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Title:
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Date:
2013-01-01

Citation:
White, C. R. & Kearney, M. R. (2013). Determinants of inter-specific variation in basal metabolic rate. Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology, 183 (1), pp.1-26. https://doi.org/10.1007/s00360-012-0676-5.

Determinants of inter-specific variation in basal metabolic rate: a review

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Abstract

Basal metabolic rate (BMR) is the rate of metabolism of a resting, postabsorptive, non-reproductive, adult bird or mammal, measured during the inactive circadian phase at a thermoneutral temperature. BMR is one of the most widely measured physiological traits, and data are available for over 1200 species. With data available for such a wide range of species, BMR is a benchmark measurement in ecological and evolutionary physiology, and is often used as a reference against which other levels of metabolism are compared. Implicit is such comparisons is the assumption that BMR is invariant for a given species, and that it therefore represents a stable point of comparison. However, BMR shows substantial variation between individuals, populations, and species. Investigation of the ultimate (evolutionary) explanations for these differences remains an active area of inquiry, and explanation of size-related trends remains a contentious area. Whereas explanations for the scaling of BMR are generally mechanistic and claim ties to the first principles of chemistry and physics, investigations of mass-independent variation typically take an evolutionary perspective and have demonstrated that BMR is ultimately linked with a range of extrinsic variables including diet, habitat temperature, and net primary productivity. Here we review explanations for size-related and mass-independent variation in the BMR of animals, and suggest ways that the various explanations can be evaluated and integrated.

Introduction

Basal metabolic rate (BMR) is perhaps the most widely reported physiological metric. ‘Basal’ has long been recognised as a poorly chosen term (Krogh, 1916) because metabolic rate can fall below BMR under a range of conditions (Geiser, 2004; Green et al., 2007; Halsey et al., 2008; Green et al., 2009). The term nevertheless remains in widespread use and has come to refer not to the lowest metabolic rate that an endotherm can achieve, but instead to metabolic rate measured under precisely defined conditions. BMR is the rate of metabolism of a resting, normothermic, postabsorptive, non-reproductive, adult bird or mammal, measured during the inactive circadian phase at a thermoneutral temperature (McNab, 1997; Frappell and Butler, 2004). BMR is usually measured by indirect calorimetry as rate of oxygen consumption, using well described techniques and commercially available equipment (Withers, 2001; Lighton, 2008). Being relatively easy to measure in the laboratory, the number of species for which data are available has grown steadily since the 1930s (Figure 1), and data are presently available for nearly 700 species of mammal (Sieg et al., 2009), and more than 500 species of bird (McNab, 2009). The highest reported BMR (of *Elephas maximus*: Benedict, 1938) is almost five orders of magnitude greater than the lowest (of *Myotis nigricans*: McNab, 1989), and size is well known to account for much of the inter-specific variation in BMR (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). However, the strong relationship between mass and BMR conceals a great deal of variation, and species of the same size can differ by up to several fold (White and Seymour, 2004). Even within a species, BMR varies seasonally (Lovegrove, 2005; Smit and McKechnie, 2010) as well as between populations (Wikelski et al., 2003; Broggi et al., 2007; Tieleman et al., 2009b) and individuals (Nespolo and Franco, 2007). That differences between individuals and species can be significant, substantial, and repeatable, has led to the speculation that this variation must be important. The present review examines the causes and consequences of this variation, approaching the topic from both ultimate (evolutionary) and proximate (mechanistic) perspectives. We focus on inter-specific variation in BMR, though we do use some examples from intra-specific studies; a more in-depth coverage of intra-specific variation is provided by Konarzewski and Książek (2012). We begin by discussing the profound influence of body mass on metabolism, and follow this with a discussion of the causes and consequences of the variation in BMR that is not explained by body mass. We conclude with the suggestion that integrative examinations of mass-dependent and mass-independent variation are likely to yield valuable insights into the evolutionary causes of the allometric scaling of metabolic rate with body mass.

Non-isometric scaling and the influence of body mass

Body mass alone explains most (generally > 90%) of the variation in BMR between species, and a great deal of ink has been spilled debating the exact form of the scaling relationship between body mass and metabolism. Like many physiological variables, BMR does not increase in direct proportion to body mass (isometrically). Instead, the relationship between body mass (M) and BMR is allometric and often well described by a power function of the form:

$$\mathrm{BMR} = a\, M^{b}$$

where a is the scaling constant, and b is the scaling exponent (see White, 2011; White and Kearney, 2012 for discussion of statistical analyses of metabolic scaling). The value of the scaling exponent has been the subject of interest since at least the 19th century, when Sarrus and Rameaux (1838, cited by Brody, 1945) suggested that metabolic rate should scale in proportion to body surface area rather than body mass. Sarrus and Rameaux's hypothesis found empirical support when Rubner (1883) reported that the metabolic rates of dogs were proportional not to their body mass, but to their body surface area. This finding came to be known as the surface law of metabolism (e.g. Brody, 1945; Kleiber, 1961). Although some subsequent studies have supported the exponent of ⅔ implied by these early analyses (e.g. Heusner, 1991; White and Seymour, 2003), the heat loss hypothesis is unlikely to be correct, since animals with relatively high body surface areas do not have relatively high BMRs (White and Seymour, 2004). Moreover, in the decades following publication of Rubner's

(1883) work, the exponent of ⅔ was supplanted by a value of ¾ (Kleiber, 1932). Later analyses expanded the data set to include a wider range of species (Benedict, 1938; Brody, 1945; Hemmingsen, 1960) and the ¾-power scaling relationship came to be known as Kleiber's law (e.g. Smil, 2000; Wang et al., 2001). Notably, however, recent analyses reject any single value of the exponent for mammals (e.g. Duncan et al., 2007; Sieg et al., 2009; White et al., 2009; Capellini et al., 2010) and demonstrate that the scaling exponent of BMR increases with body size (e.g. Clarke et al., 2010; Kolokotrones et al., 2010). These analyses further refute the idea that heat loss dictates the scaling of BMR, because the exponent of BMR for large animals with low surface area: volume ratios is significantly different from the scaling exponent of body surface area (⅔: Reynolds, 1997). Among birds, the most recent phylogenetically-informed (PI) analyses demonstrate a difference between wild-caught and captive species (McKechnie et al., 2006). Wild-caught birds scale with an exponent close to ¾, whereas captive species scale with an exponent close to ⅔ (McKechnie et al., 2006), although other studies favour different values (White et al., 2007a). Clearly, there is no consensus on a single value for the scaling exponent of BMR, and recent meta-analyses have generally stressed the lack of a single universal value (Savage et al., 2004; Glazier, 2005; White et al., 2007b). The *causes* of the non-isometric scaling of metabolism remain a lively subject of ongoing debate (e.g. Krogh, 1916; Kleiber, 1961; McMahon, 1973; Heusner, 1982; Kooijman, 1986; Heusner, 1991; Patterson, 1992; West et al., 1997; Banavar et al., 1999; West et al., 1999; Dodds et al., 2001; Banavar et al., 2002b; Darveau et al., 2002; Kozłowski et al., 2003b, a; Agutter and Wheatley, 2004; Kozłowski and Konarzewski, 2004; Weibel et al., 2004; Brown et al., 2005; Glazier, 2005; Kozłowski and Konarzewski, 2005; Weibel and Hoppeler, 2005; Demetrius, 2006; Chown et al., 2007; Gillooly and Allen, 2007; White et al., 2007b; Ginzburg and Damuth, 2008; White et al., 2008; Banavar et al., 2010; Demetrius and Tuszynski, 2010; Glazier, 2010; Roberts et al., 2010; Agutter and Tuszynski, 2011; Riveros and Enquist, 2011; Roberts et al., 2011; Seymour and White, 2011; White et al., 2011c).

Hypotheses for the scaling of metabolic rate have been reviewed in detail by a number of authors (e.g. Dodds et al., 2001; Agutter and Wheatley, 2004; Glazier, 2005; da Silva et al., 2006; O'Connor et al., 2007), and many hypotheses will not be discussed further here (e.g. Patterson, 1992; Witting, 1995; Kozłowski and Weiner, 1997; Bejan, 2000; Demetrius, 2003; Makarieva et al., 2003; Bejan, 2005; Demetrius, 2006; Ginzburg and Damuth, 2008; Demetrius and Tuszynski, 2010). Instead, we focus on those hypotheses that we view as most prominent, emphasising those that are the subject of ongoing empirical scrutiny.

Resource Distribution

The most prominent recent explanations for the scaling of metabolic rate are the resource distribution theories of West, Brown, and Enquist (West et al., 1997, 1999) and Banavar and co-workers (Banavar et al., 1999; Banavar et al., 2002b). These theories predict the scaling of metabolic rate with body size on the basis of models of resource transport. The two theories have influenced a general model for quarter-power scaling in animals, which incorporates a minimum of specific detail and requires only a few simplifying assumptions (reproduced from Banavar et al., 2010 p 15816, with minor modifications for clarity):

1. Definition of metabolic rate: Metabolic rate, B, can be measured as the rate of flow of discrete particles through a supply network. In mammals, for example, metabolic rate is routinely measured as the rate of oxygen consumption, and the oxygen molecules are transported in the blood vessels from a central source, the heart, to terminal units, the mitochondria.
2. Steady-state postulate: The flux of resources is at steady state, so supply matches demand, the rate B of particles being consumed by the terminal units matches the rate B of particles leaving the source, and the number of particles in transit does not change over time.
3. Geometric similarity: Animals, especially those in the same taxonomic or functional group, are geometrically similar, so their geometry can be characterized by length, L, surface area, A, and volume, V, and simple Euclidean geometrical scaling gives $V \sim L^3$ and $A \sim L^2$.
4. Directed transport: The average distance (d) from the source to each terminal unit is proportional to the length, L, of the animal.
5. Velocity, v, is assumed to be uniform within an animal. The average transit time, τ, scales as $\tau \sim d/v$.

6. Mass is proportional to volume: The density of protoplasm is approximately constant across animals, so mass, *M*, is proportional to volume, *V*.
7. Particles in transit are contained within animal volume: The number of resource particles in transit, *N*, scales linearly with *M* and *V*.
8. Definition of service volume: a service volume is defined as a unit of tissue that has a fixed metabolic rate independent of animal mass. Thus the number of service volumes is proportional to *B*. In an animal with volume *V*, each service volume is proportional to V/B and radius or length $l_s \sim (V/B)^{1/3}$. The service volume does not necessarily correspond to any biological structure, although in mammals the service volume can be thought of as the volume of tissue supplied by a capillary, the terminal unit of the vascular network.

