The Journal of Experimental Biology 208, 1611-1619
Published by The Company of Biologists 2005
doi:10.1242/jeb.01501

Review

Allometric scaling of mammalian metabolism

Craig R. White* and Roger S. Seymour

School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, SA, 5005 Australia

*Author for correspondence at present address: School of Biosciences, The University of Birmingham, Birmingham, B15 2TT UK (e-mail: C.R.White@bham.ac.uk)

Accepted 14 January 2005

Summary

The importance of size as a determinant of metabolic rate (MR) was first suggested by Sarrus and Rameaux over 160 years ago. Max Rubner's finding of a proportionality between MR and body surface area in dogs (in 1883) was consistent with Sarrus and Rameaux's formulation and suggested a proportionality between MR and body mass (M_b) raised to the power of 2/3. However, interspecific analyses compiled during the first half of the 20th century concluded that mammalian basal MR (BMR, ml O_2 h^{-1}) was proportional to $M_b^{3/4}$, a viewpoint that persisted for seven decades, even leading to its common application to non-mammalian groups. Beginning in 1997, the field was re-invigorated by three new theoretical explanations for 3/4-power BMR scaling. However, the debate over which theory accurately explains 3/4-power scaling may be premature, because some authors maintain that there is insufficient evidence to adopt an exponent of 3/4 over 2/3. If progress toward understanding the non-isometric scaling of BMR is ever to be made, it is first essential to know what the relationship actually is. We re-examine previous investigations of BMR scaling by standardising units and recalculating regression statistics. The proportion of large herbivores in a data set is positively correlated both with the scaling exponent (b, where BMR=aM_b^b) and the coefficient of variation (CV: the standard deviation of ln–ln residuals) of the relationship. Inclusion of large herbivores therefore both inflates b and increases variation around the calculated trendline. This is related to the long fast duration required to achieve the postabsorptive conditions required for determination of BMR, and because peak post-feeding resting MR (RMR_{pp}) scales with an exponent of 0.75±0.03 (95% CI). Large herbivores are therefore less likely to be postabsorptive when MR is measured, and are likely to have a relatively high MR if not postabsorptive.

The 3/4 power scaling of RMR_{pp} is part of a wider trend where, with the notable exception of cold-induced maximum MR (b=0.65±0.05), b is positively correlated with the elevation of the relationship (higher MR values scale more steeply). Thus exercise-induced maximum MR (b=0.87±0.05) scales more steeply than RMR_{pp}, field MR (b=0.73±0.04), thermoneutral resting MR (RMR_t, b=0.712±0.013) and BMR. The implication of this observation is that contamination of BMR data with non-basal measurements is likely to increase the BMR scaling exponent even if the contamination is randomly distributed with respect to M_b. Artificially elevated scaling exponents can therefore be accounted for by the inclusion of measurements that fail to satisfy the requirements for basal metabolism, which are strictly defined (adult, non-reproductive, postabsorptive animals resting in a thermoneutral environment during the inactive circadian phase). Similarly, a positive correlation between M_b and body temperature (T_b) and between T_b and mass-independent BMR contributes to elevation of b. While not strictly a defined condition for the measurement of BMR, the normalisation of BMR measurements to a common T_b (36.2°C) to achieve standard metabolic rate (SMR) further reduces the CV of the relationship. Clearly the value of the exponent depends on the conditions under which the data are selected. The exponent for true BMR is 0.686 (±0.014), T_b normalised SMR is 0.675 (±0.013) and RMR_t is 0.712 (±0.013).

Key words: basal metabolic rate, scaling, allometry.

Introduction

"*You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away, provided that the ground is fairly soft. A rat is killed, a man is broken, a horse splashes.*" '*On being the right size*', by J. B. S. Haldane (1928).

Size matters. Its effect is all pervasive, but it influences different variables in different ways: given that the volume (V, and therefore mass, M) of an object is proportional to the cube of some linear dimension ($M \propto L^3$), whilst its surface area (A) is proportional to the square of a linear dimension ($A \propto L^2$), we

can rearrange to find that $L \propto M^{1/3} \propto A^{1/2}$, so $A \propto M^{2/3}$. If you double an object's length, but keep its proportions the same, its surface increases fourfold, and its volume eightfold. Surface area does not have an isometric relationship with mass, and this is true of a great many physiological variables (Huxley, 1932; Gould, 1966; Packard and Boardman, 1999). Allometry (or scaling) is a technique used to describe this non-isometric variation by regressing a variable of interest against body mass, thereby describing the relationship. This relationship is often well described by a linear regression of log(y) on log(M) such that

$$\log y = \log a + b \log M_{\mathrm{b}} , \quad (1)$$

which can be rearranged to produce a power equation of the form:

$$y = a M_{\mathrm{b}}^{b} , \quad (2)$$

where y is the variable of interest, a is the allometric coefficient, M_{b} is body mass and b is the allometric exponent. Allometric procedures are used throughout the biological sciences and a great many allometric relationships have been generated (McMahon and Bonner, 1983; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Brown and West, 2000).

