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:

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

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).

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Literature cited

Addo-Bediako A, Chown SL, Gaston KJ (2002) Metabolic cold adaptation in insects: a large-scale perspective. Funct Ecol 16:332-338

Agutter PS, Tuszynski JA (2011) Analytic theories of allometric scaling. J Exp Biol 214:1055-1062

Agutter PS, Wheatley DN (2004) Metabolic scaling: consensus or controversy? Theoretical Biology and Medical Modelling 1:13 (http://www.tbiomed.com/content/11/11/13)

Åkerlund G (1969) Oxygen consumption of the ampullariid snail *Marisa cornuarietis* L. in relation to body weight and temperature. Oikos 20:529-533

Algar AC, Kerr JT, Currie DJ (2007) A test of Metabolic Theory as the mechanism underlying broad-scale species-richness gradients. Glob Ecol Biogeogr 16:170-178

Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545-1548

Anderson KJ, Jetz W (2005) The broad-scale ecology of energy expenditure of endotherms. Ecol Lett 8:310-318

Artacho P, Castañeda LE, Nespolo RF (2005) The role of quantitative genetic studies in animal physiological ecology. Rev Chil Hist Nat 78:161-167

Artacho P, Nespolo RF (2009) Natural selection reduces energy metabolism in the garden snail, *Helix aspersa* (*Cornu aspersum*). Evolution 63:1044-1050

Atkinson HJ (1973) The respiratory physiology of the marine nematodes *Enoplus Brevis* (Bastian) and *E. Communis* (Bastian). J Exp Biol 59:255-266

Bacigalupe LD, Nespolo RF, Bustamante DM, Bozinovic F (2004) The quantitative genetics of sustained energy budget in a wild mouse. Evolution 58:421-429

Banavar JR, Damuth J, Maritan A, Rinaldo A (2002a) Modelling universality and scaling. Nature 420:626

Banavar JR, Damuth J, Maritan A, Rinaldo A (2002b) Supply-demand balance and metabolic scaling. Proc Natl Acad Sci U S A 99:10506-10509

Banavar JR, Damuth J, Maritan A, Rinaldo A (2003) Allometric cascades. Nature 421:713-714

Banavar JR, Maritan A, Rinaldo A (1999) Size and form in efficient transportation networks. Nature 399:130-131

Banavar JR, Maritan A, Rinaldo A (2000) Rivers, blood and transportation networks - Reply. Nature 408:160

Banavar JR, Moses ME, Brown JH, Damuth J, Rinaldo A, Sibly RM, Maritan A (2010) A general basis for quarter-power scaling in animals. Proc Natl Acad Sci U S A 107:15816-15820

Batterham AM, Jackson AS (2003) Validity of the allometric cascade model at submaximal and maximal metabolic rates in exercising men. Respir Physiol Neurobiol 135:103-106

Batterham AM, Jackson AS (2005) Authors' response. Respir Physiol Neurobiol 146:3-4

Bejan A (2000) Shape and structure, from engineering to nature. Cambridge University Press, Cambridge

Bejan A (2005) The constructal law of organization in nature: tree-shaped flows and body size. J Exp Biol 208:1677-1686

Benedict FG (1938) Vital energetics: A study in comparative basal metabolism. Carnegie Institution of Washington, Washington, D.C.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A (2007) The delayed rise of present-day mammals. Nature 446:507-512

Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol 25:653-659

Bishop CM (1999) The maximum oxygen consumption and aerobic scope of birds and mammals: Getting to the heart of the matter. Proceedings of the Royal Society of London - Series B: Biological Sciences 266:2275-2281

Blackburn TM, Gaston KJ (1994) The distribution of body sizes of the worlds bird species. Oikos 70:127-130

Blackburn TM, Gaston KJ (1998) The distribution of mammal body masses. Diversity and Distribution 4:121-133

Blackburn TM, Gaston KJ (1999) The relationship between animal abundance and body size: a review of the mechanisms. Adv Ecol Res 28

Blackmer AL, Mauck RA, Ackerman JT, Huntington CE, Nevitt GA, Williams JB (2005) Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels. Behav Ecol 16:906-913

Boily P (2002) Individual variation in metabolic traits of wild nine-banded armadillos (*Dasypus novemcinctus*), and the aerobic capacity model for the evolution of endothermy. J Exp Biol 205:3207-3214

Bokma F (2004) Evidence against universal metabolic allometry. Funct Ecol 18:184-187

Boratyński Z, Koskela E, Mappes T, Oksanen TA (2010) Sex-specific selection on energy metabolism – selection coefficients for winter survival. J Evol Biol 23:1969-1978

Boratyński Z, Koteja P (2009) The association between body mass, metabolic rates and survival of bank voles. Funct Ecol 23:330-339

Boratyński Z, Koteja P (2010) Sexual and natural selection on body mass and metabolic rates in free-living bank voles. Funct Ecol 24:1252-1261

Bouwhuis S, Sheldon BC, Verhulst S (2011) Basal metabolic rate and the rate of senescence in the great tit. Funct Ecol:in press

Bozinovic F, Muñoz JLP, Cruz-Neto AP (2007) Intraspecific variability in the basal metabolic rate: testing the food habits hypothesis. Physiol Biochem Zool 80:452-460

Bozinovic F, Rojas JM, Broitman BR, Vásquez RA (2009) Basal metabolism is correlated with habitat productivity among populations of degus (*Octodon degus*). Comp Biochem Physiol A 152:560-564

Brody S (1945) Bioenergetics and growth. Reinhold Publishing Corporation, New York

Broggi J, Hohtola E, Koivula K, Orell M, Thomson RL, Nilsson J-Å (2007) Sources of variation in winter basal metabolic rate in the great tit. Funct Ecol 21:528-533

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004a) Response to forum commentary ofn "toward a metabolic theory of ecology". Ecology 85:1818-1821

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004b) Toward a metabolic theory of ecology. Ecology 85:1771-1789

Brown JH, West GB, Enquist BJ (2005) Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant. Funct Ecol 19:735-738

Brzęk P, Bielawska K, Książek A, Konarzewski M (2007) Anatomic and molecular correlates of divergent selection for basal metabolic rate in laboratory mice. Physiol Biochem Zool 80

Buckley LB, Rodda GH, Jetz W (2008) Thermal and energetic constraints on ectotherm abundance: a global test using lizards. Ecology 89:48-55

Buikema AL, Jr. (1972) Oxygen consumption of the cladoceran, *Daphnia pulex*, as a function of body size, light and light acclimation. Comp Biochem Physiol A 42:877-888

Burnham KP, Anderson DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. Wildl Res 28:111-119

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York

Burrin DG, Ferrell CL, Eisemann JH, Britton RA, Nienaber JA (1989) Effect of level of nutrition on splanchnic blood flow and oxygen consumption in sheep. Br J Nutr 62:23-34

Burton T, Killen SS, Armstrong JD, Metcalfe NB (2011) What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proceedings of the Royal Society B: Biological Sciences 278:3465-3473

Bushuev A, Kerimov A, Ivankina E (2011) Estimation of heritability and repeatability of resting metabolic rate in birds by the example of free-living pied flycatchers *Ficedula hypoleuca* (Aves: Passeriformes). Biology Bulletin Reviews 1:26-46

Calder WA, III (1984) Size, function, and life history. Harvard University Press, Cambridge

Capellini I, Venditti C, Barton RA (2010) Phylogeny and metabolic scaling in mammals. Ecology 91:2783-2793

Careau V, Morand-Ferron J, Thomas D (2007) Basal metabolic rate of canidae from hot deserts to cold arctic climates. J Mammal 88:394-400

Careau V, Thomas D, Pelletier F, Turki L, Landry F, Garant D, Réale D (2011) Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (*Peromyscus maniculatus*). J Evol Biol 24:2153-2163

Cavieres G, Sabat P (2008) Geographic variation in the response to thermal acclimation in rufous-collared sparrows: are physiological flexibility and environmental heterogeneity correlated? Funct Ecol 22:509-515

Chappell MA, Bachman GC (1995) Aerobic performance in Belding's ground squirrels (*Spermophilus beldingi*): variance, ontogeny, and the aerobic capacity model of endothermy. Physiol Zool 68:421-442

Chappell MA, Bech C, Buttemer WA (1999) The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. J Exp Biol 202:2269-2279

Chappell MA, Garland T, Jr, Robertson G, Saltzman W (2007) Relationships among running performance, aerobic physiology and organ mass in male Mongolian gerbils. J Exp Biol 210:4179-4197

Chaui-Berlinck JG (2006) A critical understanding of the fractal model of metabolic scaling. J Exp Biol 209:3045-3054

Chaui-Berlinck JG (2007) Response to 'Comment on "A critical understanding of the fractal model of metabolic scaling" '. J Exp Biol 210:3875-3876

