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

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15 **Abstract**

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

32

33

34 Introduction

35 Basal metabolic rate (BMR) is perhaps the most widely reported physiological metric.
36 ‘Basal’ has long been recognised as a poorly chosen term (Krogh, 1916) because metabolic rate can
37 fall below BMR under a range of conditions (Geiser, 2004; Green et al., 2007; Halsey et al., 2008;
38 Green et al., 2009). The term nevertheless remains in widespread use and has come to refer not to
39 the lowest metabolic rate that an endotherm can achieve, but instead to metabolic rate measured
40 under precisely defined conditions. BMR is the rate of metabolism of a resting, normothermic,
41 postabsorptive, non-reproductive, adult bird or mammal, measured during the inactive circadian
42 phase at a thermoneutral temperature (McNab, 1997; Frappell and Butler, 2004). BMR is usually
43 measured by indirect calorimetry as rate of oxygen consumption, using well described techniques
44 and commercially available equipment (Withers, 2001; Lighton, 2008). Being relatively easy to
45 measure in the laboratory, the number of species for which data are available has grown steadily
46 since the 1930s (Figure 1), and data are presently available for nearly 700 species of mammal (Sieg
47 et al., 2009), and more than 500 species of bird (McNab, 2009). The highest reported BMR (of
48 *Elephas maximus*: Benedict, 1938) is almost five orders of magnitude greater than the lowest (of
49 *Myotis nigricans*: McNab, 1989), and size is well known to account for much of the inter-specific
50 variation in BMR (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). However, the strong
51 relationship between mass and BMR conceals a great deal of variation, and species of the same size
52 can differ by up to several fold (White and Seymour, 2004). Even within a species, BMR varies
53 seasonally (Lovegrove, 2005; Smit and McKechnie, 2010) as well as between populations (Wikelski
54 et al., 2003; Broggi et al., 2007; Tieleman et al., 2009b) and individuals (Nespolo and Franco, 2007).
55 That differences between individuals and species can be significant, substantial, and repeatable, has
56 led to the speculation that this variation must be important. The present review examines the causes
57 and consequences of this variation, approaching the topic from both ultimate (evolutionary) and
58 proximate (mechanistic) perspectives. We focus on inter-specific variation in BMR, though we do

59 use some examples from intra-specific studies; a more in-depth coverage of intra-specific variation is
60 provided by Konarzewski and Książek (2012). We begin by discussing the profound influence of
61 body mass on metabolism, and follow this with a discussion of the causes and consequences of the
62 variation in BMR that is not explained by body mass. We conclude with the suggestion that
63 integrative examinations of mass-dependent and mass-independent variation are likely to yield
64 valuable insights into the evolutionary causes of the allometric scaling of metabolic rate with body
65 mass.

66 **Non-isometric scaling and the influence of body mass**

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

$$72 \quad \text{BMR} = a M^b$$

73 where a is the scaling constant, and b is the scaling exponent (see White, 2011; White and Kearney,
74 2012 for discussion of statistical analyses of metabolic scaling). The value of the scaling exponent
75 has been the subject of interest since at least the 19th century, when Sarrus and Rameaux (1838, cited
76 by Brody, 1945) suggested that metabolic rate should scale in proportion to body surface area rather
77 than body mass. Sarrus and Rameaux's hypothesis found empirical support when Rubner (1883)
78 reported that the metabolic rates of dogs were proportional not to their body mass, but to their body
79 surface area. This finding came to be known as the surface law of metabolism (e.g. Brody, 1945;
80 Kleiber, 1961). Although some subsequent studies have supported the exponent of $\frac{2}{3}$ implied by
81 these early analyses (e.g. Heusner, 1991; White and Seymour, 2003), the heat loss hypothesis is
82 unlikely to be correct, since animals with relatively high body surface areas do not have relatively
83 high BMRs (White and Seymour, 2004). Moreover, in the decades following publication of Rubner's

(1883) work, the exponent of $\frac{2}{3}$ was supplanted by a value of $\frac{3}{4}$ (Kleiber, 1932). Later analyses expanded the data set to include a wider range of species (Benedict, 1938; Brody, 1945; Hemmingsen, 1960) and the $\frac{3}{4}$ -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; Kolokotronis 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 ($\frac{2}{3}$: 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 $\frac{3}{4}$, whereas captive species scale with an exponent close to $\frac{2}{3}$ (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).

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

116 ***Resource Distribution***

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

- 124 1. Definition of metabolic rate: Metabolic rate, B , can be measured as the rate of flow of discrete
125 particles through a supply network. In mammals, for example, metabolic rate is routinely measured
126 as the rate of oxygen consumption, and the oxygen molecules are transported in the blood vessels
127 from a central source, the heart, to terminal units, the mitochondria.
- 128 2. Steady-state postulate: The flux of resources is at steady state, so supply matches demand, the rate
129 B of particles being consumed by the terminal units matches the rate B of particles leaving the
130 source, and the number of particles in transit does not change over time.
- 131 3. Geometric similarity: Animals, especially those in the same taxonomic or functional group, are
132 geometrically similar, so their geometry can be characterized by length, L , surface area, A , and
133 volume, V , and simple Euclidean geometrical scaling gives $V \sim L^3$ and $A \sim L^2$.
- 134 4. Directed transport: The average distance (d) from the source to each terminal unit is proportional to
135 the length, L , of the animal.
- 136 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 $3/4$ -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.,

165 2002a; West et al., 2002a; Banavar et al., 2003; Darveau et al., 2003; West et al., 2003; Kozłowski
166 and Konarzewski, 2004; Suarez et al., 2004; West et al., 2004; Brown et al., 2005; Kozłowski and
167 Konarzewski, 2005; Painter, 2005a; Suarez and Darveau, 2005; Chaui-Berlinck, 2006, 2007; Savage
168 et al., 2007; Agutter and Tuszynski, 2011).