The theory assumes only that resources are distributed from a point source through a distribution network with no particular branching pattern, and therefore applies equally to hierarchically branched and explosion networks. It also assumes the transported resources are not stored near the service volume, and hence the ideas relate strongly to those metabolites that cannot be stored in the body (e.g. O_2). The model predicts that the scaling exponent of metabolic rate is 2/3 if velocity of flow is independent of mass (consistent with an alternative model: Dodds, 2010), but can attain a maximum value of 3/4 if velocity scales with its maximum exponent, 1/12 (Banavar et al., 2010). It is worth noting, however, that real animals clearly violate some assumptions of the model. Not all animals have outward directed transport systems that distribute resources from a single point and, even for those that do, flow velocity is not uniform throughout the animal (Banavar et al., 2010). Although the central tendency of ¾-power scaling is supported by some studies (Savage et al., 2004; Moses et al., 2008), other studies emphasise the many deviations from quarter-power scaling and the resource distribution model has yet to adequately explain differences in the scaling exponent between endotherms and ectotherms (Phillipson, 1981; Glazier, 2005; White et al., 2006; White et al., 2007b; Glazier, 2010), and between rest and activity (White and Seymour, 2005a; Glazier, 2008; White et al., 2008; Glazier, 2010), although attempts to do so have been made (Gillooly and Allen, 2007). Debate regarding resource distribution models has been vociferous, focussing on issues of mathematical validity and empirical support (Banavar et al., 2000; Dodds et al., 2001; Banavar et al., 2002a; West et al., 2002a; Banavar et al., 2003; Darveau et al., 2003; West et al., 2003; Kozłowski and Konarzewski, 2004; Suarez et al., 2004; West et al., 2004; Brown et al., 2005; Kozłowski and Konarzewski, 2005; Painter, 2005a; Suarez and Darveau, 2005; Chaui-Berlinck, 2006, 2007; Savage et al., 2007; Agutter and Tuszynski, 2011).

Interestingly, much of the empirical evaluation of the predictions of the resource distribution models has focussed on the scaling of metabolic rate with body mass (e.g. Bokma, 2004; Savage et al., 2004; Glazier, 2005; Duncan et al., 2007; White et al., 2007b), and the range of other scaling exponents predicted by these models has rarely been examined (Table 1). Examining the congruence between predicted and observed values for circulatory variables, in particular, seems to be a valuable step in evaluating the core of these models, which are grounded in principles of hydrodynamics. West et al.'s (1997, 1999) models for ¾ power scaling, for example, assume that natural selection has optimized the resource distribution network to minimize transport costs. This seems reasonable because the heart contributes a significant fraction of whole-animal metabolic rate (2.4-10.4%: Loiselle and Gibbs, 1979) and individuals with low metabolic rates are favoured in at least some situations (e.g. Blackmer et al., 2005; Artacho and Nespolo, 2009). Some of the predictions of the models are supported by empirical data, suggesting that they are plausible models of resource transport (Table 1). In birds and mammals, for example, heart rate scales with an exponent close to the predicted value of -0.25 (Table 1). For fish, on the other hand, heart rate is independent of body mass (Clark and Farrell, 2011; White and Seymour, 2011).

A significant product of the resource distribution model has been its use as a foundation for a Metabolic Theory of Ecology (MTE), which aims to use metabolism as a basis for applying first principles of physics and chemistry to link the biology of individual organisms to the ecology of populations, communities, and ecosystems (Brown et al., 2004b). The fundamental equation of MTE describes variation in MR in terms of an empirically determined normalisation constant independent of body size and temperature (i_0), body mass (M), activation energy (E), Boltzmann's constant (k), and absolute temperature (T) (Gillooly et al., 2001; Brown et al., 2004b):

$$MR = i_0 \, M^{3/4} \, e^{-E/kT}$$

While early work on the MTE applied only a narrow range of parameters to describe the temperature- and mass-dependence of metabolic rate, recent work by the original proponents of MTE has acknowledged a wider range of variation in the parameters of the fundamental equation (Wang et al., 2009; DeLong et al., 2010; Dell et al., 2011). The strength of MTE lies in its ability to predict a wide range of ecological patterns (Allen et al., 2002; Brown et al., 2004b; Meehan et al., 2004; Meehan, 2006; Buckley et al., 2008; Munch and Salinas, 2009), its grounding in first principles (although some contention exists about the extent to which this holds for the temperature term: Clarke, 2006; Irlich et al., 2009), and its deliberate simplicity (Brown et al., 2004a). Not all tests of MTE support the theory (e.g. Algar et al., 2007; Duncan et al., 2007; Hawkins et al., 2007a; O'Connor et al., 2007; Downs et al., 2008), however, and it is worth noting that other theories also predict the scaling of metabolic rate with body mass with similar accuracy (see below), and application of these alternative explanations to explaining size-dependent ecological patterns is likely to be similarly successful.

Dynamic Energy Budget

In the framework of the Dynamic Energy Budget (DEB) theory (Kooijman, 2010), metabolic rate is considered to comprise a weighted sum of four processes: assimilation, maintenance, growth, and maturation. DEB theory decomposes body mass into two indirectly measurable state variables, the 'reserve' and the 'structure', and is based on generalized surface area (source) and volume (sink) relationships. It makes the key assumptions that the composition of reserve and structure each remains constant but may differ from each other ('strong homeostasis') and that, under constant food, the relative amount of reserve and structure stays constant and hence so does the entire body composition ('weak homeostasis'). Energy and matter are assimilated in proportion to structural surface area (because food enters the body across surfaces), and directed first to the reserve pool of the organism. The reserve is not necessarily metabolites ‘set aside for later’, but rather is defined by its turnover rate. It reflects the part of the dry mass of an organism that fluctuates with resource supply, and is constantly used and replenished. DEB theory assumes that no costs are paid for the maintenance of reserves, but costs are paid for their turnover and are included in the overheads of assimilation and utilization. The structure is the “permanent” biomass and does require energy for its maintenance (protein turnover and the maintenance of concentration gradients and ionic potentials, etc.) in direct proportion to structural volume.

Under DEB theory, the allometric scaling of metabolic rate arises because the contribution of non-respiring reserves to body mass increases with body size. For example, body fat (which can be considered as part of the reserve, but is by no means all of it) scales as $M^{1.19}$ in mammals (Pitts and Bullard, 1968; Calder, 1984) and has a very low mass-specific metabolic rate (Elia, 1992). For interspecific comparisons, DEB theory predicts the scaling of mass-specific standard or basal metabolic rate for fully grown animals as (Kooijman et al., 2007; Kooijman, 2010):

$$\propto \frac{L_h L^2 + L^3}{d_V L^3 + d_E L^4}$$

where respiration has contributions from growth and maintenance (assimilation is excluded because animals are postabsorptive). The parameters d_E and d_V represent the specific density (g cm^{-3}) of reserve (E) and structure (V) and the amount of structure is proportional to the cubed volumetric length L^3, so d_V is independent of mass. The ratio of reserve to structure is proportional to L, so metabolic rate scales allometrically with an exponent less than 1. Inclusion of a “heating length” multiplier L_h (a positive constant for endotherms, and zero for ectotherms) for a surface area term (L^2) in the numerator means that the scaling exponent of metabolic rate is predicted to be lower for endotherms than ectotherms, a pattern that is supported by empirical data (Phillipson, 1981; White et al., 2006; White et al., 2007b). However, the appropriateness of including a surface-specific heating term $L_h L^2$ requires further scrutiny since body surface area and basal metabolic rate are not related in mammals (White and Seymour, 2004), and it is not clear that heat loss determines basal metabolism in a mechanistic sense (da Silva et al., 2006; Seymour and White, 2011).

The mechanisms invoked by DEB theory to explain intraspecific scaling relationships are different from those that explain interspecific scaling. Interspecifically, the allometric scaling of metabolic rate arises because of the increase in reserve with mass, and differences between endotherms and ecotherms arise because of differences in the heating constant. Although the idea has not yet been formally explored, it seems likely that at least some of the variation in the interspecific scaling exponent of metabolic rate could be explained by DEB theory on the basis of size- and activity-dependent variation between species in the energy turnover of structure, and thereby the relative contributions of reserve and structure to whole-body metabolism. It is not yet clear, however, if DEB theory can explain the frequently observed covariation between metabolic level and the scaling exponent of metabolic rate (Glazier, 2005, 2008, 2009a, b, c, 2010).

Metabolic Level Boundaries

The metabolic level boundaries (MLB) hypothesis (Glazier, 2005, 2010) predicts that scaling exponents for MR will vary between two boundary constraints: surface-area limits on fluxes of metabolic resources, wastes and (or) heat that scale allometrically as $M^{2/3}$, and volume limits on energy use or power production that scale isometrically as M^1. Thus, metabolic rate is predicted to scale isometrically at low levels of sustained metabolic intensity, and the scaling exponent of metabolic rate is predicted to decrease toward 2/3 as sustained metabolic intensity increases. During intense activity, volume limits on power production by the locomotory musculature dominate, and metabolic rate is predicted to scale isometrically. The pattern of variation predicted by the metabolic level boundaries hypothesis is supported by variation in the scaling exponent for birds and mammals (Glazier, 2008, 2009a), unicellular organisms (Glazier, 2009b), and ectothermic animals (Glazier, 2009c; Killen et al., 2010). In support of the hypothesis, the body temperature of large animals has been shown to rise continually during intense aerobic exercise (e.g. Jones et al., 1989; Nagano et al., 1990b), which demonstrates the metabolic rate during intense exercise is not constrained by heat flux.

Allometric cascade

The allometric cascade (AC) theory (Darveau et al., 2002; Hochachka et al., 2003) regards the scaling of metabolic rate as a consequence of multiple causes, where the exponent *b* is the sum of the influences of multiple contributors to metabolism and control, and where the relative strength of each contributor, with its own characteristic exponent value, is determined by its control contribution. The original mathematical model derived from the allometric cascade theory has been criticised (Banavar et al., 2003; West et al., 2003), and a revised model subsequently appeared (Darveau et al., 2003; Hochachka et al., 2003):

$$MR = MR_0 \sum c_i (M/M_0)^{b_i}$$

where MR_0 is the 'characteristic metabolic rate' of an animal with a 'characteristic body mass', M_0. With M_0 of 1 unit mass (usually kg), MR_0 takes the place of the value *a*, found in the standard scaling equation, b_i is the scaling exponent of the process *i*, and c_i is its control contribution to overall flux, or the control coefficient of the process *i*.

