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Indexing cardiovascular and respiratory variables: allometric scaling principles

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1REVIEW

2BH Pypendop and JH Jones
3Indexing cardiopulmonary variables
4Indexing cardiovascular and respiratory variables: allometric scaling principles
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13Abstract

14**Objectives** To describe the allometric scaling principles underlying appropriate indexing of 15cardiovascular and respiratory measurements obtained in adult mammals, and to propose 16guidelines for indexing experimental cardiovascular and respiratory data.

17**Database used** PubMed, using the terms 'allometry', 'allometric', 'indexing', 'cardiovascular' 18and 'respiratory'.

19**Conclusions** Indexing of cardiopulmonary variables is commonly used in attempts to account for 20the effects of body size on measurements and to standardize them. Some cardiopulmonary 21variables have been indexed using various functions of body mass in a process that often ignores 22the underlying relationship between the variable of interest and body size, as described in the 23allometry literature. This can result in a failure to ideally reduce the effect of body size on

24measurements in a manner that highlights differences. We review how commonly measured 25cardiopulmonary variables are related to body mass in mammalian species according to the 26allometry literature, and offer suggestions on how this information can be used to appropriately 27index cardiopulmonary variables in a simple and informative manner.

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29*Keywords* cardiac index, cardiovascular, respiratory.

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31Introduction

32Numerous variables of interest to the anesthesiologist are known to vary as a function of body 33size. Many variables increase as body size increases (e.g. cardiac output, minute ventilation), 34whereas others decrease as body size increases (e.g. heart rate, respiratory rate) and some do not 35vary systematically with body size (e.g. blood pressure, hematocrit). Many researchers have 36 recognized the utility of expressing cardiopulmonary variables known to vary with body size as 37values indexed to another size-related variable; for example, cardiac index may be calculated as 38the quotient of cardiac output and body surface area (BSA). Such expressions reduce the 39variability of measurements, may artificially eliminate the effect of body size on the variable and 40 give a clearer indication of how an individual animal's values compare with those expected for a 41typical animal of its body size. However, a variety of methods for such indexing are found in the 42literature. The simplest, and possibly most common adjustment, is to divide the measurement by 43body mass and present it mass-specifically. Although this is appropriate for some variables, as 44will be described, many cardiopulmonary variables increase or decrease in a manner that is not 45directly proportional to body mass, and indexing them to body mass will under- or overestimate, 46respectively, the true size-adjusted value; this error will be amplified as body size difference

47 increases (Table 1). Therefore, the actual function of body mass with which the variable changes 48 should be used for indexing. Examining the veterinary anesthesia literature confirms that 49 incorrect indexing of cardiopulmonary measurements is common; for example, of 10 articles 50 recently published in this journal that reported both cardiac index and stroke index, four used 51 methods of indexing unsupported by allometric principles. In addition, in these four manuscripts, 52 cardiac output and stroke volume were incorrectly indexed using the same function of body 53 mass, which suggests that heart rate is not expected to be affected by body size (see below), a 54 supposition known to be incorrect.

55Scaling describes the structural and functional consequences of changes in size or scale among 56otherwise similar organisms (Schmidt-Nielsen 1984). Allometric scaling refers to the scaling of 57bodies or functions that do not vary in direct proportion to their size (Schmidt-Nielsen 1984). 58Many morphological and physiological variables have been shown to depend on body mass 59according to the general allometric equation $Y = Y_0 \times M^b$, where Y_0 is a constant, characteristic of 60the type of organism and equal to the value of the variable of interest in a 1 kg (assuming that M 61is expressed in kg) animal, *b* is the allometric exponent, and *M* is body mass (West et al. 1997). 62The value of *b* usually ranges from – 1 to 1 for cardiopulmonary variables; negative values 63 indicate that the variable decreases as body size increases, and positive values indicate that the 64variable increases as body size increases. When the exponent is 0, the variable is 'size-65independent': it does not vary as a function of body size (see below). A simplified interpretation 66of the effects of different exponents in allometric equations is to consider the magnitude of the 67 effect of changes in size, based on the logarithms of the exponent. For instance, if a variable 68scales as $M^{1/4}$, the variable will change by a factor of 10^1 (= 10-fold) whenever body mass 69changes by 10⁴. Because mammals span a size range of 10⁸, this indicates that variables that

70scale with mass exponents of 1/4 (e.g. circulation time) or -1/4 (e.g. resting heart rate) differ by 71approximately 100-fold (10 × 10) between the smallest and largest mammals (Fig. 1). The 72theoretical basis for the allometric equation $Y = Y_0 \times M^b$ and the common allometric exponents 73has been discussed (West et al. 1997; Dodds et al. 2001; Glazier 2005, 2010; Chaui-Berlinck 742006; Clemente 2007; West &West 2013; White & Kearney 2014), but is beyond the scope of 75this review.