169 Interestingly, much of the empirical evaluation of the predictions of the resource distribution
170 models has focussed on the scaling of metabolic rate with body mass (e.g. Bokma, 2004; Savage et
171 al., 2004; Glazier, 2005; Duncan et al., 2007; White et al., 2007b), and the range of other scaling
172 exponents predicted by these models has rarely been examined (Table 1). Examining the congruence
173 between predicted and observed values for circulatory variables, in particular, seems to be a valuable
174 step in evaluating the core of these models, which are grounded in principles of hydrodynamics.
175 West et al.'s (1997, 1999) models for $\frac{3}{4}$ power scaling, for example, assume that natural selection
176 has optimized the resource distribution network to minimize transport costs. This seems reasonable
177 because the heart contributes a significant fraction of whole-animal metabolic rate (2.4-10.4%:
178 Loisel and Gibbs, 1979) and individuals with low metabolic rates are favoured in at least some
179 situations (e.g. Blackmer et al., 2005; Artacho and Nespolo, 2009). Some of the predictions of the
180 models are supported by empirical data, suggesting that they are plausible models of resource
181 transport (Table 1). In birds and mammals, for example, heart rate scales with an exponent close to
182 the predicted value of -0.25 (Table 1). For fish, on the other hand, heart rate is independent of body
183 mass (Clark and Farrell, 2011; White and Seymour, 2011).

184 A significant product of the resource distribution model has been its use as a foundation for a
185 Metabolic Theory of Ecology (MTE), which aims to use metabolism as a basis for applying first
186 principles of physics and chemistry to link the biology of individual organisms to the ecology of
187 populations, communities, and ecosystems (Brown et al., 2004b). The fundamental equation of MTE
188 describes variation in MR in terms of an empirically determined normalisation constant independent

189 of body size and temperature (i_0), body mass (M), activation energy (E), Boltzmann's constant (k),
190 and absolute temperature (T) (Gillooly et al., 2001; Brown et al., 2004b):

191
$$MR = i_0 M^{3/4} e^{-E/kT}$$

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

205 ***Dynamic Energy Budget***

206 In the framework of the Dynamic Energy Budget (DEB) theory (Kooijman, 2010), metabolic rate is
207 considered to comprise a weighted sum of four processes: assimilation, maintenance, growth, and
208 maturation. DEB theory decomposes body mass into two indirectly measurable state variables, the
209 'reserve' and the 'structure', and is based on generalized surface area (source) and volume (sink)
210 relationships. It makes the key assumptions that the composition of reserve and structure each
211 remains constant but may differ from each other ('strong homeostasis') and that, under constant
212 food, the relative amount of reserve and structure stays constant and hence so does the entire body
213 composition ('weak homeostasis'). Energy and matter are assimilated in proportion to structural

214 surface area (because food enters the body across surfaces), and directed first to the reserve pool of
 215 the organism. The reserve is not necessarily metabolites ‘set aside for later’, but rather is defined by
 216 its turnover rate. It reflects the part of the dry mass of an organism that fluctuates with resource
 217 supply, and is constantly used and replenished. DEB theory assumes that no costs are paid for the
 218 maintenance of reserves, but costs are paid for their turnover and are included in the overheads of
 219 assimilation and utilization. The structure is the “permanent” biomass and does require energy for its
 220 maintenance (protein turnover and the maintenance of concentration gradients and ionic potentials,
 221 etc.) in direct proportion to structural volume.

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

$$228 \quad \propto \frac{L_h L^2 + L^3}{d_V L^3 + d_E L^4}$$

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

239 mammals (White and Seymour, 2004), and it is not clear that heat loss determines basal metabolism
240 in a mechanistic sense (da Silva et al., 2006; Seymour and White, 2011).

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

251 ***Metabolic Level Boundaries***

252 The metabolic level boundaries (MLB) hypothesis (Glazier, 2005, 2010) predicts that scaling
253 exponents for MR will vary between two boundary constraints: surface-area limits on fluxes of
254 metabolic resources, wastes and (or) heat that scale allometrically as $M^{2/3}$, and volume limits on
255 energy use or power production that scale isometrically as M^1 . Thus, metabolic rate is predicted to
256 scale isometrically at low levels of sustained metabolic intensity, and the scaling exponent of
257 metabolic rate is predicted to decrease toward 2/3 as sustained metabolic intensity increases. During
258 intense activity, volume limits on power production by the locomotory musculature dominate, and
259 metabolic rate is predicted to scale isometrically. The pattern of variation predicted by the metabolic
260 level boundaries hypothesis is supported by variation in the scaling exponent for birds and mammals
261 (Glazier, 2008, 2009a), unicellular organisms (Glazier, 2009b), and ectothermic animals (Glazier,
262 2009c; Killen et al., 2010). In support of the hypothesis, the body temperature of large animals has
263 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

289 driven by energy demand processes. Under basal conditions, major energy sinks are $\text{Na}^+\text{-K}^+$
290 ATPase, protein turnover, substrate cycles, and mitochondrial proton leak (Rolfe and Brand, 1997),
291 and the control coefficients for these processes contribute to the global b value for BMR, which is
292 predicted to be within the range 0.76 – 0.79 (Darveau et al., 2002), which is somewhat higher than
293 observed for mammals over most of their mass range (Kolokotronis et al., 2010). The principles of
294 allometric cascade theory also appear to be valid for resting and exercising humans (Batterham and
295 Jackson, 2003, 2005; but see Nevill and Bate, 2005 for an alternative viewpoint).

