rangle + \langle \theta_t \rangle \cdot \langle \phi_t \rangle$. Thus, the nth mixed moment of θ_t and $\tilde{\phi}_t^n$ is $\langle \theta_t \tilde{\phi}_t^n \rangle = \langle\langle \theta_t, \tilde{\phi}_t^n \rangle\rangle + \langle \theta_t \rangle \cdot \langle\langle^n \phi_t \rangle\rangle$. All of the stochastic processes involved in this study are defined implicitly as evolutionary, not stationary, random functions of t. With regard to the variable t, $\langle t \rangle$ equals t, and $\langle\langle^n t \rangle\rangle$ equals zero for every $n \in \mathbb{N}_2$. These equivalences hold for any deterministic process.

Ratio of first-order deterministic t-derivatives

Let X_t be the set of all deterministic or stochastic ratios of differentiable functions of t, and let $\mathcal{D}_t \langle X_t \rangle$ be the set of all ratios of first-order deterministic t-derivatives. Then, for any $\langle \Omega_t \rangle \in \langle X_t \rangle$, $\mathcal{D}_t$ is defined by

$$\mathcal{D}_t \langle \Omega_t \rangle = \left(\frac{D_t(u\langle \Omega_t \rangle)}{D_t(v\langle \Omega_t \rangle)} \middle| D_t(v\langle \Omega_t \rangle) \neq 0 \right),$$

where $u\langle \Omega_t \rangle$ and $v\langle \Omega_t \rangle$ are the numerator and the denominator of $\langle \Omega_t \rangle$, respectively. Therefore, $\mathcal{D}_t$ is a multivalued differential operator defined as the ratio of the standard first-order differential operator D_t:

$$\mathcal{D}_t \langle \cdot \rangle \equiv \frac{D_t(u\langle \cdot \rangle)}{D_t(v\langle \cdot \rangle)}.$$

An important property of $\mathcal{D}_t$ is that it operates linearly on sums of ratios of differentiable deterministic functions in which the denominators are common. For example, $\mathcal{D}_t \langle^1 \omega_t +^2 \omega_t \rangle$ equals $\mathcal{D}_t \langle^1 \omega_t \rangle + \mathcal{D}_t \langle^2 \omega_t \rangle$ if $\langle^1 \omega_t \rangle$ and $\langle^2 \omega_t \rangle$ are expressed with a common denominator.

The mathematical analysis of k

Let $\theta_t = \log_a y_t$ and $\phi_t = \log_a x_t$ each be a deterministic ontogenetic growth function such that $\theta_t = \log_a[f(x_t; b, k)] = \log_a b + k \phi_t$ and ϕ_t are deterministic variables that depend on t. Also, let $\Omega_t \equiv \theta_t \phi_t^{-1}$ be the ratio of θ_t to ϕ_t. Then the first-order derivative of the deterministic ontogenetic growth function θ_t with respect to the deterministic ontogenetic growth function ϕ_t is [1,5–7]

$$k \equiv \mathcal{D}_t \langle \Omega_t \rangle = \left(\frac{D_t \theta_t}{D_t \phi_t} \middle| D_t \phi_t \neq 0 \right) = \frac{d\theta_t}{d\phi_t},$$

where θ_t and ϕ_t are differentiable real-valued functions of t. Note: $d\theta_t / d\phi_t$ is a parametric derivative in which θ_t and ϕ_t are differentiable deterministic functions. The temporal distribution of k has been a subject of intense interest (see [6] and [7]). The reason for this is that ontogenetic processes govern the size of traits and the timing and rate of development of traits [7–11]. Thus, k can vary with t [5–7]; this implies that the relationship between θ_t and ϕ_t may not always be linear [5–7]. When θ_t and ϕ_t are linearly related, $D_t \theta_t$ is proportional to $D_t \phi_t$ [1]; k is constant with t, and so the relationship between θ_t and ϕ_t is described by $\log_a f$. In contrast, when θ_t and ϕ_t are nonlinearly related, $D_t \theta_t$ is not proportional to $D_t \phi_t$ [5]; k varies with t, and so the relationship between θ_t and ϕ_t is not described by $\log_a f$. Both cases have been observed experimentally (see [12] and [13]). Although deterministic log-linear allometric growth trajectories are always the result of $D_t(u\langle \Omega_t \rangle) = D_t \theta_t$ being proportional to $D_t(v\langle \Omega_t \rangle) = D_t \phi_t$, the proportionality between $D_t(u\langle \Omega_t \rangle)$ and $D_t(v\langle \Omega_t \rangle)$ is not always expected to hold under stochastic log-linear allometric growth trajectories because θ_t and ϕ_t are correlated stochastic processes; their probability distributions interact in ways that are not intuitively obvious. The following is a case in point.

Since θ_t and ϕ_t are inherently correlated stochastic processes, $\langle \Omega_t \rangle$ contains the central and mixed moments of those processes (Methods, equations 6–8). These statistical moments are described by the allometric growth factors (see Methods, equation 9) that affect the temporal distribution of $\langle \Omega_t \rangle$. Of course, $\langle \Omega_t \rangle$ must be transformed into its probabilistic derivative, $\mathcal{D}_t \langle \Omega_t \rangle$, in order to analyze the allometric growth factors that affect the temporal distribution of k. These allometric growth factors, which only appear in the probabilistic version of $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$, are essential because they provide important insight into ontogenetic allometry. Failure to account for the inherent stochasticity in Ω_t leads not only to the miscalculation of k, but also to the omission of all of the informative central and mixed moments of the random ontogenetic growth functions that govern the statistical dynamics of k. Therefore, by treating θ_t and ϕ_t as correlated stochastic processes, this study reveals and analyzes the allometric growth factors that affect the temporal distribution of k.

The probabilistic derivative, $\mathcal{D}_t \langle \Omega_t \rangle$, in which Ω_t is a ratio of correlated stochastic processes, is newly presented in this study as the inner mean derivative of a random function with respect to a random function. This derivative implies the differentiation of the expected value of a random function with respect to the expected value of a random function, whereas the outer mean derivative of a random function with respect to a random function—for instance, $\langle D_t \theta_t / D_t \phi_t \rangle$—implies the expected value of a ratio of correlated stochastic t-derivatives. In other words, $\mathcal{D}_t \langle \Omega_t \rangle$, in which $\Omega_t \equiv \theta_t \phi_t^{-1}$ is a stochastic process, defines k as a deterministic variable, whereas $\langle D_t \theta_t / D_t \phi_t \rangle$, in which $D_t \theta_t$ and $D_t \phi_t$ are stochastic, is the deterministic coefficient $\langle k \rangle$. Although all of the statistical moments of k can be derived from $D_t \theta_t / D_t \phi_t$, $\langle k \rangle$ or $\langle\langle^n k \rangle\rangle$ for any $n \in \mathbb{N}_2$ cannot vary with t because $D_t \theta_t / D_t \phi_t$ is simply a random variable, not a stochastic process. Thus, only $\mathcal{D}_t \langle \Omega_t \rangle$, by which the deterministic variable k is defined, can vary with t. This distinction between the inner mean derivative $\mathcal{D}_t \langle \Omega_t \rangle$ and the outer mean derivative $\langle D_t \theta_t / D_t \phi_t \rangle$ is important and is further addressed in the Discussion.

The concept of an inner mean derivative and an outer mean derivative only applies to the ratio of stochastic t-derivatives. The expected value of a stochastic t-derivative, such as $\langle D_t \phi_t \rangle = D_t \langle \phi_t \rangle$, is simply referred to as a mean t-derivative (see equation 4.62 in [14]). Nelson [15] introduced mean derivatives (albeit based on the conditional expectation) to address issues in stochastic mechanics (see [16] and [17] for details).