For animals working at $\dot{V}O_2$max (i.e. their maximal sustainable work rates, equivalent to maximum sustainable ATP turnover rates), major contributors to control include the lung, heart and circulation (Wagner, 1993; Jones, 1998), as well as cellular-level energy-supply and ATP-demand pathways (Thomas and Fell, 1998; Jeneson et al., 2000; Cloutier and Wellstead, 2010). Based on the control coefficients for these processes, the predicted global *b* value is 0.82 – 0.92 (Darveau et al., 2002), in good agreement with empirical data (Bishop, 1999; Weibel et al., 2004; White and Seymour, 2005a; White et al., 2007b; White et al., 2008). For animals under BMR conditions, on the other hand, all of the oxygen delivery steps have an excess capacity of at least several-fold, which allows animals to increase the metabolic rate from BMR to $\dot{V}O_2$max. Thus, the control contributions of these steps are considered to be zero under basal conditions, and the global scaling of BMR is driven by energy demand processes. Under basal conditions, major energy sinks are Na^+-K^+-ATPase, protein turnover, substrate cycles, and mitochondrial proton leak (Rolfe and Brand, 1997), and the control coefficients for these processes contribute to the global b value for BMR, which is predicted to be within the range 0.76 – 0.79 (Darveau et al., 2002), which is somewhat higher than observed for mammals over most of their mass range (Kolokotrones et al., 2010). The principles of allometric cascade theory also appear to be valid for resting and exercising humans (Batterham and Jackson, 2003, 2005; but see Nevill and Bate, 2005 for an alternative viewpoint).

Cell Size

The cell size (CS) model proposes that the mass scaling of metabolism is shaped by the evolutionary coupling of cell size and body size, since, with increasing cell size, the cell surface area:volume ratio decreases (Davison, 1955; Kozłowski et al., 2003a; Kozłowski et al., 2010). All other things being equal, the model predicts that metabolic rate should scale isometrically when evolutionary increases in body size are achieved entirely through increases in cell number (i.e. cell size scales as M^0), or as $M^{2/3}$ when increases in size are achieved through increases in cell volume (i.e. cell size increases with M). Experimental studies have supported the link between cell size and metabolic rate (Maciak et al., 2011), and the cell size model for metabolic scaling has been supported in studies of endotherms (Vinogradov, 1995; Kozłowski et al., 2003a; Opazo et al., 2005), reptiles (Starostová et al., 2009), tetrapods (Vinogradov and Anatskaya, 2006), and insects (Chown et al., 2007). Recent work, however, has demonstrated that patterns of mass-dependence of cell sizes in different animal groups are inconsistent with the assumptions of the model, and has called for revision of the model (Glazier, 2005; Kozłowski et al., 2010). Cell volume scales with exponents between 0 and 0.3 in birds and mammals (Kozłowski et al., 2010). The cell size model predicts that a cell volume scaling exponent of 0.3 should be associated with a metabolic rate scaling exponent of 0.9 (Kozłowski et al., 2003a; Kozłowski et al., 2010), which is greater than the exponents observed for these groups (McKechnie and Wolf, 2004; White and Seymour, 2005a; McKechnie et al., 2006; White et al., 2007b; White et al., 2009). The cell size model is also difficult to reconcile with the observation that the metabolism of individual cells in culture does not scale with the 2/3-power of cell volume (West et al., 2002b), though the relevance of cell preparations to the *in vivo* metabolism of cells remains an open question. Similarly, the ratio of mitochondrial volume to cell volume is a more important predictor of the respiration of isolated hepatocytes than cell volume itself (Porter and Brand, 1995).

Heat dissipation limits

The heat dissipation limit (HDL) theory (Speakman and Król, 2010) proposes that an upper boundary on sustained energy expenditure is imposed by the maximal capacity to dissipate body heat and therefore avoid the detrimental consequences of hyperthermia. In contrast to other theories, HDL seeks to explain the scaling of average daily energy expenditure (field metabolic rate), which it estimates on the basis of the exponent of maximal capacity to dissipate heat ($\propto M^{0.47-0.50}$, all other things being equal). Interestingly, the value of ~0.5 is similar to that predicted for the scaling exponent of metabolic rate at a constant temperature by an analytical model of the thermal niche of an ellipsoid furred endotherm (Porter and Kearney, 2009), as well as to the empirically-determined scaling exponent of minimum wet thermal conductance (b = 0.42 to 0.62: Schleucher and Withers, 2001; Withers et al., 2006), and the scaling exponent of daily energy expenditure (DEE) measured at any given temperature (Calder, 1984). Incorporating empirical data for the scaling of plumage/fur mass ($\propto M^{0.95-0.98}$), skin mass ($\propto M^{0.94}$), and body temperature ($\propto M^{0.05}$), the predicted scaling exponent of maximum heat dissipation capacity is about 0.63, a value close to the measured scaling exponents (shown ± SE) of FMR of 0.647 ± 0.013 in mammals and 0.658 ± 0.017 in birds (Speakman and Król, 2010). When analysed using phylogenetic independent contrasts (Felsenstein, 1985) the exponent of FMR for birds and mammals are 0.679 ± 0.032 and 0.576 ± 0.036, respectively (Speakman and Król, 2010).

The HDL theory is also supported by the observation that the daily energy turnover of lactating animals is increased by manipulating heat dissipation capacity through pelage removal or cold exposure (Johnson and Speakman, 2001; Król and Speakman, 2003; Król et al., 2007; Wu et al., 2009; Simons et al., 2011), but not by increases in litter size, by forced exercise, or by simultaneous pregnancy (Hammond and Diamond, 1994; Johnson et al., 2001a, b; Laurien-Kehnen and Trillmich, 2003). Similarly, lactating red squirrels *Tamiasciurus hudsonicus* raising large litters occupy poorly insulated nests in warm years (Guillemette et al., 2009). Support for the predictions of the theory is not universal, however, and other studies of small mammals report mixed results (Zhao and Cao, 2009; Speakman and Król, 2011; Zhao, 2011). The generality of the HDL theory also remains to be verified on animals performing other energetically-demanding activities, such as locomotion, and the theory explains the scaling of metabolic rate only in free-living endotherms, and does not apply to ectotherms. Nonetheless, for endotherms, the theory is relevant to BMR because it represents an upper limit to DEE. Given that BMR contributes a substantial component of DEE, an upper limit to DEE with a scaling exponent of ~0.63 will constrain BMR to a similarly low exponent to ensure that there is scope for activity (= DEE – BMR) across the size range of endotherms.

Evaluating explanations for metabolic scaling

It is a truism that all biological models are wrong because they are simplifications of complex systems and rarely, if ever, fully account for the variation they aim to explain. Ideally, models should maximise generality, realism, and precision, but this is not always possible and one of these is often sacrificed in favour of the others (Levins, 1966). Nevertheless, these three goals offer criteria by which competing models can be evaluated. With respect to metabolic scaling, distinguishing among competing models on the grounds of how well they predict empirical data is difficult because many models predict similar values. Metabolic rate may scale allometrically because of the geometry of resource distribution networks, leading to predictions of metabolic scaling exponents of 0.67 – 0.75 (Banavar et al., 2010) or 0.5 – 1 (Price et al., 2007). A definitive test of the resource distribution model has proven elusive, however, because like several other models it predicts a central tendency of 0.75-power scaling (West et al., 1997, 1999). Thus, while this prediction shows good general agreement with the mean scaling exponent observed in both intra-specific (Moses et al., 2008) and inter-specific (Savage et al., 2004) studies, other models make similar predictions: the Cell Size (Kozłowski et al., 2003a), Metabolic Level Boundaries (Glazier, 2010), and Dynamic Energy Budget models all predict *b* to vary between 0.67 and 1, the mid-point of which is close to 0.75. Similarly, the metabolic level boundaries (Glazier, 2010) and dynamic energy budget (Kooijman, 2010) models both predict that scaling exponents for resting endotherms will be lower than those for resting ectotherms. Given that the predictions from the models overlap so strongly, it is important that the presentation of models include clear descriptions of their unique predictions to facilitate tests that distinguish between alternatives (Shipley, 2000; Currie et al., 2004; Hawkins et al., 2007b; Glazier, 2010; White et al., 2011b; Kearney and White, 2012).

An alternative criterion by which competing explanations for metabolic scaling can be compared is their relative complexity. Simple explanations that incorporate a minimum of detail are sometimes regarded as more parsimonious than more complicated ones (Zuo et al., 2009). Implicit in such a judgement is the idea that a model should be evaluated not only on how well it fits available data, but that comparisons of alternative models should incorporate information about how many parameters are required to describe the data. Thus, of two models that describe variation in metabolic rate equally well, the ‘best’ model is the one that includes the fewest parameters. Such ideas form the basis of information theoretic approaches to model comparison (Burnham and Anderson, 2002; Johnson and Omland, 2004; Hobbs and Hilborn, 2006); in the case of metabolic scaling, such tests generally favour complex models over simple ones (Isaac and Carbone, 2010), because the additional predictive power of complex models outweighs their need to estimate extra parameters. It should be borne in mind, however, that some models are more connected to formal theories (e.g. DEB) than others (e.g. MLB); theory-based models must also be evaluated on the legitimacy of the theoretical assumptions in addition to model complexity (Kearney and White, 2012).

The two most common problems associated with tests of explanations for metabolic scaling have been a failure to account for phylogenetic non-independence in comparative data, and a reliance on correlational approaches to understand the scaling of physiological traits with body mass. While the former is rarely a problem in recent analyses (e.g. Sieg et al., 2009; White et al., 2009; Capellini et al., 2010; Kolokotrones et al., 2010), the latter is almost unavoidable because the metabolic rate and body mass are necessarily measured in intact individuals. The resultant correlation between these traits is then assessed; this approach precludes examination of the causal effect of mass on the trait of interest. Correlational approaches to distinguishing between competing explanations are problematic because many variables in addition to metabolic rate co-vary with body mass. For example, body mass is correlated with climate, diet, and life-history traits including litter size and maximum longevity (McNab, 2008; Jones et al., 2009), all of which have been shown to have confounding effects on metabolic rate (e.g. White and Seymour, 2004; McNab, 2008). A potential solution to this problem is the examination of scaling relationships for colonial organisms. The size of colonies can be manipulated experimentally and the consequences of the manipulation for scaling relationships can be examined (e.g. Nakaya et al., 2005; White et al., 2011b). An additional alternative approach is the manipulation of biotic and abiotic variables, and examination of the size-dependence of the resultant effect (Glazier, 2005). Such an approach is most commonly applied to intraspecific studies (e.g. Table 2) but could also be applied to interspecific ones, and represents a potentially powerful tool to understand the factors that constrain and influence the allometry of metabolic rate.

