

# Allometric algorithms

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*The aim of the present study is to emphasize the applicability and versatility of the allometric equation in the biological sciences. This equation ( $Y = a \cdot M^b$ ) was introduced by Huxley (1932) for intra- and interspecific comparisons of morphological, physiological and ecological variables (Y), when they are expressed as functions of body mass (M). The regression analysis of the experimental data, plotted in a double logarithmic scale, yields a straight line, which is equivalent to the logarithmic form of the above mentioned allometric equation [ $\log Y = \log(a) + (b) \cdot \log(M)$ ]. Only the exponent (b) can be calculated **a priori** for a given function, based firstly on the corresponding dimensional analysis in accordance with the MLT-system of physics, and secondly on one of the theories of biological similarity, while parameter (a) is of empirical nature. A relevant feature of the allometric equations is that they can be treated algebraically to obtain allometric ratios, mass independent numbers (MIN), and even dimensionless numbers ( $M^0L^0T^0$ ), which are valid for all organisms pertaining to the same taxonomic classification.*

**Key words:** allometry, body weight, comparative physiology, dimensional analysis, logarithmic scaling.

## INTRODUCTION

For any quantitative analysis of biological data, it is necessary to take into account that: *i-* the size spectrum of living beings (McMahon & Bonner, 1983) is of 21 orders of magnitude, which includes at one end the mycoplasmas ( $10^{-13}$  g) and on the other the blue whales ( $10^8$  g); *ii-* that the relationship between any variable (Y) and body mass (M) is generally non-linear. In biological sciences, it is customary to utilize Huxley's (1932) allometric equation for this purpose:

$$Y = a \cdot M^b \quad (1)$$

This simple power equation in its logarithmic form reads as follows:

$$\log(Y) = \log(a) + b \cdot \log(M) \quad (2)$$

The latter equation corresponds to a straight line (Fig 1), and is the most elementary procedure for the statistical treatment of experimental data. An additional advantage of allometric equations is that they can be submitted to algebraic operations, as for instance:

1) the **product** of two allometric equations yields:

$$M^x \cdot M^w = M^{(x+w)} \quad (3)$$

2) or else, the **quotient** of two equations gives:

$$M^x/M^w = M^{(x-w)} \quad (4)$$

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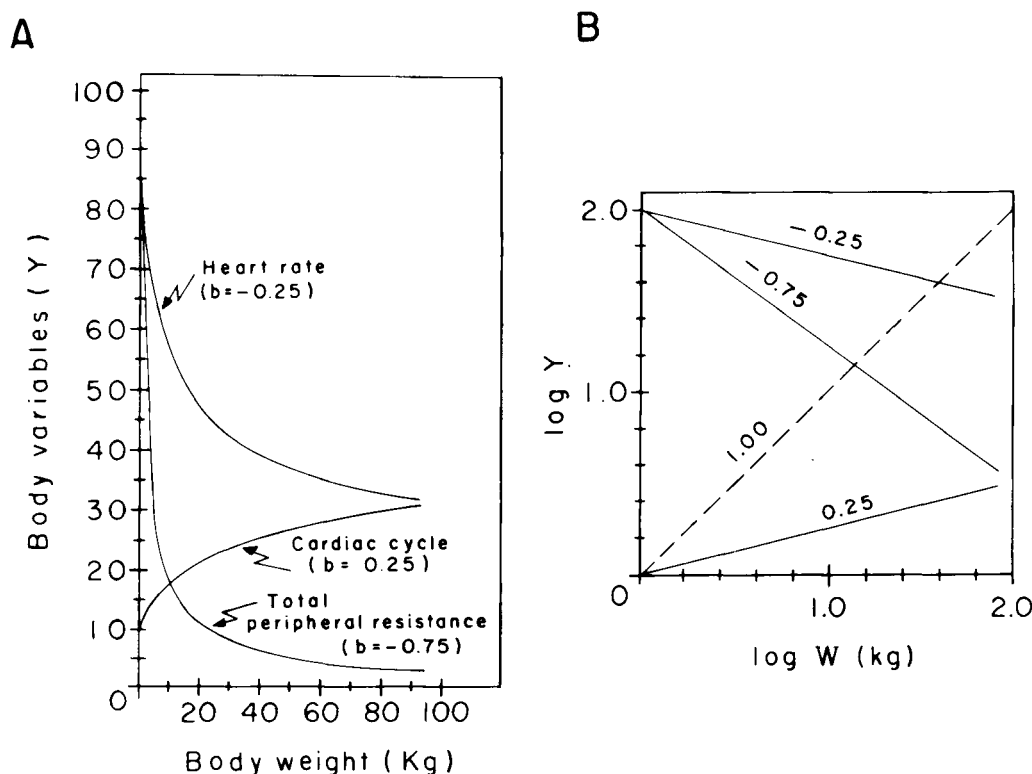