Chen X, Li B-L (2003) Testing the allometric scaling relationships with seedlings of two tree species. Acta Oecol 24:125-129

Chown SL, Marais E, Terblanche JS, Klok CJ, Lighton JRB, Blackburn TM (2007) Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. Funct Ecol 21:282-290

Clark TD, Farrell AP (2011) Effects of body mass on physiological and anatomical parameters of mature salmon: evidence against a universal heart rate scaling exponent. J Exp Biol 214:887-893

Clarke A (2006) Temperature and the metabolic theory of ecology. Funct Ecol 20:405-412

Clarke A, Rothery P, Isaac NJB (2010) Scaling of basal metabolic rate with body mass and temperature in mammals. J Anim Ecol 79:610-619

Clauset A, Erwin DH (2008) The evolution and distribution of species body size. Science 321:399-401

Clauset A, Schwab DJ, Redner S (2009) How many species have mass *M*? Am Nat 173:256-263

Cloutier M, Wellstead P (2010) The control systems structures of energy metabolism. J Royal Soc Interface 7:651-665

Crile G, Quiring DP (1940) A record of the body weight and certain organ and gland weights of 3690 animals. Ohio J Sci XL:219-259

Cruz-Neto AP, Garland T, Jr., Abe AS (2001) Diet, phylogeny, and basal metabolic rate in phyllostomid bats. Zoology 104:49-58

Csada RD, James PC, Espie RHM (1996) The "file drawer problem" of non-significant results: does it apply to biological research? Oikos 76:591-593

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol Lett 7:1121-1134

da Silva JKL, Garcia GJM, Barbosa LA (2006) Allometric scaling laws of metabolism. Physics of Life Reviews 3:229-261

Daan S, Masman D, Groenewold A (1990) Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am J Physiol 259:R333-R340

Darveau CA, Suarez RK, Andrews RD, Hochachka PW (2002) Allometric cascade as a unifying principle of body mass effects on metabolism. Nature 417:166-170

Darveau CA, Suarez RK, Andrews RD, Hochachka PW (2003) Reply to West *et al* and Banavar *et al*. Nature 421:714

Davison J (1955) Body weight, cell surface and metabolic rate in anuran Amphibia. Biological Bulletin 109:407-419

Dehnel PA (1960) Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. Biological Bulletin 118:215-249

Dehnel PA, Segal E (1956) Acclimation of oxygen consumption to temperature in the American cockroach (*Periplaneta Americana*). Biological Bulletin 111:53-61

Dell AI, Pawar S, Savage VM (2011) Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences:in press

DeLong JP, Okie JG, Moses ME, Sibly RM, Brown JH (2010) Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. Proc Natl Acad Sci U S A 107:12941-12945

Demetrius L (2003) Quantum statistics and allometric scaling of organisms. Physica A: Statistical Mechanics and its Applications 322:477-490

Demetrius L (2006) The origin of allometric scaling laws in biology. J Theor Biol 243:455-467

Demetrius L, Tuszynski JA (2010) Quantum metabolism explains the allometric scaling of metabolic rates. J Royal Soc Interface 7:507-514

Dodds PS (2010) Optimal form of branching supply and collection networks. Physical Review Letters 104:048702

Dodds PS, Rothman DH, Weitz JS (2001) Re-examination of the "'3/4-law" of metabolism. J Theor Biol 209:9-27

Dohm MR, Hayes JP, Garland T, Jr. (2001) The quantitative genetics of maximal and basal rates of oxygen consumption in mice. Genetics 159:267-277

Downs CJ, Hayes JP, Tracy CR (2008) Scaling metabolic rate with body mass and inverse body temperature: a test of the Arrhenius fractal supply model. Funct Ecol 22:239-244

Duncan RP, Forsythe DM, Hone J (2007) Testing the metabolic theory of ecology: allometric scaling exponents in mammals. Ecology 88:324-333

Dutenhoffer MS, Swanson DL (1996) Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. Physiol Zool 69:1232-1254

Ehnes RB, Rall BC, Brose U (2011) Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. Ecol Lett 14:993-1000

Eisemann JH, Nienaber JA (1990) Tissue and whole-body oxygen uptake in fed and fasted steers. Br J Nutr 64:399-411

Elia M (1992) Organ and tissue contributions to metabolic rate. In: Kinney JM, Tucker HN (eds) Energy metabolism: Tissue determinants and cellular corollaries. Raven, New York

Eliakim A, Barstow TJ, Brasel JA, Ajie H, Lee WNP, Renslo R, Berman N, Cooper DM (1996) Effect of exercise training on energy expenditure, muscle volume, and maximal oxygen uptake in female adolescents. The Journal of pediatrics 129:537-543

Ellison CT, Burton RS (2006) Disruption of mitochondrial function in interpopulation hybrids of *Tigriopus californicus*. Evolution 60:1382-1391

Farrell-Gray CC, Gotelli NJ (2005) Allometric exponents support a 3/4-power scaling law. Ecology 86:2083-2087

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1-15

Finn RN, Rønnestad I, van der Meeren T, Fyhn HJ (2002) Fuel and metabolic scaling during the early life stages of Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 243:217-234

Franz R, Hummel J, Kienzle E, Kölle P, Gunga H-C, Clauss M (2009) Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs. Proceedings of the Royal Society B 276:1731-1736

Frappell PB, Butler PJ (2004) Minimal metabolic rate, what it is, its usefulness, and its relationship to the evolution of endothermy: a brief synopsis. Physiol Biochem Zool 77:865-868

Frappell PB, Hinds DS, Boggs DF (2001) Scaling of respiratory variables and the breathing pattern in birds: An allometric and phylogenetic approach. Physiol Biochem Zool 74:75-89

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: A test and review of evidence. Am Nat 160:712-726

Froehle AW (2008) Climate variables as predictors of basal metabolic rate: new equations. Am J Hum Biol 20:510-529

Garland T, Jr, Bennett AF (1990) Quantitative genetics of maximal oxygen consumption in a garter snake. American Journal of Physiology - Regulatory, Integrative and Comparative Physiology 259:R986-R992

Garland T, Jr. (1983) The relation between maximal running speed and body mass in terrestrial mammals. Journal of Zoology 199:157-170

Garland T, Jr., Ives AR (2000) Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346-364

Geiser F (1988) Reduction of metabolism during hibernation and daily torpor in mammals and birds: Temperature effect or physiological inhibition? J Comp Physiol B 158:25-38

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239-274

Geluso K, Hayes JP (1999) Effects of dietary quality on basal metabolic rate and internal morphology of European starlings (*Sturnus vulgaris*). Physiol Biochem Zool 72:189-197

Gillooly JF, Allen AP (2007) Changes in body temperature influence the scaling of Vo_2 max and aerobic scope in mammals. Biology Letters 3:99-102

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248-2251

Ginzburg L, Damuth J (2008) The space-lifetime hypothesis: viewing organisms in four dimensions, literally. Am Nat 171:125-131

Glazier DS (1985) Relationship between metabolic rate and energy expenditure for lactation in *Peromyscus*. Comp Biochem Physiol A Comp Physiol 80:587-590

Glazier DS (2005) Beyond the ‘3/4-power law’: variation in the intra- and interspecific scaling of metabolic rate in animals. Biological Reviews 80:1-52

Glazier DS (2008) Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals. Proceedings of the Royal Society B 22:1405-1410

Glazier DS (2009a) Activity affects intraspecific body-size scaling of metabolic rate in ectothermic animals. J Comp Physiol B 179:821-828

Glazier DS (2009b) Metabolic level and size scaling of rates of respiration and growth in unicellular organisms. Funct Ecol 23:963-968

Glazier DS (2009c) Ontogenetic body-mass scaling of resting metabolic rate covaries with species-specific metabolic level and body size in spiders and snakes. Comp Biochem Physiol A 153:403-407

Glazier DS (2010) A unifying explanation for diverse metabolic scaling in animals and plants. Biological Reviews 85:111-138

Grafen A (1989) The phylogenetic regression. Philosophical Transactions of the Royal Society of London B 326:119-157

Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird. J Avian Biol 40:529-538

Green JA, Halsey LG, Butler PJ, Holder RL (2007) Estimating the rate of oxygen consumption during submersion from the heart rate of diving animals. American Journal of Physiology - Regulatory, Integrative and Comparative Physiology 292:R2028-R2038

Guerino F, Huntington GB, Erdman RA (1991) The net portal and hepatic flux of metabolites and oxygen consumption in growing beef steers given postruminal casein. J Anim Sci 69:387-395

Guillemette CU, Fletcher QE, Boutin S, Hodges RM, McAdam AG, Humphries MM (2009) Lactating red squirrels experiencing high heat load occupy less insulated nests. Biology Letters 5:166-168

Günther B, León de la Barra B (1966) A unified theory of biological similarities. J Theor Biol 13:48-59