Integrating explanations for metabolic scaling

The various explanations for metabolic scaling are not necessarily exclusive, and integration of various aspects of the associated theories and models may lead to a greater understanding of why metabolic rate scales allometrically with body mass (Ginzburg and Damuth, 2008; Glazier, 2010). For example, Clarke et al. (2010) suggest that the reason why the relationship between log(M) and log(MR) for mammals is not linear (e.g. Hayssen and Lacy, 1985; Dodds et al., 2001; Glazier, 2005;

Makarieva et al., 2008; Kolokotrones et al., 2010; White, 2011) is because at large sizes the scaling is dominated by factors that dictate 0.75-power scaling (e.g. resource distribution: West et al., 1997), whereas at small sizes this factor is overridden by considerations of heat flow and hence the exponent is closer to 0.67. They note that the pattern of variation in the scaling exponent arising from this prediction is analogous to the metabolic level boundaries hypothesis of Glazier (2005, 2010). Similar arguments could be made using several of the other theories discussed above, since they also invoke fluxes that scale allometrically (e.g. of heat across body surfaces or metabolites across cell surfaces). Indeed, since the sum of two non-isometric scaling relationships will not be a strict power function of mass (Figure 2) (see also Garland, 1983; Calder, 1984), any theory that includes additive combinations of isometric ($\propto M^1$) and allometric (e.g. $\propto M^{0.67}$) components that vary with metabolic level will match a number of observed scaling patterns, at least qualitatively. Examples of such patterns include the curvature in BMR scaling for mammals (Hayssen and Lacy, 1985; Painter, 2005b; Kolokotrones et al., 2010), differences between the scaling exponent of basal and standard metabolic rate of endotherms and ectotherms (White et al., 2007b; White et al., 2008), the high scaling exponent of hibernating endotherms compared to daily heterotherms and euthermic endotherms (Geiser, 1988; White and Seymour, 2005a), and the high scaling exponent of field metabolic rate in reptiles compared to birds and mammals (Nagy et al., 1999; Nagy, 2005; Speakman and Król, 2010). This prediction is made explicit by the MLB hypothesis, which includes fluxes of metabolic resources, wastes and (or) heat that scale allometrically (Glazier, 2005, 2008, 2010), but the principle of summed allometric and isometric components (or summed components that each scale allometrically with different exponents) of metabolic rate applies equally to combinations of organ-tissue compartments that differ in their association with body mass (see e.g. Wang et al., 2001; Glazier, 2005; Painter, 2005b; Glazier, 2010; Killen et al., 2010).

Differences in the scaling of BMR and $\dot{V}O_2$max, for example, can be explained by considering differences in the metabolic scaling exponents between tissues that contribute to energy turnover during rest and exercise (Glazier, 2005). Most metabolic activity during basal metabolism is associated with the internal organs including liver, kidney, gastrointestinal tract, heart, and brain (Krebs, 1950; Rolfe and Brown, 1997), and variation in BMR between species and individuals has therefore been attributed to variation in organ mass (Daan et al., 1990; Konarzewski and Diamond, 1995; Meerlo et al., 1997; Książek et al., 2004; Song and Wang, 2006; Brzęk et al., 2007; Raichlen et al., 2009; Williams et al., 2010) and tissue metabolism (Krebs, 1950; Wang et al., 2001). During exercise-induced maximal metabolism, on the other hand, most (>90%) metabolic activity is associated with work done by the locomotor muscles and delivery of substrates and oxygen to these (Weibel et al., 2004). There is therefore a hierarchy of contributions to organismal metabolism depending on demand (see Darveau et al., 2002; Suarez and Darveau, 2005): whole-animal metabolism is a function of organ mass and metabolism, which in turn is a function of tissue and mitochondrial metabolism, which is governed by the activity of metabolic enzymes. At rest, allometric scaling of visceral organism metabolism dominates (see e.g. Porter, 2001; Wang et al., 2001; Glazier, 2005), whereas during exercise isometric scaling of muscle metabolism dominates (see e.g. Weibel et al., 2004; Glazier, 2005). Evidence for the validity of such an approach comes from the human literature, which includes examples where specific body compartments have been shown to be more appropriate than whole body mass for standardising inter-individual differences in $\dot{V}O_2$max (Eliakim et al., 1996; Nevill et al., 2004; Nevill et al., 2006; Tolfrey et al., 2006). Similarly, muscular parameters better explain inter-specific variation in mammalian $\dot{V}O_2$max than does body mass (Weibel et al., 2004; Weibel and Hoppeler, 2005).

Decomposition of whole-animal metabolism into organ-tissue compartments that scale with different exponents can also explain the higher scaling exponent of ectotherm SMR compared to endotherm BMR (White et al., 2006; White et al., 2007b). The organs that contribute to resting metabolism are smaller in ectotherms than in endotherms (Crile and Quiring, 1940; Martin, 1981; Karasov, 1987; Franz et al., 2009) and the tissue-mass-specific metabolic intensity is lower (Hulbert and Else, 1981; Hulbert et al., 2002). Thus, if whole-animal metabolism is assumed, for simplicity, to have two compartments (e.g. muscle + bone compartment that scales as $M^{\sim 1}$, and a visceral organ + brain compartment that scales as $M^{\sim 0.67}$) and the mass-specific intensity of both compartments is higher for endotherms than ecotherms, then the scaling exponent of SMR is predicted to be lower for endotherms than ecotherms (Figure 3). This approach also predicts that the curvature in MR will be less pronounced or absent in ectotherms than endotherms, as is also apparently the case (Ehnes et al., 2011; Müller et al., 2011a). The exact values of the exponents predicted by this approach will depend on the scaling exponent of organ masses and tissue-mass-specific metabolic intensities. However, while this 'multi-compartment' approach can explain variation in the scaling exponent of whole-animal metabolic rate, it does not offer an explanation for *why* the compartments scale as they do. First principles explanations for these organ-specific scaling patterns might come from the mechanistic models discussed above, and further understanding of the ultimate (evolutionary) causes of the allometric relationship between metabolic rate and body size could be gleaned from examination of the genetic associations between traits that contribute to metabolic rate (Glazier, 2005). For example, examination of how the genetic correlation between brain size and body size varies during development has been beneficial in understanding why the scaling exponent of brain size is lower during development than for interspecific comparisons (Lande, 1979; Riska and Atchley, 1985; Lynch and Walsh, 1998).

Causes of mass-independent variation in BMR

Climate and habitat productivity

Perhaps the most prominent and well-supported abiotic correlate of mass-independent variation in BMR is environmental temperature, which is negatively related to BMR in both birds (Jetz et al., 2007; White et al., 2007a) and mammals (Lovegrove, 2003; Careau et al., 2007), including humans (Froehle, 2008). This relationship probably arises as a consequence of the need to limit endogenous heat production in hot environments (McNab and Morrison, 1963), and to maximise heat production in cold environments (BMR is positively correlated with maximum cold-induced metabolic rate in both birds and mammals: Dutenhoffer and Swanson, 1996; Rezende et al., 2002; Rezende et al., 2004). The low BMR of species from hot environments may also arise because lower differential between body and ambient temperatures means that the contribution of endogenous heat production to thermoregulation can be reduced, thereby saving energy and/or water, or because high temperature limits the sustained metabolism of endotherms (Speakman and Król, 2010). If energy expenditure attributable to maintenance (BMR) and activity (AMR = FMR - BMR) are considered independent (i.e. the 'partioned pathways' model of Ricklefs et al., 1996), as is the case in at least free-ranging great cormorants *Phalacrocorax carbo* (White et al., 2011a), then, in an environment where daily energy expenditure is restricted by heat dissipation, a reduction in BMR increases the scope for activity. Support for the idea that scope for activity (=FMR divided by BMR) is restricted by the difference between maximum rates of heat dissipation and BMR arises from the observation that scope for activity decreases from up to 8-fold for small mammals to less than 3-fold for large ones (Westerterp and Speakman, 2008), though it is not currently clear if scope for activity also with climate. While the relationship between environmental temperature and BMR is likely to have a genetic component, as has been shown for stonechats (Wikelski et al., 2003), the extent to which phenotypic plasticity contributes to the observed relationship between environmental temperature and BMR remains unclear, as cold acclimation causes an increase in metabolic rate for birds and mammals (Williams and Tieleman, 2000; Song and Wang, 2006; McKechnie et al., 2007; McKechnie, 2008). Recent comparative analysis suggest that the magnitude and direction of seasonal acclimatization in free-living birds depends upon their thermal environment: species that experience cold winters at high latitude have higher BMR in winter than summer, whereas species that inhabit warmer subtropical latitudes have lower BMR in winter (Smit and McKechnie, 2010). These acclimation and acclimatization responses act on timescales of weeks, suggesting that ambient temperature has a proximate role in influencing BMR (Swanson and Olmstead, 1999; McKechnie et al., 2007), though changes associated with environmental triggers for reproduction are also implicated as drivers of seasonal variation (Smit and McKechnie, 2010). However, there is evidence that inter-specific and inter-population differences are maintained for multiple generations in captivity, and that populations from more seasonal environments show a greater capacity for thermal acclimation than populations from stable environments (Tieleman et al., 2003; Cavieres and Sabat, 2008). These findings suggest a genetic component to climate-associated variation in BMR. Thus, there remains a clear need for common-garden experiments comparing differences in BMR between animals from warm and cold environments to separate the genetic and phenotypic components of the negative relationship between environmental temperature and BMR.

Related to the effect of temperature, BMR is often thought to be associated with environmental productivity, such that animals from highly productive environments have higher BMRs than those from less productive environments. This conclusion stems from the observation that the BMRs of arid species are generally lower than those of mesic species (e.g. Tieleman and Williams, 2000; Withers et al., 2006). However, the BMR of birds is not related to net primary productivity (White et al., 2007a). This contrasts with the situation in mammals, where environmental productivity has been shown to be positively correlated with BMR in a range of studies (Mueller and Diamond, 2001; Bozinovic et al., 2007; Bozinovic et al., 2009). BMR is similarly correlated with rainfall parameters associated with environmental productivity for marsupials (Withers et al., 2006) and small (< 1 kg) eutherians (Lovegrove, 2003). Birds and mammals also differ in the relationship between BMR and rainfall variability: the relationship is negative in mammals (Lovegrove, 2003; Withers et al., 2006), but positive (White et al., 2007a) or absent (Jetz et al., 2007) in birds. The reason for this difference between birds and mammals is unclear, but it could be genuine, reflecting perhaps a difference in mobility, or it could arise as a consequence of methodological differences between the avian and mammalian analyses. Future analyses applying uniform phylogenetically-informed methods (see e.g. Rezende and Diniz-Filho, 2012) and drawing on environmental data from a single database could resolve the issue, and could be extended to other groups for which latitudinal and climate effects on metabolic rate have been identified, such as insects (Addo-Bediako et al., 2002) and fish (White et al., 2012). The ongoing accumulation of readily available climate data (e.g. www.worldclim.org), large compilations of metabolic data (e.g. McNab, 2009; Sieg et al., 2009) and complete species-level supertrees (e.g. Bininda-Emonds et al., 2007) will facilitate such work.

Probably the most controversial correlate of BMR is diet. Early work tended to report significant associations between diet and BMR (e.g. McNab, 1969, 1986). These were, however, not supported by subsequent PI analyses (e.g. Cruz-Neto et al., 2001; Rezende et al., 2004), though problems in correctly assigning dietary categories could contribute to this discrepancy (McNab, 2003). More recent PI analyses have supported an association between diet and BMR for Carnivora (Muñoz-Garcia and Williams, 2005), and between diet and FMR for birds (Anderson and Jetz, 2005), but no association is observed between BMR and diet for birds (Table 3) or mammals in general (White, 2011; see also Clarke et al. 2010 for a discussion of covariation between diet and body temperature in mammals).

