

Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals

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Metabolic rate is traditionally assumed to scale with body mass to the 3/4-power, but significant deviations from the ‘3/4-power law’ have been observed for several different taxa of animals and plants, and for different physiological states. The recently proposed ‘metabolic-level boundaries hypothesis’ represents one of the attempts to explain this variation. It predicts that the power (log–log slope) of metabolic scaling relationships should vary between 2/3 and 1, in a systematic way with metabolic level. Here, this hypothesis is tested using data from birds and mammals. As predicted, in both of these independently evolved endothermic taxa, the scaling slope approaches 1 at the lowest and highest metabolic levels (as observed during torpor and strenuous exercise, respectively), whereas it is near 2/3 at intermediate resting and cold-induced metabolic levels. Remarkably, both taxa show similar, approximately U-shaped relationships between the scaling slope and the metabolic (activity) level. These predictable patterns strongly support the view that variation of the scaling slope is not merely noise obscuring the signal of a universal scaling law, but rather is the result of multiple physical constraints whose relative influence depends on the metabolic state of the organisms being analysed.

Keywords: allometry; birds; body mass; constraints; mammals; metabolic scaling

1. INTRODUCTION

All biological activities depend on metabolic energy, and thus understanding why rates of metabolism vary is of fundamental importance. A major factor affecting metabolic rate is body size. Respiratory metabolic rate (R) typically scales with body mass (M) according to the power function $R = aM^b$, where a is a normalization constant (antilog of the intercept in a log–log plot) and b is the scaling exponent (slope in a log–log plot). Rubner (1883) observed that the scaling exponent b was 2/3 in dogs of different size, which he explained using the theory of Sarrus & Rameaux (1839: cited in McNab 2002). According to this theory, to maintain a constant body temperature, endothermic animals must metabolically produce enough body heat to exactly balance the amount of heat lost through their body surface. Therefore, since body surface scales as $M^{2/3}$, so should metabolic rate. However, in broader comparisons of different species of mammals, Kleiber (1932) found that b was closer to 3/4 than 2/3. Since that time, it has been commonly assumed that b is typically 3/4, a generalization known as ‘Kleiber’s law’ or the ‘3/4-power law’ (Brody 1945; Hemmingsen 1960; Kleiber 1961; Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Recently, it has even been claimed that scaling based on multiples of a 1/4-power is universal, or nearly so, not only for metabolic rate, but also for the rates and durations of other biological processes dependent on metabolic energy (Brown *et al.* 2004; Savage *et al.* 2004; West & Brown 2005). In addition, influential theoretical models have been proposed to explain quarter-power scaling, thus further reifying the 3/4-power law (West *et al.* 1997, 1999; Banavar *et al.* 1999, 2002).

However, the universal status of the 3/4-power law has been seriously weakened by recent empirical and theoretical work. First, several rigorous empirical analyses, involving body sizes spanning several orders of magnitude, have shown that b often deviates substantially from 3/4, varying significantly among different taxonomic groups of animals and plants (Glazier 2005; Reich *et al.* 2006; White *et al.* 2006, 2007), and among different physiological states (Glazier 2005; Niven & Scharlemann 2005; White & Seymour 2005; Makarieva *et al.* 2005a, 2006b). Second, the models supporting the so-called 3/4-power law appear to have flawed assumptions and serious mathematical inconsistencies that have not yet been resolved, despite much debate (Dodds *et al.* 2001; Kozłowski & Konarzewski 2004, 2005; Brown *et al.* 2005; Makarieva *et al.* 2005b, 2006a; Painter 2005b,c; West & Brown 2005; Banavar *et al.* 2006; Chaui-Berlinck 2006, 2007; Etienne *et al.* 2006; Savage *et al.* 2007).