One of the most frequently investigated allometric relationships is that between M_{b} and basal metabolic rate (BMR). Given that heat produced through metabolic processes must be lost through the body surface, it can therefore be supposed that metabolic rate would also be proportional to $M_{\mathrm{b}}^{2/3}$, so that the rate of heat production would be matched to the area of the surface over which it is dissipated. The idea that the effect of body size on metabolism might reflect simple geometric and physical processes was first suggested by Sarrus and Ramaeux in 1838 (cited by Brody, 1945) and supported by Max Rubner (1883). Rubner (1883) found that the metabolic rate of resting dogs was independent of mass when divided by surface area. This finding, which came to be known as Rubner's surface law of metabolism, stood largely unchallenged for almost 50 years, until publication of Max Kleiber's influential monograph (Kleiber, 1932). Kleiber (1932, 1961) found that metabolic rate was proportional to body mass raised to an exponent significantly greater than 2/3, and a value of 3/4 was subsequently adopted. Famously, one of the advantages of an exponent expressed as a simple fraction was the simplification of slide rule calculations (Schmidt-Nielsen, 1984). Three-quarter power scaling of mammalian BMR is a central paradigm of comparative physiology that has been accepted for over 70 years and remains in widespread use. Kleiber's monograph (Kleiber, 1932), for example, continues to be cited in papers appearing in top journals (Gillooly et al., 2001; Niklas and Enquist, 2001; Whitfield, 2001; Darveau et al., 2002; Marquet, 2002; Weibel, 2002; West et al., 2002b; Cohen et al., 2003).

Since publication of Kleiber's monograph (Kleiber, 1938), a great deal of effort has been invested in the investigation of both BMR scaling and the adaptive significance of BMR variation. In the years following Kleiber (1938), Benedict (1938) significantly expanded the data set and Brody's famous mouse-to-elephant curve (Brody, 1945) captured almost all of the body mass variation available with terrestrial mammals: both studies supported an exponent of 3/4. Hemmingsen (1960) included unicellular organisms and poikilothermic vertebrates, thereby expanding the range of body masses to 18 orders of magnitude, and also supported an exponent of 3/4 (a similar approach with a similar result was recently presented by Gillooly et al., 2001). During the last 20 years, investigation of BMR variation has gained prominence, and many studies have taken the approach of inferring adaptive variation in BMR by correlating it with traits of interest. Such studies have identified BMR differences associated with, for example, phylogeny (Hayssen and Lacy, 1985; Elgar and Harvey, 1987), diet (McNab, 1988), geography (Lovegrove, 2000), aridity (Lovegrove, 2000; White, 2003), habitat productivity (Lovegrove, 2000; Mueller and Diamond, 2001), climate (Lovegrove, 2003) and relative organ masses (Konarzewski and Diamond, 1995). In addition to identifying presumably adaptive differences in BMR and presenting scaling relationships for specific groupings of mammals, many of these studies also produced scaling relationships for all data available to them (Table 1). Although calculation of a regression line conceals the adaptive variation in BMR in a single average relationship between BMR and M_{b}, the scaling of BMR independent of other factors has continued to be of interest.

Recent attention has focused on theoretical explanations for this quarter-power scaling based on the geometry of nutrient supply networks (West et al., 1997; Banavar et al., 1999, 2002b; Bejan, 2000), four-dimensional biology (West et al., 1999) and an allometric cascade that links cellular and whole animal metabolism (Darveau et al., 2002; Hochachka et al., 2003). Proponents of these theories remain unable to reach a consensus on which is correct, and have presented arguments disputing competing theories (Banavar et al., 2002a, 2003; West et al., 2002a, 2003; Darveau et al., 2003). However, the debate over which theory accurately explains quarter-power scaling may be premature, at least where mammalian BMR is concerned, because some authors maintain that there is insufficient evidence to adopt an exponent of 3/4 over 2/3 (e.g. Heusner, 1991; Dodds et al., 2001; White and Seymour, 2003). If progress toward understanding the non-isometric scaling of BMR is ever to be made, it is first essential to know what the relationship actually is.

Regression model

Traditionally, allometric analyses are conducted with ordinary least-squares (OLS) regression (e.g. Huxley, 1932; Gould, 1966; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). However, comparative data are likely not to meet two assumptions of this model. Firstly, because of shared phylogenetic descent, species data are likely not to represent statistically independent points. This results in overestimation of degrees of freedom and an increased Type I error rate. A large body of literature deals with both the documentation of

Table 1. *Ordinary least-squares allometric regression parameters for past analyses of the scaling of mammalian basal metabolic rate*