Organ-tissue contributions to mass-independent BMR

The internal organs contribute substantially to BMR, and variation in BMR between species has therefore been attributed to variation in organ mass (Daan et al., 1990; Raichlen et al., 2009) and tissue metabolism (Krebs, 1950; Wang et al., 2001). Within species, 71% of the variation in BMR of Chilean mouse oppossums is explained by variation in the mass of digestive organs (Nespolo et al., 2002), strains of mice with high BMR tend to have relatively large metabolically active organs (heart, kidney, liver, and small intestine) (Konarzewski and Diamond, 1995), and mice artificially selected for high BMR have larger small intestine, liver, kidneys, and heart than mice selected for low BMR (Książek et al., 2004; Brzęk et al., 2007). Similarly, cold-acclimated Brandt's voles

Lasiopodomys brandtii have higher BMR and heavier liver, kidneys and gastrointestinal segments than warm-acclimated ones (Song and Wang, 2006). In field voles *Microtus agrestis*, BMR is positively correlated with heart mass (Meerlo et al., 1997). However, the relationship between organ mass and BMR differs between sexes in red junglefowl *Gallus gallus* (Hammond et al., 2000), BMR is associated with only the mass of reproductive tissue in adult house sparrows *Passer domesticus* (Chappell et al., 1999), and diet-induced changes in the mass of the gastrointestinal tracts, gizzards, and livers of starlings are not associated with increases in BMR (Geluso and Hayes, 1999). Thus, while comparative studies of birds have revealed a clear effect of inter-specific variation in organ masses on BMR (Daan et al., 1990), the results of intraspecific studies are more equivocal.

A controversial correlate of metabolic rate is brain size (Imamura and Clowes, 1975; Martin, 1981; Harvey and Bennett, 1983; McNab, 1989; Nagano et al., 1990a; Pastor, 2000; Isler and van Schaik, 2006; Weisbecker and Goswami, 2010). Recent comparative analyses are generally in favour of an association between brain size and metabolism for at least eutherian mammals; the presence or absence of an association for marsupials is more equivocal and depends upon the method of analysis (Imamura and Clowes, 1975; Weisbecker and Goswami, 2010). A potential problem with comparative analyses of the association between brain size and BMR, however, is that brain size is correlated with a range of other ecological and life-history traits (e.g. Burrin et al., 1989; Eisemann and Nienaber, 1990; Huntington et al., 1990; Guerino et al., 1991; Sol et al., 2002; Sol et al., 2005), and disentangling the associations between these traits, BMR, and brain size is difficult. Intra-specific studies have also demonstrated an association between brain size and BMR for humans (Javed et al., 2010; Müller et al., 2011b) and inbred strains of mice (Konarzewski and Diamond, 1995), and artificial selection studies offer an alternative experimental approach to examining the association. Brain weight has been shown to respond to artificial selection in mice in only 6-10 generations (Roderick et al., 1976), and comparison of BMR in lines divergently selected for low and high brain size should help resolve the issue.

Mitochondrial contributions to mass-independent BMR

Approximately 90% of oxygen consumption is associated with ATP production by mitochondria, with ~19-28% used by Na^+-K^+-ATPase and ~20% associated with mitochondrial proton leak (Rolfe and Brand, 1997). Variation in BMR between populations and individuals within a species have been attributed to variation in mitochondrial function (Speakman et al., 2004; Tieleman et al., 2009a), and individual mice with high metabolic rates have more uncoupled mitochondria than those with low metabolic rates (Speakman et al., 2004). However, differences in BMR between eutherians and marsupials are not explained by differences in mitochondrial proton leak (Polymeropoulos et al., 2011), nor are differences in BMR between individual humans (Larsen et al., 2011). Differences in BMR between individual humans are explained instead by differences in mitochondrial oxygen affinity (Larsen et al., 2011). Inter-individual and inter-population differences in mitochondrial function have been linked to fitness-enhancing traits in ectotherms (e.g. Ellison and Burton, 2006; Seebacher and Wilson, 2006), and similar links between BMR, mitochondrial function, and Darwinian fitness surely await discovery in endotherms. In addition to measurement of mitochondrial activity, attention should also be given to variation in the density of mitochondria, as variation in total mitochondrial volume accounts for significant variation in aerobic capacity (Weibel et al., 2004). Since aerobic capacity is often correlated with BMR (e.g. Hayes and Garland, 1995; see also Table 4) and mitochondrial processes contribute significantly to BMR, it seems likely that BMR will be correlated with the metabolic intensity and abundance of mitochondria, as well as mitochondrial morphology, which is related to proton leak across the inner mitochondrial membrane (Porter et al., 1996).

Approaches to understanding mass-independent variation

Quantitative genetic analyses and artificial selection experiments are a promising approach for elucidating the evolutionary factors that influence BMR. Several of these are ongoing, including divergent selection on BMR directly in laboratory mice (Książek et al., 2004); divergent selection on locomotor activity, predatory behaviour, and ability to cope with herbivorous diet in bank voles *Myodes* (*Clethrionomys*) *glareolus* (Sadowska et al., 2008); and selection on maximum rate of oxygen consumption ($\dot{V}O_{2max}$) during treadmill exercise, as well as selection to generate a negative correlation between $\dot{V}O_{2max}$ and BMR (see Swallow et al., 2009; Wone et al., 2011). Results available to date have demonstrated support for as association between diet and BMR, although the ability to cope with a low-quality herbivorous diet shows a positive additive genetic correlation with BMR (Sadowska et al., 2009), rather than the negative association expected from studies of the effect of dietary manipulation on BMR (Veloso and Bozinovic, 1993; Koteja, 1996; Perissinotti et al., 2009; Zhao and Wang, 2009). Seven generations of selection for high $\dot{V}O_{2max}$ has so far yielded a 12.3% increase in $\dot{V}O_{2max}$ in selected lines compared to control lines, and a non-significant 3.5% increase in BMR (Wone et al., 2011).

Selection on BMR directly has generated lines of mice that differ significantly in BMR and $\dot{V}O_{2max}$ elicited by forced swimming (Książek et al., 2004). The body-mass-corrected masses of four visceral organs (small intestine, liver, kidneys, and heart) are also consistently and substantially higher in mice selected for high BMR than those selected for low BMR (Książek et al., 2004); these differences are considered large enough to claim the existence of positive genetic correlations between BMR and the masses of examined viscera (Książek et al., 2004). It will be interesting to examine the outcomes of the suite of selection experiments not only for BMR, but also on the traits that are believed to underlie variation in BMR including the sizes of visceral organs and mitochondrial characteristics. Brain and liver mass are heritable in mice (Jones et al., 1992), as are the masses of brain, heart, liver, and kidney in baboons *Papio hamadryas* (Mahaney et al., 1993), and the liver in wild mice *Phyllotis darwini* (Bacigalupe et al., 2004). Baboons show additive genetic correlations between the masses of brain and liver, as well as between liver and kidneys (Mahaney et al., 1993), but no additive genetic correlations were detected between liver, heart, lungs, small intestine, and caecum in *Phyllotis darwini* (Bacigalupe et al., 2004). Given the phenotypic associations observed between visceral organs and BMR as well as between mitochondrial characteristics and BMR, the likely heritability of these traits, and the genetic associations among visceral organs, it seems plausible that genetic associations between BMR and these traits will also be revealed. Such analyses will yield valuable information regarding the mechanistic bases of variation in BMR that arises as a consequence of direct selection on BMR, or as a consequence of correlated responses in BMR associated with selection on other traits.

Consequences of variation in BMR for animal performance

Mass-independent variation in BMR amounts to up to several-fold between individuals, populations, and species, and understanding the consequences of this variation for organismal performance is essential to understanding the selection pressures that act on energy expenditure in the wild. In this regard, the most strident criticism of the BMR concept is that while the strict conditions prescribed for its measurement facilitate comparison by ensuring that all animals are in a similar physiological state, these conditions potentially come with the sacrifice of biological relevance. Basal conditions can be paraphrased as the measurement of a starving, stationary, sleeping animal, suggesting that the measurement is likely to have little practical utility in understanding the evolution of energy expenditure. Nevertheless, the observation that BMR varies significantly has led to the idea that the variation is important and might therefore be the subject of natural selection, either directly on BMR itself, or indirectly on a trait related to BMR. Indeed, BMR is repeatable (Nespolo and Franco, 2007), has low to moderate heritability (Table 5; see also Table 6 for heritabilities of metabolic rate for ecotherms), varies between individuals, responds to artificial selection (Książek et al., 2004), and is correlated with a wide range of other traits (Table 4, see also Biro and Stamps, 2010; Burton et al., 2011). This suggests that BMR could be the subject of selection, but studies demonstrating this in wild populations are rare.

Measurements of the association between juvenile survival and SMR in snails *Helix aspersa* suggest that maintenance metabolism is under a combination of directional and stabilising selection

(Artacho and Nespolo, 2009), such that individuals with low and intermediate metabolic rates are favoured over those with high metabolic rates. Natural selection therefore eliminates individuals with high metabolic rates but does not necessarily favour individuals with the absolute lowest metabolic rates. Similarly, inbreeding results in an increase in resting metabolic rate in crickets *Gryllodes sigillatus*, suggesting that low quality individuals have higher metabolic rates than high quality individuals (Ketola and Kotiaho, 2009). This contrasts with the finding that BMR is positively related to over-winter survival in short-tailed field voles *Microtus agrestis* (Jackson et al., 2001) and reproductive success in bank voles *Myodes* (*Clethrionomys*) *glareolus* (Boratyński and Koteja, 2010), although BMR is not related to over-winter survival in bank voles (Boratyński and Koteja, 2009). This discrepancy presumably arises for the same reason that stabilising selection was observed by Artacho and Nespolo (2009): high BMR may be an advantage in some situations, but a liability in others, and *vice versa*. Thus, high BMR and maximum rates of thermogenesis increase over-winter survival by improving cold tolerance (Hayes and O'Conner, 1999; Jackson et al., 2001), but low BMR improves starvation resistance (Rixon and Stevenson, 1957). Male Leach’s storm-petrels *Oceanodroma leucorhoa* with low BMR breed earlier and produce chicks that grow faster than males with relatively high BMR (Blackmer et al., 2005), but mice with low BMR die sooner than those with high BMR (Speakman et al., 2004). Other studies have found no link between BMR and reproductive traits in mice (Hayes et al., 1992; Johnson et al., 2001a; Johnston et al., 2007), a positive correlation between energy expenditure during lactation and BMR in *Peromyscus* mice (Glazier, 1985), no link between interspecific differences in age at first reproduction and BMR (Lovegrove, 2009), and a positive relationship between BMR and maximum running speed (Lovegrove, 2004).

The level of BMR therefore appears to be maintained as a consequence of a series of trade-offs such that low BMR is an advantage during food deprivation or reproduction, but high BMR is an advantage during cold exposure or predation events. This list is very unlikely to be exhaustive and other relationships presumably await discovery. However, an unanswered and intriguing question concerns the extent to which the “file drawer problem” (Csada et al., 1996) influences our current understanding of the consequences of variation in BMR, and it is presently unclear how many non-significant relationships between BMR and other traits remain unpublished.