296 **Cell Size**

297 The cell size (CS) model proposes that the mass scaling of metabolism is shaped by the evolutionary
298 coupling of cell size and body size, since, with increasing cell size, the cell surface area:volume ratio
299 decreases (Davison, 1955; Kozłowski et al., 2003a; Kozłowski et al., 2010). All other things being
300 equal, the model predicts that metabolic rate should scale isometrically when evolutionary increases
301 in body size are achieved entirely through increases in cell number (i.e. cell size scales as M^0), or as
302 $M^{2/3}$ when increases in size are achieved through increases in cell volume (i.e. cell size increases
303 with M). Experimental studies have supported the link between cell size and metabolic rate (Maciak
304 et al., 2011), and the cell size model for metabolic scaling has been supported in studies of
305 endotherms (Vinogradov, 1995; Kozłowski et al., 2003a; Opazo et al., 2005), reptiles (Starostová et
306 al., 2009), tetrapods (Vinogradov and Anatskaya, 2006), and insects (Chown et al., 2007). Recent
307 work, however, has demonstrated that patterns of mass-dependence of cell sizes in different animal
308 groups are inconsistent with the assumptions of the model, and has called for revision of the model
309 (Glazier, 2005; Kozłowski et al., 2010). Cell volume scales with exponents between 0 and 0.3 in
310 birds and mammals (Kozłowski et al., 2010). The cell size model predicts that a cell volume scaling
311 exponent of 0.3 should be associated with a metabolic rate scaling exponent of 0.9 (Kozłowski et al.,
312 2003a; Kozłowski et al., 2010), which is greater than the exponents observed for these groups
313 (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 $\pm$ 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

339 cold exposure (Johnson and Speakman, 2001; Król and Speakman, 2003; Król et al., 2007; Wu et al.,
340 2009; Simons et al., 2011), but not by increases in litter size, by forced exercise, or by simultaneous
341 pregnancy (Hammond and Diamond, 1994; Johnson et al., 2001a, b; Laurien-Kehnen and Trillmich,
342 2003). Similarly, lactating red squirrels *Tamiasciurus hudsonicus* raising large litters occupy poorly
343 insulated nests in warm years (Guillemette et al., 2009). Support for the predictions of the theory is
344 not universal, however, and other studies of small mammals report mixed results (Zhao and Cao,
345 2009; Speakman and Król, 2011; Zhao, 2011). The generality of the HDL theory also remains to be
346 verified on animals performing other energetically-demanding activities, such as locomotion, and the
347 theory explains the scaling of metabolic rate only in free-living endotherms, and does not apply to
348 ectotherms. Nonetheless, for endotherms, the theory is relevant to BMR because it represents an
349 upper limit to DEE. Given that BMR contributes a substantial component of DEE, an upper limit to
350 DEE with a scaling exponent of ~ 0.63 will constrain BMR to a similarly low exponent to ensure that
351 there is scope for activity ($= \text{DEE} - \text{BMR}$) across the size range of endotherms.

352 ***Evaluating explanations for metabolic scaling***

353 It is a truism that all biological models are wrong because they are simplifications of complex
354 systems and rarely, if ever, fully account for the variation they aim to explain. Ideally, models
355 should maximise generality, realism, and precision, but this is not always possible and one of these is
356 often sacrificed in favour of the others (Levins, 1966). Nevertheless, these three goals offer criteria
357 by which competing models can be evaluated. With respect to metabolic scaling, distinguishing
358 among competing models on the grounds of how well they predict empirical data is difficult because
359 many models predict similar values. Metabolic rate may scale allometrically because of the
360 geometry of resource distribution networks, leading to predictions of metabolic scaling exponents of
361 $0.67 - 0.75$ (Banavar et al., 2010) or $0.5 - 1$ (Price et al., 2007). A definitive test of the resource
362 distribution model has proven elusive, however, because like several other models it predicts a
363 central tendency of 0.75-power scaling (West et al., 1997, 1999). Thus, while this prediction shows

364 good general agreement with the mean scaling exponent observed in both intra-specific (Moses et al.,
365 2008) and inter-specific (Savage et al., 2004) studies, other models make similar predictions: the Cell
366 Size (Kozłowski et al., 2003a), Metabolic Level Boundaries (Glazier, 2010), and Dynamic Energy
367 Budget models all predict b to vary between 0.67 and 1, the mid-point of which is close to 0.75.
368 Similarly, the metabolic level boundaries (Glazier, 2010) and dynamic energy budget (Kooijman,
369 2010) models both predict that scaling exponents for resting endotherms will be lower than those for
370 resting ectotherms. Given that the predictions from the models overlap so strongly, it is important
371 that the presentation of models include clear descriptions of their unique predictions to facilitate tests
372 that distinguish between alternatives (Shipley, 2000; Currie et al., 2004; Hawkins et al., 2007b;
373 Glazier, 2010; White et al., 2011b; Kearney and White, 2012).