Reference	*N*	Mass range	% Large herb.	*a*	*b*	95% CI	r^2	CV
Rubner (1883)	7	1.0	0	10.3	0.61	0.07	0.99	0.05
Kleiber (1932)	13	3.7	30.8	2.6	0.74	0.02	0.999	0.07
Benedict (1938)	32	5.7	28.1	1.8	0.76	0.02	0.99	0.24
Brody (1945)	69	5.4	39.1	2.3	0.731	0.011	0.996	0.15
Hayssen and Lacy (1985)	293	5.2	4.4	4.3	0.69	0.02	0.94	0.44
Elgar and Harvey (1987)	265	6.0	6.8	4.2	0.71	0.02	0.94	0.49
McNab (1988)	320	5.3	4.1	3.4	0.71	0.02	0.95	0.38
Heusner (1991)	391	6.2	4.3	3.8	0.71	0.02	0.95	0.41
Lovegrove (2000)	487	5.0	2.5	4.1	0.69	0.02	0.94	0.40
Symonds and Elgar (2002)	112	5.6	6.3	3.2	0.73	0.03	0.95	0.48
White and Seymour (2003)	571	4.6	0	4.0	0.686	0.014	0.94	0.35
White and Seymour (2003)	469	4.4	0	4.2	0.675	0.013	0.96	0.29
Savage et al. (2004)	626	6.2	3.5	3.7	0.712	0.013	0.95	0.39

Basal metabolic rate (BMR)=aM_b^b. All regressions were recalculated to standardise units (BMR in ml O_2 h^{-1}; M_b in g).

Mass range is in orders of magnitude; % Large herb., percentage of a data set represented by the orders Artiodactyla, Perrisodactyla and Proboscidea; CV, coefficient of variation, the standard deviation of ln–ln residuals (Garland, 1984).

this problem and a discussion of how to properly account for it (e.g. Felsenstein, 1985; Harvey and Pagel, 1991; Garland et al., 1992; Rohlf, 2001). Although none of the regressions presented here account for shared descent, BMR scaling patterns observed for mammals and birds are not greatly altered by the inclusion of such information (White and Seymour, 2003; McKechnie and Wolf, 2004). Secondly, OLS regression assumes that M_b is independent of the variable of interest and measured without error, which may not be the case. In such a situation, reduced major axis (RMA) regression may be more appropriate for inferring functional relationships (Sokal and Rohlf, 1995). Although the classic allometry studies use OLS regression (Huxley, 1932; Gould, 1966; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984), the use of RMA regression is becoming more common (e.g. Nunn and Barton, 2000; Green, 2001; Niklas, 2004). The RMA exponent b_{RMA} can be calculated by dividing the OLS exponent by the square root of the coefficient of determination r^2 (Sokal and Rohlf, 1995), so the difference between the regression models diminishes as r^2 increases. Where r^2 is low, however, the OLS exponent is likely to be an underestimate. Throughout this review, OLS regression results are presented (Table 1, Figs 1–7), and RMA regressions are tabulated for the main findings (Table 2).

Species composition and digestive state

A striking feature of the early analyses of mammalian BMR scaling (Kleiber, 1932; Benedict, 1938; Brody, 1945) is the consistent over-representation of large herbivorous lineages (Artiodactyla, Perissodactyla and Proboscidea). Whereas these groups (henceforth referred to as 'large herbivores') represent only 5% of Mammalia (Nowak, 1999), they comprise 28–39% of the data in these seminal analyses (Table 1). Large herbivores are more appropriately represented in more recent studies, but considerable variation remains between analyses. A comparison of recent BMR scaling studies (since 1984) reveals that the inclusion of large herbivores both increases the coefficient of variation of the relationship (the standard deviation of ln–ln residuals; Garland, 1984) and increases the scaling exponent (Fig. 1). These observations can both be explained by the difficulty in obtaining the conditions necessary for the measurement of BMR, which are strictly defined (McNab, 1997). BMR measurements must be obtained in the inactive circadian phase for animals that are adult, non-reproductive, conscious, resting in a thermoneutral environment, and post-absorptive. Achieving this final condition is difficult in animals that use microbial fermentation to digest cellulose, and such animals are typically fasted for

Table 2. *Ordinary least-squares (OLS) and reduced major axis (RMA) allometric regression parameters for the scaling of mammalian metabolic rate*

	OLS		RMA		
	a	*b*	*a*	*b*	95% CI
SMR	4.17	0.675	3.85	0.689	0.013
BMR	3.98	0.686	3.61	0.706	0.014
RMR_t	3.66	0.712	3.33	0.729	0.013
FMR	9.99	0.73	4.53	0.75	0.04
RMR_{pp}	7.91	0.75	7.70	0.76	0.03
MMR_c	31.56	0.65	28.3	0.68	0.05
MMR_e	16.71	0.87	0.4	0.88	0.05

Mammalian metabolic rate (MR)=aM_b^b. All regressions are presented in standardised units (BMR in ml O_2 h^{-1}; M_b in g). SMR, standard metabolic rate; BMR, basal metabolic rate; RMR_t, thermoneutral resting metabolic rate; FMR, field metabolic rate; RMR_{pp}, peak postprandial resting metabolic rate; MMR_c, cold-induced maximum metabolic rate; MMR_e, exercise-induced maximum metabolic rate; see text for details.