Looking forward: the evolution of BMR and allometric scaling

BMR is ultimately linked with a range of extrinsic variables including habitat temperature, net primary productivity, and diet, and BMR is correlated with variation in survival, reproduction, and lifespan. An enduring area of interest that remains active, despite decades of research, concerns understanding the mechanistic basis of the allometric scaling of metabolic rate with body mass (e.g. Agutter and Wheatley, 2004; Savage et al., 2008; White and Kearney, 2012). However, if the non-isometric scaling of metabolic rate is ever to be understood, it is first necessary to know exactly what the relationship is. Recent meta-analyses (Glazier, 2005; White et al., 2007b), and PI analyses of hundreds of species of birds (McKechnie and Wolf, 2004; McKechnie et al., 2006; Kabat et al., 2008) and mammals (Duncan et al., 2007; Sieg et al., 2009; White et al., 2009; Capellini et al., 2010) have failed to support any single value of the allometric scaling exponents relating BMR to body mass. Without very substantial increases in the size of the data set, these conclusions are unlikely to change (White and Seymour, 2005b). Thus, an emerging challenge is to understand, for example, the differences in metabolic scaling between endotherms and ectotherms (Farrell-Gray and Gotelli, 2005; White et al., 2007b), and between metabolic levels (White and Seymour, 2005a; Glazier, 2008, 2009a). One promising area for understanding the allometry of metabolic rate is the use of experimental manipulation of intra-specific scaling exponents in species that span a wide range of body masses during development. During development, many species of ectotherm grow over several orders of magnitude in body size (e.g. Soling and Kleineke, 1976; Killen et al., 2007; Moran and Wells, 2007), and the scaling of metabolic rate in ecotherms has proven amenable to experimental manipulation (e.g. Table 2) (Glazier, 2005). Such experimental studies, which might involve manipulation of any of the factors known to influence metabolism, potentially represent powerful tools to understand the factors that constrain and influence the allometric scaling exponent relating metabolic rate to body mass.

Further progress toward understanding why metabolic rate scales allometrically is also likely to be made by complimenting the ongoing emphasis on mechanistic explanations with an approach that views metabolic scaling as an evolutionary outcome of trait associations, and explicitly incorporates the factors associated with mass-independent variation in metabolic rate between species (e.g. temperature, productivity, reproductive output) (see e.g. Glazier, 2005; Killen et al., 2010). Quantitative genetic tools have previously been applied to other problems of allometric scaling (e.g. Lande, 1979; Riska and Atchley, 1985; Lynch and Walsh, 1998), and are increasingly being applied to understanding other aspects of metabolic evolution (Artacho et al., 2005; Hayes, 2010; Nespolo et al., 2011, see also Konarzewski and Książek, 2012). The application of this tool set also has the potential to yield substantial benefits not only to the understanding of mass-independent variation, but also to the scaling of metabolic rate with body mass. As an example, because the genetic correlation between body mass and metabolic rate is positive and often less than 1 (Table 7), allometric scaling of metabolic rate with body mass can arise in a simple evolutionary model that includes random variation in body mass and correlated changes in metabolic rate (Figure 4; see Appendix B for modelling procedures). The scaling exponent of metabolic rate in such a model can take a wide range of values, depending on the strength of the association between metabolic rate and body mass (Figure 4). While this example is obviously simplistic, it nonetheless demonstrates that the evolution of allometric scaling might be explained without the need to invoke first principles mechanistic hypotheses grounded in chemistry or physics (see also Witting, 1995; Kozłowski and Weiner, 1997; Glazier, 2005 for other examples). Taking the resource distribution hypotheses as an example, this evolutionary approach based on trait associations assumes not that the geometry of the resource distribution network dictates metabolic scaling, but that the geometry of the resource distribution network has evolved to support the pattern of metabolic scaling (see also Weibel and Hoppeler, 2005). For evolutionary models of allometric scaling to be of any value, however, it is essential that plausible models of evolution and trait association are specified, and, critically, that appropriate tests are either presented in conjunction with the models, or that clear descriptions of the unique predictions of the models are presented, so that appropriate tests can be designed (Shipley, 2000; Currie et al., 2004; Hawkins et al., 2007b; Glazier, 2010; White et al., 2011b; Kearney and White, 2012).

Acknowledgements

Lesley Alton, Doug Glazier, Phil Matthews and four anonymous reviewers provided detailed comments on an earlier version of the manuscript, and Jon Green, Lewis Halsey, Karyn Johnson, James Maino, and Dustin Marshall provided helpful suggestions; Ian Hume showed exemplary patience in guiding the manuscript through several phases of development. Our research is funded by the Australian Research Council (Projects DP0987626, DP110101776, DP110102813).

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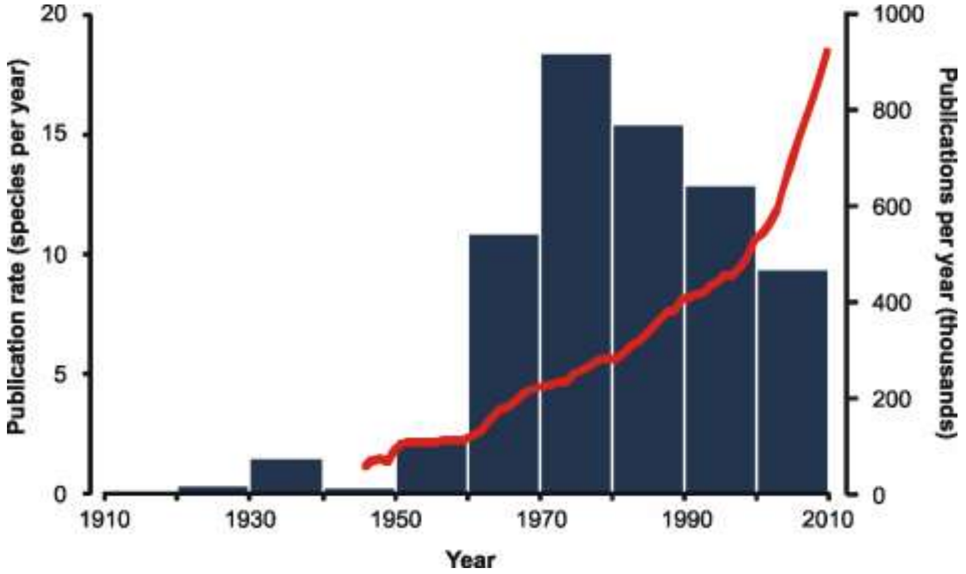

Figure 1. Total annual publication output across all fields indexed by PubMed (Publications per year, red line) and publication rate of data for mammalian basal metabolic rate (BMR, filled bars). BMR data are from a recent compilation (Sieg et al., 2009). Where BMR data for a species have been published multiple times, only the first instance is included.

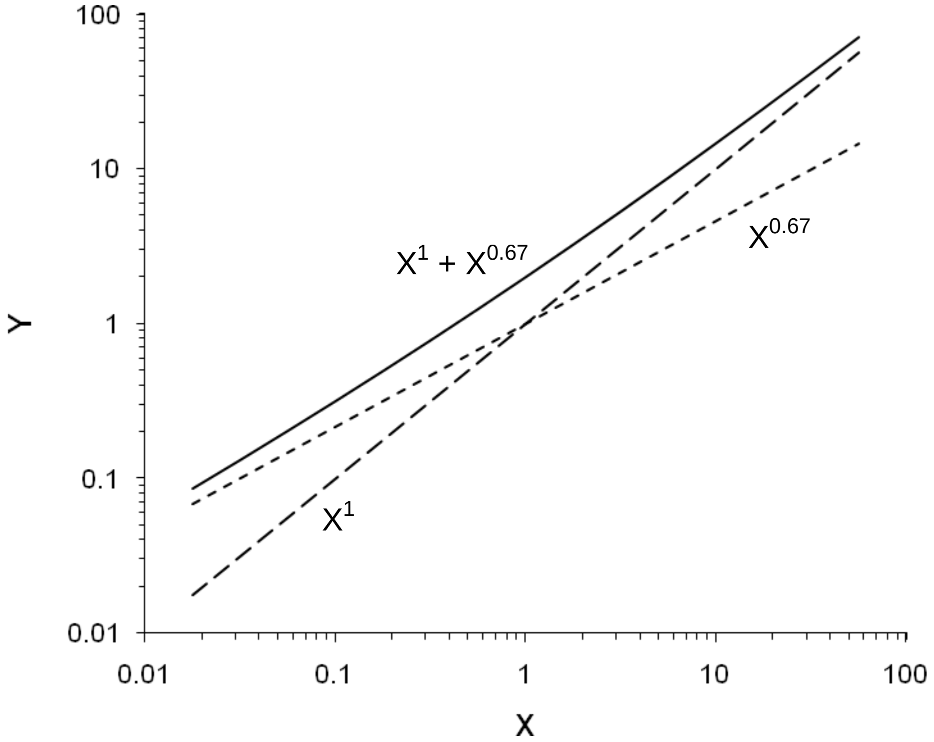

Figure 2. Summing isometric and allometric relationships introduces curvature into the relationship between logY and logX.