As a result, Glazier (2005) proposed a new model, the metabolic-level boundaries (MLB) hypothesis, to help explain the extensive variation in metabolic scaling that has been observed (other models are also reviewed in Glazier 2005). According to the MLB hypothesis, the scaling slope b should vary between two extreme boundary limits: 2/3 as a result of surface-related constraints on fluxes of resources, wastes and heat, and 1 as a result of mass (volume) constraints on energy use or power production (cf. Kooijman 2000). Variation in b is mediated by the overall metabolic level of the organisms being considered, which determines the relative influences of surface area and volume on the scaling of metabolic rate. In resting organisms, b should be negatively related to metabolic level because when maintenance costs are high, metabolic scaling should be chiefly limited by fluxes of resources, wastes and (or) heat across surfaces (scaling

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Table 1. Scaling slopes ($b \pm 95\%$ confidence limits) and antilog intercepts (a) of log metabolic rate ($\text{ml O}_2 \text{ h}^{-1}$) versus log wet body mass (g) of birds and mammals in various physiological states. (The b values ($p < 0.05$ in all cases) were determined by conventional LSR analysis with each species regarded as an independent data point, except where indicated (PIC, phylogenetically independent contrasts; RMA, reduced major axis analysis; MA, major axis analysis; RRA, robust regression analysis; BBM, binned body mass classes). N is the sample size, which is the number of species, or number of estimates with number of species in parentheses. The b values in italics are those used in figure 1.)

physiological state	taxon	b	a	N	source
low metabolic level					
hibernation (5°C)	mammals	<i>0.941</i> ± 0.086	0.047	29	Geiser (1988)
hibernation (20°C)	mammals	<i>0.794</i> ± 0.064	0.373	36	Geiser (1988)
hibernation (4.3–10.1°C)	mammals	<i>0.879</i> ± 0.082	0.044	27 (16)	Weiner (1989)
torpor (15–16°C)	birds	<i>1.028</i> ± 0.210	0.155	8	Lasiewski (1963), Lasiewski & Lasiewski (1967) and Lasiewski <i>et al.</i> (1967)
resting metabolic level					
	mammals	<i>0.676</i> ± 0.013	4.98	456	White <i>et al.</i> (2006)
	mammals (RMA)	<i>0.69</i> ± 0.013	5.10	456	White <i>et al.</i> (2006)
	mammals (BBM)	<i>0.737</i> ± 0.026	3.25	52 (626)	Savage <i>et al.</i> (2004)
	mammals	0.690	4.11	487	Lovegrove (2000)
