

Statistical origin of allometry

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Statistical origin of allometry

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Abstract – The allometry relationship (AR) between two properties of a living network X and Y is $X = aY^b$ where one or both of the variables is a measure of size and the allometry coefficient a and exponent b are fit to data. Many investigators have focused on determining the proper value of b entailed by an appropriate biological model, whereas others have argued that the allometry coefficient plays the more important role. Herein we use metabolic data to determine a probability density function (*pdf*) for the allometry coefficient $P(a)$ with constant allometry exponent and a *pdf* for the allometry exponent $\Psi(b)$ with a constant allometry coefficient. The two distributions are found to imply that the allometry parameters co-vary and an explicit functional relation between them is determined. The empirical *pdf* $P(a)$ is a Pareto distribution and establishes an inconsistency between reductionistic and statistical models of the interspecies AR. This inconsistency is resolved using the probability calculus to establish that the scaling of the *pdf* is the proper origin of allometry.

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Introduction. – Allometry is the study of size and its consequences [1] both within a given organism and between species in a given taxa. It was first recognized by Cuvier [2] in 1812 that brain mass increases more slowly than total body mass (TBM) proceeding from small to large species within a taxon. This observation was first expressed mathematically as an allometry relation (AR) in 1892 by Snell [3]. Four decades later Sir Julian Huxley [4] proposed that two parts of the same organism have different but proportional rates of growth. In this way if Y is a measure of the size of a living network with growth rate θ and X is a subnetwork observable with growth rate ε he conjectured that

$$\frac{1}{\varepsilon X} \frac{dX}{dt} = \frac{1}{\theta Y} \frac{dY}{dt}. \quad (1)$$

Equation (1) can be directly integrated to obtain the time-independent intraspecies allometry growth law involving the host network Y and the subnetwork X :

$$X = \alpha Y^\beta, \quad (2)$$

where the allometry coefficient α and exponent $\beta (= \varepsilon/\theta)$ are empirically determined parameters [1,5,6]. A modern derivation of eq. (2) was given by Stevens [7] who

distinguished between intraspecies and interspecies allometry and demonstrated that such a scaling relation always arises when the variables involved are self-similar. Consequently, ARs fall into the category of homogeneous scaling relations of the form $X(\lambda Y) = \lambda^\beta X(Y)$, see for example [8].

Two distinct methods dominate the many derivations of the theoretical AR, eq. (2). The first method is based on first-principles reductionistic arguments starting from an assumed form for the underlying mechanisms and deducing the necessity of eq. (2). A mechanism-based derivation of AR using a fractal nutrient transport model was given by West *et al.* [9] for X the basal metabolic rate (BMR) of an organism and Y the total body mass (TBM) from which they deduced $\beta = 3/4$. This argument, like other reductionistic approaches, dating back to Sarrus and Rameaux [10] in 1839, focuses on determining the proper value of the allometry exponent β entailed by an appropriate biological model. The latter authors [10] reasoned that the heat generated by a warm-blooded animal is proportional to its volume and the heat loss is approximately proportional to the animal's free surface thereby deducing the "surface law" with $\beta = 2/3$.

The second method is phenomenological and involves statistics; collecting data, identifying patterns (laws) in the data and developing methods of statistical analysis.

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Warton *et al.* [11] point out that fitting a line to a bivariate data set is not a simple task and the AR literature is filled with debate over the proper methodology. Sir Julian readily adopted the statistical approach of linear regression of $\ln X = \ln \alpha + \beta \ln Y$ on multiple data sets to determine the allometry coefficient α and exponent β . The sophisticated statistical techniques such as the principle component analysis [11] were not available to Sir Julian and although they can be found in the modern AR literature least-square regression still seems to be the method of choice [12,13].

A third method that is rarely used in the AR literature [14] is the probability calculus, which we apply herein.

In the second section the fluctuations in metabolic ARs are shown to yield a Pareto *pdf* in the allometry coefficient with the allometry exponent held fixed and a Laplace *pdf* in the allometry exponent with the allometry coefficient held fixed. The allometry parameters are shown to co-vary and the functional relation between the allometry exponent and coefficient is derived. In the third section the probability calculus is used to derive the empirical AR from the scaling of the *pdf* for the allometry variables X and Y . In the fourth section we draw some conclusions.