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

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

407 ***Integrating explanations for metabolic scaling***

408 The various explanations for metabolic scaling are not necessarily exclusive, and integration of
409 various aspects of the associated theories and models may lead to a greater understanding of why
410 metabolic rate scales allometrically with body mass (Ginzburg and Damuth, 2008; Glazier, 2010).
411 For example, Clarke et al. (2010) suggest that the reason why the relationship between $\log(M)$ and
412 $\log(MR)$ for mammals is not linear (e.g. Hayssen and Lacy, 1985; Dodds et al., 2001; Glazier, 2005;

413 Makarieva et al., 2008; Kolokotronis et al., 2010; White, 2011) is because at large sizes the scaling
 414 is dominated by factors that dictate 0.75-power scaling (e.g. resource distribution: West et al., 1997),
 415 whereas at small sizes this factor is overridden by considerations of heat flow and hence the
 416 exponent is closer to 0.67. They note that the pattern of variation in the scaling exponent arising from
 417 this prediction is analogous to the metabolic level boundaries hypothesis of Glazier (2005, 2010).
 418 Similar arguments could be made using several of the other theories discussed above, since they also
 419 invoke fluxes that scale allometrically (e.g. of heat across body surfaces or metabolites across cell
 420 surfaces). Indeed, since the sum of two non-isometric scaling relationships will not be a strict power
 421 function of mass (Figure 2) (see also Garland, 1983; Calder, 1984), any theory that includes additive
 422 combinations of isometric ($\propto M^1$) and allometric (e.g. $\propto M^{0.67}$) components that vary with metabolic
 423 level will match a number of observed scaling patterns, at least qualitatively. Examples of such
 424 patterns include the curvature in BMR scaling for mammals (Hayssen and Lacy, 1985; Painter,
 425 2005b; Kolokotronis et al., 2010), differences between the scaling exponent of basal and standard
 426 metabolic rate of endotherms and ectotherms (White et al., 2007b; White et al., 2008), the high
 427 scaling exponent of hibernating endotherms compared to daily heterotherms and euthermic
 428 endotherms (Geiser, 1988; White and Seymour, 2005a), and the high scaling exponent of field
 429 metabolic rate in reptiles compared to birds and mammals (Nagy et al., 1999; Nagy, 2005; Speakman
 430 and Król, 2010). This prediction is made explicit by the MLB hypothesis, which includes fluxes of
 431 metabolic resources, wastes and (or) heat that scale allometrically (Glazier, 2005, 2008, 2010), but
 432 the principle of summed allometric and isometric components (or summed components that each
 433 scale allometrically with different exponents) of metabolic rate applies equally to combinations of
 434 organ-tissue compartments that differ in their association with body mass (see e.g. Wang et al., 2001;
 435 Glazier, 2005; Painter, 2005b; Glazier, 2010; Killen et al., 2010).

436 Differences in the scaling of BMR and $\dot{V}O_2\text{max}$, for example, can be explained by
 437 considering differences in the metabolic scaling exponents between tissues that contribute to energy

438 turnover during rest and exercise (Glazier, 2005). Most metabolic activity during basal metabolism
 439 is associated with the internal organs including liver, kidney, gastrointestinal tract, heart, and brain
 440 (Krebs, 1950; Rolfe and Brown, 1997), and variation in BMR between species and individuals has
 441 therefore been attributed to variation in organ mass (Daan et al., 1990; Konarzewski and Diamond,
 442 1995; Meerlo et al., 1997; Książek et al., 2004; Song and Wang, 2006; Brzęk et al., 2007; Raichlen
 443 et al., 2009; Williams et al., 2010) and tissue metabolism (Krebs, 1950; Wang et al., 2001). During
 444 exercise-induced maximal metabolism, on the other hand, most (>90%) metabolic activity is
 445 associated with work done by the locomotor muscles and delivery of substrates and oxygen to these
 446 (Weibel et al., 2004). There is therefore a hierarchy of contributions to organismal metabolism
 447 depending on demand (see Darveau et al., 2002; Suarez and Darveau, 2005): whole-animal
 448 metabolism is a function of organ mass and metabolism, which in turn is a function of tissue and
 449 mitochondrial metabolism, which is governed by the activity of metabolic enzymes. At rest,
 450 allometric scaling of visceral organism metabolism dominates (see e.g. Porter, 2001; Wang et al.,
 451 2001; Glazier, 2005), whereas during exercise isometric scaling of muscle metabolism dominates
 452 (see e.g. Weibel et al., 2004; Glazier, 2005). Evidence for the validity of such an approach comes
 453 from the human literature, which includes examples where specific body compartments have been
 454 shown to be more appropriate than whole body mass for standardising inter-individual differences in
 455 $\dot{V}O_2\text{max}$ (Eliakim et al., 1996; Nevill et al., 2004; Nevill et al., 2006; Tolfrey et al., 2006). Similarly,
 456 muscular parameters better explain inter-specific variation in mammalian $\dot{V}O_2\text{max}$ than does body
 457 mass (Weibel et al., 2004; Weibel and Hoppeler, 2005).

458 Decomposition of whole-animal metabolism into organ-tissue compartments that scale with
 459 different exponents can also explain the higher scaling exponent of ectotherm SMR compared to
 460 endotherm BMR (White et al., 2006; White et al., 2007b). The organs that contribute to resting
 461 metabolism are smaller in ectotherms than in endotherms (Crile and Quiring, 1940; Martin, 1981;
 462 Karasov, 1987; Franz et al., 2009) and the tissue-mass-specific metabolic intensity is lower (Hulbert

463 and Else, 1981; Hulbert et al., 2002). Thus, if whole-animal metabolism is assumed, for simplicity,
 464 to have two compartments (e.g. muscle + bone compartment that scales as M^{-1} , and a visceral organ
 465 + brain compartment that scales as $M^{-0.67}$) and the mass-specific intensity of both compartments is
 466 higher for endotherms than ectotherms, then the scaling exponent of SMR is predicted to be lower for
 467 endotherms than ectotherms (Figure 3). This approach also predicts that the curvature in MR will be
 468 less pronounced or absent in ectotherms than endotherms, as is also apparently the case (Ehnes et al.,
 469 2011; Müller et al., 2011a). The exact values of the exponents predicted by this approach will
 470 depend on the scaling exponent of organ masses and tissue-mass-specific metabolic intensities.
 471 However, while this ‘multi-compartment’ approach can explain variation in the scaling exponent of
 472 whole-animal metabolic rate, it does not offer an explanation for *why* the compartments scale as they
 473 do. First principles explanations for these organ-specific scaling patterns might come from the
 474 mechanistic models discussed above, and further understanding of the ultimate (evolutionary) causes
 475 of the allometric relationship between metabolic rate and body size could be gleaned from
 476 examination of the genetic associations between traits that contribute to metabolic rate (Glazier,
 477 2005). For example, examination of how the genetic correlation between brain size and body size
 478 varies during development has been beneficial in understanding why the scaling exponent of brain
 479 size is lower during development than for interspecific comparisons (Lande, 1979; Riska and
 480 Atchley, 1985; Lynch and Walsh, 1998).