Fig 1. Three allometric equations of cardiovascular system represented (A) in current coordinate (Cartesian system), and (B) as log-log plot of the same variables, including as a reference  $b = 1.0$  (isometry).

3) finally, the **power** of an allometric equation is:

$$(M^x)^w = M^{xw} \quad (5)$$

In consequence, the above mentioned three algebraic operations can be applied to numerous variables in an iterative manner, so that the results may be algorithms of great biological interest. We have used the term "algorithm", from the Arab mathematician Al-Khuwarizmi (around 825 AD), to indicate that we are dealing with "a rule of procedures for solving a mathematical problem in a finite number of steps that generally involves the repetition of an operation".

#### SCALING

All problems which are related with size (L) or mass (M) of a living being are of obvious importance, not only with regard to the morphology or the physiology of each or-

ganism, but also for its ethological and ecological implications.

One of the aims of comparative physiology is to establish quantitative differences between organisms of different size and, for this purpose, it is customary to define one organism as the **prototype** (p) and the other as the **model** (m), where prototype means a large or a small scale organism to which a model organism is geometrically, chemically or physically related. For the dimensional analysis, the MLT-system is preferentially utilized, where **M** = mass, **L** = length, and **T** = time. Any biological function (Y) can be defined as the product of three power functions of these variables (M, L, T), so that:

$$Y = M^\alpha L^\beta T^\gamma \quad (6)$$

as specified in Table I, where the corresponding exponents ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) are indicated for each variable.

**Table I**

Dimensional analysis of thirteen variables of biological interest

Item	Variable	Definition	Dimensions		
			M $\alpha$	L $\beta$	T $\gamma$
1	Mass	Unit of matter	1	0	0
2	Length	Unit of space	0	1	0
3	Time (period)	Duration of one cycle	0	0	1
4	Area	Length squared	0	2	0
5	Volume	Cube of a length	0	3	0
6	Flow	Volume per unit time	0	3	-1
7	Frequency	The reciprocal of one period	0	0	-1
8	Energy; work	Force times distance	1	2	-2
9	Power	Work per unit time	1	2	-3
10	Pressure	Force per unit area	1	-1	-2
11	Resistance	Pressure gradient per unit flow	1	-4	-1
12	Concentration	Mass per unit volume	1	-3	0
13	Compliance	Change of volume per change of pressure	-1	4	2

**Table II**

Comparison of the different theories of similarity

Item	Similarity	Yates's coefficients			References
		p	q	r	
1	Mechanical	1	0.33	0.17	Galileo, 1638 (see Levi-Civita & Amaldi, 1950)
2	Biological	1	0.33	0.33	Lambert & Teissier, 1927
3	Elastic	1	0.25	0.25	McMahon, 1973
4	Empirical regression coefficients	0.96	0.35	0.30	Günther <i>et al.</i> , 1992

#### DIFFERENT THEORIES OF BIOLOGICAL SIMILARITY

The theories of biological similarity (Lambert & Teissier, 1927; McMahon, 1973), which are based on the MLT-system of physics, can be utilized to predict the allometric exponent ( $b$ ) of Huxley's allometric equation (eqn 1) and, in consequence, these predictions can be "falsified" in the sense of Popper (1980) by comparing the calculated or theoretical reduced exponent ( $b_R$ ) with the corresponding empirical values ( $b_E$ ), which are obtained by means of the linear regression analysis of the experimental data (for more details see Günther, 1975 a, b). It is necessary to insist that from the dimensional analysis (Levi-Civita & Amaldi, 1950), we can obtain only the numerical values of the exponents ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) of the corresponding fundamental units (MLT). The already known theories of biological similarities (Table II) differ only with regard to the coefficients for each of these exponents. The numerical

values of the three exponents are unknown and, therefore, Yates (1979) proposed the following algebraic equation to obtain the coefficients ( $p$ ,  $q$ ,  $r$ ) for the reduced allometric exponent ( $b_R$ ):

$$b_R = p\alpha + q\beta + r\gamma \quad (7)$$

The statistical solution for equation 7 was obtained by means of multiple regression analysis (Günther *et al.*, 1992) of 203 empirical allometric exponents which appeared in literature (Calder, 1984; Peters, 1983). The simplified equation (of statistical origin) is the following one:

$$b_R = 0.96\alpha + 0.35\beta + 0.30\gamma \quad (8)$$

#### A DIMENSIONAL NETWORK

From the MLT-system of physics it is possible to deduce the corresponding dimensional formulae for numerous functions, as