Halsey LG, Butler PJ, Blackburn TM (2006) A phylogenetic analysis of the allometry of diving. Am Nat 167:276-287

Halsey LG, Butler PJ, Fahlman A, Woakes A, Handrich Y (2008) Behavioral and physiological significance of minimum resting metabolic rate in king penguins. Physiol Biochem Zool 81:74-86

Hammond K, Diamond J (1994) Limits to dietary nutrient intake and intestinal nutrient uptake in lactating mice. Physiol Zool 67:282-303

Hammond KA, Chappell MA, Cardullo RA, Lin R-S, Johnsen TS (2000) The mechanistic basis of aerobic performance variation in red junglefowl. J Exp Biol 203:2053-2064

Harvey PH, Bennett PM (1983) Brain size, energetics, ecology and life history patterns. Nature 306:314-315

Hawkins BA, Albuquerque FS, Araújo MB, Beck J, Bini LM, Cabrero-Sañudo FJ, Castro-Parga I, Diniz-Filho JAF, Ferrer-Castán D, Field R, Gómez JF, Hortal J, Kerr JT, Kitching IJ, León-Cortés JL, Lobo JM, Montoya D, Moreno JC, Ollalla-Tárraga MÁ, Pausas JG, Qian H, Rahbek C, Rodríguez MÁ, Sanders NJ, Williams P (2007a) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. Ecology 88:1877-1888

Hawkins BA, Diniz-Filho JAF, Bini LM, Araújo MB, Field R, Hortal J, Kerr JT, Rahbek C, Rodríguez MÁ, Sanders NJ (2007b) Metabolic theory and diversity gradients: Where do we go from here? Ecology 88:1898-1902

Hayes JP (1989) Altitudinal and seasonal effects on aerobic metabolism of deer mice. J Comp Physiol B 159:453-459

Hayes JP (2010) Metabolic rates, genetic constraints, and the evolution of endothermy. J Evol Biol 23:1868-1877

Hayes JP, Garland T, Jr. (1995) The evolution of endothermy: testing the aerobic capacity model. Evolution 19:836-847

Hayes JP, Garland T, Jr., Dohm MR (1992) Individual variation in metabolism and reproduction of *Mus*: are energetics and life history linked? Funct Ecol 6:5-14

Hayes JP, O'Conner CS (1999) Natural selection on thermogenic capacity of high-altitude deer mice. Evolution 53:1280-1287

Hayssen V, Lacy RC (1985) Basal metabolic rates in mammals: Taxonomic differences in the allometry of BMR and body mass. Comp Biochem Physiol A 81:741-754

Hemmingsen AM (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. Reports of the Steno Memorial Hospital and the Nordisk Insulinlaboratorium 9:1-110

Heusner AA (1982) Energy metabolism and body size: 1. Is the 0.75 mass exponent of Kleibers equation a statistical artifact? Respir Physiol 48:1-12

Heusner AA (1991) Size and power in mammals. J Exp Biol 160:25-54

Hobbs NT, Hilborn R (2006) Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecol Appl 16:5-19

Hochachka PW, Darveau CA, Andrews RD, Suarez RK (2003) Allometric cascade: a model for resolving body mass effects on metabolism. Comp Biochem Physiol A 134:675-691

Hogstad O (1987) It is expensive to be dominant. The Auk 104:333-336

Hulbert AJ, Else PL (1981) Comparison of the “mammal machine” and the “reptile machine”: energy use and thyroid activity. American Journal of Physiology - Regularoy, Integrative and Comparative Physiology 241:R350-R356

Hulbert AJ, Else PL, Manolis SC, Brand MD (2002) Proton leak in hepatocytes and liver mitochondria from archosaurs (crocodiles) and allometric relationships for ectotherms. J Comp Physiol B 172:387-397

Huntington GB, Eisenmann JH, Whitt JM (1990) Portal blood flow in beef steers: comparison of techniques and relation to hepatic blood flow, cardiac output and oxygen uptake. J Anim Sci 68:1666-1673

Ihaka R, Gentleman R (1996) R: A language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299-314

Imamura M, Clowes GH, Jr. (1975) Hepatic blood flow and oxygen consumption in starvation, sepsis and septic shock. Surgery, Gynecology and Obstetrics 141:27-37

Irlich UM, Terblanche JS, Blackburn TM, Chown SL (2009) Insect rate-temperature relationships: environmental variation and the metabolic theory of ecology. Am Nat 174:819-835

Isaac NJB, Carbone C (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. Ecol Lett:doi: 10.1111/j.1461-0248.2010.01461.x

Isler K, van Schaik CP (2006) Metabolic costs of brain size evolution. Biology Letters 2:557-560

Jackson DM, Trayhurn P, Speakman JR (2001) Associations between energetics and over-winter survival in the short-tailed field vole *Microtus agrestis*. J Anim Ecol 70:633-640

Javed F, He Q, Davidson LE, Thornton JC, Albu J, Boxt L, Krasnow N, Elia M, Kang P, Heshka S, Gallagher D (2010) Brain and high metabolic rate organ mass: contributions to resting energy expenditure beyond fat-free mass. Am J Clin Nutr 91:907-912

Jeneson JAL, Westerhoff HV, Kushmerick MJ (2000) A metabolic control analysis of kinetic controls in ATP free energy metabolism in contracting skeletal muscle. Am J Physiol 279:C813-C832

Jetz W, Freckleton RP, McKechnie AE (2007) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. PLoS ONE 3:e3261

Jeyasingh PD (2007) Plasticity in metabolic allometry: the role of dietary stoichiometry. Ecol Lett 10:282-289

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101-108

Johnson MS, Speakman JR (2001) Limits to sustained energy intake: V. Effect of cold-exposure during lactation in *Mus musculus*. J Exp Biol 204:1967-1977

Johnson MS, Thomson SC, Speakman JR (2001a) Limits to sustained energy intake II. Inter-realtionships between resting metabolic rate, life-history traits and morphology in *Mus musculus*. J Exp Biol 204:1937-1446

Johnson MS, Thomson SC, Speakman JR (2001b) Limits to sustained energy intake: I. Lactation in the laboratory mouse *Mus musculus*. J Exp Biol 204:1925-1935

Johnston SL, Souter DM, Erwin SS, Tolkamp BJ, Yearsley JM, Gordon IJ, Illius AW, Kyriazakis I, Speakman JR (2007) Associations between basal metabolic rate and reproductive performance in C57BL/6J mice. J Exp Biol 210:65-74

Jones JH (1998) Optimization of the mammalian respiratory system: symmorphosis versus single species adaptation. Comparative Biochemistry and Physiology B 120:125-138

Jones JH, Taylor CR, Lindholm A, Straub R, Longworth KE, Karas RH (1989) Blood gas measurements during exercise: errors due to temperature correction. J Appl Physiol 67:879-884

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648

Jones LD, Nielsen MK, Britton RA (1992) Genetic variation in liver mass, body mass, and liver:body mass in mice. J Anim Sci 70:2999-3006

Kabat AP, Blackburn TM, McKechnie AE, Butler PJ (2008) Phylogenetic analysis of the allometric scaling of therapeutic regimes for birds. Journal of Zoology 275:359-367

Karasov WH (1987) Nutrient requirements and the design and function of guts in fish, reptiles, and mammals. In: Dejours P, Bolis L, Taylor CR, Weibel ER (eds) Comparative physiology: life in water and on land. Liviana Press, Padova

Kearney MR, White CR (2012) Testing metabolic theories.In review

Ketola T, Kotiaho JS (2009) Inbreeding, energy use and condition. J Evol Biol 22:770-781

Ketola T, Kotiaho JS (2012) Inbreeding depression in the effects of body mass on energy use. Biol J Linn Soc 105:309-317

Khazaeli AA, Van Voorhies W, Curtsinger JW (2005) Longevity and metabolism in *Drosophila melanogaster*: genetic correlations between life span and age-specific metabolic rate in populations artificially selected for long life. Genetics 169:231-242

Killen SS, Atkinson D, Glazier DS (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecol Lett 13:184-193

Killen SS, Costa I, Brown JA, Gamperl AK (2007) Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. Proceedings of the Royal Society B 274:431-438

Kingsolver JG, Pfennig DW (2004) Individual-level selection as a cause of Cope's rule of phyletic size increase. Evolution 58:1608-1612

Kleiber M (1932) Body size and metabolism. Hilgardia 6:315-353

Kleiber M (1961) The fire of life. John Wiley & Sons, Inc., New York, London

Kolokotrones T, Savage VM, Deeds EJ, Fontana W (2010) Curvature in metabolic scaling. Nature 464:753-756

Konarzewski M, Diamond J (1995) Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 49:1239-1248

Konarzewski M, Książek A (2012) Sources of intraspecific variation in the mass-specific basal metabolic rate: a review