The probabilistic version of $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$ is not readily calculable because the numerator and the denominator of Ω_t are correlated stochastic processes; the expected value of a ratio of correlated stochastic processes is generally not equal to the ratio of expected values of the stochastic processes [18]. Therefore, this study equates $\langle \Omega_t \rangle$ to its Taylor series expansion in order to reveal the central and mixed moments of the stochastic processes on which $\mathcal{D}_t$ operates (Methods, equations 6–8). Although $\langle \Omega_t \rangle$ can be expanded as $\upsilon_t \equiv \langle \langle \theta_t, \phi_t^{-1} \rangle \rangle + \langle \theta_t \rangle \cdot \langle \phi_t^{-1} \rangle$ (which is not the Taylor series for $\langle \Omega_t \rangle$), $\mathcal{D}_t \upsilon_t$, like its identity $\mathcal{D}_t \langle \Omega_t \rangle$, is not readily calculable because ϕ_t^{-1} is stochastic. Subsequently, the Taylor series expansion of $\langle \Omega_t \rangle$ is essential for evaluating the probabilistic version of $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$. Also, $\langle \Omega_t \rangle$ contains the term $\varphi_t \equiv \tilde{\phi}_t \langle \phi_t \rangle^{-1}$, which is the ratio of $\tilde{\phi}_t$ to $\langle \phi_t \rangle$ (Methods, equation 8). Naturally, φ_t and $\tilde{\phi}_t$ share similar statistical properties; for example, $\langle \varphi_t \rangle$ equals zero at every t, and $\langle \varphi_t^n \rangle$ equals $\langle \langle {}^n \varphi_t \rangle \rangle$ for every $n \in \mathbb{N}_2$.

Results: The statistical dynamics of k

Using the definitions and notations described above, the inner mean derivative of the random ontogenetic growth function θ_t with respect to the random ontogenetic growth function ϕ_t is (see Methods, equations 6–11, for derivation)

$$k \equiv \mathcal{D}_t \langle \Omega_t \rangle = \sum_{n=0}^{\infty} \left(\frac{(-1)^n D_t \langle \theta_t \varphi_t^n \rangle}{D_t \langle \phi_t \rangle} \middle| D_t \langle \phi_t \rangle \neq 0 \right) = \sum_{n=0}^{\infty} \left(\frac{(-1)^n d \langle \theta_t \varphi_t^n \rangle}{d \langle \phi_t \rangle} \right) = \sum_{n=0}^{\infty} k_n, \quad (1)$$

where $\langle \theta_t \varphi_t^n \rangle$ and $\langle \phi_t \rangle$ are differentiable real-valued functions of t. Equation (1) is the exact probabilistic version of k. This equation is also the exact general solution for the inner mean derivative of a random function with respect to a random function and can thus be applied to any ratio of correlated stochastic t-derivatives; no simplifying assumptions were made to derive equation (1). Note: $k_n = (-1)^n d \langle \theta_t \varphi_t^n \rangle / d \langle \phi_t \rangle$ for each $n \in \mathbb{N}_0$ is a parametric derivative in which $\langle \theta_t \varphi_t^n \rangle$ and $\langle \phi_t \rangle$ are differentiable deterministic functions.

Each of the nth terms in equation (1) is the statistical relative growth rate, k_n, which can be expanded as (see Methods, equations 12 and 13, for derivation)

$$k_n = \frac{(-1)^n d \langle \langle \theta_t, \varphi_t^n \rangle \rangle}{d \langle \phi_t \rangle} + \langle \theta_t \rangle \cdot \frac{(-1)^n d \langle \langle {}^n \varphi_t \rangle \rangle}{d \langle \phi_t \rangle} + \langle \langle {}^n \varphi_t \rangle \rangle \cdot \frac{(-1)^n d \langle \theta_t \rangle}{d \langle \phi_t \rangle}, \quad (2)$$

where the summed terms

$${}^1\mathfrak{F}_n = \frac{(-1)^n d \langle \langle \theta_t, \varphi_t^n \rangle \rangle}{d \langle \phi_t \rangle}, \quad {}^2\mathfrak{F}_n = \langle \theta_t \rangle \cdot \frac{(-1)^n d \langle \langle {}^n \varphi_t \rangle \rangle}{d \langle \phi_t \rangle},$$

$$\text{and } {}^3\mathfrak{F}_n = \langle \langle {}^n \varphi_t \rangle \rangle \cdot \frac{(-1)^n d \langle \theta_t \rangle}{d \langle \phi_t \rangle}$$

describe the allometric growth factors that affect the temporal distribution of k. The 0th term in equation (1) is $k_0 = {}^1\mathfrak{F}_0 + {}^2\mathfrak{F}_0 + {}^3\mathfrak{F}_0$ (where ${}^1\mathfrak{F}_0 = 0$ at every t and ${}^2\mathfrak{F}_0 = 0$ at every t), which becomes k either when Ω_t is deterministic or when $\sum_{n=1}^{\infty} k_n$ is zero at every t. Traditionally, $k_0 = {}^3\mathfrak{F}_0$ is calculated as k and is the ratio of $D_t \langle \theta_t \rangle$ to $D_t \langle \phi_t \rangle$ [19]. Note, however, that

evaluating only k_0 when $\sum_{n=1}^{\infty} k_n$ is not zero does not yield an exact k because the other terms—k_1, $k_2, \ldots, k_n$—must also be considered. Thus neglecting $\sum_{n=1}^{\infty} k_n \neq 0$ clearly leads to a miscalculated k. Moreover, k (or k_n for every $n \in \mathbb{N}_0$) can vary with t; nonlinear allometries can occur, even though the stochastic process θ_t and the stochastic process ϕ_t are linearly related.

The statistical dynamics of k can be readily analyzed by the summed terms (${}^1\mathfrak{F}_n$, ${}^2\mathfrak{F}_n$, and ${}^3\mathfrak{F}_n$) in equation (2). Consider the following example: let the stochastic processes, y_t and x_t, belong to the finite family of $q e^{rt}$—the exponential growth-law functions in which only r is a random variable—such that the random ontogenetic growth function θ_t is $\theta_t = s_y + r_y t$ and the random ontogenetic growth function ϕ_t is $\phi_t = s_x + r_x t$. Then, if $s_x = \log_e q_x$ equals zero, equation (2) is (see Methods, equations 14–16, for derivation)

$$k_n = \frac{(-1)^n \langle \langle r_y, \tilde{r}_x^n \rangle \rangle}{\langle r_x \rangle^{n+1}} + \frac{(-1)^n \langle \langle {}^n r_x \rangle \rangle}{\langle r_x \rangle^n} \cdot \frac{\langle r_y \rangle}{\langle r_x \rangle}. \quad (3)$$

The allometric growth factors in equation (3) are

$${}^1\mathfrak{F}_n = \frac{(-1)^n \langle \langle r_y, \tilde{r}_x^n \rangle \rangle}{\langle r_x \rangle^{n+1}}, \quad {}^2\mathfrak{F}_n = 0,$$

$$\text{and } {}^3\mathfrak{F}_n = \frac{(-1)^n \langle \langle {}^n r_x \rangle \rangle}{\langle r_x \rangle^n} \cdot \frac{\langle r_y \rangle}{\langle r_x \rangle}.$$

Equation (3) is an example of equation (2) in which the derivatives are explicitly defined. The appeal of this example (besides that it can be realistic for a particular organism) is that the allometric growth factors (${}^1\mathfrak{F}_n$ and ${}^3\mathfrak{F}_n$) contain the slopes (r_y and r_x) from θ_t and ϕ_t, thus making it easy to interpret the biology of ${}^1\mathfrak{F}_n$ and ${}^3\mathfrak{F}_n$. For instance, $k_0 = {}^3\mathfrak{F}_0$ is simply $\langle r_y \rangle \cdot \langle r_x \rangle^{-1}$; it is the ratio of $\langle r_y \rangle$ (the expected value of the specific growth rate of y_t) to $\langle r_x \rangle$ (the expected value of the specific growth rate of x_t). So, naturally, when the mean growth rate of y_t increases relative to the mean growth rate of x_t, k_0 also increases. Note that k differs from k_0 because $\sum_{n=1}^{\infty} {}^1\mathfrak{F}_n$ and $\sum_{n=2}^{\infty} {}^3\mathfrak{F}_n$ are nonzero sums. If k_0 is 1 and $\sum_{n=1}^{\infty} {}^1\mathfrak{F}_n$ and $\sum_{n=2}^{\infty} {}^3\mathfrak{F}_n$ were both zero sums, then relative growth would be isometric [2]; however, since $\sum_{n=1}^{\infty} {}^1\mathfrak{F}_n$ and $\sum_{n=2}^{\infty} {}^3\mathfrak{F}_n$ are really nonzero sums, relative growth deviates from isometry. This is a simple and yet realistic example illustrating the fact that k can be miscalculated if $\sum_{n=1}^{\infty} {}^1\mathfrak{F}_n \neq 0$ and $\sum_{n=2}^{\infty} {}^3\mathfrak{F}_n \neq 0$ are not taken into account.