481 **Causes of mass-independent variation in BMR**

482 ***Climate and habitat productivity***

483 Perhaps the most prominent and well-supported abiotic correlate of mass-independent variation in
 484 BMR is environmental temperature, which is negatively related to BMR in both birds (Jetz et al.,
 485 2007; White et al., 2007a) and mammals (Lovegrove, 2003; Careau et al., 2007), including humans
 486 (Froehle, 2008). This relationship probably arises as a consequence of the need to limit endogenous

487 heat production in hot environments (McNab and Morrison, 1963), and to maximise heat production
488 in cold environments (BMR is positively correlated with maximum cold-induced metabolic rate in
489 both birds and mammals: Dutenhoffer and Swanson, 1996; Rezende et al., 2002; Rezende et al.,
490 2004). The low BMR of species from hot environments may also arise because lower differential
491 between body and ambient temperatures means that the contribution of endogenous heat production
492 to thermoregulation can be reduced, thereby saving energy and/or water, or because high temperature
493 limits the sustained metabolism of endotherms (Speakman and Król, 2010). If energy expenditure
494 attributable to maintenance (BMR) and activity ($AMR = FMR - BMR$) are considered independent
495 (i.e. the 'partitioned pathways' model of Ricklefs et al., 1996), as is the case in at least free-ranging
496 great cormorants *Phalacrocorax carbo* (White et al., 2011a), then, in an environment where daily
497 energy expenditure is restricted by heat dissipation, a reduction in BMR increases the scope for
498 activity. Support for the idea that scope for activity ($=FMR$ divided by BMR) is restricted by the
499 difference between maximum rates of heat dissipation and BMR arises from the observation that
500 scope for activity decreases from up to 8-fold for small mammals to less than 3-fold for large ones
501 (Westerterp and Speakman, 2008), though it is not currently clear if scope for activity also with
502 climate. While the relationship between environmental temperature and BMR is likely to have a
503 genetic component, as has been shown for stonechats (Wikelski et al., 2003), the extent to which
504 phenotypic plasticity contributes to the observed relationship between environmental temperature
505 and BMR remains unclear, as cold acclimation causes an increase in metabolic rate for birds and
506 mammals (Williams and Tieleman, 2000; Song and Wang, 2006; McKechnie et al., 2007;
507 McKechnie, 2008). Recent comparative analysis suggest that the magnitude and direction of seasonal
508 acclimatization in free-living birds depends upon their thermal environment: species that experience
509 cold winters at high latitude have higher BMR in winter than summer, whereas species that inhabit
510 warmer subtropical latitudes have lower BMR in winter (Smit and McKechnie, 2010). These
511 acclimation and acclimatization responses act on timescales of weeks, suggesting that ambient

512 temperature has a proximate role in influencing BMR (Swanson and Olmstead, 1999; McKechnie et
513 al., 2007), though changes associated with environmental triggers for reproduction are also
514 implicated as drivers of seasonal variation (Smit and McKechnie, 2010). However, there is evidence
515 that inter-specific and inter-population differences are maintained for multiple generations in
516 captivity, and that populations from more seasonal environments show a greater capacity for thermal
517 acclimation than populations from stable environments (Tieleman et al., 2003; Cavieres and Sabat,
518 2008). These findings suggest a genetic component to climate-associated variation in BMR. Thus,
519 there remains a clear need for common-garden experiments comparing differences in BMR between
520 animals from warm and cold environments to separate the genetic and phenotypic components of the
521 negative relationship between environmental temperature and BMR.

522 Related to the effect of temperature, BMR is often thought to be associated with
523 environmental productivity, such that animals from highly productive environments have higher
524 BMRs than those from less productive environments. This conclusion stems from the observation
525 that the BMRs of arid species are generally lower than those of mesic species (e.g. Tieleman and
526 Williams, 2000; Withers et al., 2006). However, the BMR of birds is not related to net primary
527 productivity (White et al., 2007a). This contrasts with the situation in mammals, where
528 environmental productivity has been shown to be positively correlated with BMR in a range of
529 studies (Mueller and Diamond, 2001; Bozinovic et al., 2007; Bozinovic et al., 2009). BMR is
530 similarly correlated with rainfall parameters associated with environmental productivity for
531 marsupials (Withers et al., 2006) and small (< 1 kg) eutherians (Lovegrove, 2003). Birds and
532 mammals also differ in the relationship between BMR and rainfall variability: the relationship is
533 negative in mammals (Lovegrove, 2003; Withers et al., 2006), but positive (White et al., 2007a) or
534 absent (Jetz et al., 2007) in birds. The reason for this difference between birds and mammals is
535 unclear, but it could be genuine, reflecting perhaps a difference in mobility, or it could arise as a
536 consequence of methodological differences between the avian and mammalian analyses. Future

537 analyses applying uniform phylogenetically-informed methods (see e.g. Rezende and Diniz-Filho,
538 2012) and drawing on environmental data from a single database could resolve the issue, and could
539 be extended to other groups for which latitudinal and climate effects on metabolic rate have been
540 identified, such as insects (Addo-Bediako et al., 2002) and fish (White et al., 2012). The ongoing
541 accumulation of readily available climate data (e.g. www.worldclim.org), large compilations of
542 metabolic data (e.g. McNab, 2009; Sieg et al., 2009) and complete species-level supertrees (e.g.
543 Bininda-Emonds et al., 2007) will facilitate such work.