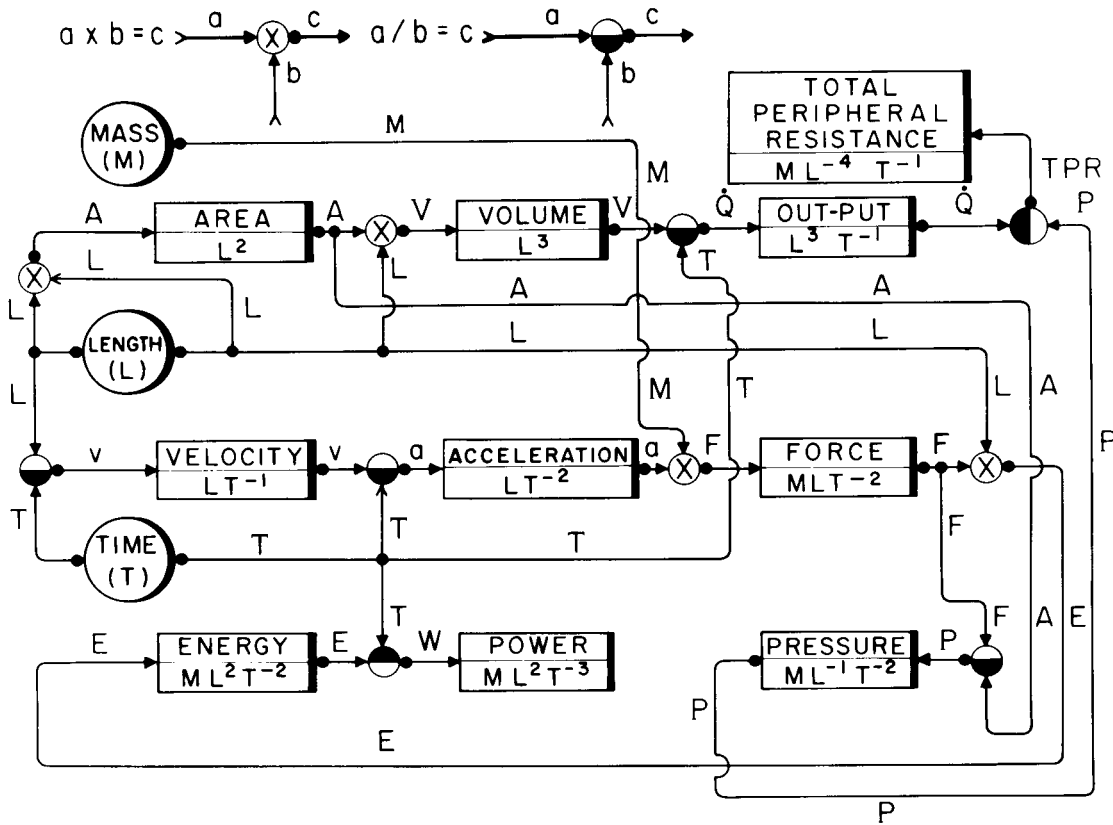


Fig 2. Functional relationships among biological variables defined in accordance with the MLT-system of physics. For each variable, the corresponding name and its physical dimension are indicated.

shown in Figure 2. As it has been said, from each dimensional formula, the corresponding allometric “reduced” exponent ( $b_R$ ) can be calculated in accordance with equation 8.

These theoretically predicted values ( $b_R$ ) can be compared with the empirical allometric exponents ( $b_E$ ), which normally are obtained from the regression analysis of the experimental data. The correlation between  $b_R$  and  $b_E$  for 12 variables of biological interest is shown in Figure 3.