Fluctuations in allometry parameters. – Careful reading of Huxley’s book reveals that it is not eq. (2) that is fit to data because the data only occasionally consist of individual measurements of X and Y . The data primarily consists of averages over collections of such measurements on individual specimens and are denoted by $\langle X \rangle$ and $\langle Y \rangle$. This change in variables is not discussed in the text of his book but is explicitly stated in the table captions. This same duality permeates the literature [1,5,6] subsequent to Huxley in which the theoretical discussions focus on (X, Y) [9] but the data fits usually use $(\langle X \rangle, \langle Y \rangle)$ [13,15,16]. The data within a single species often has little variation and the theoretical AR adequately describes the intraspecies scaling [12,17]. On the other hand, data across species within a given taxa relate average quantities and an empirical AR describes the interspecies scaling.

To reconcile these very different descriptions of AR, the theoretical and empirical ones, we consider the average of eq. (2) over an ensemble of realizations of the data $\langle X \rangle = \alpha \langle Y^\beta \rangle$ and note that $\langle Y^\beta \rangle \neq \langle Y \rangle^\beta$ if $\beta \neq 1$. In order to derive the empirical AR from eq. (2) we introduce $X = \langle X \rangle + \delta X$ and $Y = \langle Y \rangle + \delta Y$ into the equation. After some algebra the allometry coefficient can be expressed as $a = \alpha + \delta a$, where δa is the fluctuation from the empirical value. Thus, we rewrite eq. (2) as $\langle X \rangle = (\alpha + \delta a) \langle Y \rangle^\beta$, which when $\delta a/\alpha \ll 1$ simplifies to the empirical AR:

$$\langle X \rangle = \alpha \langle Y \rangle^\beta \quad (3)$$

which has the form of the theoretical AR with the variables replaced with their average values.

It is evident that in order to derive the empirical AR from the theoretical one the *pdf* of the allometry coefficient fluctuations must be very narrow. The

intraspecies AR may well satisfy this condition, see for example, Glazier [17]. However the interspecies AR may not. We emphasize that eq. (3) only follows from eq. (2) when $\delta a/\alpha \ll 1$ implying that the distribution of fluctuation must be very narrow. This condition on the fluctuations in the allometry coefficient can be directly tested using available data. Note that we assume that all the fluctuations are associated with the allometry coefficient with the allometry exponent held fixed. We discuss the implications of this perspective more fully in due course.

Savage [18] made similar observations and established criteria for the conditions under which the fluctuations in TBM yield $\langle M^\beta \rangle \approx \langle M \rangle^\beta$ in terms of the standard deviation of the fluctuations. He observed that this is not a good approximation when applied to taxonomy groupings that have a large mass range. We compliment his analysis and determine the empirical distribution from which the corrections to such averages are determined and explore the implications of having a large error when replacing the average of a function with the function of the average in an AR.

Allometry coefficient. Heusner [15] studied the most commonly quoted interspecies AR, those being between BMR $X = B$ and TBM $Y = M$, which we write as

$$\langle B \rangle = a \langle M \rangle^b. \quad (4)$$

He conjectured that the allometry exponent b has a fixed value β and the allometry coefficient a remains the central mystery of allometry. Meakin [8] asserted that in homogeneous scaling relations it is the coefficient that embodies the “real physics” behind power-law relations. This latter view has also emerged in allometry, see Etienne *et al.* [19] and references therein. We explore the implications of Heusner’s conjecture to test the assumption $\delta a/\alpha \ll 1$ and treat the interspecies allometry coefficient as a random variable:

$$a' = \frac{a}{\alpha} = \frac{\langle B \rangle}{\alpha \langle M \rangle^\beta}, \quad (5)$$

with the allometry exponent $b = \beta$ held fixed. Thus there is a single value of the allometry coefficient calculated for each $(\langle B \rangle, \langle M \rangle)$ -pair.