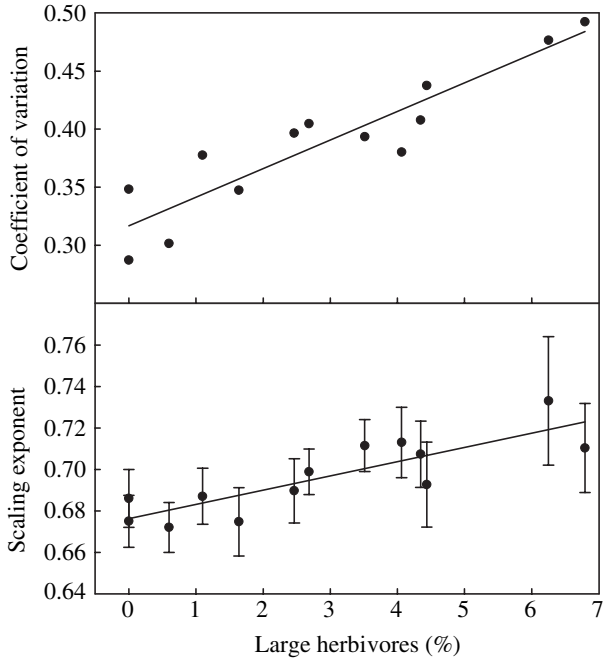

Fig. 1. Relationship between the percentage of large herbivores in a basal metabolic rate (BMR) data set and the coefficient of variation (CV, the standard deviation of residuals from a ln–ln allometric relationship; Garland, 1984) and scaling exponent (shown ±95% CI) of the allometric relationship between BMR and body mass. Both correlations are significant (CV: r=0.92, P<0.0001; scaling exponent: r=0.85, P=0.0003). Data sources are provided in Table 1.

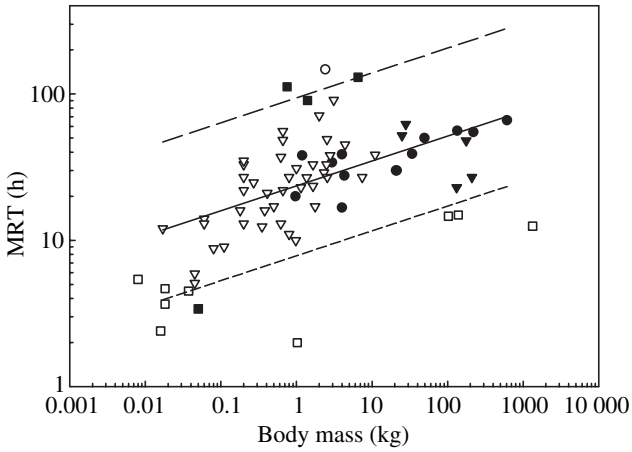

Fig. 2. Relationship between mean retention time of particles in the digestive tract (MRT, h) and body mass (M_b, g) for a range of herbivorous species that ferment in the cecum (unfilled triangles), foregut (filled circles), or colon (filled triangles). Solid line is the allometric relationship between MRT and M_b (MRT=7.3$M_b^{0.17\pm0.05\ [95\%\ CI]}$, r^2=0.43, N=60). Short broken line represents the earliest appearance of particles (=MRT/3), long broken line represents the final appearance of particles (=4×MRT). Filled squares, cecum fermenting species not included in the regression analysis because standardised residuals were more than 2 S.D. from the regression mean; unfilled circle, a foregut fermenting species excluded for the same reason. Insectivores, carnivores and piscivores (unfilled squares) are included for comparison, and have MRT values 2–13 times shorter than that predicted for herbivores of similar size. Data from Krockenberger and Bryden (1994), Morris et al. (1994) Stevens and Hume (1995), Caton et al. (1996), Comport and Hume (1998), Bodley et al. (1999), Campbell et al. (1999), McClelland et al. (1999), Felicetti et al. (2000), Gibson and Hume (2000), Hume et al. (2000), Pei et al. (2001).

less than 72 h prior to measurement of oxygen consumption (e.g. Rogerson, 1968; Weiner, 1977; Renecker and Hudson, 1986). However, ruminants may require 7 days to arrive at a postabsorptive state (Blaxter, 1962), although such a state may in fact be unachievable (McNab, 1997).

To examine the influence of body size on the fast duration required to achieve postabsorptive conditions, reference can be made to the mean retention time of particles in the digestive tract (MRT: the average time food requires to pass through the digestive tract), which has been suggested to correlate with required fast duration (Blaxter, 1989). In herbivorous mammals, MRT scales positively with an exponent of 0.17±0.05 (95% CI), regardless of whether the main site of fermentation is the foregut, hindgut or caecum (Fig. 2). A MRT of 12 h is therefore predicted for a 20 g herbivore, compared to nearly 3 days for a 500 kg one. However, the final appearance of faeces following feeding can take 4 times longer than the MRT (Blaxter, 1989), suggesting that MRT may approximate only the minimum time required to achieve a postabsorptive condition. Given that large herbivores are typically fasted for no more than 72 h, if at all, prior to determination of metabolic rate, it seems likely that such measurements fail to satisfy the conditions required for determination of BMR.