	mammals (RRA)	<i>0.678</i> ± 0.014		391	Heusner (1991)
	mammals	<i>0.693</i> ± 0.022	4.36	293	Hayssen & Lacy (1985)
	birds	<i>0.64</i> ± 0.03	6.07	83	White <i>et al.</i> (2006)
	birds (RMA)	<i>0.66</i> ± 0.03	5.36	83	White <i>et al.</i> (2006)
	birds	<i>0.669</i> ± 0.030	6.17	126	McKechnie & Wolf (2004)
	birds (PIC)	<i>0.677</i>	4.67	126	McKechnie & Wolf (2004)
	birds	<i>0.635</i> ± 0.043	8.51	37	Rezende <i>et al.</i> (2002)
	birds (PIC)	<i>0.721</i> ± 0.087	5.70	37	Rezende <i>et al.</i> (2002)
	birds	<i>0.68</i> ± 0.06	8.92	45	Frappell <i>et al.</i> (2001)
	birds (PIC)	<i>0.68</i> ± 0.10	8.43	44	Frappell <i>et al.</i> (2001)
	birds	<i>0.638</i> ± 0.028	7.75	82	Tieleman & Williams (2000)
	birds (PIC)	<i>0.677</i> ± 0.054	5.38	82	Tieleman & Williams (2000)
	birds	<i>0.677</i>	6.98	263	Daan <i>et al.</i> (1991)
	birds (MA)	<i>0.67</i> ± 0.03	4.86	399	Bennett & Harvey (1987)
field metabolic level					
	mammals	<i>0.734</i> ± 0.038	9.94	79	Nagy <i>et al.</i> (1999)
	mammals (RMA)	<i>0.75</i> ± 0.04	4.53	79	White & Seymour (2005)
	mammals (BBM)	<i>0.749</i> ± 0.054	9.31	35 (79)	Savage <i>et al.</i> (2004)
	mammals	0.72	1.40	111 (86)	Anderson & Jetz (2005)
	mammals (PIC)	0.73	1.40	110 (86)	Anderson & Jetz (2005)
	birds	<i>0.681</i> ± 0.036	21.66	95	Nagy <i>et al.</i> (1999)
	birds	0.68	2.10	132 (96)	Anderson & Jetz (2005)
	birds (PIC)	0.67	2.10	131 (96)	Anderson & Jetz (2005)
	birds	<i>0.703</i> ± 0.042	19.84	81	Tieleman & Williams (2000)
	birds (PIC)	<i>0.671</i> ± 0.065	16.65	81	Tieleman & Williams (2000)
high metabolic level					
cold-exposed					
	mammals	<i>0.65</i> ± 0.05	31.56	70	White & Seymour (2005)
	mammals (RMA)	<i>0.68</i> ± 0.05	28.3	70	White & Seymour (2005)
	mammals	<i>0.668</i> ± 0.060	30.34	56 (28)	Weiner (1989)
	birds	<i>0.600</i> ± 0.033	56.10	47	Rezende <i>et al.</i> (2002)
	birds (PIC)	<i>0.651</i> ± 0.088	44.36	47	Rezende <i>et al.</i> (2002)
high metabolic level					
strenuous activity					
	mammals	<i>0.872</i> ± 0.059	17.17	34	Weibel <i>et al.</i> (2004)
	mammals (BBM)	<i>0.828</i> ± 0.070	26.06	21 (28)	Savage <i>et al.</i> (2004)
	athletic				
	mammals	<i>0.942</i> ± 0.050	17.11	10	Weibel <i>et al.</i> (2004)
	mammals	<i>0.857</i> ± 0.040	18.00	67 (45)	Weiner (1989)
	mammals	<i>0.841</i> ± 0.045	22.93	18	Koteja (1987)
	birds & mammals	<i>0.879</i> ± 0.020	35.02	15	Bishop (1999)
	birds	<i>0.837</i> ± 0.107	33.65	39 (35)	Norberg (1996)