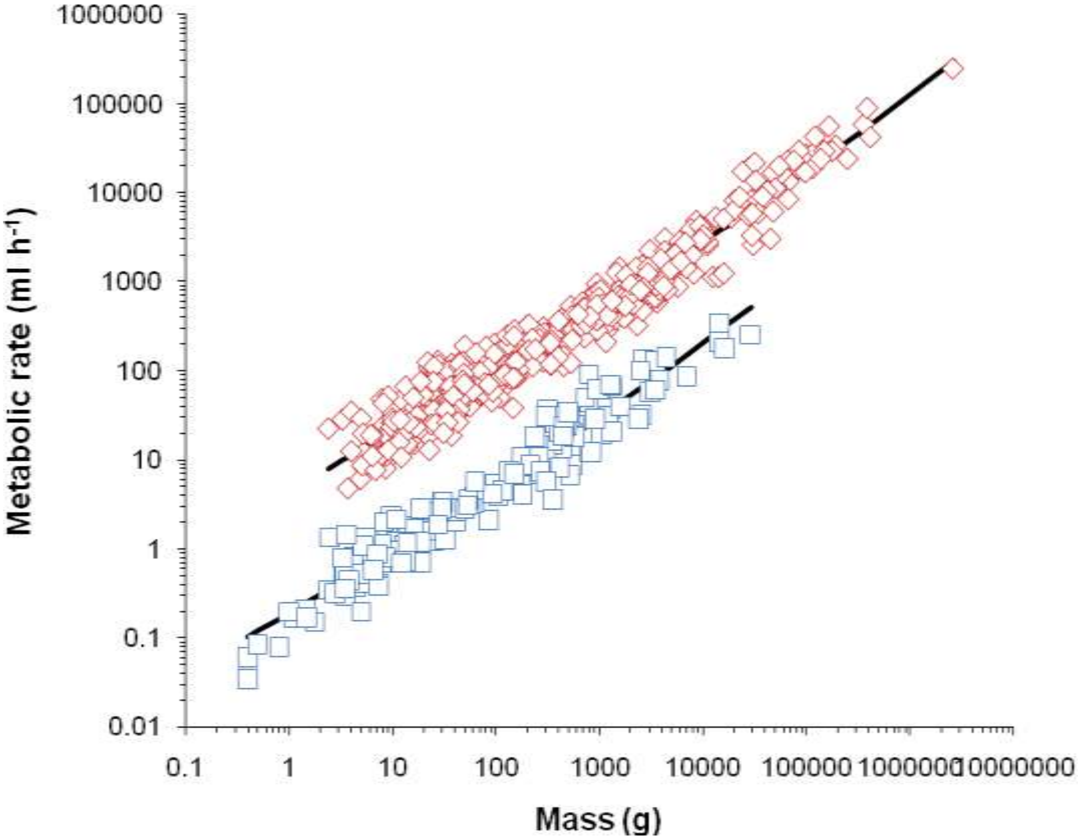

Figure 3. Relationships between mammalian BMR (unfilled diamonds: Sieg et al., 2009) and reptile SMR (unfilled squares: White et al., 2006) and mass (M, g) estimated by fitting summed allometric ($\propto M^{0.67}$) and isometric ($\propto M^{1}$) components by iteration (Gauss-Newton algorithm) using JMP v8.0.1 (SAS Institute, Cary, NC, USA). Mammal BMR = 4.30 $M^{0.67}$ + 0.084 mass^{1}; Reptile SMR = 0.18 $M^{0.67}$ + 0.012 M^{1}. Data for reptiles were normalised to a body temperature of 25 °C using a Q_{10} value of 2.44 (White et al., 2006).

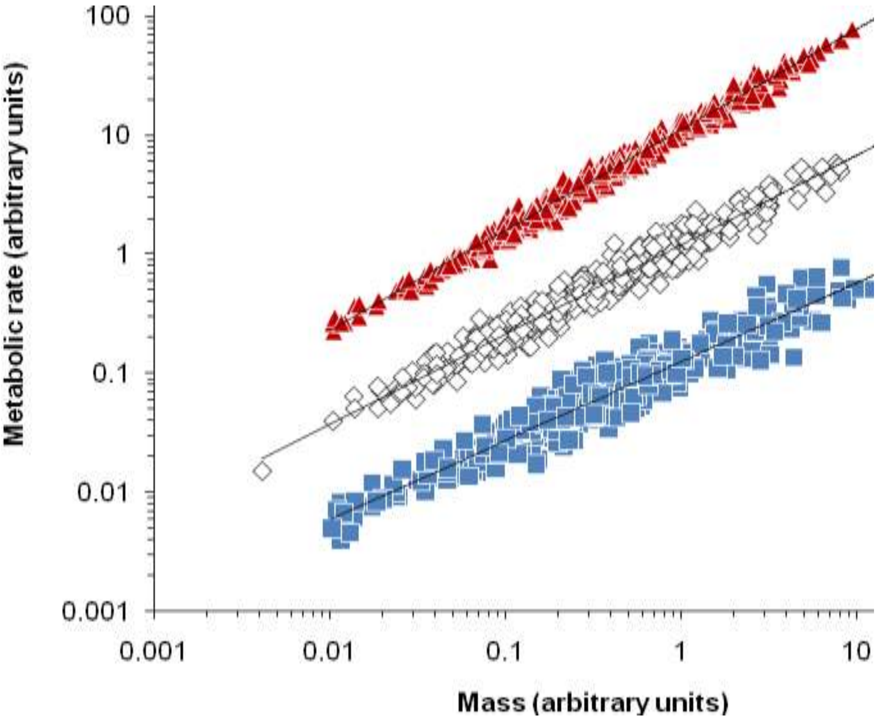

Figure 4. Simulated associations between metabolic rate (MR) and mass (M) generated according to the methods in Appendix B. The scaling exponent (b) and strength of the association is dependent on the relationship between changes in MR and changes in M (filled triangles: the change in MR at each time step is equal to 0.7 to 1 times the change in M, b = 0.84; unfilled diamonds: change in MR is 0.5 to 1 times the change in M, b = 0.75; filled squares: change in MR is 0.33 to 1 times the change in M, b = 0.66). The model does not predict the elevation of the relationship; filled triangles and filled squares are offset by for clarity by +1 and -1 orders of magnitude, respectively.

Table 1. Selected scaling exponents (b) for the cardiovascular system predicted by the fractal resource distribution model of West, Brown, and Enquist (WBE: West et al., 1997) and the Resource Distribution Network model of Banavar et al. (RDN: Banavar et al., 2010).

Variable	**WBE**	**RDN**	**Observed**
Cardiac frequency	-0.25		Mammals: -0.23 (Seymour and Blaylock, 2000) Birds: -0.28 (Seymour and Blaylock, 2000) Fish: ~0 (White and Seymour, 2011)
Aorta radius	0.375	0.33	0.33 (Peters, 1983)
Aorta length	0.25	0.33	0.32 (Günther and León de la Barra, 1966)
Aorta pressure	0		0.05 (Seymour and Blaylock, 2000)
Blood velocity	0	0 to 0.083	0.07 (Peters, 1983)
Respiratory frequency	-0.25		-0.56 to -0.25 (Stahl, 1967; Frappell et al., 2001; Mortola and Limoges, 2006; Terblanche et al., 2008; Mortola and Seguin, 2009)

Table 2. Examples of manipulative studies of the scaling of metabolic rate (see Glazier, 2005 for an extensive compilation of further examples).

Treatment	**Species**	**Reference**
Diet	*Daphnia*	(Jeyasingh, 2007)
Light intensity	*Daphnia pulex*	(Buikema, 1972)
	Atlantic cod *Gadus morhua*	(Finn et al., 2002)
Oxygen availability	Marine nematode *Enoplus brevis*	(Atkinson, 1973)
pH	Ornate rainbowfish *Rhadinoventrus ornatus*	(Vaca and White, 2010)
Salinity	Crab *Hemigrapsus oregonensis*	(Dehnel, 1960)
	Crab *Hemigrapsus nudus*	(Dehnel, 1960)
	Rainbow trout *Salmo gardneri*	(Rao, 1971)
Starvation	Shore crab *Carcinus maenus*	(Marsden et al., 1973)
	Sand Dollar *Mellita quinquiesperforata*	(Lane and Lawrence, 1979)
Temperature	American cockroach *Periplaneta americana*	(Dehnel and Segal, 1956)
	Freshwater snail *Marisa cornuarietis*	(Åkerlund, 1969)
	Shore crab *Carcinus maenus*	(Marsden et al., 1973)
	Sea anemone *Metridium senile*	(Walsh and Somero, 1981)
	Wood louse *Porcellio laevis*	(Lardies et al., 2004)
	Vendance *Coregonus albula*	(Ohlberger et al., 2007)
Water availability	Manchurian ash *Fraxinus mandshurica*	(Chen and Li, 2003)
	Amur cork tree *Phellodendron amurense*	(Chen and Li, 2003)
Colony size	*Botrylloides simodensis* (colonial ascidian)	(Nakaya et al., 2005)
	Hippoporina indica (Colonial marine bryozoan)	(White et al., 2011b)
Inbreeding	Cricket *Gryllodes sigillatus*	(Ketola and Kotiaho, 2012)

Table 3. Parameter estimates for a model for avian basal metabolic rate (BMR, ml h^{-1}) as assessed by phylogenetic generalised least squares ($\lambda = 0.83$ and AIC = -395.2; AIC for an equivalent non-phylogenetic model is 247.0). Significant ($p < 0.05$) parameters are indicated with *; n.s. is non-significant. See Appendix A for a description of the analysis.

Parameter	**Estimate**	**s.e.**
Intercept	-1.11^{*}	0.06
logM	0.72^{*}	0.02
Diet		
Aquatic vegetation	$0.03^{\text{n.s.}}$	0.07
Aquatic invertebrates	$0.06^{\text{n.s.}}$	0.05
Fruit	$-0.04^{\text{n.s.}}$	0.03
Flying insects	$-0.06^{\text{n.s.}}$	0.05
Grass	$0.07^{\text{n.s.}}$	0.08
Leaves	$0.04^{\text{n.s.}}$	0.04
Insects	$0.01^{\text{n.s.}}$	0.02
Omnivore	$0.07^{\text{n.s.}}$	0.04
Pollen	$0.08^{\text{n.s.}}$	0.04
Seeds	$-0.01^{\text{n.s.}}$	0.03
Vertebrates	$-0.01^{\text{n.s.}}$	0.04

Table 4. A selection of significant correlates of metabolic rate in animals (values in parentheses are additive genetic correlations).

Species	**MR level**	**Correlate**	**Direction**	**Reference**
Laboratory rat *Rattus norvegicus*	RMR	Starvation resistance	-	(Rixon and Stevenson, 1957)
Great tit *Parus major*	RMR	Social dominance	+	(Røskaft et al., 1986)
Pied flycatchers *Ficedula hypoleuca*	RMR	Social dominance	+	(Røskaft et al., 1986)
Willow tit *Parus montanus*	RMR	Social dominance	+	(Hogstad, 1987)
Deer mouse *Peromyscus maniculatus*	BMR	$\dot{V}O_2$max	+	(Hayes, 1989)
Belding's ground squirrel *Spermophilus beldingi*	RMR	$\dot{V}O_2$max	+	(Chappell and Bachman, 1995)
Masu salmon *Oncorhynchus masou*	RMR	Social dominance	+	(Yamamoto et al., 1998)
House sparrows *Passer domesticus*	$BMR_{juvenile}$	Juvenile $\dot{V}O_2$max	+	(Chappell et al., 1999)
Short-tailed field vole *Microtus agrestis*	RMR	Over-winter survival	+	(Jackson et al., 2001)
Nine-banded armadillos *Dasypus novemcinctus*	BMR	MMR_{cold}	+	(Boily, 2002)
Short-tailed field vole *Microtus agrestis*	RMR	Daily energy expenditure*	+	(Speakman et al., 2003)
Laboratory mice *Mus musculus*	RMR	Longevity	+	(Speakman et al., 2004)
Leach’s storm-petrel *Oceanodroma leucorhoa*	BMR ♂	Offspring growth	-	(Blackmer et al., 2005)
Leach’s storm-petrel *Oceanodroma leucorhoa*	BMR ♂	Hatch date	+	(Blackmer et al., 2005)
Bank vole *Myodes glareolus*	BMR	MMR_{swim}	(+)	(Sadowska et al., 2005)
Laboratory mouse *Mus musculus*	BMR	Gestational weight loss	+	(Johnston et al., 2007)
Garden snail *Helix aspersa*	SMR	Juvenile survival	- and stabilising	(Artacho and Nespolo, 2009)
Laboratory mice *Mus musculus*	BMR	$MMR_{exercise}$	(+)	(Wone et al., 2009)
Bank vole *Myodes glareolus*	BMR	Postweaning growth rate	(+)	(Sadowska et al., 2009)
Bank vole *Myodes glareolus*	BMR	Ability to cope with poor diet	(+)	(Sadowska et al., 2009)
Bank vole *Myodes glareolus*	BMR ♂	Reproductive success	+	(Boratyński and Koteja, 2010)
Bank voles *Myodes glareolus*	BMR ♀	Over-winter survival	+	(Boratyński et al., 2010)