**MORPHOMETRY AND PHYSIOMETRY OF THE MAMMALIAN CARDIOVASCULAR SYSTEM**

The applicability of Huxley’s allometric equation is illustrated in Figure 4, where 17 different cardiovascular variables are characterized by means of the corresponding reduced exponent ( $b_R$ ), as calculated after equation 8. The same procedure can be extrapolated to any other physiological system, with the specific aim to establish intra- or

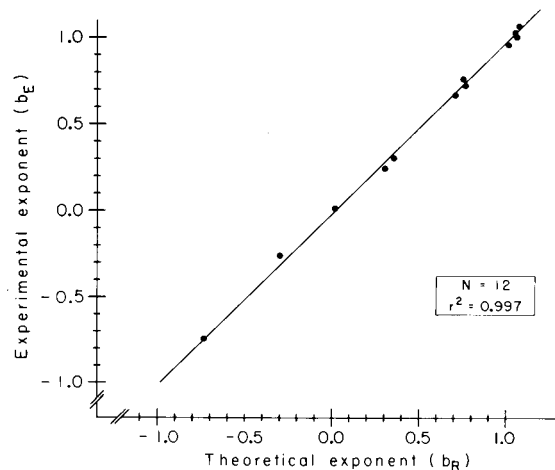
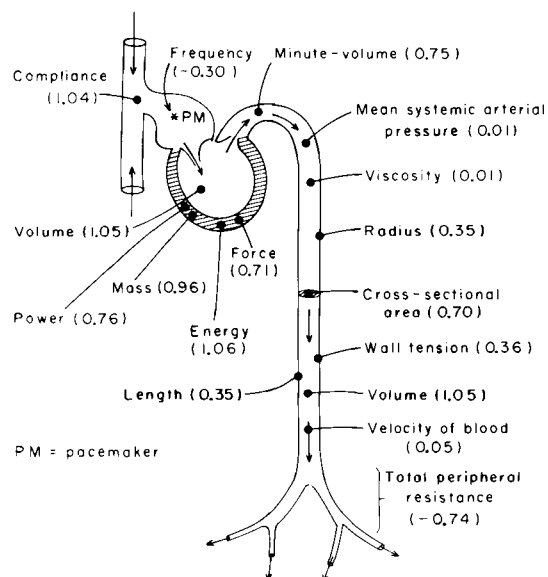


Fig 3. Regression analysis of the theoretical allometric reduced exponent ( $b_R$ ) of 12 variables of biological interest and the corresponding experimental values ( $b_E$ ).

interspecies quantitative comparisons for a given variable (see Table III). For instance, and following Laplace’s law, we obtain for wall tensions ( $T = P \cdot R$ ) in cylindrical



$$b_R = 0.96\alpha + 0.35\beta + 0.30\gamma$$

Fig 4. Seventeen allometric reduced exponents ( $b_R$ , within parentheses) of morphological and physiological variables of the cardiovascular system of mammals.

structures that the product of pressure ( $b_R = 0.01$ ) and radius ( $b_R = 0.35$ ) yields  $b_R = 0.36$ , as shown in Figure 4.

On the other hand, for the total peripheral resistance (TPR), we have  $TPR = (SAP)/$

( $Q_b$ ), being  $Q_b$  the minute-volume of blood ejected by the left ventricle. In this case the final result will be:

$$TPR = (SAP)/(Q_b) = M^{0.01}/M^{0.75} = M^{-0.74} \quad (9)$$

Furthermore, the functional relationship among many variables can be defined in a quantitative manner by means of a series of operations with several allometric reduced exponents ( $b_R$ ). To illustrate this procedure, we summarize in Figure 5 all cardiovascular functions which finally yield the systemic arterial pressure (SAP).