Konarzewski M, Książek A, Łapo I (2005) Artificial selection in metabolic rates and related traits in rodents. Integrative and Comparative Biology 45:416-425

Kooijman SALM (1986) Energy budgets can explain body size relations. J Theor Biol 121:269-282

Kooijman SALM (2010) Dynamic Energy Budget Theory for Metabolic Organisation. Cambridge University Press, Cambridge

Kooijman SALM, Baas J, Bontje D, Broerse M, Jager T, Van Gestel CAM, Van Hattum B (2007) Scaling relationships based on partition coefficients and body sizes have similarities and interactions. SAR QSAR Environ Res 18:315-330

Koteja P (1996) Limits to the energy budget in a rodent, *Peromyscus maniculatus*: Does gut capacity set the limit? Physiol Zool 69:994-1020

Kozłowski J, Czarnołęski M, François-Krassowska A, Maciak S, Pis T (2010) Cell size is positively correlated between different tissues in passerine birds and amphibians, but not necessarily in mammals. Biology Letters:doi: 10.1098/rsbl.2010.0288

Kozłowski J, Konarzewski M (2004) Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? Funct Ecol 18:283-289

Kozłowski J, Konarzewski M (2005) West, Brown and Enquist's model of allometric scaling again: the same questions remain. Funct Ecol 19:739-743

Kozłowski J, Konarzewski M, Gawelczyk AT (2003a) Cell size as a link between noncoding DNA and metabolic rate scaling. Proceedings of the National Academy of Sciences of the USA 100:14080-14085

Kozłowski J, Konarzewski M, Gawelczyk AT (2003b) Intraspecific body size optimization produces intraspecific allometries. In: Blackburn TM, Gaston KJ (eds) Macroecology: concepts and consequences. Blackwell Science Ltd, Malden, pp 299-320

Kozłowski J, Weiner J (1997) Interspecific allometries are by-products of body size optimization. Am Nat 149:352-380

Krebs HA (1950) Body size and tissue respiration. Biochim Biophys Acta 4:249-269

Krogh A (1916) Respiratory exchange of animals and man. Longmans, Green and Co., London

Król E, Murphy RW, Speakman JR (2007) Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. J Exp Biol 240:4233-4243

Król E, Speakman JR (2003) Limits to sustained energy intake VI. Energetics of lactation in laboratory mice at thermoneutrality. J Exp Biol 206:4255-4266

Książek A, Konarzewski M, Łapo I (2004) Anatomic and energetic correlates of divergent selection for basal metabolic rate in laboratory mice. Physiol Biochem Zool 77:890-899

Lacy RC, Lynch CB (1979) Quantitative genetic analysis of temperature regulation in *Mus musculus*. I. Partitioning of variance. Genetics 91:743-753

Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. Evolution 33:402-416

Lane JM, Lawrence JM (1979) The effect of size, temperature, oxygen level and nutritional condition on oxygen uptake in the sand dollar, *Mellita quinquiesperforata* (Leske). Biological Bulletin 157:275-287

Lantová P, Zub K, Koskela E, Síchová K, Borowski Z (2011) Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example. Physiol Behav 104:378-383

Lardies MA, Catalán TP, Bozinovic F (2004) Metabolism and life-history correlates in a lowland and highland population of a terrestrial isopod. Can J Zool 82:677-687

Larivée ML, Boutin S, Speakman JR, McAdam AG, Humphries MM (2010) Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. Funct Ecol 24:597-607

Larsen FJ, Schiffer TA, Sahlin K, Ekblom B, Weitzberg E, Lundberg JO (2011) Mitochondrial oxygen affinity predicts basal metabolic rate in humans. The FASEB Journal:doi:10.1096/fj.1011-182139

Laurien-Kehnen C, Trillmich F (2003) Lactation performance of guinea pigs (*Cavia porcellus*) does not respond to experimental manipulation of pup demands. Behav Ecol Sociobiol 53:145-152

Levins R (1966) The strategy of model building in population biology. Am Sci 54:421-431

Lighton JRB (2008) Measuring metabolic rates: a manual for scientists. Oxford University Press, Oxford

Loiselle DS, Gibbs CL (1979) Species differences in cardiac energetics. Am J Physiol 237:H90-H98

Lovegrove BG (2003) The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. J Comp Physiol B 173:87-112

Lovegrove BG (2004) Locomotor mode, maximum running speed, and basal metabolic rate in placental mammals. Physiol Biochem Zool 77:916-928

Lovegrove BG (2005) Seasonal thermoregulation power in mammals. J Comp Physiol B 175:234-247

Lovegrove BG (2009) Age at first reproduction and growth rate are independent of basal metabolic rate in mammals. J Comp Physiol B 179:391-401

Lynch CB, Sulzbach DS (1984) Quantitative genetic analysis of temperature regulation in *Mus musculus*. II. Diallel analysis of individual traits. Evolution 38:527-540

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland

Maciak S, Konarzewski M, Kozłowski J, Janko KC, L., Kotusz J, Boron A, Juchno D, Kujawa R (2011) Standard metabolic rate (SMR) is inversely related to erythrocyte and genome size in allopolyploid fish of *Cobitis taenia* hybrid complex. Funct Ecol:in press

Mahaney MC, Williams-Blangero S, Blangero J, Leland MM (1993) Quantitative genetics of relative organ weight variation in captive baboons. Hum Biol 65:991-1003

Makarieva AM, Gorshkov VD, Li B-L, Chown SL, Reich PB, Gavrilov VM (2008) Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. Proceedings of the National Academy of Sciences 105:16994-16999

Makarieva AM, Gorshkov VD, Li B (2003) A note on metabolic rate dependence on body size in plants and animals. J Theor Biol 221:301-307

Marsden ID, Newell RC, Ahsanullah M (1973) The effect of starvation on the metabolism of the shore crab, Carcinus maenas. Comp Biochem Physiol A 45:195-213

Martin RD (1981) Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293:57-60

Martins EP, Hansen TF (1997) Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646-667

Mattila TM, Bokma F (2008) Extant mammal body masses suggest punctuated equilibrium. Proceedings of the Royal Society B 275:2195-2199

Maurer BA, Brown JH, Rusler RD (1992) The micro and macro in body size evolution. Evolution 46:939-953

McKechnie AE (2008) Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. J Comp Physiol B 178:235-247

McKechnie AE, Chetty K, Lovegrove BG (2007) Phenotypic flexibility in the basal metabolic rate of laughing doves: responses to short-term thermal acclimation. J Exp Biol 210:97-106

McKechnie AE, Freckleton RP, Jetz W (2006) Phenotypic plasticity in the scaling of avian basal metabolic rate. Proceedings of the Royal Society B 273:931-937

McKechnie AE, Wolf BO (2004) The allometry of avian basal metabolic rate: Good predictions need good data. Physiol Biochem Zool 77:502-521

McMahon T (1973) Size and shape in biology. Science 179:1201-1204

McNab BK (1969) The economics of temperature regulation in neotropical bats. Comp Biochem Physiol 31:227-268

McNab BK (1986) The influence of food habits on the energetics of eutherian mammals. Ecol Monogr 56:1-20

McNab BK (1989) Brain size and its relation to the rate of metabolism in mammals. Am Nat 133:157-167

McNab BK (1997) On the utility of uniformity in the definition of basal rate of metabolism. Physiol Zool 70:718-720

McNab BK (2003) Standard energetics of phyllostomid bats: the inadequacies of phylogenetic-contrast analyses. Comp Biochem Physiol A 135:357-368

McNab BK (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. Comp Biochem Physiol A 151:5-28

McNab BK (2009) Ecological factors affect the level and scaling of avian BMR. Comp Biochem Physiol A 152:22-45

McNab BK, Morrison P (1963) Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecol Monogr 33:63-82

Meehan TD (2006) Energy use and animal abundance in litter and soil communities. Ecology 87:1650-1658

Meehan TD, Jetz W, Brown JH (2004) Energetic determinants of abundance in winter landbird communities. Ecol Lett 7:532-537

Meerlo P, Bolle L, Visser GH, Masman D, Daan S (1997) Basal metabolic rate in relation to body composition and daily energy expenditure in the field vole, *Microtus agrestis*. Physiol Zool 70:362-369

Moran D, Wells RMG (2007) Ontogenetic scaling of fish metabolism in the mouse-to-elephant mass magnitude range. Comp Biochem Physiol A 148:611-620

Mortola JP, Limoges M-J (2006) Resting breathing frequency in aquatic mammals: A comparative analysis with terrestrial species. Respir Physiol Neurobiol 154:500-514

Mortola JP, Seguin J (2009) Resting breathing frequency in aquatic birds: a comparative analysis with terrestrial species. Journal of Zoology 279:210-218