544 Probably the most controversial correlate of BMR is diet. Early work tended to report
545 significant associations between diet and BMR (e.g. McNab, 1969, 1986). These were, however, not
546 supported by subsequent PI analyses (e.g. Cruz-Neto et al., 2001; Rezende et al., 2004), though
547 problems in correctly assigning dietary categories could contribute to this discrepancy (McNab,
548 2003). More recent PI analyses have supported an association between diet and BMR for Carnivora
549 (Muñoz-Garcia and Williams, 2005), and between diet and FMR for birds (Anderson and Jetz,
550 2005), but no association is observed between BMR and diet for birds (Table 3) or mammals in
551 general (White, 2011; see also Clarke et al. 2010 for a discussion of covariation between diet and
552 body temperature in mammals).

553 ***Organ-tissue contributions to mass-independent BMR***

554 The internal organs contribute substantially to BMR, and variation in BMR between species has
555 therefore been attributed to variation in organ mass (Daan et al., 1990; Raichlen et al., 2009) and
556 tissue metabolism (Krebs, 1950; Wang et al., 2001). Within species, 71% of the variation in BMR of
557 Chilean mouse opossums is explained by variation in the mass of digestive organs (Nespolo et al.,
558 2002), strains of mice with high BMR tend to have relatively large metabolically active organs
559 (heart, kidney, liver, and small intestine) (Konarzewski and Diamond, 1995), and mice artificially
560 selected for high BMR have larger small intestine, liver, kidneys, and heart than mice selected for
561 low BMR (Książek et al., 2004; Brzęk et al., 2007). Similarly, cold-acclimated Brandt's voles

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

571 A controversial correlate of metabolic rate is brain size (Imamura and Clowes, 1975; Martin,
572 1981; Harvey and Bennett, 1983; McNab, 1989; Nagano et al., 1990a; Pastor, 2000; Isler and van
573 Schaik, 2006; Weisbecker and Goswami, 2010). Recent comparative analyses are generally in favour
574 of an association between brain size and metabolism for at least eutherian mammals; the presence or
575 absence of an association for marsupials is more equivocal and depends upon the method of analysis
576 (Imamura and Clowes, 1975; Weisbecker and Goswami, 2010). A potential problem with
577 comparative analyses of the association between brain size and BMR, however, is that brain size is
578 correlated with a range of other ecological and life-history traits (e.g. Burrin et al., 1989; Eisemann
579 and Nienaber, 1990; Huntington et al., 1990; Guerino et al., 1991; Sol et al., 2002; Sol et al., 2005),
580 and disentangling the associations between these traits, BMR, and brain size is difficult. Intra-
581 specific studies have also demonstrated an association between brain size and BMR for humans
582 (Javed et al., 2010; Müller et al., 2011b) and inbred strains of mice (Konarzewski and Diamond,
583 1995), and artificial selection studies offer an alternative experimental approach to examining the
584 association. Brain weight has been shown to respond to artificial selection in mice in only 6-10
585 generations (Roderick et al., 1976), and comparison of BMR in lines divergently selected for low and
586 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

612 locomotor activity, predatory behaviour, and ability to cope with herbivorous diet in bank voles
613 *Myodes (Clethrionomys) glareolus* (Sadowska et al., 2008); and selection on maximum rate of
614 oxygen consumption ($\dot{V}O_{2\max}$) during treadmill exercise, as well as selection to generate a negative
615 correlation between $\dot{V}O_{2\max}$ and BMR (see Swallow et al., 2009; Wone et al., 2011). Results available
616 to date have demonstrated support for an association between diet and BMR, although the ability to
617 cope with a low-quality herbivorous diet shows a positive additive genetic correlation with BMR
618 (Sadowska et al., 2009), rather than the negative association expected from studies of the effect of
619 dietary manipulation on BMR (Veloso and Bozinovic, 1993; Koteja, 1996; Perissinotti et al., 2009;
620 Zhao and Wang, 2009). Seven generations of selection for high $\dot{V}O_{2\max}$ has so far yielded a 12.3%
621 increase in $\dot{V}O_{2\max}$ in selected lines compared to control lines, and a non-significant 3.5% increase in
622 BMR (Wone et al., 2011).

623 Selection on BMR directly has generated lines of mice that differ significantly in BMR and
624 $\dot{V}O_{2\max}$ elicited by forced swimming (Książek et al., 2004). The body-mass-corrected masses of four
625 visceral organs (small intestine, liver, kidneys, and heart) are also consistently and substantially
626 higher in mice selected for high BMR than those selected for low BMR (Książek et al., 2004); these
627 differences are considered large enough to claim the existence of positive genetic correlations
628 between BMR and the masses of examined viscera (Książek et al., 2004). It will be interesting to
629 examine the outcomes of the suite of selection experiments not only for BMR, but also on the traits
630 that are believed to underlie variation in BMR including the sizes of visceral organs and
631 mitochondrial characteristics. Brain and liver mass are heritable in mice (Jones et al., 1992), as are
632 the masses of brain, heart, liver, and kidney in baboons *Papio hamadryas* (Mahaney et al., 1993),
633 and the liver in wild mice *Phyllotis darwini* (Bacigalupe et al., 2004). Baboons show additive
634 genetic correlations between the masses of brain and liver, as well as between liver and kidneys
635 (Mahaney et al., 1993), but no additive genetic correlations were detected between liver, heart, lungs,
636 small intestine, and caecum in *Phyllotis darwini* (Bacigalupe et al., 2004). Given the phenotypic

637 associations observed between visceral organs and BMR as well as between mitochondrial
638 characteristics and BMR, the likely heritability of these traits, and the genetic associations among
639 visceral organs, it seems plausible that genetic associations between BMR and these traits will also
640 be revealed. Such analyses will yield valuable information regarding the mechanistic bases of
641 variation in BMR that arises as a consequence of direct selection on BMR, or as a consequence of
642 correlated responses in BMR associated with selection on other traits.