76Kleiber's law

77In 1883, the German physiologist Max Rubner demonstrated that in dogs spanning an order of 78magnitude difference in body size, metabolic heat production varied in proportion to BSA, or 79 $M^{2/3}$ (Rubner 1883). In 1932, the distinguished physiologist Max Kleiber reported that metabolic 80rates (in kcal per day) for mammals and birds spanning a body mass range of 0.15 kg to 679 kg 81were best described by a relationship proportional to $M^{0.74}$, usually expressed rounded off to $M^{3/4}$ 82(Kleiber 1932). It should be noted that in the allometry literature, mass exponents derived from 83empirical data are typically expressed as decimal values (e.g. 0.74), whereas those denoting a 84generalized underlying relationship are expressed as fractions (e.g. 3/4). A few years later, 85studies using an even larger range of body sizes (mouse to elephant) reported similar findings 86(Brody et al. 1934; Benedict 1938). Kleiber (1975) noted that these empirical allometric 87exponents were not significantly different from 0.75, and $M^{3/4}$ has become the most common 88scaling exponent relating body size to metabolism for interspecific comparisons. 89Cardiopulmonary variables scaling this way include cardiac output, minute ventilation and 90oxygen consumption.

91Several authors have pointed out that Kleiber's 'law' is an empirical approximation rather than a 92law, and that the 3/4 exponent is likely not to be universally applicable (Hayssen & Lacy 1985;

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93Glazier 2005, 2010; White et al. 2007; Kolokotrones et al. 2010; Hulbert 2014; White & Kearney 942014). Nevertheless, data analysis of the basal metabolic rate of adult mammals often yields the 953/4 exponent (or exponents that are not statistically different from 3/4), although some authors 96have suggested that the 'true' exponent is closer to 2/3, and that 3/4 is probably related to 97contamination of the dataset with non-basal measurements (White & Seymour 2003, 2005; 98Glazier 2005).

99Interspecific and intraspecific size effects

100Kleiber's law was empirically derived by collecting data from a variety of species, including 101both mammals and birds. His conclusion has been criticized based on the fact that, within a 102species, the effect of size on metabolism and cardiopulmonary variables appears to be best 103described by $M^{2/3}$, as originally reported by Rubner (1883) and later reinforced by Heusner 104(1982). It has since been argued that scaling within a species (intraspecific) appears to more 105closely fit a mass exponent of 2/3, whereas scaling between species (interspecific) seems to 106better fit a mass exponent of 3/4; there are experimental and theoretical justifications for the use 107of both allometric exponents (Feldman & McMahon 1983). Similarly to the 3/4 exponent, it has 108been suggested that the 2/3 exponent does not apply in all contexts and that the exponents may 109take a variety of values depending on the measurement being made (Glazier 2005).

110Allometric scaling of cardiopulmonary variables in mammals

111Values for Y_0 and b in the allometric equation $Y = Y_0 \times M^b$ for various cardiopulmonary variables 112reported in the literature are presented in Table 2. Some additional relationships can be 113hypothesized based on the variables for which there are experimental data. For example, arterial 114oxygen concentration is considered not to vary with body size (West & Brown 2005), which 115implies that oxygen delivery should vary as a function of body mass similarly to cardiac output.