Red squirrels *Tamiasciurus hudsonicus*	RMR	Over-winter survival	-	(Larivée et al., 2010)
Root vole *Microtus oeconomus*	RMR	Proactive behaviour	+	(Lantová et al., 2011)
Deer mouse *Peromyscus maniculatus*	RMR	Exploratory behaviour	(+)	(Careau et al., 2011)
Atlantic salmon *Salmo salar*	SMR	Social dominance	+	(Reid et al., 2011)
Atlantic salmon *Salmo salar*	SMR	Feeding rate	+	(Reid et al., 2011)
Atlantic salmon *Salmo salar*	SMR	Growth rate	-	(Reid et al., 2011)

*Extrinsic association caused by environmental differences between habitats, rather than an intrinsic one. Note that a number of other studies have found no association between metabolic rate and a range of traits (Hayes et al., 1992; Chappell et al., 1999; Hammond et al., 2000; Dohm et al., 2001; Johnson et al., 2001a; Nespolo et al., 2005; Sadowska et al., 2005; Vézina et al., 2006; Chappell et al., 2007; Boratyński and Koteja, 2009; Bouwhuis et al., 2011; Timonin et al., 2011; Schimpf et al., 2012). See also Biro and Stamps (2010) and Burton et al. (2011) for compilations of associations between metabolic rate and other traits.

Table 5. Narrow-sense heritability (h^2) of basal metabolic rate (BMR), standard metabolic rate (SMR), sustained metabolic rate (susMR), cold-induced maximum metabolic rate (MMR), and exercise-induced maximum metabolic rate ($\dot{V}O_{2max}$) of birds and mammals. * indicates $p < 0.05$.

Species	Measurement	h^2 ± SE	Reference
Laboratory mouse *Mus musculus*	BMR	0.08 ± 0.06	(Lacy and Lynch, 1979)
Laboratory mouse *Mus musculus*	RMR	0.21 ± 0.04*	(Lynch and Sulzbach, 1984)
Hsd:ICR strain, *Mus domesticus*	BMR	0.09	(Dohm et al., 2001)
	$\dot{V}O_2$max	0.64*	(Dohm et al., 2001)
Leaf-eared mouse *Phyllotis darwini*	BMR	0.15	(Nespolo et al., 2003)
Leaf-eared mouse *Phyllotis darwini*	BMR	0.21 ± 0.21	(Bacigalupe et al., 2004)
	susMR	0.20 ± 0.38	(Bacigalupe et al., 2004)
Laboratory mouse *Mus musculus*	BMR	0.38 ± 0.21*	(Konarzewski et al., 2005)
	Swim $\dot{V}O_2$max	0.40 ± 0.21*	(Konarzewski et al., 2005)
Leaf-eared mouse *Phyllotis darwini*	BMR	0.11 ± 0.18	(Nespolo et al., 2005)
	MMR	0.69 ± 0.35*	(Nespolo et al., 2005)
Bank vole *Clethrionomys glareolus*	BMR	0.40*	(Sadowska et al., 2005)
	Swim $\dot{V}O_2$max	0.40*	(Sadowska et al., 2005)
	MMR	0.43*	(Sadowska et al., 2005)
Zebra finch *Taeniopygia guttata*	BMR	0.25 ± 0.04*	(Rønning et al., 2007)
Blue tit *Cyanistes caeruleus*	RMR	0.59 ± 0.25	(Nilsson et al., 2009)
Stonechat *Saxicola torquate rubicola*	$BMR_{residual}$	0.48 ± 0.16	(Tieleman et al., 2009b)
Stonechat *Saxicola torquata axillaris*	$BMR_{residual}$	0.20 ± 0.35	(Tieleman et al., 2009b)
Stonechat *Saxicola torquate maura*	BMR (g^{-1})	0.37 ± 0.47	(Tieleman et al., 2009b)
Laboratory mouse *Mus musculus*	$BMR_{residual}$	0.19 ± 0.07*	(Wone et al., 2009)
	$\dot{V}O_2max_{residual}$	0.16 ± 0.06*	(Wone et al., 2009)
Pied Flycatcher *Ficedula hypoleuca*	RMR	0.43 ± 0.17*	(Bushuev et al., 2011)
Deer mouse *Peromyscus maniculatus*	$RMR_{residual}$	0.39 ± 0.20	(Careau et al., 2011)

Table 6. Broad-sense (H^2) and narrow sense (h^2) heritability of metabolic rate in ectothermic animals (* $p < 0.05$, *** $p < 0.001$).

Species	Measurement	Heritability ± SE	Reference
Garter snake *Thamnophis sirtalis*	Maximum	$H^2 = 0.88^{***}$	(Garland and Bennett, 1990)
Drosophila melanogaster			
5 d post-eclosion	Routine MR	$H^2 = 0.07^{***}$	(Khazaeli et al., 2005)
	Routine MR	$H^2 = 0.14^{***}$	(Khazaeli et al., 2005)
16 d post-eclosion	Routine MR	$H^2 = 0.48^{***}$	(Khazaeli et al., 2005)
	Routine MR	$H^2 = 0.45^{***}$	(Khazaeli et al., 2005)
29 d post-eclosion	Routine MR	$H^2 = 0.43^{***}$	(Khazaeli et al., 2005)
	Routine MR	$H^2 = 0.26^{***}$	(Khazaeli et al., 2005)
47 d post-eclosion	Routine MR	$H^2 = 0.30^{***}$	(Khazaeli et al., 2005)
	Routine MR	$H^2 = 0.29^{***}$	(Khazaeli et al., 2005)
Sand cricket *Gryllus firmus*	Resting	$H^2 = 0.045 \pm 0.04$	(Nespolo et al., 2007)
	Average	$H^2 = 0.052 \pm 0.06$	(Nespolo et al., 2007)
	Minimum	$H^2 = 0.10 \pm 0.06$	(Nespolo et al., 2007)
	Maximum	$H^2 = 0.085 \pm 0.05$	(Nespolo et al., 2007)
Cricket *Gryllodes sigillatus*	Resting	$h^2 = 0.142 \pm 0.187$	(Ketola and Kotiaho, 2009)
	Exercise	$h^2 = 0.718^* \pm 0.313$	(Ketola and Kotiaho, 2009)

Table 7. Additive genetic correlations between metabolic rate and body mass in animals, shown ± SEE.

Species	MR level	Correlation	Reference
Zebra finch *Taeniopygia guttata*	BMR	0.914 ± 0.081	(Rønning et al., 2007)
Blue tit *Cyanistes caeruleus*	RMR	1.178 ± 0.456	(Nilsson et al., 2009)
Stonechat *Saxicola torquata rubicola*	BMR	0.400 ± 0.349	(Tieleman et al., 2009b)
Stonechat *Saxicola torquata axillaris*	BMR	0.780 ± 0.360	(Tieleman et al., 2009b)
Deer mouse *Peromyscus maniculatus*	BMR	0.72 ± 0.23	(Careau et al., 2011)

Appendix A. Phylogenetic methods for the analysis of the effect of diet on avian basal metabolic rate.

The relationship between log transformed basal metabolic rate (BMR), log transformed body mass (M) and dietary categories was analysed using phylogenetic generalised least squares (PGLS) (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000) in the APE (Analysis of Phylogenetics and Evolution) package (Paradis et al., 2004) within R (Ihaka and Gentleman, 1996) according to established procedures (Halsey et al., 2006; Duncan et al., 2007; White et al., 2009). Data for avian BMR matched to a phylogenetic hypothesis were obtained from a published analysis of the scaling of BMR (Kabat et al., 2008), and were matched to dietary categories provided by McNab (2009). Matched BMR and diet data were available for a total of 287 species. Since the true branch lengths in the phylogeny are unknown, two branch length assumptions were compared: all branches set equal to 1, and an alternative assumption that branch lengths were proportional in length to the number of taxa descended from the node to which the branch leads (Grafen, 1989). A measure of phylogenetic correlation, λ (Pagel, 1999; Freckleton et al., 2002), was estimated by fitting PGLS models with different values of λ and finding the value that maximizes the log likelihood. The degree to which trait evolution deviates from Brownian motion ($\lambda = 1$) was accommodated by modifying the covariance matrix using the maximum likelihood value of λ, which is a multiplier of the off-diagonal elements of the covariance matrix (i.e., those quantifying the degree of relatedness between species). All models were compared on the basis of Akaike's Information Criterion (AIC) as a measure of model fit (Burnham and Anderson, 2001, 2002). The relative support of alternative models was compared on the basis of Δ_i (= AIC – minimum AIC); models having $\Delta_i \leq 2$ have substantial support, those where $4 \leq \Delta_i \leq 7$ have considerably less support, while models having $\Delta_i > 10$ have essentially no support (Burnham and Anderson, 2001).

Appendix B. Methods for the generation of an allometric association between metabolic rate and body mass.

The model for allometric scaling is based on Monte Carlo simulations developed to understand the causes of the observed right-skewed lognormal distribution of mammalian body masses (Maurer et al., 1992; Blackburn and Gaston, 1994, 1998, 1999). Initially, 400 ‘species’ with a mass (M) of 1 and a metabolic rate (MR) of 1 were generated. For each species, a random change in M was then generated by multiplying M by a normal deviate with a mean of 0 and standard deviation of 0.02 and then adding M. This was then repeated a total of 5000 times for each ‘species’. Thus, for each of the 5000 time steps, mass varied randomly with a standard deviation of 2% of the value of M at the previous time step. Because the genetic correlation between MR and M is positive and often less than 1 (Table 7), factorial changes in MR at each time step were randomly smaller than the changes in MR (see e.g. Figure 4). This procedure generates lognormal distributions of M and MR, consistent with the idea that body size evolves multiplicatively, and could be made more realistic by the introduction of size-biased selection and extinction, and anagenetic size change within species between speciation and extinction events (e.g. Stanley, 1973; Maurer et al., 1992; Kingsolver and Pfennig, 2004; Clauset and Erwin, 2008; Mattila and Bokma, 2008; Clauset et al., 2009). The consequences of variation in MR for allometric scaling could be examined by including selections against low (e.g. Jackson et al., 2001) or high (e.g. Artacho and Nespolo, 2009) MR.