We consider the data relating the average BMR to the average TBM for 391 species of mammal examined by Heusner [15] as well as by Dodds *et al.* [16]. A regression of the logarithmic transformation of eq. (4)

$$\ln \langle B \rangle = \ln \alpha + \beta \ln \langle M \rangle \quad (6)$$

on these data that minimizes the mean-square error is a straight line on double logarithmic graph paper. This straight line is found to have slope $\beta = 0.71$ so that empirically $2/3 < \beta < 3/4$ with the allometry coefficient fitting the smallest available TBM being $\alpha = 0.02$. Savage *et al.* [13] obtained the same value of β as Heusner [15], Dodds *et al.* [16] and us, using 626 species where the 95%

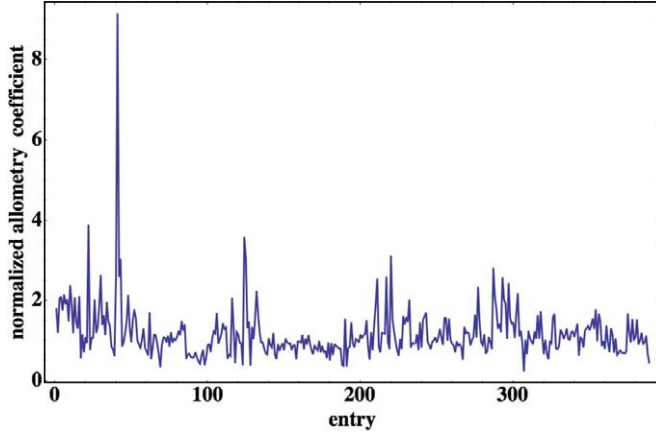


Fig. 1: (Colour on-line) This figure depicts the random nature of the normalized allometry coefficient $a' = a/\alpha$ with $\beta = 0.71$ for 391 mammalian species tabulated in Huesner [15]. Each entry is calculated from a $(\langle B \rangle, \langle M \rangle)$ -data point calculated using eq. (5). Line segments connect the data points to aid the eye in assessing variability.

confidence interval excluded both $3/4$ and $2/3$. They [13] subsequently logarithmically binned the data to change the slope to be compatible with $3/4$.

The fluctuations in the allometry coefficient normalized to α with the allometry exponent held fixed at the empirical value $\beta = 0.71$ as determined by eq. (5) are depicted in fig. 1.

In fig. 2 we depict the histogram of the fluctuations in the allometry coefficient shown in fig. 1. The data in fig. 1 are partitioned into twenty equal-sized bins on a logarithmic scale and a histogram is constructed by counting the number of data points within each of the bins as indicated by the dots in fig. 2. The solid line segment in this latter figure is the best mean-square fit to these twenty numbers.

The functional form for the histogram given by the curve in fig. 2 is expressed in eq. (7) and the quality of the fit to the residue data is determined by the correlation coefficient to be $r^2 = 0.98$. The normalized histogram $N(\ln a')$ on the interval $(0, \infty)$ using $N(\ln a') d \ln a' = P(a') da'$ yields the *pdf*:

$$a' P(a') = \frac{\mu}{2} \begin{cases} a'^{\mu}, & a' \leq 1, \\ \frac{1}{a'^{\mu}}, & a' \geq 1, \end{cases} \quad (7)$$

and empirically $\mu = 2.79$. Note that it is difficult to determine the value of the power-law index from data and so the fitted value obtained here should be viewed with some caution [20]. Equation (7) is an inverse power-law *pdf* or asymptotically a Pareto distribution describing the variability of a trait across multiple species, which in this case is BMR. The Pareto distribution indicates that the condition that the allometry coefficient *pdf* be narrow, the condition required to derive the empirical AR from the theoretical one, is not satisfied. The size of a typical