116West et al. (1997) developed a general theoretical model in an attempt to explain many of the 117empirical allometric relationships between cardiovascular and respiratory variables and body 118size. Their work suggests that the actual (theoretical) value of *b* may be slightly different from 119the observed value, which is compatible with the statistical derivation of these observed values 120(Table 3). Variables with a mass exponent of 0 are expected to be size-independent and thus not 121to vary with body size. Examples of such variables include hematocrit or hemoglobin 122concentration, and arterial oxygen tension (PaO₂) and carbon dioxide tension (PaCO₂). Blood 123pressure has typically been considered to be size-independent, although a recent study challenges 124this assumption (White & Seymour 2014). Although the PaO₂ required for 50% hemoglobin 125saturation (P₅₀) scales in mammals with a negative mass exponent (Schmidt-Nielsen & Larimer 1261958), at sea level at rest, hemoglobin is close to being fully saturated with oxygen at normal 127PaO₂ in healthy mammals. Because the two determinants of arterial oxygen concentration are 128hemoglobin concentration and PaO₂, both of which are considered to be size-independent, 129arterial oxygen concentration is also expected to be size-independent. Variables with a mass 130exponent of 1 change in direct proportion to body mass. Such variables include blood volume, 131heart mass, stroke volume, lung volume and tidal volume. The mass exponent for the majority of 132the remaining variables is 3/4 interspecifically (2/3 intraspecifically) and applies to variables 133such as oxygen consumption, cardiac output and minute ventilation that increase with body size, 134but not in direct proportion to it. Most biological frequencies, such as heart rate or respiratory 135rate, scale with a mass exponent of -1/4 (or -0.25), which indicates that they are lower in larger 136animals. Circulation time scales with an exponent of 1/4 as it is derived from the ratio of blood 137volume (exponent: 1) and cardiac output (exponent: 3/4). Similarly, vascular resistance, which is 138 related to the ratio of pressure (exponent: 0) and cardiac output (exponent: 3/4), is expected to

139scale with a mass exponent of -3/4. Oxygen delivery is related to the product of arterial oxygen 140concentration (exponent: 0) and cardiac output, and thus is expected to vary as $M^{3/4}$.

1411mplications for indexing experimental cardiovascular and respiratory data

142The literature on allometric scaling describes the relationships between body size and most 143common cardiovascular and respiratory variables. This information should be used when 144interpreting cardiopulmonary data with consideration of the effect of body size. As Table 1 145shows, indexing these variables to an incorrect function of body mass would result in an 146incomplete and inaccurate interpretation. It should also be noted that if body size were fairly 147homogeneous in the sample being studied, there would be no effect on the variability of the 148measurements whether one applied the appropriate function of body mass, an inappropriate 149function of body mass, or used the raw measurements. If all subjects in the sample have similar 150body mass, correcting for body mass or any function of body mass will be equivalent to dividing 151the measurements by a constant, which does not affect their relative variability. Nevertheless, in 152this situation, the only logical approaches are either to not correct for body size or to correct for 153the appropriate function of body size, and the latter may allow better comparisons with other 154published data.

155Exponents for indexing cardiovascular and respiratory data are reported in Table 3, and 156exponents for a few additional variables are described in the text above. It should be noted that 157these exponents are for comparisons between species such as when data are obtained in multiple 158species, or if the goal for correcting the raw data for body size is to allow for the making of 159interspecies comparisons or estimates. Because the literature suggests that the slope for 160metabolic rate, and therefore probably many of the cardiovascular and respiratory variables, is 161lower when individuals of a single species are examined (Heusner 1982; Feldman & McMahon 1621983; Schmidt-Nielsen 1984), it may be appropriate to modify the exponents in Table 3 for 163comparisons and correction of data within a species. In this case, the 3/4 and – 3/4 exponents 164would become 2/3 and – 2/3, respectively, and the 1/4 and – 1/4 exponents would become 1/3 165and – 1/3, respectively. The existence of two different sets of exponents describing the effect of 166size within and between species may be related to similarities in body shape among animals of 167the same species, compared with systematic changes in dimensions dictated by size in animals of 168different species. Previous authors have suggested that, within a species, geometric similarity 169underlies the effect of body size, whereas elastic similarity may be more important between 170animal species (Feldman & McMahon 1983).

171Table 2 also reports the value of Y_0 in the $Y = Y_0 \times M^b$ allometric equation, or the expected value 172of the variable in a 1 kg animal (log 0 = 1) if the unit of mass is kg. This Y_0 factor is irrelevant for 173the correction of experimental data for the effect of body size. The data should only be corrected 174for (divided by) M^b , using the appropriate value for b; indeed, according to the equation above, 175 $Y/M^b = Y_0$, where Y is the measurement, showing that the intercept of the allometric equation Y_0 176is included in the actual measurement.