643 **Consequences of variation in BMR for animal performance**

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

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

662 (Artacho and Nespolo, 2009), such that individuals with low and intermediate metabolic rates are
663 favoured over those with high metabolic rates. Natural selection therefore eliminates individuals
664 with high metabolic rates but does not necessarily favour individuals with the absolute lowest
665 metabolic rates. Similarly, inbreeding results in an increase in resting metabolic rate in crickets
666 *Gryllodes sigillatus*, suggesting that low quality individuals have higher metabolic rates than high
667 quality individuals (Ketola and Kotiaho, 2009). This contrasts with the finding that BMR is
668 positively related to over-winter survival in short-tailed field voles *Microtus agrestis* (Jackson et al.,
669 2001) and reproductive success in bank voles *Myodes (Clethrionomys) glareolus* (Boratyński and
670 Koteja, 2010), although BMR is not related to over-winter survival in bank voles (Boratyński and
671 Koteja, 2009). This discrepancy presumably arises for the same reason that stabilising selection was
672 observed by Artacho and Nespolo (2009): high BMR may be an advantage in some situations, but a
673 liability in others, and *vice versa*. Thus, high BMR and maximum rates of thermogenesis increase
674 over-winter survival by improving cold tolerance (Hayes and O'Conner, 1999; Jackson et al., 2001),
675 but low BMR improves starvation resistance (Rixon and Stevenson, 1957). Male Leach's storm-
676 petrels *Oceanodroma leucorhoa* with low BMR breed earlier and produce chicks that grow faster
677 than males with relatively high BMR (Blackmer et al., 2005), but mice with low BMR die sooner
678 than those with high BMR (Speakman et al., 2004). Other studies have found no link between BMR
679 and reproductive traits in mice (Hayes et al., 1992; Johnson et al., 2001a; Johnston et al., 2007), a
680 positive correlation between energy expenditure during lactation and BMR in *Peromyscus* mice
681 (Glazier, 1985), no link between interspecific differences in age at first reproduction and BMR
682 (Lovegrove, 2009), and a positive relationship between BMR and maximum running speed
683 (Lovegrove, 2004).

684 The level of BMR therefore appears to be maintained as a consequence of a series of trade-
685 offs such that low BMR is an advantage during food deprivation or reproduction, but high BMR is an
686 advantage during cold exposure or predation events. This list is very unlikely to be exhaustive and

687 other relationships presumably await discovery. However, an unanswered and intriguing question
688 concerns the extent to which the “file drawer problem” (Csada et al., 1996) influences our current
689 understanding of the consequences of variation in BMR, and it is presently unclear how many non-
690 significant relationships between BMR and other traits remain unpublished.

691 **Looking forward: the evolution of BMR and allometric scaling**

692 BMR is ultimately linked with a range of extrinsic variables including habitat temperature,
693 net primary productivity, and diet, and BMR is correlated with variation in survival, reproduction,
694 and lifespan. An enduring area of interest that remains active, despite decades of research, concerns
695 understanding the mechanistic basis of the allometric scaling of metabolic rate with body mass (e.g.
696 Agutter and Wheatley, 2004; Savage et al., 2008; White and Kearney, 2012). However, if the non-
697 isometric scaling of metabolic rate is ever to be understood, it is first necessary to know exactly what
698 the relationship is. Recent meta-analyses (Glazier, 2005; White et al., 2007b), and PI analyses of
699 hundreds of species of birds (McKechnie and Wolf, 2004; McKechnie et al., 2006; Kabat et al.,
700 2008) and mammals (Duncan et al., 2007; Sieg et al., 2009; White et al., 2009; Capellini et al., 2010)
701 have failed to support any single value of the allometric scaling exponents relating BMR to body
702 mass. Without very substantial increases in the size of the data set, these conclusions are unlikely to
703 change (White and Seymour, 2005b). Thus, an emerging challenge is to understand, for example, the
704 differences in metabolic scaling between endotherms and ectotherms (Farrell-Gray and Gotelli,
705 2005; White et al., 2007b), and between metabolic levels (White and Seymour, 2005a; Glazier, 2008,
706 2009a). One promising area for understanding the allometry of metabolic rate is the use of
707 experimental manipulation of intra-specific scaling exponents in species that span a wide range of
708 body masses during development. During development, many species of ectotherm grow over
709 several orders of magnitude in body size (e.g. Soling and Kleineke, 1976; Killen et al., 2007; Moran
710 and Wells, 2007), and the scaling of metabolic rate in ectotherms has proven amenable to
711 experimental manipulation (e.g. Table 2) (Glazier, 2005). Such experimental studies, which might

712 involve manipulation of any of the factors known to influence metabolism, potentially represent
713 powerful tools to understand the factors that constrain and influence the allometric scaling exponent
714 relating metabolic rate to body mass.