The possible confounding influence of ruminants was also recognized by Kleiber (1932), who presented his analysis both with and without these species. However, his fortuitous selection of data (r^2=0.999, Table 1) meant that removal of any species altered the calculated regression little and rendered this exclusion unproductive. Contrary to Kleiber's finding (Kleiber, 1932), the exclusion of large herbivores from recent data sets does decrease the scaling exponent and also decreases variation around the regression line (Fig. 1). To account for this finding, it is first necessary to understand the scaling of metabolic rate during digestion. Peak postfeeding resting metabolic rate (RMR_{pp}) is the highest metabolic rate measured in a resting animal following food intake, and scales with an exponent of 0.75±0.03 (Fig. 3), which is higher than all mammalian BMR scaling exponents produced since 1984 (Table 1). The peak factorial increase in metabolism following feeding (=RMR_{pp}/BMR) is therefore positively correlated with body mass in mammals, as has been documented intraspecifically for Burmese pythons *Python molurus* (Secor and Diamond, 1997) and cane toads *Bufo marinus* (Secor and Faulkner, 2002). Inclusion of non-postabsorptive measurements is therefore likely to increase the scaling exponent for BMR, even if such measurements are randomly distributed with respect to body mass. When non-postabsorptive measurements for large herbivores are included, however, the error is even greater,

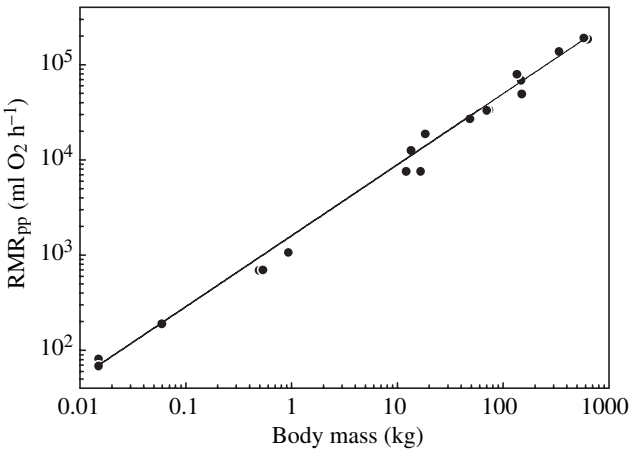

Fig. 3. Relationship between peak postfeeding resting metabolic rate (RMR_{pp}, ml O_2 h^{-1}) and body mass (M_b, g). RMR_{pp} is the highest metabolic rate observed in resting animals following feeding and is related to M_b according to $RMR_{pp}=7.91M_b^{0.75\pm0.03\ (95\%\ CI)}$, $r^2=0.99$, $N=19$. Data from Lusk (1915), Brody (1945), Gallivan and Ronald (1981), Costa and Kooyman (1984), Diamond et al. (1985), McDonald et al. (1988), MacArthur and Campbell (1994), Markussen et al. (1994), Rosen and Trites (1997), Sherwood (1997), Clements et al. (1998), Campbell et al. (1999).

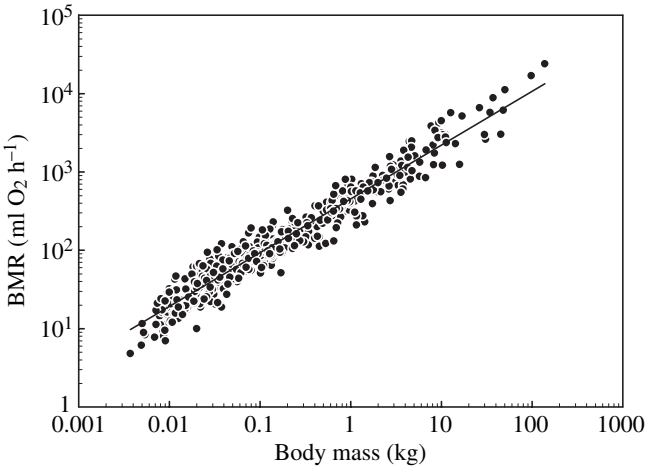

Fig. 4. Relationship between basal metabolic rate (BMR, ml O_2 h^{-1}) and body mass (M_b, g). $BMR=3.98M_b^{0.686\pm0.014\ (95\%\ CI)}$, $r^2=0.94$, $N=571$. Data were selected according to McNab (1997) and taken from White and Seymour (2003). Lineages for which basal conditions were unlikely to be achieved (large herbivores, Macropodidae, Lagomorpha, and Soricidae) were excluded for reasons discussed in the text.

because larger species have greater factorial increases in metabolic rate and, being near the upper limit of the mass range, they have high leverage and exert a disproportionately large influence on exponent calculation. To arrive at a precise estimate of the scaling exponent relating BMR and M_b, it is therefore necessary to exclude these large herbivores, together with other lineages for which basal conditions are unlikely to be achieved (Macropodidae, Lagomorpha, and Soricidae). Macropods and lagomorphs are excluded because they have microbial fermentation in the stomach or hindgut (Stevens and Hume, 1995), while shrews (Soricidae) are excluded because resting and postabsorptive conditions may be mutually exclusive (Speakman et al., 1993). With the exclusion of these suspected non-basal lineages, White and Seymour (2003) found that BMR scales with an exponent of 0.686±0.014 (Fig. 4). Relaxation of the requirements for estimation of BMR to include species that may not be postabsorptive (thermoneutral RMR or RMR_t: Speakman et al., 2003) results in an increase of the scaling exponent to 0.712±0.013 (recalculated from Savage et al., 2004).