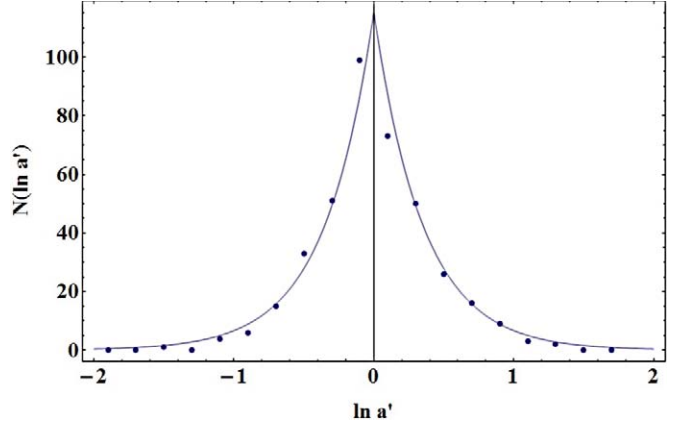


Fig. 2: (Colour on-line) The histogram of the normalized deviations from the prediction of the allometry relation $a' = a/\alpha$ using the data from fig. 1 partitioned into 20 equal-sized bins on a logarithmic scale. The solid line segment is the linear regression on eq. (7) to the twenty histogram numbers, which yields the power-law index $\mu = 2.79$ and the quality of the fit measured by the correlation coefficient $r^2 = 0.98$.

fluctuation can be estimated using the standard deviation calculated using eq. (7) and turns out to be 0.017 so that $\delta a/\alpha \sim O(1)$.

Consequently, reductionistic arguments directed towards deriving eq. (2) must be carefully considered to properly account for fluctuations. The interspecies AR given by eq. (3) cannot be derived from the theoretical AR when the condition for that derivation is violated. Note that the same distribution for the allometry coefficient with $\mu = 3.89$ was obtained using the BMR for 533 species of birds listed by McNab [21]. We do not record the latter figure here since it does not differ in any qualitatively significant way from fig. 2.

Allometry exponent. A complementary phenomenological approach to that in the preceding subsection that seems equally reasonable mathematically is to assume that the allometry coefficient is constant and the variation is due to the random nature of the allometry exponent. The fluctuations in the allometry exponent are obtained from eq. (4) in terms of the deviation from the fitted value to be

$$\delta b = \frac{\ln(B/\alpha)}{\ln M} - \beta. \quad (8)$$

If we assume $\beta = 0.71$ then eq. (8) provides us with the statistical fluctuations in the allometry exponent shown in fig. 3. Thus, there is a single value of the allometry exponent calculated for each $(\langle B \rangle, \langle M \rangle)$ -pair and we determine the *pdf* for the random allometric exponent under the assumption that $a = \alpha$.

The variability in the allometry exponent determined by the data constructed from eq. (8) is depicted in fig. 3. In fig. 4 these data from fig. 3 are used to construct a histogram exactly as we did for the allometry coefficient. The solid line segment in fig. 4 is the best fit to the twenty

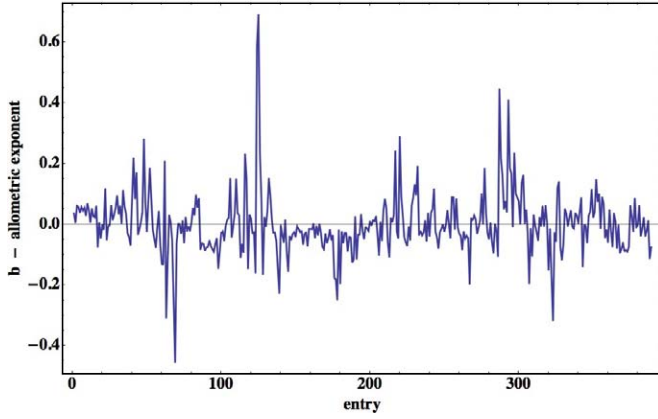


Fig. 3: (Colour on-line) This figure depicts the random nature of the allometry exponent with $\alpha = 0.02$ for 391 mammalian species tabulated in Huesner [15]. Line segments connect the data points to aid the eye in assessing the variability. Each entry is calculated from a $(\langle B, \langle M \rangle)$ -data point calculated using eq. (8).

numbers of the histogram with minimum mean-square error. The functional form for the histogram of deviations from the allometry exponent β is determined by the curve in fig. 4 and the quality of the fit to the histogram is determined by the correlation coefficient $r^2 = 0.97$. The histogram is fit by the Laplace *pdf*

$$\Psi(b) = \frac{\gamma}{2} \exp[-\gamma |b - \beta|] \quad (9)$$

with the empirical value $\gamma = 12.85$.