Moses ME, Hou C, Woodruff WH, West GB, Nekola JC, Zuo W, Brown JH (2008) Revisiting a model of ontogenetic growth: estimating model parameters from theory and data. Am Nat 171:632-645

Mueller P, Diamond J (2001) Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. Proceedings of the National Academy of Sciences 98:12551-12554

Müller DWH, Codron D, Werner J, Fritz J, Hummell J, Griebeler EM, Clauss M (2011a) Dichotomy of eutherian reproduction and metabolism. Oikos:in press

Müller MJ, Langemann D, Gehrke I, Later W, Heller M, Glüer CC, Heymsfield SB, Bosy-Westphal A (2011b) Effect of constitution on mass of individual organs and their association with metabolic rate in humans—a detailed view on allometric scaling. PLoS ONE 6:e22732

Munch SB, Salinas S (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. Proceedings of the National Academy of Sciences 106:13860-13864

Muñoz-Garcia A, Williams JB (2005) Basal metabolic rate in carnivores is associated with diet after controlling for phylogeny. Physiol Biochem Zool 78:1039-1056

Nagano K, Gelman S, Bradley EL, Parks D (1990a) Hypothermia, hepatic oxygen supply-demand, and ischemia-reperfusion injury in pigs. Am J Physiol Gastrointest Liver Physiol 258:G910-G918

Nagano K, Gelman S, Parks DA, Bradley EL, Jr. (1990b) Hepatic oxygen supply-uptake relationship and metabolism during anesthesia in miniature pigs. Anesthesiology 72

Nagy KA (2005) Field metabolic rate and body size. J Exp Biol 208:1621-1625

Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles and birds. Annu Rev Nutr 19:247-277

Nakaya F, Saito Y, Motokawa T (2005) Experimental allometry: effect of size manipulation on metabolic rate of colonial ascidians. Proceedings of the Royal Society B 272:1963-1969

Nespolo RF, Bacigalupe LD, Bozinovic F (2003) Heritability of energetics in a wild mammal, the leaf-eared mouse (*Phyllotis darwini*). Evolution 57:1679-1688

Nespolo RF, Bacigalupe LD, Figueroa CC, Koteja P, Opazo JC (2011) Using new tools to solve an old problem: the evolution of endothermy in vertebrates. Trends Ecol Evol 26:414-423

Nespolo RF, Bacigalupe LD, Sabat P, Bozinovic F (2002) Interplay among energy metabolism, organ mass and digestive enzyme activity in the mouse-opossum *Thylamys elegans*: the role of thermal acclimation. J Exp Biol 205:2697-2703

Nespolo RF, Bustamante DM, Bacigalupe LD, Bozinovic F (2005) Quantitative genetics of bioenergetics and growth-related traits in the wild mammal, *Phyllotis darwini*. Evolution 59:1829-1837

Nespolo RF, Castañeda LE, Roff DA (2007) Quantitative genetic variation of metabolism in the nymphs of the sand cricket, *Gryllus firmus*, inferred from an analysis of inbred-lines. Biol Res 40:5-12

Nespolo RF, Franco M (2007) Whole-animal metabolic rate is a repeatable trait: a meta-analysis. J Exp Biol 210:2000-2005

Nevill A, Holder R, Markovic G (2006) Scaling maximum oxygen uptake using lower leg muscle volume provides further insight into the pitfalls of whole body-mass power laws. J Appl Physiol 101:1006-1007

Nevill AM, Bate S (2005) Allometric cascade model and metabolic rate. Respir Physiol Neurobiol 146:1-2

Nevill AM, Markovic G, Vucetic V, Holder R (2004) Can greater muscularity in larger individuals resolve the 34 power-law controversy when modelling maximum oxygen uptake? Ann Hum Biol 31:436-445

Nilsson J-Å, Åkesson M, Nilsson JF (2009) Heritability of resting metabolic rate in a wild population of blue tits. J Evol Biol 22:1867-1874

O'Connor MP, Kemp SJ, Agosta SJ, Hansen F, Sieg AE, Wallace BP, McNair JN, Dunham AE (2007) Reconsidering the mechanistic basis of the metabolic theory of ecology. Oikos 116:1058-1072

Ohlberger J, Staaks G, Hölker F (2007) Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendance (*Coregonus albula*). J Comp Physiol B 177:905-916

Opazo JC, Soto-Gamboa M, Fernández MJ (2005) Cell size and basal metabolic rate in hummingbirds. Rev Chil Hist Nat 78:261-265

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401:877-884

Painter P (2005a) Supply-demand balance in outward-directed networks and Kleiber's law. Theoretical Biology and Medical Modelling 2:45

Painter PR (2005b) Data from necropsy studies and *in vitro* tissue studies lead to a model for allometric scaling of basal metabolic rate. Theoretical Biology and Medical Modelling 2:39

Paradis E, Claude J, Strimmer K (2004) APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 20:289-290

Pastor CM (2000) Hepatic and splanchnic oxygen consumption during acute hypoxemic hypoxia in anesthetized pigs. Critical Care Medicine 28:765-773

Patterson MR (1992) A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. Science 255:1421-1423

Perissinotti PP, Antenucci CD, Zenuto R, Luna F (2009) Effect of diet quality and soil hardness on metabolic rate in the subterranean rodent *Ctenomys talarum*. Comp Biochem Physiol A 154:298-307

Peters RH (1983) The ecological implications of body size. Cambridge University press, Cambridge

Phillipson J (1981) Bioenergetic options and phylogeny. In: Townsend CR, Calow P (eds) Physiological Ecology: An Evolutionary Approach to Resource Use. Sinauer Associates, Sunderland

Pitts GC, Bullard TR (1968) Some interspecific aspects of body composition in mammals. In: Reid JT, Bensadoun A, Bull LS (eds) Body composition in animals and man. National Academy of Science, Washington, DC

Polymeropoulos ET, Heldmaier G, Frappell PB, McAllan BM, Withers KW, Klingenspor M, White CR, Jastroch M (2011) Phylogenetic differences of mammalian basal metabolic rate are not explained by mitochondrial basal proton leak. Proceedings of the Royal Society B:10.1098/rspb.2011.0881

Porter RK (2001) Allometry of mammalian cellular oxygen consumption. CMLS Cellular and Molecular Life Sciences 58:815-822

Porter RK, Brand MD (1995) Causes of differences in respiration rate of hepatocytes from mammals of different body mass. American Journal of Physiology - Regulatory, Integrative and Comparative Physiology 269:R1213-R1224

Porter RK, Hulbert AJ, Brand MD (1996) Allometry of mitochondrial proton leak: influence of membrane surface area and fatty acid composition. American Journal of Physiology - Regularoy, Integrative and Comparative Physiology 271:R1550-R1560

Porter WP, Kearney M (2009) Size, shape, and the thermal niche of endotherms. Proceedings of the National Academy of Sciences 106:19666-19672

Price CA, Enquist BJ, Savage VM (2007) A general model for allometric covariation in botanical form and function. Proc Natl Acad Sci U S A 104:13204-13209

Raichlen DA, Gordon AD, Muchlinski MN, Snodgrass JJ (2009) Causes and significance of variation in mammalian basal metabolism. J Comp Physiol B:in press

Rao GMM (1971) Influence of activity and salinity on the weight-dependent oxygen consumption of the rainbow trout *Salmo gairdneri*. Marine Biology 8:205-212-212

Reid D, Armstrong JD, Metcalfe NB (2011) Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. Funct Ecol:in press

Reynolds PS (1997) Phylogenetic analysis of surface areas of mammals. J Mammal 78:859-868

Rezende EL, Bozinovic F, Garland T, Jr (2004) Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. Evolution 58:1361-1374

Rezende EL, Diniz-Filho JAF (2012) Phylogenetic analyses: comparing species to infer adaptations and physiological mechanisms. Comprehensive Physiology 2:639-674

Rezende EL, Swanson DL, Novoa FF, Bozinovic F (2002) Passerines versus nonpasserines: So far, no statistical differences in the scaling of avian energetics. J Exp Biol 205:101-107

Ricklefs RE, Konarzewski M, Daan S (1996) The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. Am Nat 147:1047-1071

Riska B, Atchley WR (1985) Genetics of growth predict patterns of brain-size evolution. Science 229:668-671

Riveros AJ, Enquist BJ (2011) Metabolic scaling in insects supports the predictions of the WBE model. J Insect Physiol:DOI: 10.1016/j.jinsphys.2011.1001.1011

Rixon RH, Stevenson JAF (1957) Factors influencing survival of rats in fasting. Metabolic rate and body weight loss. Am J Physiol 188:332-336

Roberts MF, Lightfoot EN, Porter WP (2010) A new model for the body size–metabolism relationship. Physiol Biochem Zool 83:395-405