The statistical relative growth rate, $k_1 = {}^1\mathfrak{F}_1 + {}^3\mathfrak{F}_1$ (where ${}^3\mathfrak{F}_1 = 0$), in equation (3) is

$$k_1 = {}^1\mathfrak{F}_1 = \frac{-\langle \langle r_y, r_x \rangle \rangle}{\langle r_x \rangle^2}.$$

The nonzero coefficient, $\langle \langle r_y, r_x \rangle \rangle$, is the probability covariance between the random variable r_y and the random variable r_x; it is a measure of the joint distribution of r_y and r_x. The more closely r_y and r_x are positively associated, the lower the value of k_1 because $-\langle \langle r_y, r_x \rangle \rangle$ is less than zero. In contrast, the more closely r_y and r_x are negatively associated, the higher the value of k_1 because $-\langle \langle r_y, r_x \rangle \rangle$ is greater than zero. And so whether k_0 is being subtracted or added by k_1 solely depends on the direction of association between r_y and r_x.

The allometric growth factor (${}^3\mathfrak{F}_n$) contains the term $\langle \langle {}^n \varphi_t \rangle \rangle$, which in equation (3) is

$$\langle\langle^n\varphi_t\rangle\rangle \equiv \frac{\langle\langle^n\phi_t\rangle\rangle}{\langle\phi_t\rangle^n} = \frac{\langle\langle^n r_x\rangle\rangle}{\langle r_x\rangle^n}.$$

Clearly, $\varphi_t = \tilde{r}_x\langle r_x\rangle^{-1}$ is a random variable, not a stochastic process. Thus, for instance, $\langle\langle^2\varphi_t\rangle\rangle$ is a nonzero positive coefficient that represents the ratio of $\langle\langle^2 r_x\rangle\rangle$ (the probability variance of r_x) to $\langle r_x\rangle^2$ (the squared expected value of r_x). Consequently, $\langle\langle^2\varphi_t\rangle\rangle$ describes the ontogenetic variance of x_t, and $\langle\langle^3\varphi_t\rangle\rangle$ describes the ontogenetic asymmetry of x_t. Both genetic and environmental factors can affect $\langle\langle^2\varphi_t\rangle\rangle$ and $\langle\langle^3\varphi_t\rangle\rangle$, and these two ontogenetic statistical moments (or biological processes) influence k in a manner that is not intuitively obvious unless equation (1) is used.

It is important to note that the allometric growth factor, $^2\mathfrak{F}_n$, is zero in equation (3) only because φ_t is a random variable, not a stochastic process; $\varphi_t = \tilde{r}_x\langle r_x\rangle^{-1}$ does not vary with t because s_x is constrained to zero, and thus $D_t\langle\langle^n\varphi_t\rangle\rangle$ equals zero at every t. Since s_x is constrained to zero, k does not vary with t.

Now suppose only s_y and s_x are random variables in the random ontogenetic growth functions, $\theta_t = s_y + r_y t$ and $\phi_t = s_x + r_x t$. Then, if $\langle s_x\rangle = \langle\log_e q_x\rangle$ equals zero, equation (2) is (*see* Methods, equations 17–19, for derivation)

$$k_n = \frac{-(-1)^n n\langle\langle s_y, s_x^n\rangle\rangle t^{-n-1}}{r_x^{n+1}} +$$
$$\langle\theta_t\rangle\cdot\frac{-(-1)^n n\langle\langle^n s_x\rangle\rangle t^{-n-1}}{r_x^{n+1}} + \qquad (4)$$
$$\frac{(-1)^n\langle\langle^n s_x\rangle\rangle t^{-n}}{r_x^n}\cdot\frac{r_y}{r_x},$$

where $\langle\theta_t\rangle = \langle s_y\rangle + r_y t$ is a deterministic process and $s_x = \tilde{s}_x$ is a mean-centered random variable. In this case, $\varphi_t = s_x r_x^{-1} t^{-1}$ is a stochastic process because $\langle\langle^n\phi_t\rangle\rangle$ for each $n\in\mathbb{N}_2$ does not vary with t, and yet $\langle\phi_t\rangle$ increases with t since there is growth. The allometric growth factors in equation (4) are

$$^1\mathfrak{F}_n = \frac{-(-1)^n n\langle\langle s_y, s_x^n\rangle\rangle t^{-n-1}}{r_x^{n+1}},$$
$$^2\mathfrak{F}_n = \langle\theta_t\rangle\cdot\frac{-(-1)^n n\langle\langle^n s_x\rangle\rangle t^{-n-1}}{r_x^{n+1}},$$
$$\text{and } ^3\mathfrak{F}_n = \frac{(-1)^n\langle\langle^n s_x\rangle\rangle t^{-n}}{r_x^n}\cdot\frac{r_y}{r_x}.$$

It is apparent that, unlike equation (3), equation (4) contains the deterministic variable t. Thus, k varies with t, and its values can either be greater than 1 (that is, positively allometric at every t) or less than 1 (that is, negatively allometric at every t) or an arrangement of both (that is, reversal in ontogenetic polarity) [10]. Note that $k_0 = {}^3\mathfrak{F}_0 = r_y r_x^{-1}$ in equation (4) is constant with t; this implies that $\langle\theta_t\rangle$ and $\langle\phi_t\rangle$ are linearly related, and so the relationship between $\langle\theta_t\rangle$ and $\langle\phi_t\rangle$ is described by $\log_e f$. All other statistical relative growth rates (k_n for every $n\in\mathbb{N}_1$), however, are derived from relationships that are not described by $\log_e f$ and therefore vary with t. For example, $\langle\langle\theta_t, \varphi_t\rangle\rangle = \langle\langle s_y, s_x\rangle\rangle r_x^{-1} t^{-1}$ and $\langle\phi_t\rangle = r_x t$ are nonlinearly related, and so $k_1 = {}^1\mathfrak{F}_1$, which is derived from the relationship between $\langle\langle\theta_t, \varphi_t\rangle\rangle$ and $\langle\phi_t\rangle$, varies with t. Consequently, nonlinear allometries occur in

this case, even though the stochastic process θ_t and the stochastic process ϕ_t are linearly related.