as $M^{2/3}$; see also §4), whereas when they are low and amply met by surface-dependent processes, metabolic scaling should be more related to the energy demand required to sustain the tissues, which is directly proportional to tissue mass or volume (scaling as M^1). This negative relationship between b and metabolic level should extend to dormant or ectothermic organisms with very low metabolic levels, where b should be near 1, and to cold-exposed endothermic animals with relatively high metabolic rates, where b should be near $2/3$. However, in active

animals, b should be positively related to metabolic level because as activity increases metabolic rate is increasingly affected by the energy demand of muscular tissue, which scales in direct proportion to muscle mass, which in turn scales as M^1 (Calder 1984; Weibel *et al.* 2004; Glazier 2005). During bursts of maximal activity, b should approach 1 because metabolic rate is chiefly driven by the resource demand of metabolizing tissues, rather than by surface-dependent resource supply or waste removal (cf. Hammond & Diamond 1997; Weibel & Hoppeler 2005).

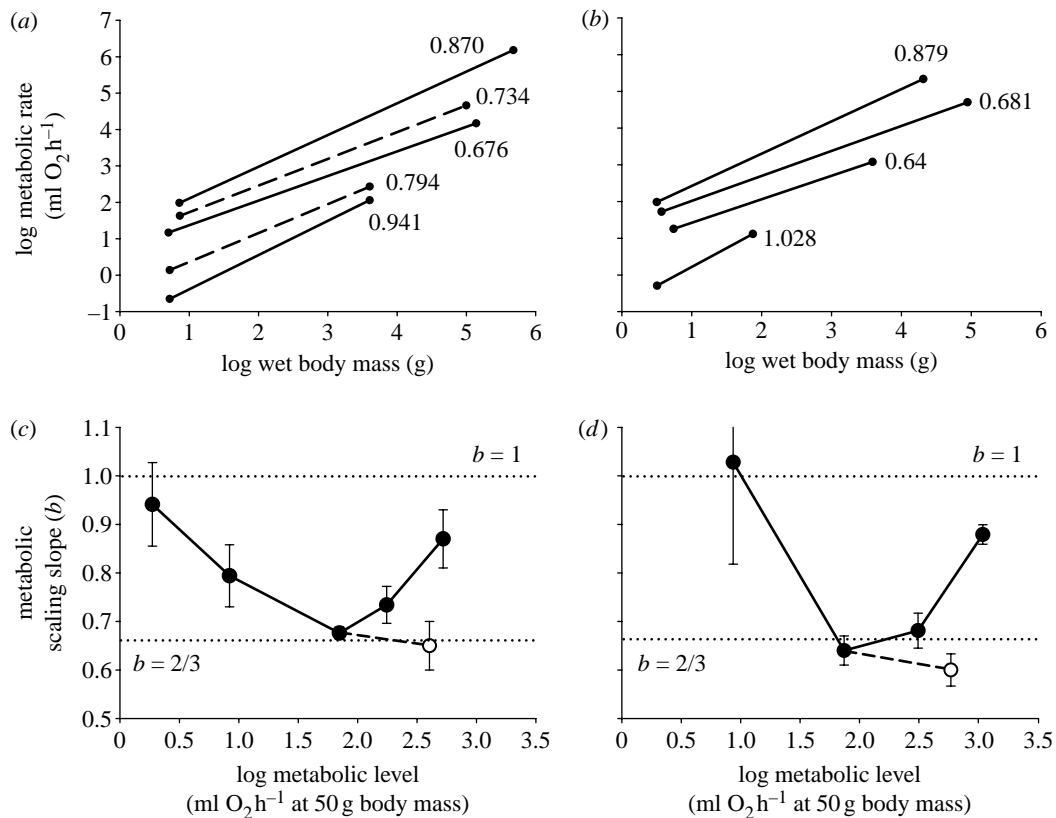


Figure 1. Scaling of metabolic (respiration) rate in relation to wet body mass in (a,c) mammals and (b,d) birds exhibiting various physiological states (data from sources in table 1). (a,b) The dots at the ends of each log–log least-squares regression line denote the minimum and maximum body masses for each sample. The scaling slopes of solid lines are significantly different from $3/4$, whereas the slopes of dashed lines are not significantly different from $3/4$. The physiological states for the scaling lines are in ascending order for mammals: hibernating at 5°C , torpid at 20°C , resting, field active and maximally active; and for birds: torpid at $15\text{--}16^{\circ}\text{C}$, resting, field active and maximally active. (c,d) Scaling slopes ($b \pm 95\%$ confidence limits) versus metabolic level at 50 g body mass. Filled circles denote various levels of activity from minimal to maximal, whereas open circles indicate cold-exposed metabolic rates. For the different levels of activity, note the approximately U-shaped relationship shown for both mammals and birds with extreme values of the scaling slopes near $2/3$ and 1 (indicated by dotted lines), as predicted by the MLB hypothesis.

This is briefly made possible by stored oxygen and energy in the muscle tissues and their temporary tolerance to accumulation of wastes (e.g. lactic acid). Overall, the MLB hypothesis predicts a U-shaped (or V-shaped) relationship between the metabolic scaling slope b and metabolic level.

Here, the MLB hypothesis is tested in birds and mammals, the only taxa for which sufficient data were available on metabolic scaling in all of the several physiological states mentioned above.

2. MATERIAL AND METHODS

The MLB hypothesis was tested by examining metabolic scaling relationships that were based on the largest, most taxonomically comprehensive datasets available, and those which represented a diversity of statistical methods. Most scaling relationships included 10 or more species (table 1), as well as body mass ranges exceeding two orders of magnitude (figure 1), except for torpid birds ($N=8$; body mass range = 1.37 orders of magnitude). Minimal metabolic rates were represented by torpid animals at the lowest body temperatures for which sufficient data were available (5°C for mammals and $15\text{--}16^{\circ}\text{C}$ for birds). Resting metabolic rates (RMRs) were measured under basal conditions (White *et al.* 2006). Field metabolic rates were estimated in free-living animals using the doubly labelled water method (Nagy *et al.* 1999). Maximal metabolic rates (MMRs) of thermoregulation were estimated