Body temperature

Body mass and temperature are primary determinants of metabolic rate (Gillooly et al., 2001). Although there is no functional link in endotherms between metabolic rate and T_b within the thermal neutral zone, where BMR is measured, repeated attempts have been made to explain the BMR differences between birds and mammals, and eutherians and marsupials, in terms of differences in T_b (Hemmingsen, 1960; Dawson and Hulbert, 1970; White and Seymour, in press). In endotherms, the level of BMR is determined by factors presently uncertain but apparently related to cellular function (Hulbert and Else, 2000), while T_b is clearly regulated by the central nervous system (Bligh, 1976). As defined, the measurement conditions for BMR do not account for T_b differences between species, so descriptive scaling of BMR should not be compensated for them. Compensation is necessary, however, when comparing groups that differ in T_b or searching for uniform explanations for scaling effects that do not depend on T_b. T_b is significantly correlated ($r\approx0.55$) with the residual variation in mammalian BMR (White and Seymour, 2003) and, when normalised to a common T_b according to the Q_{10} principle, the BMR values of birds and mammals do not differ in allometric coefficient or exponent, nor do the BMR values of eutherians and marsupials (White and Seymour, in press). An approach that accounts for T_b differences has two further benefits: firstly, it allows for investigation of the influence of body mass on BMR without the confounding influence of T_b, which is also positively correlated with body mass (Withers et al., 2000; White and Seymour, 2003). Secondly, incorporation of T_b into predictive multiple regression models allows for improved estimation of BMR when both body mass and temperature are available.

To standardise the metabolic rates of mammals to a common T_b, it is necessary to determine the relationship between MR and T_b, find the mean T_b, and then apply the appropriate Q_{10} to the temperature difference (T_b – normalised BMR is henceforth referred to as standard metabolic rate: SMR). White and Seymour (2003) determined an appropriate Q_{10} for this procedure by calculating the r^2 value for the linear regression relating log(SMR) and log(mass), normalised to a T_b of 36.2°C using Q_{10} values ranging from 2.0 to 4.0. A value of 3.0 was finally selected because it minimised r^2. Within the range 2.0–4.0, Q_{10} has a quantifiable effect on the scaling exponent

estimated for the relationship between SMR and body mass, but none of the exponents differs significantly from 2/3 (White and Seymour, in press). Alternatively, Q_{10} can be estimated from the relationship between the natural log of mass-independent BMR and T_b (= BMR$\times M_b^{-b}$, where SMR=aM_b^b. However, estimation of Q_{10} in this manner requires the scaling exponent for SMR (not BMR), which cannot be obtained without Q_{10}. The relationship between BMR and T_b is described by the equation:

$$\ln(\text{BMR} \times M_b^{-b}) = cT_b + \ln(d) , \quad (3)$$

which can be rearranged to form:

$$\text{BMR} \times M_b^{-b} = de^{cT_b} , \quad (4)$$

The quantity e^{10c} then represents the factorial change in BMR associated with a 10°C change in body temperature, or Q_{10}. Determination of Q_{10} in this manner is advantageous because, by making use of linear regression, it is possible to produce confidence limits for c, and therefore also for Q_{10}. A drawback of this method, however, is that it requires an estimate of the SMR scaling exponent. Where such an estimate is not available it can be derived using a multiple regression approach (described below) or by iteratively solving for both b and c. The latter approach entails first estimating b by normalising data to a common T_b using a reasonable Q_{10} (e.g. 2.5). This value of b is then used in the approach described above to estimate a new Q_{10}, which is in turn used to produce a new estimate of b, and so on. By accounting for the effect of T_b, White and Seymour (2003) found that mammalian SMR scales with an exponent of 0.675±0.013, which is not significantly different from 2/3 (Fig. 5). This exponent was subsequently used to estimate the Q_{10} relating T_b and BMR, which was equal to 2.8 (White and Seymour, in press).

Separate determination of b and Q_{10} is useful in situations where it is of particular interest to identify one or the other. This allows for derivation of relationships between BMR and either T_b or M_b, an approach that provides intuitively simple results. However, one of the great strengths of scaling is in the predictive power that it provides. For species that are difficult to obtain or measure, BMR can be estimated only from M_b, because M_b alone accounts for 94% of the variation in BMR (White and Seymour, 2003). Such predictions can be further improved by incorporating T_b in a multiple regression approach. By regressing ln(BMR) against T_b and ln(M_b), it is possible to derive both b and Q_{10} from a relationship of the form:

$$\ln(\text{BMR}) = b\ln(M_b) + cT_b + \ln(a) , \quad (5)$$

which can be rearranged to form:

$$\text{BMR} = a(M_b^b) \times e^{cT_b} . \quad (6)$$

Interestingly, the Q_{10} for euthermic mammals (2.8; 95% CI, 2.4–3.2) is not significantly different to that found for hibernating (Q_{10}=2.2; 95% CI, 1.7–2.8) or torpid ones (Q_{10}=2.4; 95% CI, 1.6–3.5), although the exact values for hibernating and torpid animals are quite uncertain. Once normalised to a euthermic T_b (36.2°C), the metabolic rate of torpid mammals is equivalent to that of euthermic mammals, whilst small hibernating mammals show an additional suppression of metabolic rate. As such, the SMR scaling exponent for hibernating mammals (b=0.87; 95% CI, 0.79–0.94) is significantly different to that of euthermic (b=0.675; 95% CI, 0.663–0.688) and torpid ones (b=0.67; 95% CI, 0.56–0.77; Fig. 5).