Intricate temporal distributions of k can arise from the case described by equation (4). For example, suppose $\sum_{n=3}^{\infty} k_n$ at every t is negligible compared to $\sum_{n=0}^{2} k_n$ at every t. Then equation (1) is

$$k \equiv \mathcal{D}_t\langle\Omega_t\rangle \approx k_0 + \gamma_1 t^{-2} - \gamma_2 t^{-3},$$

where $\gamma_1 = [\langle\langle s_y, s_x\rangle\rangle - k_0\langle\langle^2 s_x\rangle\rangle] r_x^{-2}$ and $\gamma_2 = 2[\langle\langle s_y, s_x^2\rangle\rangle + \langle s_y\rangle\cdot\langle\langle^2 s_x\rangle\rangle] r_x^{-3}$ are probabilistic coefficients. Now there could be a condition in which the temporal distribution of k is not monotonic and is either positively allometric or negatively allometric: k has a stationary point at $t_s = \frac{3}{2}\gamma_2\gamma_1^{-1}$ (set $D_t k = 0$ and solve for t), where the stationary value of k is $k_s = k_0 + \frac{4}{27}\gamma_1^3\gamma_2^{-2}$ (substitute t_s for t in k); thus, the temporal distribution of k is not monotonic. This is an interesting case because k, which could be either greater than 1 or less than 1 at every t, increases with t, reaches k_s (the maximum rate of relative growth), and then decreases with t. This is classic case of accelerated and decelerated rates of relative growth within a given t period. Note that k_s depends on the probabilistic coefficients, k_0, γ_1, and γ_2. When Ω_t is deterministic, k_s is undefined. Since, however, Ω_t is inherently stochastic, the terms in γ_1 and in γ_2 affect k_s and t_s. For instance, if $\langle\langle s_y, s_x\rangle\rangle$ increases while k_0, γ_2, and all other terms in γ_1 remain constant, then k_s increases, assuming γ_1 and γ_2 are positive. Moreover, increasing $\langle\langle s_y, s_x\rangle\rangle$ decreases the t at which k_s is reached; this is because t_s is inversely proportional to γ_1, which is directly related to $\langle\langle s_y, s_x\rangle\rangle$. If stochasticity disappears, then γ_1 and γ_2 also vanish and t_s becomes undefined. So k_0, γ_1, and γ_2 affect not only k_s, but also the t at which k_s is reached. This is a clear case of how γ_1 and γ_2—coefficients that only appear in the probabilistic version of $k \equiv \mathcal{D}_t\langle\Omega_t\rangle$—affect the timing and rate of development of traits. Thus, ignoring the effects of stochasticity on both θ_t and ϕ_t omits all of the informative ontogenetic statistical moments (e.g., $\langle\langle s_y, s_x\rangle\rangle$) that govern the temporal distribution of k. Furthermore, even though the relationship between the realizations of stochastic θ_t and the realizations of stochastic ϕ_t is described by $\log_e f$, k differs from k_0 and can vary with t. This important fact should always be considered when analyzing allometric growth.

It is interesting to note that as t approaches infinity, equation (4) or any of its approximations reaches an asymptotic value of $k_0 = \lim_{t\to\infty} (k_0 + \gamma_1 t^{-2} - \gamma_2 t^{-3})$. The t at which this asymptotic value is first reached is an indication of the cessation of the variability of k with respect to t. In other words, nonlinear allometries disappear as t approaches infinity. So as the allometric growth process evolves over t, two distinct phases are observed: the first phase is a non-uniform temporal distribution of k, and the second phase is a uniform temporal distribution of k. This two-phase allometric growth process may be more realistic than a growth process that exclusively corresponds to either the first or second phase. It should be made clear, though, that only the second phase is indicative to a log-linear allometric growth trajectory, since k_0 (not k) is constant with t. And so the probabilistic coefficients, γ_1 and γ_2, essentially have an insignificant impact on only the second phase of the allometric growth process. Clearly, the first phase of the allometric growth process can entail an intricate temporal distribution of k, such as the one provided in the previous paragraph.

Equations (3) and (4) are realistic examples of the types of temporal distributions of k that may arise from the random

exponential growth-law function, qe^{rt}, to which the stochastic processes, y_t and x_t, belong. The important distinction between equations (3) and (4) is the type of variable $\varphi_t \equiv \tilde{\phi}_t \langle \phi_t \rangle^{-1}$ assumes: φ_t is a random variable (not a stochastic process) in equation (3); φ_t is a stochastic process in equation (4). As a result, k defined by equation (3) does not vary with t, whereas k defined by equation (4) varies with t. In either case, it is q or r that is a random variable. Nonetheless, it is entirely possible to have a case in which q and r are both random variables.

With regard to the convergence of equation (1), $\varphi_t \equiv \tilde{\phi}_t \langle \phi_t \rangle^{-1}$ has an important role: equation (1) is guaranteed to converge at every t if the realizations of stochastic φ_t are between -1 and 1 at every t; this is because the realizations of $\varphi_t^n \equiv \tilde{\phi}_t^n \langle \phi_t \rangle^{-n}$ approach zero at every t as n approaches infinity.

Discussion

Although statistical models for relative growth have been developed (*see* [7] and [20]), their models, which show variability in $k \equiv k_0$ with respect to t, are not probabilistic because they do not incorporate actual stochasticity into $f(x_t; b, k)$; they do not treat y_t and x_t as correlated random functions. Also, although a probabilistic model for static (not ontogenetic) allometry, in which x is treated as an independent random variable (not as a stochastic process), has been proposed (*see* [21]), their model cannot address the statistical moments that govern the temporal distribution of k because their model is used to analyze the effects of stochasticity only on $D_x f(x; b, k)$. Consequently, equation (1) is entirely new and has no analog to any statistical model for relative growth previously developed.

Equation (1) is the exact general solution for the inner mean derivative of the random ontogenetic growth function θ_t with respect to the random ontogenetic growth function ϕ_t. This equation, which is the exact probabilistic version of k, is general because it does not entail any simplifying assumptions. Thus, the generality of equation (1) makes it possible to analyze all of the informative ontogenetic statistical moments (or biological processes) that govern the temporal distribution of k:

$$k \equiv \mathcal{D}_t \langle \Omega_t \rangle = \sum_{n=0}^{\infty} \left(\frac{(-1)^n D_t \langle \theta_t \varphi_t^n \rangle}{D_t \langle \phi_t \rangle} \middle| D_t \langle \phi_t \rangle \neq 0 \right).$$

This expression makes it apparent that k is composed of an infinite series of ratios of first-order t-derivatives. The statistical complexity of k arises from the derivative in the numerator, which is the t-derivative of the nth mixed moment of θ_t and φ_t^n. Each of these nth statistical moments is governed by the interactions between θ_t and φ_t^n. So most of the informative ontogenetic statistical moments are captured by the mean t-derivative, $D_t \langle \theta_t \varphi_t^n \rangle$; this is evident by expanding $(-1)^n D_t \langle \theta_t \varphi_t^n \rangle$ (*see* Methods, equations 12 and 13, for derivation):

$$(-1)^n D_t \langle \theta_t \varphi_t^n \rangle =$$
$$(-1)^n \left[D_t \langle \langle \theta_t, \varphi_t^n \rangle \rangle + \langle \theta_t \rangle \cdot D_t \langle \langle^n \varphi_t \rangle \rangle + \langle \langle^n \varphi_t \rangle \rangle \cdot D_t \langle \theta_t \rangle \right]. \quad (5)$$

The summed terms in equation (5) compose the allometric growth factors ($^1\mathfrak{F}_n$, $^2\mathfrak{F}_n$, and $^3\mathfrak{F}_n$) in equation (2). These allometric growth factors are important to interpret because they describe the central and mixed moments of the random ontogenetic growth functions that govern the statistical dynamics of k. Clearly, equation (5) is calculable, since each of the nth terms of $\langle \theta_t \varphi_t^n \rangle$ is a differentiable deterministic function of t.

To biologically interpret equation (5), one must specify the finite family of functions to which the stochastic processes, y_t and x_t, belong (*see*, for example, equations 3 and 4).

Equations (3) and (4) are examples of how to model and analyze the statistical dynamics of k. These examples are derived from the random exponential growth-law function that is theoretically assumed for a particular organism. Thus relaxing this assumption leads to the practical (experimental) side of modeling the statistical dynamics of k. Traditionally, $\langle \theta_t \rangle$ and $\langle \phi_t \rangle$ are experimentally measured, plotted with respect to each other, and then related by a differentiable function from which k_0 is derived [19]. This study, however, shows that k_0 is not the only statistical relative growth rate that needs to be considered when evaluating k (*see* equations 1 and 2). The other statistical relative growth rates (k_n for every $n \in \mathbb{N}_1$) should also be quantified in a similar manner. For example, $\langle \theta_t \varphi_t \rangle$ and $\langle \phi_t \rangle$ can be experimentally measured, plotted with respect to each other, and then related by a differentiable function from which k_1 can be derived. Thus, the probabilistic version of $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$ is a very practical metric: it only requires measuring the mixed and central moments of θ_t and ϕ_t.