by exposure to cold in a He-O_2 atmosphere (Rezende *et al.* 2002; White & Seymour 2005), whereas that of locomotion were estimated in strenuously running mammals and flying or running birds (Bishop 1999; Weibel *et al.* 2004). The datasets featured in figure 1 were taken from the most rigorous and comprehensive studies available, though similar patterns are observed for other datasets as well (see table 1; and White *et al.* 2007). Most of the scaling relationships were calculated using conventional least-squares regression (LSR). Scaling slopes determined by other statistical procedures were almost always very close to that determined by LSR (table 1; see also §4). Relative metabolic levels of the scaling relationships for different physiological states were calculated for animals with 50 g wet body mass, because this intermediate value is well within the body mass ranges of all the scaling relationships analysed here. This method was deemed adequate because it yielded similar results to those based on other methods of estimating metabolic level (e.g. the intercept at 1 g mass; and the mass-specific metabolic rate at the midpoint of each regression line; see also §4).

3. RESULTS

As predicted by the MLB hypothesis, the metabolic scaling slopes (b) of mammals and birds in various states of activity vary mostly between $2/3$ and 1 , and with an approximately U-shaped relationship with metabolic level

(figure 1c,d, table 1). In both taxa, b approaches 1 at the lowest and highest metabolic levels, and is near 2/3 for resting and cold-exposed animals, as predicted.

4. DISCUSSION

The relationships between the scaling slope (b) and metabolic level are very similar in mammals and birds, and thus represent a remarkable case of convergent evolution between these independently evolved endothermic taxa. These patterns are robust as they are seen regardless of what statistical method is used to estimate the scaling parameters (see table 1; and also below).

The relationships between b and metabolic level are also seen regardless of the body mass used for comparison, or the method used to estimate metabolic level. This is because the relative elevation of the scaling lines observed at various activity levels are maintained over the entire ranges of body masses analysed (figure 1a,b). Therefore, for this and other reasons, the relationships observed between b and metabolic level are not statistical artefacts, as might be expected for closely proximate regression lines that intersect one another (Glazier 2005).

Although in most cases the statistical method used appears to have little effect on the present results, one deviation deserves special discussion. By using a 'binning' procedure that gives equal weight to all body size intervals, Savage *et al.* (2004) showed that the RMR of mammals scales with a slope of 0.737, which is significantly different from 2/3, unlike that shown by most other recent analyses (table 1). However, this deviant result appears to be a statistical artefact because, since the larger size intervals contain far fewer species than the smaller size intervals, the binning procedure actually gives greater weight to each large mammal species, which collectively are known to have a steeper scaling slope than smaller mammals (Hayssen & Lacy 1985; Heusner 1991; Lovegrove 2000; Dodds *et al.* 2001; Glazier 2005; Kozłowski & Konarzewski 2005).

In mammals, the dependence of b on body size interval may be a function, at least in part, of including large herbivores in the scaling analysis. Since large herbivores process their food for long periods of time, it is probable that short-term fasting does not completely remove the heat increment of feeding (as required for basal conditions), thus artificially elevating their metabolic rate, which in turn causes b to be biased upward (White & Seymour 2005). Removing large herbivores from the analysis results in the overall scaling exponent of mammals being indistinguishable from 2/3 (White & Seymour 2005).

Alternatively, since fur insulation in large mammals is more effective in preventing heat loss (Heldmaier 1989), the effect of surface area constraints (proportional to $M^{2/3}$) on their metabolic scaling may be reduced relative to that for small mammals, thus causing b to be more related to tissue demand (proportional to M^1). This interpretation nicely fits into the framework of the MLB hypothesis, and is consistent with the observation that b in the largest mammals appears to approach 1 (Makariev *et al.* 2003; Painter 2005a).