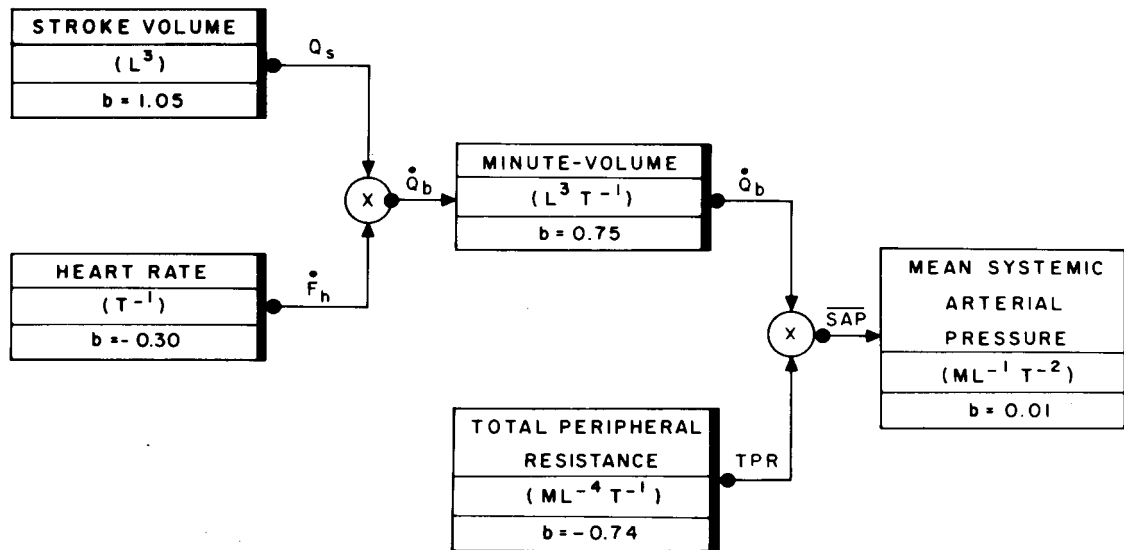
#### ALLOMETRY OF THE MAMMALIAN RESPIRATORY SYSTEM

In Table IV, we can find the allometric parameters ( $a$  and  $b$ ) for 14 variables concerning the respiratory apparatus of Eutherian mammals under resting conditions. For instance, Schmidt-Nielsen (1984, p 102) established five ratios between pairs of respiratory variables, which in each case yielded dimensionless ( $M^0$ ) and invariant numbers (Table V). These ratios indicate that for all mammals, irrespective of their sizes, five constant ratios could be established.

Table III

Allometric characteristics of the mammalian cardiovascular system

Item	Variable	Unit	Parameter a	Exponent b	References
1	Volume of the heart	ml	5.72	0.98	Peters, 1983, p 257
2	Stroke volume	ml	0.74	1.03	Peters, 1983, p 257
3	Blood volume	ml	76	1.00	Peters, 1983, p 257
4	Pulse frequency	s <sup>-1</sup>	4.03	-0.25	Peters, 1983, p 257
5	Cardiac output	ml · s <sup>-1</sup>	3.4	0.74	Peters, 1983, p 258
6	Aortic length	m	0.164	0.32	Peters, 1983, p 259
7	Aortic cross-section	m <sup>2</sup>	1.8 x 10 <sup>-5</sup>	0.67	Peters, 1983, p 259
8	Aortic blood velocity	m · s <sup>-1</sup>	0.298	0.07	Peters, 1983, p 259
9	Systemic arterial pressure	Pascal (Pa)	1.5 x 10 <sup>4</sup>	0.032	Peters, 1983, p 260
10	Total peripheral resistance	Pa · s · m <sup>-3</sup>	0.255	-0.68	Peters, 1983, p 260
11	Cardiac work	Joule	8.91 x 10 <sup>-3</sup>	1.06	Peters, 1983, p 260
12	Cardiac power	Watt	0.038	0.77	Peters, 1983, p 260
13	Inferior vena cava length	cm	13.3	0.33	Calder, 1984, p 110
14	Mass of the heart	g	5.88	0.98	Calder, 1984, p 112
15	Thickness of ventricular wall	mm	2.50	0.46	Calder, 1984, p 115
16	Aortic diameter	cm	0.34	0.36	Calder, 1984, p 110
17	Inferior vena cava diameter	cm	0.48	0.41	Calder, 1984, p 110
18	Left ventricular mass	g	1.65	1.11	Peters, 1983, p 267
19	End-systolic volume (left ventricle)	ml	0.59	0.99	Peters, 1983, p 257
20	End-diastolic volume (left ventricle)	ml	1.76	1.02	Peters, 1983, p 257



- I )  $Q_s \times F_h \times TPR = \overline{SAP}$  ( Functional equation )
- II )  $M^{1.05} \times M^{-0.30} \times M^{-0.74} = M^{0.01}$  ( Allometric equation )
- III  $[L^3] \times [T^{-1}] \times [ML^{-4} T^{-1}] = [ML^{-1} T^{-2}]$  ( Dimensional analysis )

Fig. 5. Allometric sequence of circulatory variables, which finally lead to mean systemic arterial pressure (SAP).