Co-variation of allometry parameters. We have obtained two separate distributions for the same data. In the first distribution fluctuations were associated with the allometry coefficient and the allometry exponent was held constant, in the second distribution the fluctuations were associated with the allometry exponent and the allometry coefficient was held constant. As pointed out by Glazier [12] species within a taxon represent a cloud of different metabolic rates and not just the linear metabolic level determined by linear regression. His metaphoric cloud is incorporated into the present discussion by abandoning the assumption that the allometry coefficient and exponent are independent of one another and requiring that the probability of a given fluctuation is the same regardless of representation so that

$$\mathcal{P}(a) da = \Psi(b) db. \quad (10)$$

In order to calculate a non-zero Jacobian of the transformation between the two allometry parameters requires that they be functionally related. We assume $b = \beta - c \ln a$, so that by inserting the allometry exponent *pdf* eq. (9) into (10), using the Jacobian $|db/da| = c/a$, and simplifying we obtain

$$\mathcal{P}(a) = \frac{\gamma c}{2} \begin{cases} a^{\gamma c - 1}, & \text{for } a \leq \alpha, \\ \frac{1}{a^{\gamma c + 1}}, & \text{for } a \geq \alpha. \end{cases} \quad (11)$$

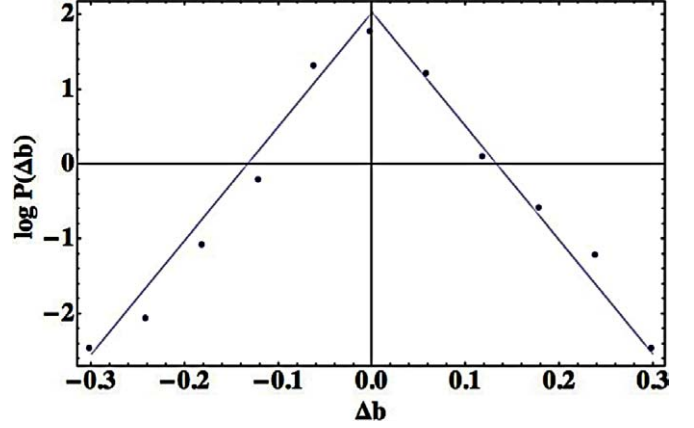


Fig. 4: (Colour on-line) The histogram of the deviations from the prediction of the AR using the data depicted in fig. 3 partitioned into 20 equal-sized bins on a logarithmic scale. The solid line segment is the best fit of eq. (9) with $\Delta b \equiv b - \beta$ to the twenty histogram numbers, and the quality of the fit is measured by the correlation coefficient $r^2 = 0.97$ with $\gamma = 12.85$.

Comparing eq. (11) with eq. (7) we can identify $\mu = \gamma c$ and obtain the *pdf* for the allometry coefficient $P(a') da' = \mathcal{P}(a) da$. Using the empirical values $\mu = 2.79$ and $\gamma = 12.85$ we obtain $c = 0.217$ and consequently the empirical transformation can be written as

$$b = 0.71 - 0.50 \log_{10} a. \quad (12)$$

Note that this functional dependency of the allometry exponent on the allometry coefficient is consistent with the empirical co-variation relation obtained by Glazier [12] who used a completely different method. The numerical value of the allometry exponent 0.71 in the transformation eq. (12) is within a few percent of that obtained by Glazier [12]. The reasons why the value of the coefficient in the allometry coefficient term differs from that of Glazier [12] are two: we are using a different data set to fit the parameters and as is well known it is very difficult to obtain an accurate power-law index from data [20].

Evolution of probabilities. – This statistical result that the fluctuations of the interspecies AR can be very large weakens the predictions of reductionist theories. Said differently the condition that the distribution of fluctuations be narrow in order to derive the empirical AR from the theoretical one is violated by the Pareto PDF for the allometry coefficient using interspecies metabolic data. In order to resolve this contradiction more generally we use the probability calculus and consider a probability analog of Sir Julian's assumption.