Roberts MF, Lightfoot EN, Porter WP (2011) Basal metabolic rate of endotherms can be modeled using heat-transfer principles and physiological concepts: Reply to “Can the basal metabolic rate of endotherms be explained by biophysical modeling?”. Physiol Biochem Zool 84:111-114

Roderick TH, Wimer RE, Wimer CC (1976) Genetic manipulation of neuroanatomical traits. In: McGaugh JL, Petrinovich LF, Krech D (eds) Knowing, thinking, and believing, Plenum Press

Rolfe DF, Brown GC (1997) Cellular energy utilization and molecular origin of standard metabolic rate in mammals. Physiol Rev 77:731-758

Rolfe DFS, Brand MD (1997) The physiological significance of mitochondrial proton leak in animal cells and tissues. Biosci Rep 17:9-16

Rønning B, Jensen H, Moe B, Bech C (2007) Basal metabolic rate: heritability and genetic correlations with morphological traits in the zebra finch. J Evol Biol 20:1815-1822

Røskaft E, Järvi T, Bakken M, Bech C, Reinertsen RE (1986) The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Anim Behav 34:838-842

Rubner M (1883) Über den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. Zeischrift für Biologie 19:536-562

Sadowska ET, Baliga-Klimczyk K, Chrząścik KM, Koteja P (2008) Laboratory model of adaptive radiation: A selection experiment in the bank vole. Physiol Biochem Zool 81:627-640

Sadowska ET, Baliga-Klimczyk K, Labocha MK, Koteja P (2009) Genetic correlations in a wild rodent: grass-eaters and fast-growers evolve high basal metabolic rates. Evolution 63:1530-1539

Sadowska ET, Labocha MK, Baliga K, Stanisz A, Wróblewska AK, Jagusiak W, Koteja P (2005) Genetic correlations between basal and maximum metabolic rates in a wild rodent: consequences for evolution of endothermy. Evolution 59:672-681

Savage VM, Deeds EJ, Fontana W (2008) Sizing up allometric scaling theory. PLoS Computational Biology 4:e1000171

Savage VM, Enquist BJ, West GB (2007) Comment on ‘A critical understanding of the fractal model of metabolic scaling’. J Exp Biol 210:3873-3874

Savage VM, Gillooly JF, Woodruff WH, West G, B., Allen AP, Enquist BJ, Brown JH (2004) The predominance of quarter-power scaling in biology. Funct Ecol 18:257-282

Schimpf NG, Matthews PGD, White CR (2012) Cockroaches that exchange respiratory gases discontinuously survive food and water restriction. Evolution 66:597-604

Schleucher E, Withers PC (2001) Re-evaluation of the allometry of wet thermal conductance for birds. Comp Biochem Physiol A 129:821-827

Schmidt-Nielsen K (1984) Scaling: Why is animal size so important? Cambridge University Press, Cambridge

Seebacher F, Wilson RS (2006) Fighting fit: thermal plasticity of metabolic function and fighting success in the crayfish *Cherax destructor*. Funct Ecol 20:1045-1053

Seymour RS, Blaylock AJ (2000) The principle of Laplace and scaling of ventricular wall stress and blood pressure in mammals and birds. Physiol Biochem Zool 73:389-405

Seymour RS, White CR (2011) Can the basal metabolic rate of endotherms be explained by biophysical modeling? Response to “A new model for the body size–metabolism relationship”. Physiol Biochem Zool 84:107-110

Shipley B (2000) Cause and correlation in biology. Cambridge University Press, Cambridge

Sieg AE, O'Conner MP, McNair JN, Grant BW, Agosta SJ, Dunham AE (2009) Mammalian metabolic allometry: do intraspecific variation, phylogeny, and regression models matter? Am Nat 174:720-733

Simons MJP, Reimert I, van der Vinne V, Hambly C, Vaanholt LM, Speakman JR, Gerkema MP (2011) Ambient temperature shapes reproductive output during pregnancy and lactation in the common vole (*Microtus arvalis*): a test of the heat dissipation limit theory. J Exp Biol 214:38-49

Smil V (2000) Laying down the law. Nature 403:597

Smit B, McKechnie AE (2010) Avian seasonal metabolic variation in a subtropical desert: basal metabolic rates are lower in winter than in summer. Funct Ecol 24:330-339

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the USA 102:5460-5465

Sol D, Timmermans S, Lefebvre L (2002) Behavioural flexibility and invasion success in birds. Anim Behav 63:495-502

Soling H-D, Kleineke J (1976) Species dependent regulation of hepatic gluconeogenesis in higher animals. In: Hanson RW, Mehlman MA (eds) Gluconeogenesis: its regulation in mammalian species. John Wiley & Sons, New York, pp 369-462

Song Z-G, Wang D-H (2006) Basal metabolic rate and organ size in Brandt's voles (*Lasiopodomys brandtii*): Effects of photoperiod, temperature and diet quality. Physiology and Behavior 89:704-710

Speakman JR, Ergon T, Cavanagh R, Reid K, Scantlebury DM, Lambin X (2003) Resting and daily energy expenditures of free-living field voles are positively correlated but reflect extrinsic rather than intrinsic factors. Proceedings of the National Academy of Sciences of the USA 100:14057-14062

Speakman JR, Król E (2010) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. J Anim Ecol 79:726-746

Speakman JR, Król E (2011) Limits to sustained energy intake. XIII. Recent progress and future perspectives. J Exp Biol 214:230-241

Speakman JR, Talbot DA, Selman C, Snart S, McLaren JS, Redman P, Krol E, Jackson DM, Johnson MS, Brand MD (2004) Uncoupled and surviving: individual mice with high metabolism have greater mitochondrial uncoupling and live longer. Aging Cell 3:87-95

Stahl WR (1967) Scaling of respiratory variables in mammals. J Appl Physiol 22:453-460

Stanley SM (1973) An explanation for Cope's rule. Evolution 27:1-26

Starostová Z, Kubička L, Konarzewski M, Kozłowski J, Kratochvíl L (2009) Cell size but not genome size affects scaling of metabolic rate in eyelid geckos. Am Nat 147:E100–E105

Suarez RK, Darveau C-A, Childress JJ (2004) Metabolic scaling: a many-splendoured thing. Comp Biochem Physiol A 139:531-541

Suarez RK, Darveau CA (2005) Multi-level regulation and metabolic scaling. J Exp Biol 208:1627-1634

Swallow JG, Hayes JP, Koteja P, Garland T, Jr (2009) Selection experiments and experimental evolution of performance and physiology. In: Garland T, Jr, Rose MR (eds) Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments. University of California Press, Berkeley, California, pp 301-351

Swanson DL, Olmstead KL (1999) Evidence for a proximate influence of winter temperature on metabolism in passerine birds. Physiol Biochem Zool 72:566-575

Terblanche JS, White CR, Blackburn TM, Marais E, Chown SL (2008) Scaling of gas exchange cycle frequency in insects. Biology Letters 4:127-129

Thomas S, Fell DA (1998) A control analysis exploration of the role of ATP utilisation in glycolytic-flux control and glycolytic-metabolite-concentration regulation. Eur J Biochem 258:956-967

Tieleman BI, Versteegh MA, Fries A, Helm B, Dingemanse NJ, Gibbs HL, Williams JB (2009a) Genetic modulation of energy metabolism in birds through mitochondrial function. Proceedings of the Royal Society B 276:1685-1693

Tieleman BI, Versteegh MA, Helm B, Dingemanse NJ (2009b) Quantitative genetics parameters show partial independent evolutionary potential for body mass and metabolism in stonechats from different populations. Journal of Zoology 278:129-136

Tieleman BI, Williams JB (2000) The adjustment of avian metabolic rates and water fluxes to desert environments. Physiol Biochem Zool 73:461-479

Tieleman BI, Williams JB, Buschur ME, Brown CR (2003) Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? Ecology 84:1800-1815

Timonin ME, Carrière CJ, Dudych AD, Latimer JGW, Unruh ST, Willis CKR (2011) Individual differences in the behavioural responses of meadow voles to an unfamiliar environment are not correlated with variation in resting metabolic rate. Journal of Zoology 284:198-205

Tolfrey K, Barker A, Thom JM, Morse CI, Narici MV, Batterham AM (2006) Scaling of maximal oxygen uptake by lower leg muscle volume in boys and men. J Appl Physiol 100:1851-1856

Vaca HF, White CR (2010) Environmental modulation of metabolic allometry in ornate rainbowfish *Rhadinocentrus ornatus*. Biology Letters 6:136-138

Veloso C, Bozinovic F (1993) Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent Ecology 74:2003-2010

Vézina F, Jalvingh KM, Dekinga A, Piersma T (2006) Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. J Exp Biol 209:3952-3952

Vinogradov AE (1995) Nucleotypic effect in homeotherms: Body-mass-corrected basal metabolic rate of mammals is related to genome size. Evolution 49:1249-1259