177Because BSA varies as $M^{2/3}$, as does intraspecific metabolic rate, it is often used to index 178cardiopulmonary data for comparisons within a species. As we have discussed, and as Table 3 179shows, this is only appropriate for variables that vary in proportion to intraspecific metabolic 180rate. In addition, one of the arguments cited as supporting the indexing of cardiopulmonary 181measurements mass-specifically (to *M*) rather than to BSA, even for variables known to vary as 182 $M^{2/3}$, is that formulae for calculating BSA may be inaccurate. It should be apparent from the 183present discussion that this is irrelevant because cardiopulmonary measurements do not actually 184vary as a function of BSA *per se*; rather, BSA just happens [in reflection of geometric similarity 185and as has been confirmed empirically in interspecific comparisons (Hemmingsen 1950)] to vary 186as $M^{2/3}$ and hence the relationship between M and BSA has the same exponent (slope of a log–log 187allometric plot) as cardiovascular and respiratory variables that vary with intraspecific metabolic 188rate. Because only the exponent is relevant for indexing, dividing the measurement by a BSA 189that can be read off a chart may be pragmatic, but it is simpler, and arguably more correct, to 190simply divide these measurements by $M^{2/3}$, which avoids any question of the accuracy of the 191BSA calculation and can be simply determined with a hand calculator. For example, if a 5 kg cat 192is found to have a cardiac output of 1 L minute⁻¹, its cardiac index could be calculated as 1931/5^{0.67} = 0.34 L minute⁻¹ $M^{-0.67}$.

194It should be noted that because there is some uncertainty regarding the actual values of the 195allometric exponents, and because the values of the exponents may vary with the conditions 196under study, analysis of covariance may be a preferable approach to traditional indexing to 197account for the effect of body size on cardiopulmonary measurements (Packard & Boardman 1981988, 1999). This approach has been utilized to account for the degree of interrelatedness 199between species in the development of phylogenetically informed allometry (Garland et al. 2002005).

201In conclusion, we suggest that when cardiovascular and respiratory variables are indexed to 202account for the effect of body size, this indexing should: 1) use body mass raised to the 203appropriate exponent according to the allometric scaling literature; 2) use different exponents for 204inter- *versus* intraspecific comparisons; and 3) ensure that variables which scale intraspecifically 205with metabolic rate ($M^{2/3}$) are indexed for the effect of body size by dividing the measurements 206by $M^{2/3}$ rather than by BSA.

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208The authors have no conflict of interest to report.

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275**Table 1** Effect of indexing a hypothetical variable specifically to body mass (*M*), or to a function 276of body mass related to metabolic rate [$M^{3/4}$ (interspecific) or $M^{2/3}$ (intraspecific)]. The effect of 277body size on this hypothetical variable is described by 100 × $M^{0.75}$

		Measurement	Measurement	Measurement
<i>M</i> (kg)	Measurement			
		indexed to M	indexed to $M^{3/4}$	indexed to $M^{2/3}$
1	100	100	100	100
2	168	84	100	106
5	334	67	100	114
10	562	56	100	120
20	946	47	100	127
50	1880	38	100	137
100	3162	32	100	145
500	10,574	21	100	164
1000	17,783	18	100	174
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279**Table 2** Values for Y_0 and *b* in the allometric equation $Y = Y_0 \times M^b$ for various cardiopulmonary