Table IV

Allometric characteristics of the mammalian respiratory system

Item	Variable	Units	Parameter a	Exponent b	References
1	Tidal volume	ml	7.69	1.04	Peters, 1983, p 255
2	Vital capacity	ml	56.7	1.03	Peters, 1983, p 254
3	Air flow	ml • min <sup>-1</sup>	6.32	0.80	Peters, 1983, p 255
4	Total compliance	ml • Pa <sup>-1</sup>	1.59 x 10 <sup>-9</sup>	1.04	Peters, 1983, p 256
5	Breathing power	Watt	1.57 x 10 <sup>-3</sup>	0.78	Peters, 1983, p 256
6	Frequency of respiration	s <sup>-1</sup>	0.891	-0.26	Peters, 1983, p 255
7	Oxygen consumption rate	ml • min <sup>-1</sup>	11.6	0.76	Calder, 1984, p 92
8	Lung volume	ml	45.2	1.05	Peters, 1983, p 254
9	Tracheal volume	ml	0.920	1.15	Peters, 1983, p 254
10	Dead space volume	ml	2.76	0.96	Peters, 1983, p 254
11	Lung capillary area	m <sup>2</sup>	2.73	0.952	Peters, 1983, p 256
12	Lung compliance	ml • Pa <sup>-1</sup>	21.4 x 10 <sup>-9</sup>	1.08	Peters, 1983, p 256
13	Total airway resistance	Pa (m <sup>3</sup> • s) <sup>-1</sup>	2.36 x 10 <sup>6</sup>	-0.70	Peters, 1983, p 256

AN ALLOMETRIC CASCADE

Instead of multiplying several allometric equations, as mentioned before, we will try now the opposite operation, namely to calculate the ratios (division) between several functions of the kidneys in Eutherian mammals (Calder, 1984). The first question might be: How much blood flows through both

kidneys in comparison with the cardiac output? The next problem could be: Which is the amount of the glomerular filtration rate as a fraction of the total renal blood flow? Finally: How much of the glomerular filtrate is reabsorbed by all tubules, and how much fluid appears finally as urine? The answers to these questions are summarized in Table VI.

**Table V**

Allometric ratios of the respiratory system of mammals.  
(After Schmidt-Nielsen, 1984, pp 102-103)

Item	Ratio	Unit	Allometric equation	Allometric ratio	Comments
1	$V_T/VC$	ml/ml	$7.69 M^{1.04} / 56.7 M^{1.03}$	$0.136 M^{0.01}$	This ratio is mass-independent and dimensionless. The tidal volume ( $V_T$ ) is equivalent to 1/7 of the vital capacity ( $V_C$ )
2	$C/VC$	(ml/cm H <sub>2</sub> O)/ml	$1.56 M^{1.04} / 56.7 M^{1.03}$	$0.028 M^{0.01}$	When the lung of vertebrates is submitted to a pressure increase of 1 cm H <sub>2</sub> O, its volume expands in 0.028 ml of air for each ml of its volume
3	$V_T/C$	ml/(ml/cm H <sub>2</sub> O)	$7.69 M^{1.04} / 1.56 M^{1.04}$	$4.93 M^{0.0}$	The pressure required to increase the lung volume in one tidal volume ( $V_T$ ) is the same in all mammals, namely 4.93 cm H <sub>2</sub> O
4	$W/VO_2$	(g-cm/min)/(ml O <sub>2</sub> /min)	$962 M^{0.78} / 11.6 M^{0.76}$	$4.05 \times 10^{-4} M^{0.02}$	The power (Watt) of the respiratory muscles is equal to 0.04 % of the metabolic power, also in Watt *
5	$VO_2/V_E$	(ml O <sub>2</sub> /min)/(ml/min)	$11.6 M^{0.76} / 379 M^{0.80}$	$0.031 M^{-0.04}$	The oxygen consumption per minute ( $VO_2$ ) represents only 3 % of the pulmonary ventilation ( $V_E$ )

$V_T$ : tidal air (ml);  $VC$ : vital capacity (ml);  $C$ : compliance (DV/Dp);  $W$ : respiratory power ( $W = g\text{-cm/min}$ );  $VO_2$ : metabolic power, expressed as O<sub>2</sub> consumption (ml O<sub>2</sub>/min);  $V_E$ : volume of expired air (ml) per minute.