The ontogenetic growth functions, θ_t and ϕ_t, must be linearly related in order to satisfy the log-linear allometric function, $\log_a f$. Thus, θ_t and ϕ_t can be generalized as $\theta_t = s_y + r_y \lambda_t$ and $\phi_t = s_x + r_x \lambda_t$, where deterministic or stochastic λ_t is any differentiable function of t. In equations (3) and (4), λ_t is simply t; but, to describe more intricate ontogenetic growth distributions, λ_t could also be $\sum_{m=1}^{z} \zeta_m t^m$ for any $z \in \mathbb{N}_2$, where ζ_m for each $m \in \mathbb{N}_1$ is a deterministic or stochastic parameter. Note that $D_t \theta_t$ and $D_t \phi_t$ equals $r_y \cdot D_t \lambda_t$ and $r_x \cdot D_t \lambda_t$, respectively; this is true for any distribution of λ_t. Subsequently, $\langle k \rangle = \langle D_t \theta_t / D_t \phi_t \rangle$ equals $\langle r_y r_x^{-1} \rangle$, which is the expected value of the ratio of r_y to r_x.

For most organisms, $k_0 = D_t \langle \theta_t \rangle / D_t \langle \phi_t \rangle$ is constant with t; this implies that $\langle \langle r_y, \lambda_t \rangle \rangle$ and $\langle \langle r_x, \lambda_t \rangle \rangle$ are typically zero at every t. In equations (3) and (4), where λ_t is t, $\langle \langle r_y, t \rangle \rangle$ and $\langle \langle r_x, t \rangle \rangle$ are naturally zero because t is naturally deterministic; thus, k_0 is naturally constant with t in these equations. There are some organisms (predominantly plants) that show $k \equiv k_0$ varying with t [22]. Indeed, this case, in which k_0 varies with t, is interesting to study, but complicates the biological analysis of $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$ because the biological interpretation of $\langle \langle r_y, \lambda_t \rangle \rangle \neq 0$ or $\langle \langle r_x, \lambda_t \rangle \rangle \neq 0$ cannot explicitly be defined. Therefore, when analytically modeling $k \equiv \mathcal{D}_t \langle \Omega_t \rangle$, there is good reason to assume that $\langle \langle r_y, \lambda_t \rangle \rangle$ and $\langle \langle r_x, \lambda_t \rangle \rangle$ are zero at every t. Keep in mind, though, that while stochastic θ_t and stochastic ϕ_t are linearly related, k_0 can vary with t.

It is important to note that if $\varphi_t \equiv \tilde{\phi}_t \langle \phi_t \rangle^{-1}$ is not a stochastic process, then k (which differs from k_0) does not vary with t (*see* equation 3). If, however, $\varphi_t \equiv \tilde{\phi}_t \langle \phi_t \rangle^{-1}$ is a stochastic process, then k not only differs from k_0, but also varies with t (*see* equation 4); this implies that the statistical relative growth rates (k_n for every $n \in \mathbb{N}_1$) are derived from relationships that are not described by $\log_e f$, even though the stochastic process θ_t and the stochastic process ϕ_t are linearly related.

Another important point to note is that $\mathcal{D}_t \langle \Omega_t \rangle$ is mathematically different from the expected value of a ratio of correlated stochastic t-derivatives. If $D_t \theta_t$ and $D_t \phi_t$ are correlated stochastic t-derivatives, then the outer mean derivative, $\langle k \rangle = \langle D_t \theta_t / D_t \phi_t \rangle$, is generally not identical with equation (1). Stated more explicitly,

$$\langle k \rangle = \left(\left\langle \frac{D_t \theta_t}{D_t \phi_t} \right\rangle \middle| \langle D_t \phi_t \rangle \neq 0 \right) =$$
$$\sum_{n=0}^{\infty} \frac{(-1)^n \langle D_t \theta_t \cdot (D_t \tilde{\phi}_t)^n \rangle}{\langle D_t \phi_t \rangle^{n+1}} = \sum_{n=0}^{\infty} \langle k \rangle_n$$

and

$$\langle k \rangle_n = \frac{(-1)^n \langle\langle D_t\theta_t, (D_t\tilde{\phi}_t)^n\rangle\rangle}{\langle D_t\phi_t \rangle^{n+1}} + \frac{(-1)^n \langle D_t\theta_t \rangle \cdot \langle (D_t\tilde{\phi}_t)^n \rangle}{\langle D_t\phi_t \rangle^{n+1}}$$

are generally not identical with equations (1) and (2), respectively. Note: $\langle k \rangle$ and $\langle k \rangle_n$ are derived in exactly the same manner as $\langle \Omega_t \rangle$ (*see* Methods, equation 8) and $\langle \Omega_t \rangle_n$ (*see* Methods, equation 9). Now compare the following limits: the outer mean derivative is

$$\langle \lim_{\Delta t \to 0} \frac{\Delta\theta_t/\Delta t}{\Delta\phi_t/\Delta t} \rangle = \lim_{\Delta t \to 0} \langle \frac{\Delta\theta_t/\Delta t}{\Delta\phi_t/\Delta t} \rangle \equiv \lim_{\Delta t \to 0} \langle \frac{\theta(t+\Delta t) - \theta(t)}{\phi(t+\Delta t) - \phi(t)} \rangle,$$

whereas the inner mean derivative is

$$\mathcal{D}_t\langle \Omega_t \rangle = \lim_{\Delta t \to 0} \frac{\Delta(u\langle \Omega_t \rangle)/\Delta t}{\Delta(v\langle \Omega_t \rangle)/\Delta t} \equiv \lim_{\Delta t \to 0} \frac{u\langle \Omega(t+\Delta t) \rangle - u\langle \Omega(t) \rangle}{v\langle \Omega(t+\Delta t) \rangle - v\langle \Omega(t) \rangle}.$$

Thus, in $\langle k \rangle$, the limit operates on the ratio of stochastic $\Delta\theta_t$ to stochastic $\Delta\phi_t$; but in $k \equiv \mathcal{D}_t\langle \Omega_t \rangle$, the limit operates on the ratio of deterministic $\Delta(u\langle \Omega_t \rangle)$ to deterministic $\Delta(v\langle \Omega_t \rangle)$. So $k \equiv \mathcal{D}_t\langle \Omega_t \rangle$ is identical with $\langle k \rangle = \langle D_t\theta_t/D_t\phi_t \rangle$ when both θ_t and ϕ_t are deterministic or when only θ_t is stochastic. When, however, only ϕ_t is stochastic or when both θ_t and ϕ_t are stochastic, $\mathcal{D}_t\langle \Omega_t \rangle$ is generally not identical with $\langle D_t\theta_t/D_t\phi_t \rangle$ (*see* equation 4); the only exception is the special case when $\varphi_t \equiv \tilde{\phi}_t\langle \phi_t \rangle^{-1}$ is not a stochastic process, but a random variable (*see* equation 3). As a result, the outer mean derivative $\langle D_t\theta_t/D_t\phi_t \rangle$ is a special case of the inner mean derivative $\mathcal{D}_t\langle \Omega_t \rangle$. Also, $\langle k \rangle_0 = \langle D_t\theta_t \rangle/\langle D_t\phi_t \rangle$ is equal to $k_0 = D_t\langle \theta_t \rangle/D_t\langle \phi_t \rangle$.