Vinogradov AE, Anatskaya OV (2006) Genome size and metabolic intensity in tetrapods: a tale of two lines. Proceedings of the Royal Society B: Biological Sciences 273:27-32

Wagner PD (1993) Algebraic analysis of the determinants of Vo_{2max}. Respir Physiol 93:221-237

Walsh PJ, Somero GN (1981) Temperature adaptation in sea anemones: Physiological and biochemical variability in geographically separate populations of *Metridium senile*. Marine Biology 62:25-34-34

Wang Z, Brown JH, Tang Z, Fang J (2009) Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America. Proceedings of the National Academy of Sciences 106:13388-13392

Wang Z, O'Conner TP, Heshka S, Heymsfield SB (2001) The reconstruction of Kleiber's law at the organ-tissue level. J Nutr 131:2967-2970

Weibel ER, Bacigalupe LD, Schmidt B, Hoppeler H (2004) Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as a determinant factor. Respiration Physiology and Neurobiology 140:115-132

Weibel ER, Hoppeler H (2005) Exercise-induced maximal metabolic rate scales with muscle aerobic capacity. J Exp Biol 208:1635-1644

Weisbecker V, Goswami A (2010) Brain size, life history, and metabolism at the marsupial/placental dichotomy. Proceedings of the National Academy of Sciences 107:16216-16221

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122-126

West GB, Brown JH, Enquist BJ (1999) The fourth dimension of life: Fractal geometry and allometric scaling of organisms. Science 284:1677-1679

West GB, Brown JH, Enquist BJ (2004) Growth models based on first principles or phenomenology? Funct Ecol 18:188-196

West GB, Enquist BJ, Brown JH (2002a) Modelling universality and scaling - Reply. Nature 420:626-627

West GB, Savage VM, Gillooly JF, Enquist BJ, Woodruff WH, Brown JH (2003) Why does metabolic rate scale with body size? Nature 421:713

West GB, Woodruff WH, Brown JH (2002b) Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. Proceedings of the National Academy of Sciences 99:2473-2478

Westerterp KR, Speakman JR (2008) Physical activity energy expenditure has not declined since the 1980s and matches energy expenditures of wild mammals. Int J Obes 32:1256-1263

White CR (2011) Allometric estimation of metabolic rates in animals. Comp Biochem Physiol A 158:346-357

White CR, Alton LA, Frappell PB (2012) Metabolic cold adaptation in fish occurs at the level of whole animal, mitochondria, and enzyme. Proc R Soc Lond B Biol Sci 279:1740-1747

White CR, Blackburn TM, Martin GR, Butler PJ (2007a) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. Proceedings of the Royal Society B 274:287-293

White CR, Blackburn TM, Seymour RS (2009) Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. Evolution 63:2658-2667

White CR, Cassey P, Blackburn TM (2007b) Allometric exponents do not support a universal metabolic allometry. Ecology 88:315-323

White CR, Grémillet D, Green JA, Martin GR, Butler PJ (2011a) Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants. Ecology 92:475-486

White CR, Kearney MR (2012) Allometry. Comprehensive Physiology:in review

White CR, Kearney MR, Matthews PGD, Kooijman SALM, Marshall DJ (2011b) A manipulative test of competing theories for metabolic scaling. Am Nat 178:746-754

White CR, Kearney MR, Matthews PGD, Kooijman SALM, Marshall DJ (2011c) A manipulative test of competing theories for metabolic scaling. Am Nat:in press

White CR, Phillips NF, Seymour RS (2006) The scaling and temperature dependence of vertebrate metabolism. Biology Letters 2:125-127

White CR, Seymour RS (2003) Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. Proceedings of the National Academy of Sciences of the USA 100:4046-4049

White CR, Seymour RS (2004) Does BMR contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological and life-history variables. Physiol Biochem Zool 77:929-941

White CR, Seymour RS (2005a) Allometric scaling of mammalian metabolism. J Exp Biol 208:1611-1619

White CR, Seymour RS (2005b) Sample size and mass range effects on the allometric exponent of basal metabolic rate. Comp Biochem Physiol A 142:74-78

White CR, Seymour RS (2011) Physiological functions that scale to body mass in fish. In: Farrell AP (ed) Encyclopedia of Fish Physiology: From Genome to Environment. Academic Press, San Diego, pp 1573 - 1582

White CR, Terblanche JS, Kabat AP, Blackburn TM, Chown SL, Butler PJ (2008) Allometric scaling of maximum metabolic rate: the influence of temperature. Funct Ecol 22:616-623

Wikelski M, Spinnery L, Schelsky W, Scheuerlein A, Gwinner E (2003) Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings of the Royal Society B 270:2383-2388

Williams JB, Miller RA, Harper JM, Wiersma P (2010) Functional linkages for the pace of life, life-history, and environment in birds. Integrative and Comparative Biology 50:855-868

Williams JB, Tieleman BI (2000) Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. J Exp Biol 203:3153-3159

Withers PC (2001) Design, calibration and calculation for flow-through respirometry systems. Aust J Zool 49:445-461

Withers PC, Cooper CE, Larcombe AN (2006) Environmental correlates of physiological variables in marsupials. Physiol Biochem Zool 79:437-453

Witting L (1995) The body mass allometries as evolutionarily determined by the foraging of mobile organisms. J Theor Biol 177:129-137

Wone B, Donovan ER, Hayes JP (2011) Metabolomics of aerobic metabolism in mice selected for increased maximal metabolic rate. Comparative Biochemistry and Physiology Part D: Genomics and Proteomics 6:399-405

Wone B, Sears MW, Labocha MK, Donovan ER, Hayes JP (2009) Genetic variances and covariances of aerobic metabolic rates in laboratory mice. Proceedings of the Royal Society B 276:3695-3704

Wu S-H, Zhang L-N, Speakman JR, Wang D-H (2009) Limits to sustained energy intake. XI. A test of the heat dissipation limitation hypothesis in lactating Brandt's voles (*Lasiopodomys brandtii*). J Exp Biol 212:3455-3465

Yamamoto T, Ueda H, Higashi S (1998) Correlation among dominance status, metabolic rate and otolith size in masu salmon. J Fish Biol 52:281-290

Zhao Z-J (2011) Energy budget during lactation in striped hamsters at different ambient temperatures. J Exp Biol 214:988-995

Zhao Z-J, Cao J (2009) Effect of fur removal on the thermal conductance and energy budget in lactating Swiss mice. J Exp Biol 212:2541-2549

Zhao Z-J, Wang D-H (2009) Plasticity in the physiological energetics of Mongolian gerbils is associated with diet quality. Physiol Biochem Zool:in press

Zuo W, Moses ME, Hou C, Woodruff WH, West GB, Brown JH (2009) Response to comments on “Energy uptake and allocation during ontogeny”. Science 325:1206-c

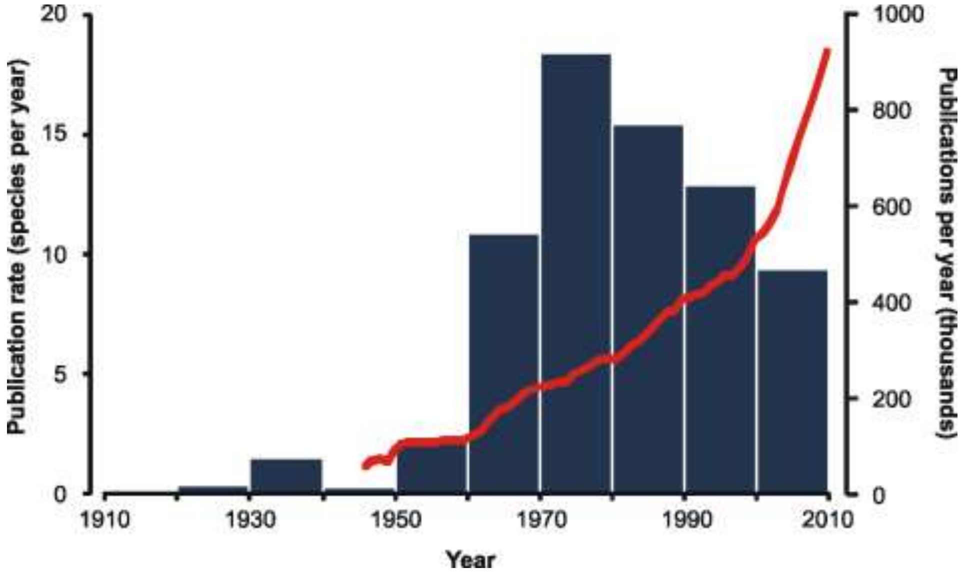

Figure 1. Total annual publication output across all fields indexed by PubMed (Publications per year, red line) and publication rate of data for mammalian basal metabolic rate (BMR, filled bars). BMR data are from a recent compilation (Sieg et al., 2009). Where BMR data for a species have been published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