\* The energy (g-cm/min) is recalculated to Joules per second (Watts), and 1 ml O<sub>2</sub> when metabolized corresponds to 20.1 Joules.

**Table VI**

Allometric cascade of the renal system and its circulatory support.  
(Modified from Calder, 1984, p 133)

Item	Function	Allometric equation	Ratios and Percentages
1	Cardiac output (CO)	$187 M^{0.81}$	
2	Renal blood flow (RBF)	$43.1 M^{0.77}$	
3	Glomerular filtration (GFR)	$5.36 M^{0.72}$	
4	Urine production (UP)	$0.042 M^{0.75}$	
5	RBF / CO	$43.1 M^{0.77} / 187 M^{0.81}$	$0.230 M^{-0.04} = 23\%$
6	GFR / RBF	$5.36 M^{0.72} / 43.1 M^{0.77}$	$0.124 M^{-0.05} = 12.8\%$
7	UP / GFR	$0.042 M^{0.75} / 5.36 M^{0.72}$	$0.0078 M^{0.03} = 0.8\%$

### DISCUSSION

The integrative nature of different organs or functions can be analyzed in a quantitative manner by means of the corresponding allometric equations, which are generally expressed as functions of body mass (M), due to the fact that M is universally accepted as a convenient reference system in the biological sciences. Adolph (1949) has summarized this holistic approach in the following manner: "Many physiological properties go hand in hand with one another; their determination is reciprocal and not unique. It seems likely that an organism is an integrated system by virtue of the fact that none of its properties

is entirely uncorrelated, but that most are demonstrably interlinked; and not just by simple chains, but by a great number of criss-crossed linkages".

Despite the fact that the great majority of morphological, physiological and ecological variables are correlated with body mass (M), Schmidt-Nielsen (1984, p 141) suggested that there exists also a certain number of non-scalable physiological variables, *i.e.*, that they are mass-independent numbers (MIN), as for instance: *i*- viscosity of the blood; *ii*- plasma protein concentration; *iii*- hematocrit; *iv*- blood pressure; *v*- red cell size; *vi*- capillary diameter.

To obtain mass independent numbers (MIN) and in some instances even adimensional conditions ( $M^0L^0T^0$ ), Stahl's (1962, 1963, 1965, 1967) *allometric cancellation method* can be recommended, since this procedure consists in the multiplication or division of the corresponding allometric equations, with the specific purpose to obtain finally Stahl's "residual mass exponent" (RME), which should be equal or very close to zero ( $M^0$ ). For instance, interspecies or intraspecies comparisons can easily be obtained by employing Stahl's cancellation method. A specific example (Calder, 1984, p 144) may be the comparison of the heart rate and the respiratory rate in mammals of different size. The corresponding allometric equations are:

1) for the **heart rate**:

$$F_h = 241 \cdot M^{-0.25} \quad (10)$$

2) for the **respiratory frequency**:

$$F_r = 53.5 \cdot M^{-0.25} \quad (11)$$

The **ratio** between equations 10 and 11 is:

$$F_h/F_r = 241 \cdot M^{-0.25} / 53.5 \cdot M^{-0.25} = 4.5 \cdot M^{0.01} \quad (12)$$

which means that, for all mammals, we have 4.5 heart beats for each respiratory cycle.

Another example is the metabolic scope. Thus, the relationship between the maximal oxygen consumption ( $VO_2 \text{ max}$ ) and the standard oxygen consumption ( $VO_2 \text{ st}$ ) in 14 species of wild mammals (Schmidt-Nielsen, 1984, p 155) is:

$$VO_2 \text{ max}/VO_2 \text{ st} = 1.94 \cdot M^{0.79} \cdot 0.188 \cdot M^{0.75} = 10.3 \cdot M^{0.04} \quad (13)$$

In conclusion, the maximal oxygen consumption is 10 times greater than the oxygen consumption at rest in mammals.

The above are only a few examples of the applicability of the allometric equations to obtain ratios of intraspecific or interspecific validity, based either on Stahl's (1962, 1963, 1965, 1967) cancellation method, or else, by means of the mass-independent numbers (MIN), which yields also Stahl's residual mass exponents (RME) close to zero.

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#### APPENDIX

The aim of this Appendix is to represent, for the first time to our knowledge, the two parameters (a, b) of the allometric equations (see eqn 1) as a single point in the Cartesian plane. Usually, the numerical values of both parameters (a, b) are given in the form of Tables (as examples see Tables A-I and A-II). In the present case, due to the wide range of the numerical values of parameter a it is convenient to use a semilogarithmic plot.