In conclusion, equation (1) is completely versatile and has much to offer with regard to analyzing the allometric growth factors ($^1\mathfrak{F}_n$, $^2\mathfrak{F}_n$, and $^3\mathfrak{F}_n$) that affect the temporal distribution of k. When the derivatives in equation (2) are defined explicitly via specifying the random ontogenetic growth functions (θ_t and ϕ_t), the allometric growth factors become biologically interpretable; they also become tractable in simulations, which are useful for modeling the statistical rates of relative growth for various distributions of λ_t (*see* Methods, Simulating the probabilistic version of k). Thus, each of the statistical relative growth rates (k_0, $k_1,\ldots, k_n$), which are infinitely summed to form equation (1), can be analyzed in detail to reveal new insight into the statistical dynamics of relative growth.

Lastly, this study ignored the statistical dynamics of b because only k is an important descriptor of relative growth. But to obtain a complete characterization of the statistical dynamics of allometric growth, b or $\log_a b = \beta$ must also be considered. Since the stochastic analysis of k has been fully developed in this study (*see* Methods, equations 6–11), the exact probabilistic version of β can easily be formulated:

$$\beta \equiv \mathcal{D}_t\langle \Xi_t \rangle = \sum_{n=0}^{\infty} \left(\frac{(-1)^n D_t\langle \Omega_t\Phi_t^n \rangle}{D_t\langle \phi_t^{-1} \rangle} \middle| D_t\langle \phi_t^{-1} \rangle \neq 0 \right) =$$
$$\sum_{n=0}^{\infty} \left(\frac{(-1)^n d\langle \Omega_t\Phi_t^n \rangle}{d\langle \phi_t^{-1} \rangle} \right) = \sum_{n=0}^{\infty} \beta_n,$$

where $\Xi_t \equiv \Omega_t(\phi_t^{-1})^{-1}$ is the ratio of Ω_t to ϕ_t^{-1} and $\Phi_t \equiv \tilde{\phi}_t^{-1}\langle \phi_t^{-1} \rangle^{-1}$ is the ratio of $\tilde{\phi}_t^{-1}$ to $\langle \phi_t^{-1} \rangle$. Each of the nth terms

of β is the allometric growth descriptor, β_n:

$$\beta_n = \frac{(-1)^n d\langle\langle \Omega_t, \Phi_t^n \rangle\rangle}{d\langle \phi_t^{-1} \rangle} + \langle \Omega_t \rangle \cdot \frac{(-1)^n d\langle\langle {}^n\Phi_t \rangle\rangle}{d\langle \phi_t^{-1} \rangle} +$$
$$\langle\langle {}^n\Phi_t \rangle\rangle \cdot \frac{(-1)^n d\langle \Omega_t \rangle}{d\langle \phi_t^{-1} \rangle}.$$

The summed terms in β_n describe the allometric growth factors that affect the temporal distribution of β. The equation (β_n) contains all of the ontogenetic statistical moments that govern the temporal distribution of β. And just like k, one could analyze the statistical dynamics of β simply by examining the summed terms in β_n. Note that, like φ_t in equation (1), if Φ_t is a stochastic process, then β varies with t.

Methods: The stochastic analysis of k

Let $\theta_t = \log_a y_t$ and $\phi_t = \log_a x_t$ each be a random ontogenetic growth function such that θ_t and ϕ_t are correlated stochastic processes. Then, if $\Omega_t \equiv \theta_t\phi_t^{-1}$ is the ratio of θ_t to ϕ_t, the expected value of Ω_t is

$$\langle \Omega_t \rangle \equiv \left(\left\langle \frac{\theta_t}{\phi_t} \right\rangle \middle| \langle \phi_t \rangle \neq 0 \right) = \left\langle \frac{\theta_t}{\langle \phi_t \rangle + \tilde{\phi}_t} \right\rangle. \qquad (6)$$

Equation (6) contains the central and mixed moments of θ_t and $\tilde{\phi}_t^n$. These statistical moments can be revealed by expanding equation (6) using the Taylor series generated by the function, g, defined by the denominator $[\langle \phi_t \rangle + \tilde{\phi}_t]^{-1} = g(\tilde{\phi}_t)$ when α equals zero at every $t \in [0, +\infty)$:

$$[\langle \phi_t \rangle + \tilde{\phi}_t]^{-1} = \sum_{n=0}^{\infty} \frac{D^n g(\alpha)}{n!} [\tilde{\phi}_t - \alpha]^n = \sum_{n=0}^{\infty} \frac{(-1)^n \varphi_t^n}{\langle \phi_t \rangle}, \qquad (7)$$

where $\varphi_t \equiv \tilde{\phi}_t\langle \phi_t \rangle^{-1}$ is the ratio of $\tilde{\phi}_t$ to $\langle \phi_t \rangle$. Substituting equation (7) into equation (6) yields

$$\langle \Omega_t \rangle \equiv \left(\left\langle \frac{\theta_t}{\phi_t} \right\rangle \middle| \langle \phi_t \rangle \neq 0 \right) = \sum_{n=0}^{\infty} \frac{(-1)^n \langle \theta_t\varphi_t^n \rangle}{\langle \phi_t \rangle} = \sum_{n=0}^{\infty} \langle \Omega_t \rangle_n, \qquad (8)$$

where each of the nth terms in equation (8) is $\langle \Omega_t \rangle_n$:

$$\langle \Omega_t \rangle_n = \frac{(-1)^n \langle\langle \theta_t, \varphi_t^n \rangle\rangle}{\langle \phi_t \rangle} + \frac{(-1)^n \langle \theta_t \rangle \cdot \langle\langle {}^n\varphi_t \rangle\rangle}{\langle \phi_t \rangle}. \qquad (9)$$

The summed terms in equation (9) are the allometric growth factors that affect the temporal distribution of $\langle \Omega_t \rangle$. Rice and Papadopoulos [23] use a similar mathematical approach (that is, the Taylor series expansion of the expected value of the change in mean phenotype) to reveal important biological factors governing evolution.

Equation (8), which is the Taylor (or Maclaurin) series expansion of $\langle \Omega_t \rangle$, can also be expressed as $\sum_{n=0}^{\infty} (-1)^n \langle \theta_t\tilde{\phi}_t^n \rangle / \langle \phi_t \rangle^{n+1}$. This particular expression, however, has no explicit common denominator, as its denominator has an unfixed exponent; thus, $\mathcal{D}_t$ cannot operate linearly on this expression, and consequently fails to define k from this expression. In contrast, equation (1), in which $\mathcal{D}_t$ operates specifically on equation (8), uniquely defines the probabilistic version of k. Equation (8) is thus essential for evaluating $\mathcal{D}_t\langle \Omega_t \rangle$: the t-derivative of the numerator

in equation (8) is

$$D_t(u\langle\Omega_t\rangle) = \sum_{n=0}^{\infty} (-1)^n D_t\langle\theta_t\varphi_t^n\rangle, \qquad (10)$$

and the t-derivative of the denominator in equation (8) is

$$D_t(v\langle\Omega_t\rangle) = D_t\langle\phi_t\rangle. \qquad (11)$$

Therefore, equation (1) (that is, the inner mean derivative of the random ontogenetic growth function θ_t with respect to the random ontogenetic growth function ϕ_t) is the ratio of equation (10) to equation (11):

$$k \equiv \mathcal{D}_t\langle\Omega_t\rangle = \sum_{n=0}^{\infty}\left(\frac{(-1)^n D_t\langle\theta_t\varphi_t^n\rangle}{D_t\langle\phi_t\rangle}\bigg| D_t\langle\phi_t\rangle \neq 0\right) =$$

$$\sum_{n=0}^{\infty}\left(\frac{(-1)^n d\langle\theta_t\varphi_t^n\rangle}{d\langle\phi_t\rangle}\right) = \sum_{n=0}^{\infty} k_n.$$