Consider the dynamics of a complex network that is heterogeneous in the random variable and whose fluctuations in time contain historical information. We choose a fractional derivative in time given by a Riemann-Liouville operator of order ν [22,23] O_t^ν and a Reisz potential in

the phase space variable z of order η [24] O_z^η and formally represent the fractional diffusion equation (FDE) as

$$G(O_t^\nu, O_z^\eta) P(z, t) = 0, \quad (13)$$

where G is a linear function of the operators. However rather than reviewing the fractional calculus as it applies to the FDE [22,23,25] we instead examine the scaling properties of its solution. The Fourier transform of an analytic function $f(z)$ is $\tilde{f}(k)$ and the Laplace transform of an analytic function $g(t)$ is $\hat{g}(u)$. Consequently the FDE can be expressed in Fourier-Laplace space as $G^*(u, k)P^*(k, u) = 0$, and the asterisk denotes the Fourier-Laplace transform.

The Fourier-Laplace transform of the *pdf* can be written [25] as

$$P^*(k, u) = \frac{u^{v-1}}{u^v + K_\eta |k|^\eta} \quad (14)$$

and K_η is a constant. The *pdf* that solves the FDE is given by the inverse Fourier-Laplace transform of eq. (14) and is [25]

$$P(z, t) = \frac{1}{t^{\mu_z}} F_z\left(\frac{z}{t^{\mu_z}}\right) \quad (15)$$

with $\mu_z = v/\eta$. Here $F_z(q)$ is an analytic function of the similarity variable $q = z/t^{\mu_z}$, t is the time and μ_z is a scaling parameter indexed to the allometry variable of interest. The scaling distribution eq. (15) indicates that the phenomenon is a fractal stochastic process.

It is reasonable to assume that the distribution of an ensemble of host networks and the distribution of an ensemble of subnetworks strongly coupled to its host are closely related. For the phenomena considered herein the ensemble distributions are those for fractal processes with different fractal dimensions. Therefore we assume that both X and Y are described by eq. (15) with the appropriate changes in indices. The average value of the phase space variable is

$$\langle Z \rangle = \bar{Z} t^{\mu_z} \quad (16)$$

with the constant

$$\bar{Z} = \int q F_z(q) dq \quad (17)$$

and we obtain time-dependent averages for both $\langle X \rangle$ and $\langle Y \rangle$. Taking the time derivatives of these averages and eliminating the time from the two equations yields the differential growth of the average values

$$\frac{1}{\mu_x \langle X \rangle} \frac{d \langle X \rangle}{dt} = \frac{1}{\mu_y \langle Y \rangle} \frac{d \langle Y \rangle}{dt}. \quad (18)$$

Equation (18) integrates directly to the empirical AR, eq. (4), see West and West [26] for more details. The allometry parameters are determined to be $b = \mu_x/\mu_y$ and $a = \bar{X}/\bar{Y}^b$. Thus, in analogy with Sir Julian's assumption of the ratio of growth rates being constant, we determine that the ratio of indices from the *pdf*'s yield a proportional relative growth of the two averages.

Conclusions. — Herein we proved that the empirical AR can only be derived from the theoretical AR when the magnitude of the fluctuations in the allometry coefficient are sufficiently small. This condition was tested for interspecies AR using metabolic aviary and mammalian data and it was found that the empirical AR could not be derived from the theoretical one. The argument required changing representations from one in which the network observables are random and the allometry parameters are empirical constants, to the equivalent representation in which the average network observables are constant and the allometry parameters are random. From the latter representation we determined that the allometry parameters are not independent of one another and the functional relation between them agrees with that obtained from a phenomenological analysis of a great deal of data by Glazier [12].

The failure of the empirical AR to follow from the theoretical one implies that the reductionist arguments used to derive the theoretical AR, such as the fractal nutrient transport models based on fractal geometry [9], must be more carefully considered to properly incorporate random fluctuations. The scaling of interspecies metabolic AR is not a consequence of fractal geometry, but results from fractal statistics and the subsequent scaling of the *pdf*'s as we argue in the third section.

Meakin [8] observed that the exponents are universal in many homogeneous scaling phenomena and the coefficients provide the only means to control physical properties and behavior. This observation is consistent with the results of our analysis that AR is entailed by scaling of the *pdf* for the statistical fluctuations of the allometry parameters. However his analysis did not address the two-variable fitting used herein from which we were able to deduce a relation between the allometry exponent and allometry coefficient in agreement with the linear regression analysis of Glazier [12]. Consequently, the allometry exponent is not universal. Additional measurements are necessary to distinguish between the probabilistic modeling of the allometry parameters and the mechanistic modeling of others [19].

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