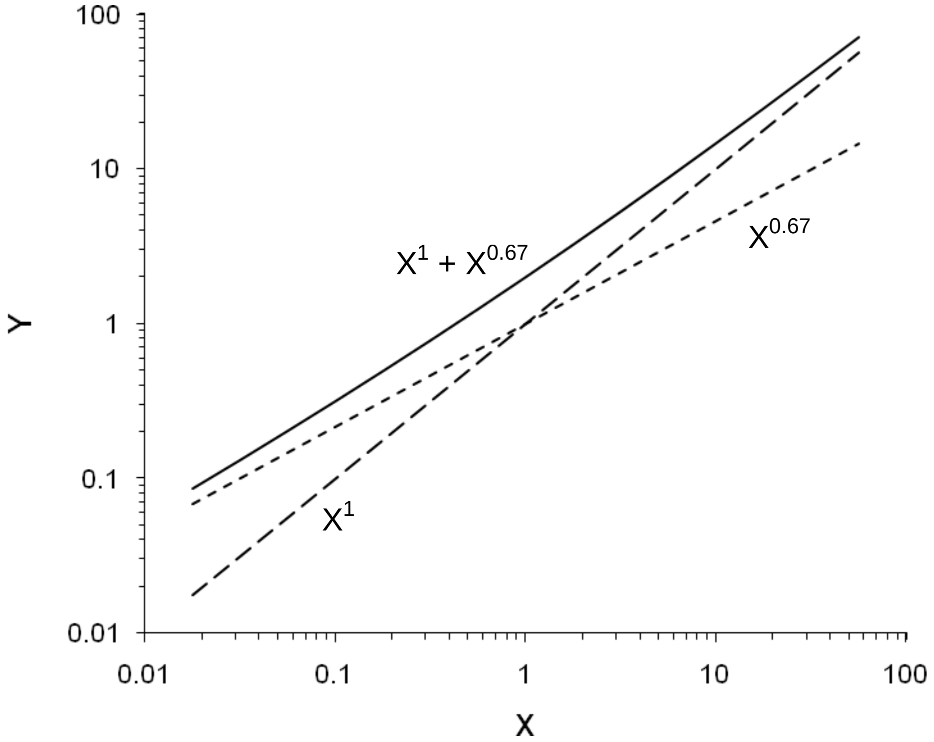

Figure 2. Summing isometric and allometric relationships introduces curvature into the relationship between logY and logX.

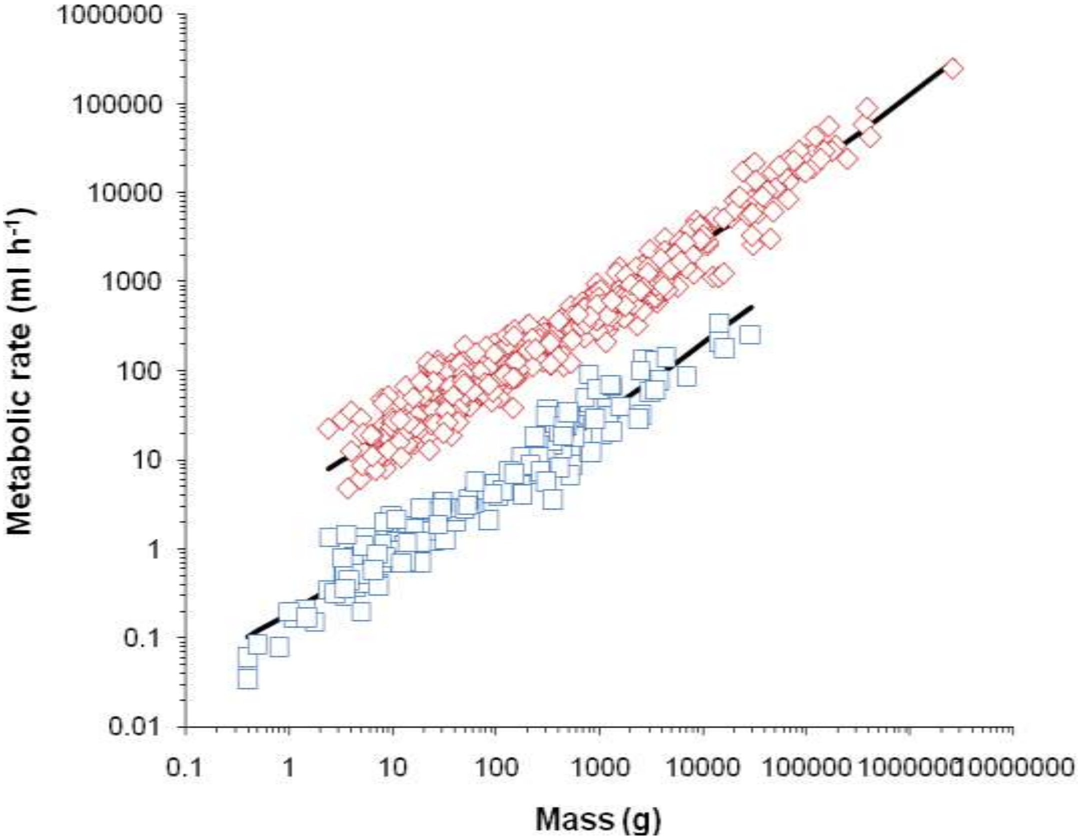

Figure 3. Relationships between mammalian BMR (unfilled diamonds: Sieg et al., 2009) and reptile SMR (unfilled squares: White et al., 2006) and mass (M, g) estimated by fitting summed allometric ($\propto M^{0.67}$) and isometric ($\propto M^1$) components by iteration (Gauss-Newton algorithm) using JMP v8.0.1 (SAS Institute, Cary, NC, USA). Mammal BMR = $4.30\ M^{0.67} + 0.084\ \text{mass}^1$; 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).

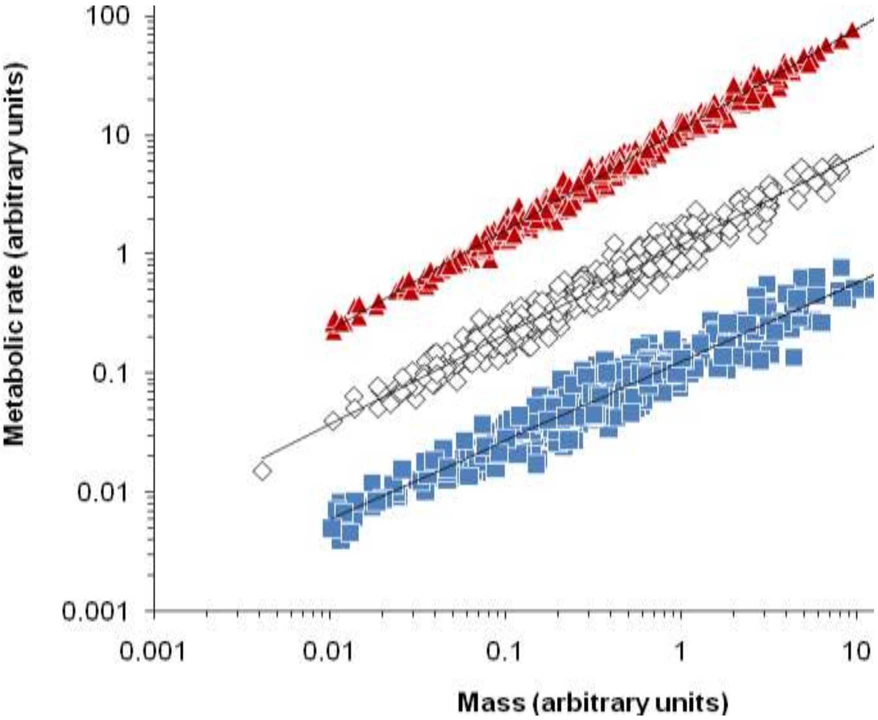

Figure 4. Simulated associations between metabolic rate (MR) and mass (M) generated according to the methods in Appendix B. The scaling exponent (b) and strength of the association is dependent on the relationship between changes in MR and changes in M (filled triangles: the change in MR at each time 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 (λ = 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 $^{n.s.}$	0.07
Aquatic invertebrates	0.06 $^{n.s.}$	0.05
Fruit	-0.04 $^{n.s.}$	0.03
Flying insects	-0.06 $^{n.s.}$	0.05
Grass	0.07 $^{n.s.}$	0.08
Leaves	0.04 $^{n.s.}$	0.04
Insects	0.01 $^{n.s.}$	0.02
Omnivore	0.07 $^{n.s.}$	0.04
Pollen	0.08 $^{n.s.}$	0.04
Seeds	-0.01 $^{n.s.}$	0.03
Vertebrates	-0.01 $^{n.s.}$	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	$h^2 \pm$ 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.

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