**Table A-I**

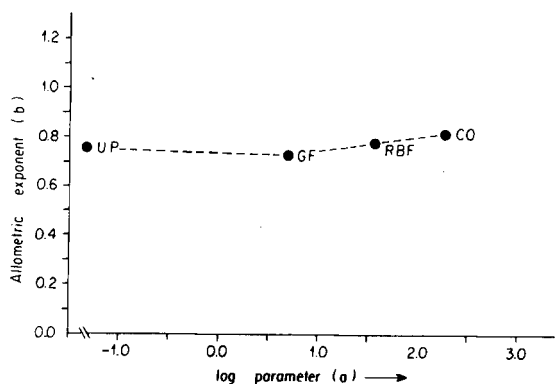
Allometric functional cascade of the renal system in mammals (Data from Calder, 1984)

Item	Function (ml/min)	Parameter (a)	log (a)	Exponent b ± SEM
1	Cardiac output	187	2.2718	0.81 ± 0.01
2	Renal blood flow	43.1	1.6344	0.77 ± 0.08
3	Glomerular filtration	5.36	0.7291	0.72 ± 0.04
4	Urine production	0.042	- 1.3767	0.75 ± 0.10

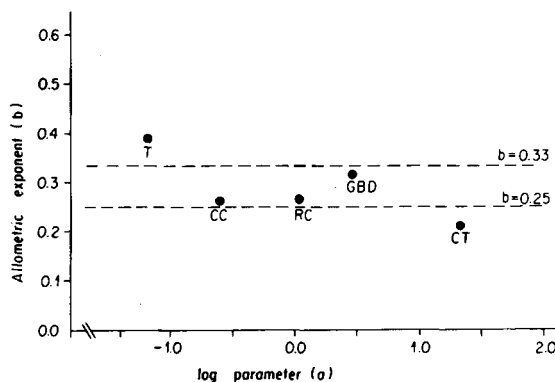
**Table A-II**

Allometric equations related to time functions (Data from Calder, 1984)

Item	Function (ml/min)	Parameter (a)	log (a)	Exponent b
1	Cardiac cycle	0.25	- 0.6021	0.25
2	Respiratory cycle	1.12	0.0492	0.26
3	Gut beat duration	2.85	0.4548	0.31
4	Circulation of blood volume	21	1.322	0.21
5	Twitch contraction cycle of soleus muscle	0.064	- 1.1938	0.39



**Fig A-1.** Two-dimensional semilogarithmic diagram of allometric equations related to circulatory and renal volume flows ( $\text{ml} \cdot \text{min}^{-1}$ ) in mammals. Ordinate, allometric exponent (b). Abscissa, logarithm of parameter (a). CO, cardiac output; RBF, renal blood flow; GF, glomerular filtration; UP, urine production. [Data from Calder (1984), p 133].



**Fig A-2.** Two dimensional diagram of allometric equations related to several time functions (s) of mammals. Ordinate, allometric exponent (b). Abscissa: logarithm of parameter (a). CT, circulation time of blood volume; GBD, gut beat duration; RC, respiratory cycle; CC, cardiac cycle; T, twitch contraction cycle of soleus muscle. The two reference lines correspond to the mean values ( $b = 0.33$  and  $b = 0.25$ ) of periodic phenomena in mammals. [Data from Calder (1984), pp 142-143].

As shown in Figure A-1, the exponents (b) of the renal flow cascade are almost the same, while in the abscissa (log a) the reduction of flows (ml/min) is dramatic, if one compares cardiac output (187 ml/min) with urine production (0.042 ml/min), *i.e.*, 4500 times less.

Another example is illustrated in Figure A-2, where different periodic phenomena are represented as points in the Cartesian plane. Again, the semilogarithmic plot allows to compare two time functions of similar allometric exponent (b). For instance, the cir-

ulation time (CT) with the cardiac cycle (CC), which yields a ratio of 84 times, or the gut beat duration (GBD) of the intestinal smooth muscles with the twitch of striated soleus muscle (T), being the ratio 44.5 times.

It is worth mentioning, that the conclusions we obtained from the two ratios are valid for all mammals, irrespective of their sizes.

In sum, the semilogarithmic plot of the characteristic allometric parameters in a Cartesian plane permits an easy visualization of functional relationships.