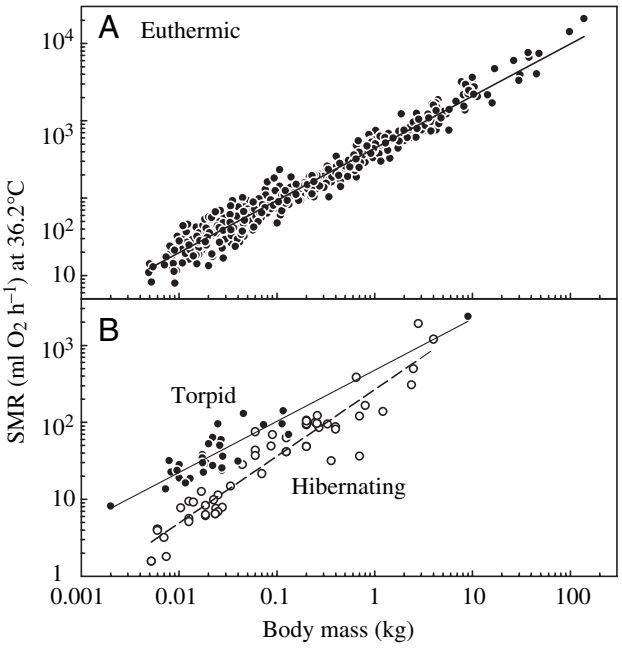

Fig. 5. Relationship between body mass (M_b, g) and standard metabolic rate (SMR, ml O_2 h^{-1}) for (A) euthermic and (B) hypothermic mammals, normalised to a body temperature of 36.2°C (see text for details): a Q_{10} of 2.8 was used for euthermic mammals, 2.4 for mammals in daily torpor (filled circles) and 2.2 for hibernating ones (unfilled circles). Equations of the regression lines: euthermic mammal SMR=4.14$M_b^{0.675\pm0.013\ (95\%\ CI)}$, r^2=0.96, N=469; torpid mammal (solid line) SMR=4.81$M_b^{0.67\pm0.1}$, r^2=0.86, N=30; hibernating mammal (broken line) SMR=0.669$M_b^{0.87\pm0.08}$, r^2=0.90, N=59. Data for euthermic mammals from White and Seymour (2003), data for hypothermic ones from Geiser (1988).

Scaling of non-basal metabolic rate

Investigation of the influence of body mass on metabolic rate is certainly not unique to the basal condition. Sufficient data have accumulated for examination of the scaling of metabolic rate under a range of conditions, some of which are discussed elsewhere in this issue or received recent attention (Nagy et al., 1999; Savage et al., 2004; Weibel et al., 2004). In addition to RMP_{pp}, RMR_t and SMR, these include maximum metabolic rate (MMR) induced either by exercise (MMR_e; Seeherman et al., 1981) or cold exposure (MMR_c, measured in an atmosphere comprising 21% oxygen in helium; Rosenmann and Morrison, 1974; Thomas et al., 1998), and field metabolic rate (FMR; measured by the doubly labeled water technique; Speakman, 1997). Discussion of the specifics of each of these relationships