An additional noteworthy result of this study is that in both birds and mammals, b increases significantly with increases in locomotor activity, but does not with increases in thermoregulatory demands resulting from exposure to

cold. As predicted by the MLB hypothesis, MMRs during locomotion are more related to (muscle) tissue demand (proportional to M^1), whereas that during thermoregulation are more related to surface-dependent loss of heat (proportional to $M^{2/3}$). These differences may help explain why some studies have found that MMR is a constant multiple of RMR, whereas others have found that the ratio of MMR to RMR varies with body size. To facilitate understanding, the effects of locomotor and thermoregulatory demands on metabolic rate should be kept separate, which has not always been done in the past.

The observation that resting and cold-induced metabolic rates in both mammals and birds tend to scale as $M^{2/3}$ further suggests that, during these physiological states, external surface area constraints on heat loss (scaling as $M^{2/3}$: Rubner 1883; Calder 1984; Reynolds 1997; White & Seymour 2005) predominate over internal surface area constraints, which are expected to scale as $M^{3/4}$ according to theory (West *et al.* 1997, 1999). The ability of birds and mammals to use a variety of behavioural and physiological mechanisms to regulate heat loss does not abolish the influence of surface area, as claimed by West & Brown (2005). The effect of surface area may still be prominent, especially if these mechanisms are employed equally (or nearly so) among species of different body size. This is expected to be true for the highly controlled thermal conditions at which the basal and cold-induced metabolic rates of birds and mammals are measured.

It is also unlikely that the relatively high b of MMR in running mammals (and other active animals) is a simple result of a positive correlation between body temperature and mass, as claimed by Gillooly & Allen (2007). First, as Gillooly & Allen (2007) themselves admit, their postulated effect of temperature on metabolic rate can explain only approximately 50% or less of the difference in b between the resting and maximally active conditions, if the most current and comprehensive datasets on mammals are examined (resting $b=0.68$; active $b=0.87$: see table 1). This is true even if the athletic species are removed from the sample (the scaling exponent for MMR is still relatively high: 0.85; Weibel *et al.* 2004).

Second, and more importantly, data on the relative timing of changes in metabolic rate and body temperature in running horses strongly suggest that muscle activity increases metabolic rate (heat production), which then elevates body temperature, the reverse of the causation emphasized by Gillooly & Allen (2007; Mukai *et al.* in press; J. H. Jones, H. Hoppeler & E. R. Weibel 2007, personal observations). These data show that once running starts, metabolic rate increases to peak levels almost immediately, whereas an increase in muscle temperature lags behind and does not peak until after running has ceased. Furthermore, once a peak metabolic rate is reached, it is unaffected by the later increase in muscle temperature.

Third, steep scaling of MMR is also observed in ectothermic vertebrates, despite their showing little change in body temperature during activity (Glazier 2005).

Other patterns of metabolic scaling in mammals and birds also support the MLB hypothesis. As predicted, heterotherms, desert dwellers, and 'ectothermic' African mole rats and newly born or hatched young, all of which have a relatively low RMR, tend to show relatively steep

scaling slopes (Glazier 2005). The higher b for MMR in athletic versus non-athletic mammals (0.94 versus 0.85; Weibel *et al.* 2004) also conforms to the MLB hypothesis, because the relative effect of muscle resource demand (scaling as M^1) on b is predicted to be higher in relatively muscular athletic mammals.

The effect of metabolic level on b is even seen within species. For example, in the laboratory rat, an increase of activity level results in a significant increase in b , whereas cold exposure does not change b (Refinetti 1989), just as observed at the interspecific level. Also in humans, increases in activity cause significant increases in b , with values approaching 1 during maximal exercise (Rogers *et al.* 1995; Batterham & Jackson 2003).

This and other evidence provided by Glazier (2005), Makarieva *et al.* (2005a), Niven & Scharlemann (2005), Reich *et al.* (2006) and White *et al.* (2006, 2007) strongly support the MLB hypothesis, but is inconsistent with the 3/4-power law and models proposed to explain it. In fact, of the 37 b values in table 1 with calculated 95% confidence limits, 78% (29) are significantly different from 3/4. Therefore, metabolism does not scale with body mass according to a single universal law, but rather appears to depend on multiple physical constraints, whose relative influence depends on the metabolic state of the organisms being analysed. In essence, the scaling of metabolism with body mass itself scales with overall metabolic (activity) level.

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