280variables in mammals, with *M* in kg

Heart rate (beats minute ⁻¹) 241 -0.25 (Stahl 1967)Cardiac output (mL minute ⁻¹)1870.81(Stahl 1967)Heart mass (g)5.80.98(Stahl 1965)Stroke volume (mL)0.78*1.03(West et al. 199Blood volume (mL)65.60.995(Stahl 1967)Circulation time (seconds)17.40.25(Schmidt-Nielse)Mean arterial pressure (mmHg)870.026(Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹)0.47 -0.78 (Calder 1984)Lung mass (g)11.30.99(Stahl 1967)Total lung capacity (mL)53.51.06(Stahl 1967)Vital capacity (mL)56.71.03(Stahl 1967)	Variable	Y_0	b	Reference
Cardiac output (mL minute ⁻¹)1870.81(Stahl 1967)Heart mass (g) 5.8 0.98 (Stahl 1965)Stroke volume (mL) 0.78^* 1.03 (West et al. 199Blood volume (mL) 65.6 0.995 (Stahl 1967)Circulation time (seconds) 17.4 0.25 (Schmidt-NielseMean arterial pressure (mmHg) 87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g) 11.3 0.99 (Stahl 1967)Total lung capacity (mL) 53.5 1.06 (Stahl 1967)Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Heart rate (beats minute ⁻¹)	241	- 0.25	(Stahl 1967)
Heart mass (g)5.80.98(Stahl 1965)Stroke volume (mL) 0.78^* 1.03 (West et al. 199)Blood volume (mL) 65.6 0.995 (Stahl 1967)Circulation time (seconds) 17.4 0.25 (Schmidt-NielseMean arterial pressure (mmHg) 87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g) 11.3 0.99 (Stahl 1967)Total lung capacity (mL) 53.5 1.06 (Stahl 1967)Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Cardiac output (mL minute ⁻¹)	187	0.81	(Stahl 1967)
Stroke volume (mL) 0.78^* 1.03 (West et al. 199Blood volume (mL) 65.6 0.995 (Stahl 1967)Circulation time (seconds) 17.4 0.25 (Schmidt-NielseMean arterial pressure (mmHg) 87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g) 11.3 0.99 (Stahl 1967)Total lung capacity (mL) 53.5 1.06 (Stahl 1967)Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Heart mass (g)	5.8	0.98	(Stahl 1965)
Blood volume (mL) 65.6 0.995 (Stahl 1967)Circulation time (seconds) 17.4 0.25 (Schmidt-NielseMean arterial pressure (mmHg) 87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g) 11.3 0.99 (Stahl 1967)Total lung capacity (mL) 53.5 1.06 (Stahl 1967)Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Stroke volume (mL)	0.78*	1.03	(West et al. 1997
Circulation time (seconds)17.4 0.25 (Schmidt-NielseMean arterial pressure (mmHg)87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g)11.3 0.99 (Stahl 1967)Total lung capacity (mL)53.5 1.06 (Stahl 1967)Vital capacity (mL)56.7 1.03 (Stahl 1967)	Blood volume (mL)	65.6	0.995	(Stahl 1967)
Mean arterial pressure (mmHg) 87 0.026 (Calder 1984)Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 -0.78 (Calder 1984)Lung mass (g) 11.3 0.99 (Stahl 1967)Total lung capacity (mL) 53.5 1.06 (Stahl 1967)Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Circulation time (seconds)	17.4	0.25	(Schmidt-Nielse
Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹) 0.47 - 0.78 (Calder 1984) Lung mass (g) 11.3 0.99 (Stahl 1967) Total lung capacity (mL) 53.5 1.06 (Stahl 1967) Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Mean arterial pressure (mmHg)	87	0.026	(Calder 1984)
Lung mass (g)11.30.99(Stahl 1967)Total lung capacity (mL)53.51.06(Stahl 1967)Vital capacity (mL)56.71.03(Stahl 1967)	Systemic vascular resistance (mmHg minute ⁻¹ mL ⁻¹)	0.47	- 0.78	(Calder 1984)
Total lung capacity (mL) 53.5 1.06 (Stahl 1967) Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Lung mass (g)	11.3	0.99	(Stahl 1967)
Vital capacity (mL) 56.7 1.03 (Stahl 1967)	Total lung capacity (mL)	53.5	1.06	(Stahl 1967)
	Vital capacity (mL)	56.7	1.03	(Stahl 1967)
Functional residual capacity (mL) 24.1 1.13 (Stahl 1967)	Functional residual capacity (mL)	24.1	1.13	(Stahl 1967)
Tidal volume (mL) 7.69 1.04 (Stahl 1967)	Tidal volume (mL)	7.69	1.04	(Stahl 1967)
Respiratory rate (breaths minute ⁻¹) 53.5 -0.26 (Stahl 1967)	Respiratory rate (breaths minute ⁻¹)	53.5	- 0.26	(Stahl 1967)
Minute volume (mL minute ⁻¹) 379 0.80 (Stahl 1967)	Minute volume (mL minute ⁻¹)	379	0.80	(Stahl 1967)
Respiratory system compliance (mL cm H_2O^{-1}) 1.56 1.04 (Stahl 1967)	Respiratory system compliance (mL cm H_2O^{-1})	1.56	1.04	(Stahl 1967)
Oxygen consumption (mL minute ⁻¹) 11.6 0.76 (Stahl 1967)	Oxygen consumption (mL minute ^{-1})	11.6	0.76	(Stahl 1967)
Hemoglobin concentration (g dL ^{-1})12.90(Schmidt-Nielse	Hemoglobin concentration (g dL ^{-1})	12.9	0	(Schmidt-Nielse
Alveolar surface (m^2) 3.340.95(Gehr et al. 198)	Alveolar surface (m ²)	3.34	0.95	(Gehr et al. 1982
Diffusion capacity for oxygen (mL O_2 second ⁻¹ mmHg ⁻¹) 0.065 0.99 (Gehr et al. 198	Diffusion capacity for oxygen (mL O ₂ second ⁻¹ mmHg ⁻¹)	0.065	0.99	(Gehr et al. 1982
Arterial-to-mixed venous oxygen concentration difference (mL dL ^{-1})† 6.2 – 0.05	Arterial-to-mixed venous oxygen concentration difference (mL dL $^{-1}$)†	6.2	- 0.05	
Venous oxygen tension (mmHg) 41.3 – 0.005 (Calder 1984)	Venous oxygen tension (mmHg)	41.3	- 0.005	(Calder 1984)
Venous carbon dioxide tension (mmHg)42- 0.03(Calder 1984)	Venous carbon dioxide tension (mmHg)	42	- 0.03	(Calder 1984)