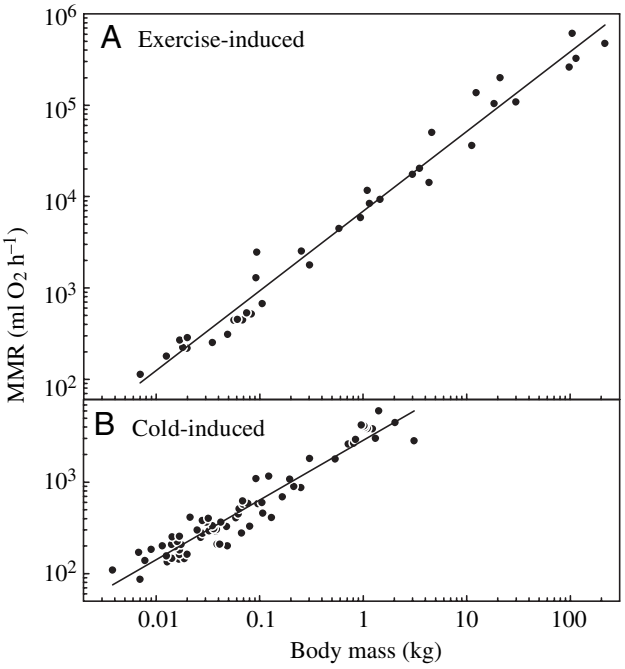

Fig. 6. Relationship between body mass (M_b, g) and maximum metabolic rate (MMR, ml O_2 h^{-1}) induced either by exercise (A, MMR_e) or exposure to cold in a He–O_2 atmosphere (B, MMR_c). Equations of the regression lines: $MMR_e=16.7M_b^{0.87\pm0.05\ (95\%\ CI)}$, $r^2=0.98$, $N=36$; $MMR_c=31.6=M_b^{0.65\pm0.05}$, $r^2=0.92$, $N=70$. MMR_e data from Seeherman et al. (1981), Taylor et al. (1981), Koteja (1987). MMR_c data from Hinds and Rice-Warner (1992), Hinds et al. (1993), Chappell and Dawson (1994), Holloway and Geiser (2001), Nespolo et al. (2001).

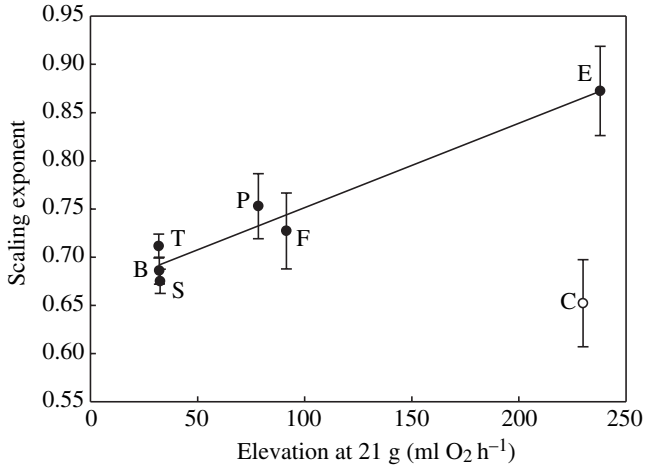

Fig. 7. Relationship between the scaling exponent (± 95% CI) of various mammalian metabolic rates (filled symbols: S, standard; B, basal; T, thermoneutral resting; P, peak post-feeding; F, field; E, exercise induced maximum) and the elevation of the allometric relationship at a mass of 21 g (modal mammalian body mass from Blackburn and Gaston, 1998). The relationship is significant ($r=0.97$, $P=0.001$), with the data for cold-induced maximum metabolic rate (C, unfilled symbol) excluded.

is well beyond the scope of this review; however, examination of the scaling of non-basal metabolic rate can provide insight into the effect that the inclusion of non-basal data may have on the scaling of basal metabolic rate. Perhaps not surprisingly, MMR_c scales with an exponent not significantly different from 2/3 (Fig. 6B), and therefore scales with an exponent similar to surface area (Reynolds, 1997). This might be expected given that MMR_c is measured under conditions that maximise heat loss. Unfortunately, measurements of both body surface area and MMR_c are available for too few species to determine if there is any relationship between the residual variation in these traits. For the remaining MR values, b is significantly positively correlated with the elevation of the relationship (Fig. 7), so higher MRs scale more steeply: MMR_e ($b=0.87\pm0.05$; Fig. 6A) scales with an exponent greater than RMR_{pp} ($b=0.75\pm0.03$; Fig. 3), FMR ($b=0.73\pm0.04$; Nagy et al., 1999), RMR_t ($b=0.712\pm0.013$; Savage et al., 2004), BMR ($b=0.686\pm0.014$; Fig. 4) and SMR ($b=0.675\pm0.013$; Fig. 5). This pattern is observed both for OLS and RMA regression exponents (Table 2). As is the case for the inclusion of non-postabsorptive measurements, the inclusion of non-basal measurements is therefore likely to increase the scaling exponent even if these measurements are randomly distributed with respect to body mass. Whereas it might be expected that non-basal measurements would increase only the elevation of the scaling relationship and leave the exponent unaffected, past failures to strictly adhere to the requirements for the measurement of BMR are therefore likely to have contributed to the generation of inflated scaling exponents.

Conclusion

Basal metabolic rate is, and is likely to remain, a benchmark measurement in comparative physiology. It represents the minimum energy cost of steady-state existence and is a useful index of energy expenditure: after the removal of body mass effects, BMR is significantly correlated with the residuals for a variety of physiological and ecological variables including maximum metabolic rate, field metabolic rate, resting heart rate, lifespan, litter size and population density (White and Seymour, in press). Part of the attraction of BMR is its relative ease of measurement and the fact that it for allows direct comparison of different species by placing them in the same physiological state. However, to achieve this aim it is necessary to adhere rigorously to the conditions specified for the measurement of BMR. Doing so results in determination of a scaling exponent for true BMR of 0.686±0.014. Similarly, McKechnie and Wolf (2004) have recently shown that when BMR data for birds are rigorously selected, BMR scales with an exponent of 0.669.

We thank Hans Hoppeler, Ewald Weibel, and all of the participants in the '*Size as a determinant of biological processes*' conference for an enjoyable meeting, and a series of entertaining and informative talks and discussions. Two referees provided comments that improved an earlier version of this manuscript.

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