Now the identity $\langle\theta_t\varphi_t^n\rangle = \langle\langle\theta_t, \varphi_t^n\rangle\rangle + \langle\theta_t\rangle\cdot\langle\langle^n\varphi_t\rangle\rangle$ can be used to expand $(-1)^n D_t\langle\theta_t\varphi_t^n\rangle$:

$$(-1)^n D_t\langle\theta_t\varphi_t^n\rangle =$$
$$(-1)^n\left[D_t\langle\langle\theta_t, \varphi_t^n\rangle\rangle + D_t(\langle\theta_t\rangle\cdot\langle\langle^n\varphi_t\rangle\rangle)\right]; \qquad (12)$$

the product rule is used to expand $D_t(\langle\theta_t\rangle\cdot\langle\langle^n\varphi_t\rangle\rangle)$:

$$D_t(\langle\theta_t\rangle\cdot\langle\langle^n\varphi_t\rangle\rangle) = \langle\theta_t\rangle\cdot D_t\langle\langle^n\varphi_t\rangle\rangle + \langle\langle^n\varphi_t\rangle\rangle\cdot D_t\langle\theta_t\rangle. \qquad (13)$$

Substituting equation (13) into equation (12) and dividing by $D_t\langle\phi_t\rangle$ yields the expanded form of the statistical relative growth rate, $k_n = (-1)^n d\langle\theta_t\varphi_t^n\rangle/d\langle\phi_t\rangle$:

$$k_n = \frac{(-1)^n d\langle\langle\theta_t, \varphi_t^n\rangle\rangle}{d\langle\phi_t\rangle} + \langle\theta_t\rangle\cdot\frac{(-1)^n d\langle\langle^n\varphi_t\rangle\rangle}{d\langle\phi_t\rangle} +$$
$$\langle\langle^n\varphi_t\rangle\rangle\cdot\frac{(-1)^n d\langle\theta_t\rangle}{d\langle\phi_t\rangle},$$

which is identical with equation (2). The summed terms in equation (2) are the allometric growth factors ($^1\mathfrak{F}_n$, $^2\mathfrak{F}_n$, and $^3\mathfrak{F}_n$) that affect the temporal distribution of k:

$$^1\mathfrak{F}_n = \frac{(-1)^n d\langle\langle\theta_t, \varphi_t^n\rangle\rangle}{d\langle\phi_t\rangle} = \frac{(-1)^n D_t\langle\langle\theta_t, \varphi_t^n\rangle\rangle}{D_t\langle\phi_t\rangle} =$$
$$\frac{(-1)^n[\langle\phi_t\rangle^{-n}\cdot D_t\langle\langle\theta_t, \tilde{\phi}_t^n\rangle\rangle + \langle\langle\theta_t, \tilde{\phi}_t^n\rangle\rangle\cdot D_t\langle\phi_t\rangle^{-n}]}{D_t\langle\phi_t\rangle},$$

$$^2\mathfrak{F}_n = \langle\theta_t\rangle\cdot\frac{(-1)^n d\langle\langle^n\varphi_t\rangle\rangle}{d\langle\phi_t\rangle} = \langle\theta_t\rangle\cdot\frac{(-1)^n D_t\langle\langle^n\varphi_t\rangle\rangle}{D_t\langle\phi_t\rangle} =$$
$$\frac{(-1)^n\langle\theta_t\rangle[\langle\phi_t\rangle^{-n}\cdot D_t\langle\langle^n\phi_t\rangle\rangle + \langle\langle^n\phi_t\rangle\rangle\cdot D_t\langle\phi_t\rangle^{-n}]}{D_t\langle\phi_t\rangle},$$

and

$$^3\mathfrak{F}_n = \langle\langle^n\varphi_t\rangle\rangle\cdot\frac{(-1)^n d\langle\theta_t\rangle}{d\langle\phi_t\rangle} = \frac{\langle\langle^n\phi_t\rangle\rangle}{\langle\phi_t\rangle^n}\cdot\frac{(-1)^n D_t\langle\theta_t\rangle}{D_t\langle\phi_t\rangle}.$$

When $\varphi_t \equiv \tilde{\phi}_t\langle\phi_t\rangle^{-1}$ is a stochastic process, the product or quotient rule can be used in $^1\mathfrak{F}_n$ and in $^2\mathfrak{F}_n$ to calculate their derivatives. Note that $D_t\langle\langle\theta_t, \varphi_t^n\rangle\rangle = D_t\left(\langle\langle\theta_t, \tilde{\phi}_t^n\rangle\rangle\cdot\langle\phi_t\rangle^{-n}\right)$ and $D_t\langle\langle^n\varphi_t\rangle\rangle = D_t(\langle\langle^n\phi_t\rangle\rangle\cdot\langle\phi_t\rangle^{-n})$ represent deterministic t-derivatives of the product of two deterministic functions.

Now suppose for a particular organism the random ontogenetic growth functions, θ_t and ϕ_t, are defined by $\theta_t = s_y + r_y t$ and $\phi_t = \left(s_x + r_x t|_{s_x=0}\right) = r_x t$ in which only r_y and r_x are random variables. Then the allometric growth factors, which are the summed terms in equation (2), are as follows:

$$^1\mathfrak{F}_n = \frac{(-1)^n D_t\langle\langle s_y + r_y t, \tilde{r}_x^n\langle r_x\rangle^{-n}\rangle\rangle}{D_t\langle r_x t\rangle} =$$
$$\frac{(-1)^n D_t\left(\langle\langle r_y, \tilde{r}_x^n\rangle\rangle\cdot\langle r_x\rangle^{-n} t\right)}{D_t(\langle r_x\rangle t)} = \frac{(-1)^n\langle\langle r_y, \tilde{r}_x^n\rangle\rangle}{\langle r_x\rangle^{n+1}}, \qquad (14)$$

$$^2\mathfrak{F}_n = \langle s_y + r_y t\rangle\cdot\frac{(-1)^n D_t\langle\langle^n(\tilde{r}_x\langle r_x\rangle^{-1})\rangle\rangle}{D_t\langle r_x t\rangle} =$$
$$[s_y + \langle r_y\rangle t]\cdot\frac{(-1)^n D_t\langle\langle^n(\tilde{r}_x\langle r_x\rangle^{-1})\rangle\rangle}{D_t(\langle r_x\rangle t)} = \qquad (15)$$
$$\frac{(-1)^n[s_y + \langle r_y\rangle t]\cdot 0}{\langle r_x\rangle} = 0,$$

and

$$^3\mathfrak{F}_n = \langle\langle^n(\tilde{r}_x\langle r_x\rangle^{-1})\rangle\rangle\cdot\frac{(-1)^n D_t\langle s_y + r_y t\rangle}{D_t\langle r_x t\rangle} =$$
$$\frac{\langle\langle^n r_x\rangle\rangle}{\langle r_x\rangle^n}\cdot\frac{(-1)^n D_t\left(s_y + \langle r_y\rangle t\right)}{D_t(\langle r_x\rangle t)} = \qquad (16)$$
$$\frac{(-1)^n\langle\langle^n r_x\rangle\rangle}{\langle r_x\rangle^n}\cdot\frac{\langle r_y\rangle}{\langle r_x\rangle},$$

where $\varphi_t = \tilde{r}_x\langle r_x\rangle^{-1}$ is a random variable, not a stochastic process. Summing equations (14), (15), and (16) then yields equation (3):

$$k_n = \frac{(-1)^n\langle\langle r_y, \tilde{r}_x^n\rangle\rangle}{\langle r_x\rangle^{n+1}} + \frac{(-1)^n\langle\langle^n r_x\rangle\rangle}{\langle r_x\rangle^n}\cdot\frac{\langle r_y\rangle}{\langle r_x\rangle}.$$