281*Calculated from Y_0 values for cardiac output and heart rate. †Calculated from values for oxygen

282 consumption and cardiac output.

283**Table 3** Theoretical values for *b* in the allometric equation $Y = Y_0 \times M^b$ for various

Variable		Reference	
Heart rate (beats minute ⁻¹)	- 1/4	(West et al. 1997)	
Cardiac output (mL minute ⁻¹)		(West et al. 1997)	
Heart mass (g)		(Schmidt-Nielsen 1984)	
Stroke volume (mL)		(West et al. 1997)	
Blood volume (mL)		(West et al. 1997)	
Circulation time (seconds)		(West et al. 1997)	
Mean arterial pressure (mmHg)		(West et al. 1997)	
Systemic vascular resistance (mmHg minute mL ^{-1})		(West et al. 1997)	
Lung volume (mL)		(West et al. 1997)	
Tidal volume (mL)		(West et al. 1997)	
Respiratory rate (breaths minute ^{-1})		(West et al. 1997)	
Minute volume (mL minute ⁻¹)*		(West et al. 1997)	
Oxygen consumption (mL minute ⁻¹)		(West et al. 1997)	
Hemoglobin concentration (g dL ⁻¹)		(Schmidt-Nielsen 1984)	
Alveolar surface (m ²)†		(West et al. 1997)	
Diffusion capacity for oxygen (mL O_2 second ⁻¹ mmHg ⁻¹)		(West et al. 1997)	
Arterial-to-mixed venous oxygen concentration difference (mL dL ⁻¹)‡		(West et al. 1997)	

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cardiopulmonary variables in mammals, with \boldsymbol{M} in kg

285*Calculated from respiratory rate and tidal volume. †Calculated from number of alveoli and

286surface of alveolus. ‡Calculated from oxygen consumption and cardiac output.

287**Figure 1** Allometric relationships of variables with commonly encountered mass exponents 288discussed in the text. All data have been standardized so that the value for the smallest mammal 289(0.001–0.0015 kg, Etruscan shrew *Suncus etruscus*) has a value of 1, and the largest mammal 290(approximately 150–190 tonne, blue whale *Balaenoptera musculus*) scales accordingly. (a) Body 291mass and relative values of allometric variables are plotted on linear axes for variables scaling 292with mass exponents of 1 (solid line), 3/4 (long-dash line) and 2/3 (medium-dash line). (b) Body 293mass and relative values of allometric variables are plotted on linear axes as in (a) but with scales 294expanded to visualize data for variables scaling with mass exponents of 1/4 (short-dash line), 0 295(dotted line), – 1/4 (dash-dot line) and – 1/3 (long- and short-dash line). Note differences in 296ordinate scaling around breaks in axes in (a) and (b). (c) Body mass and relative values of 297allometric variables shown in (a) and (b) are plotted on logarithmic axes to show that log-298transformation of the data yields a straight line with slope equal to the mass exponent. The 299intercept value (value of a mammal with body mass of 1 kg because log 1 = 0) equals the value 300of the variable for a mammal of 1 kg body mass.