If, however, θ_t and ϕ_t are defined by $\theta_t = s_y + r_y t$ and $\phi_t = \left(s_x + r_x t|_{\langle s_x\rangle=0}\right) = \tilde{s}_x + r_x t$ in which only s_y and s_x are random variables, then the allometric growth factors are

$$^1\mathfrak{F}_n = \frac{(-1)^n D_t\langle\langle s_y + r_y t, s_x^n r_x^{-n} t^{-n}\rangle\rangle}{D_t\langle s_x + r_x t\rangle} =$$
$$\frac{(-1)^n D_t\left(\langle\langle s_y, s_x^n\rangle\rangle r_x^{-n} t^{-n}\right)}{D_t(r_x t)} = \qquad (17)$$
$$\frac{-(-1)^n n\langle\langle s_y, s_x^n\rangle\rangle t^{-n-1}}{r_x^{n+1}},$$

$$^2\mathfrak{F}_n = \langle s_y + r_y t\rangle \cdot \frac{(-1)^n D_t\langle\langle^n(s_x r_x^{-1} t^{-1})\rangle\rangle}{D_t\langle s_x + r_x t\rangle} =$$

$$[\langle s_y\rangle + r_y t]\cdot \frac{(-1)^n D_t\left(\langle\langle^n s_x\rangle\rangle r_x^{-n} t^{-n}\right)}{D_t(r_x t)} = \qquad (18)$$

$$\langle\theta_t\rangle \cdot \frac{-(-1)^n n \langle\langle^n s_x\rangle\rangle t^{-n-1}}{r_x^{n+1}},$$

and

$$^3\mathfrak{F}_n = \langle\langle^n(s_x r_x^{-1} t^{-1})\rangle\rangle \cdot \frac{(-1)^n D_t\langle s_y + r_y t\rangle}{D_t\langle s_x + r_x t\rangle} =$$

$$\frac{\langle\langle^n s_x\rangle\rangle t^{-n}}{r_x^n} \cdot \frac{(-1)^n D_t\left(\langle s_y\rangle + r_y t\right)}{D_t(r_x t)} = \qquad (19)$$

$$\frac{(-1)^n \langle\langle^n s_x\rangle\rangle t^{-n}}{r_x^n} \cdot \frac{r_y}{r_x},$$

where $\varphi_t = s_x r_x^{-1} t^{-1}$ is a stochastic process and $s_x = \tilde{s}_x$ is a mean-centered random variable. Summing equations (17), (18), and (19) then yields equation (4):

$$k_n = \frac{-(-1)^n n \langle\langle s_y, s_x^n\rangle\rangle t^{-n-1}}{r_x^{n+1}} + \langle\theta_t\rangle \cdot \frac{-(-1)^n n \langle\langle^n s_x\rangle\rangle t^{-n-1}}{r_x^{n+1}} +$$

$$\frac{(-1)^n \langle\langle^n s_x\rangle\rangle t^{-n}}{r_x^n} \cdot \frac{r_y}{r_x}.$$

Methods: Simulating the probabilistic version of k

Simulating $k \equiv \mathcal{D}_t\langle\Omega_t\rangle$ using $\theta_t = s_y + r_y\lambda_t$ and $\phi_t = s_x + r_x\lambda_t$ as correlated random functions can easily be done: first specify the

terms in θ_t and in ϕ_t that are stochastic and then provide their (joint) probability distributions. Because the stochastic process θ_t and the stochastic process ϕ_t are linearly related and because $\langle\langle r_y, \lambda_t\rangle\rangle$ and $\langle\langle r_x, \lambda_t\rangle\rangle$ are assumed to be zero at every t, $k_0 = D_t\langle\theta_t\rangle/D_t\langle\phi_t\rangle$ is constant with t. Thus, the parametric derivative, $k_0 = \langle r_y\rangle \cdot \langle r_x\rangle^{-1}$, is readily calculable, since $\langle r_y\rangle$ and $\langle r_x\rangle$ are known from the distribution of r_y and the distribution of r_x, respectively. In contrast, k_n for each $n \in \mathbb{N}_1$ is not readily calculable, but can easily be assessed in simulations by first evaluating $\langle\theta_t\varphi_t^n\rangle$ for each $n \in \mathbb{N}_1$ and then relating $\langle\theta_t\varphi_t^n\rangle$ to $\langle\phi_t\rangle$ by a differentiable function from which the derivative (i.e., k_n) can be calculated. So, for example, k_1 is the parametric derivative, $D_t\langle\theta_t\varphi_t\rangle/D_t\langle\phi_t\rangle$; to evaluate $\langle\theta_t\varphi_t\rangle$ properly in simulations, the following identity of $\langle\theta_t\varphi_t\rangle$ should be used: $\langle\theta_t\varphi_t\rangle = (\langle\theta_t\phi_t\rangle - \langle\theta_t\rangle\cdot\langle\phi_t\rangle)\langle\phi_t\rangle^{-1}$; this is because $\langle\phi_t\rangle$ is evaluated together with (not separate from) $\langle\theta_t\phi_t\rangle$ and $\langle\theta_t\rangle$ in simulations. Therefore, the binomial expansion of $\langle\theta_t\varphi_t^n\rangle$ is useful for numerically evaluating $\langle\theta_t\varphi_t^n\rangle$:

$$\langle\theta_t\varphi_t^n\rangle = \sum_{i=0}^{n}\binom{n}{i}\frac{(-1)^i\langle\theta_t\phi_t^{n-i}\rangle\cdot\langle\phi_t\rangle^i}{\langle\phi_t\rangle^n}.$$

References

1. Huxley JS (1924) Constant differential growth-ratios and their significance. Nature 114: 895–896.
2. Huxley JS, Teissier G (1936) Terminology of relative growth. Nature 137: 780–781.
3. Stevens CF (2009) Darwin and Huxley revisited: the origin of allometry. J Biology 8: 14.1–14.7.
4. Li H, Huang Z, Gai J, Wu S, Zeng Y, et al. (2007) A conceptual framework for mapping quantitative trait loci regulating ontogenetic allometry. PLoS ONE 2: e1245.
5. Huxley JS (1932) Problems of Relative Growth. New York: Lincoln MacVeagh, Dial Press.
6. Laird AK (1965) Dynamics of relative growth. Growth 29: 249–263.
7. Laird AK, Barton AD, Tyler SA (1968) Growth and time: an interpretation of allometry. Growth 32: 347–354.
8. Alberch P, Gould SJ, Oster GF, Wake DB (1979) Size and shape in ontogeny and phylogeny. Paleobiology 5: 296–317.
9. Atchley WR (1984) Ontogeny, timing of development, and genetic variance-covariance structure. Am Nat 123: 519–540.
10. Klingenberg CR (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol Rev 73: 79–123.
11. McKinney ML, McNamara KJ (1991) Heterochrony: The Evolution of Ontogeny. New York: Plenum Press.
12. Klingenberg CP, Spence JR (1993) Heterochrony and allometry: lessons from the water strider genus Limnoporus. Evolution 47: 1834–1853.

13. Klingenberg CP, Zimmermann M (1992) Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. Am Nat 140: 601–620.
14. Lutes LD, Sarkani S (2004) Random Vibrations: Analysis of Structural and Mechanical Systems Elsevier.
15. Nelson E (1966) Derivation of the Schrödinger equation from Newtonian mechanics. Phys Reviews 150: 1079–1085.
16. Nelson E (1967) Dynamical Theory of Brownian Motion. Princeton, NJ: Princeton University Press.
17. Azarina SV, Gliklikh YE (2009) Stochastic differential equations and inclusions with mean derivatives relative to the past. Int J Diff Eqs 4: 27–41.
18. Heijmans R (1999) When does the expectation of a ratio equal the ratio of expectations? Statistical Papers 40: 107–115.
19. West D, West BJ (2011) Statistical origin of allometry. EPL 94: 1–6.
20. Bervian G, Fontoura NF, Haimovici M (2006) Statistical model of variable allometric growth: otolith growth in Micropogonias furnieri (Actinopterygii, Sciaenidae). J Fish Biol 68: 196–208.
21. Pleasants AB, Wake GC, Rae AL (1997) The allometric hypothesis when the size variable is uncertain: issues in the study of carcass composition by serial slaughter. J Austral Math Soc Ser B 38: 477–488.
22. Niklas KJ (2004) Plant allometry: is there a grand unifying theory?. Biol Rev 79: 871–889.
23. Rice SH, Papadopoulos A (2009) Evolution with stochastic fitness and stochastic migration. PLoS ONE 4: e7130.