715 Further progress toward understanding why metabolic rate scales allometrically is also likely
716 to be made by complimenting the ongoing emphasis on mechanistic explanations with an approach
717 that views metabolic scaling as an evolutionary outcome of trait associations, and explicitly
718 incorporates the factors associated with mass-independent variation in metabolic rate between
719 species (e.g. temperature, productivity, reproductive output) (see e.g. Glazier, 2005; Killen et al.,
720 2010). Quantitative genetic tools have previously been applied to other problems of allometric
721 scaling (e.g. Lande, 1979; Riska and Atchley, 1985; Lynch and Walsh, 1998), and are increasingly
722 being applied to understanding other aspects of metabolic evolution (Artacho et al., 2005; Hayes,
723 2010; Nespolo et al., 2011, see also Konarzewski and Książek, 2012). The application of this tool
724 set also has the potential to yield substantial benefits not only to the understanding of mass-
725 independent variation, but also to the scaling of metabolic rate with body mass. As an example,
726 because the genetic correlation between body mass and metabolic rate is positive and often less than
727 1 (Table 7), allometric scaling of metabolic rate with body mass can arise in a simple evolutionary
728 model that includes random variation in body mass and correlated changes in metabolic rate (Figure
729 4; see Appendix B for modelling procedures). The scaling exponent of metabolic rate in such a
730 model can take a wide range of values, depending on the strength of the association between
731 metabolic rate and body mass (Figure 4). While this example is obviously simplistic, it nonetheless
732 demonstrates that the evolution of allometric scaling might be explained without the need to invoke
733 first principles mechanistic hypotheses grounded in chemistry or physics (see also Witting, 1995;
734 Kozłowski and Weiner, 1997; Glazier, 2005 for other examples). Taking the resource distribution
735 hypotheses as an example, this evolutionary approach based on trait associations assumes not that the
736 geometry of the resource distribution network dictates metabolic scaling, but that the geometry of the

737 resource distribution network has evolved to support the pattern of metabolic scaling (see also
738 Weibel and Hoppeler, 2005). For evolutionary models of allometric scaling to be of any value,
739 however, it is essential that plausible models of evolution and trait association are specified, and,
740 critically, that appropriate tests are either presented in conjunction with the models, or that clear
741 descriptions of the unique predictions of the models are presented, so that appropriate tests can be
742 designed (Shipley, 2000; Currie et al., 2004; Hawkins et al., 2007b; Glazier, 2010; White et al.,
743 2011b; Kearney and White, 2012).

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

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Figure 2. Summing isometric and allometric relationships introduces curvature into the relationship between $\log Y$ and $\log X$.

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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).

1630
1631 Figure 4. Simulated associations between metabolic rate (MR) and mass (M) generated according to
1632 the methods in Appendix B. The scaling exponent (b) and strength of the association is dependent
1633 on the relationship between changes in MR and changes in M (filled triangles: the change in MR at
1634 each time step is equal to 0.7 to 1 times the change in M, $b = 0.84$; unfilled diamonds: change in MR
1635 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
1636 change in M, $b = 0.66$). The model does not predict the elevation of the relationship; filled triangles
1637 and filled squares are offset by for clarity by +1 and -1 orders of magnitude, respectively.
1638

1639 Table 1. Selected scaling exponents (b) for the cardiovascular system predicted by the fractal
 1640 resource distribution model of West, Brown, and Enquist (WBE: West et al., 1997) and the Resource
 1641 Distribution Network model of Banavar et al. (RDN: Banavar et al., 2010).
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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)

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1644 Table 2. Examples of manipulative studies of the scaling of metabolic rate (see Glazier, 2005 for an
1645 extensive compilation of further examples).
1646

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

1647

1648 Table 3. Parameter estimates for a model for avian basal metabolic rate (BMR, ml h⁻¹) as assessed by
1649 phylogenetic generalised least squares ($\lambda = 0.83$ and AIC = -395.2; AIC for an equivalent non-
1650 phylogenetic model is 247.0). Significant ($p < 0.05$) parameters are indicated with *; n.s. is non-
1651 significant. See Appendix A for a description of the analysis.
1652

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

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1655 Table 4. A selection of significant correlates of metabolic rate in animals (values in parentheses are
1656 additive genetic correlations).
1657

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

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

1667 Table 5. Narrow-sense heritability (h^2) of basal metabolic rate (BMR), standard metabolic rate
1668 (SMR), sustained metabolic rate (susMR), cold-induced maximum metabolic rate (MMR), and
1669 exercise-induced maximum metabolic rate ($\dot{V}O_{2\max}$) of birds and mammals. * indicates $p < 0.05$.
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Species	Measurement	$h^2 \pm SE$	Reference
Laboratory mouse <i>Mus musculus</i>	BMR	0.08 ± 0.06	(Lacy and Lynch, 1979)
Laboratory mouse <i>Mus musculus</i>	RMR	$0.21 \pm 0.04^*$	(Lynch and Sulzbach, 1984)
Hsd:ICR strain, <i>Mus domesticus</i>	BMR	0.09	(Dohm et al., 2001)
	$\dot{V}O_{2\max}$	0.64^*	(Dohm et al., 2001)
Leaf-eared mouse <i>Phyllotis darwini</i>	BMR	0.15	(Nespolo et al., 2003)
Leaf-eared mouse <i>Phyllotis darwini</i>	BMR	0.21 ± 0.21	(Bacigalupe et al., 2004)
	susMR	0.20 ± 0.38	(Bacigalupe et al., 2004)
Laboratory mouse <i>Mus musculus</i>	BMR	$0.38 \pm 0.21^*$	(Konarzewski et al., 2005)
	Swim $\dot{V}O_{2\max}$	$0.40 \pm 0.21^*$	(Konarzewski et al., 2005)
Leaf-eared mouse <i>Phyllotis darwini</i>	BMR	0.11 ± 0.18	(Nespolo et al., 2005)
	MMR	$0.69 \pm 0.35^*$	(Nespolo et al., 2005)
Bank vole <i>Clethrionomys glareolus</i>	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 <i>Taeniopygia guttata</i>	BMR	$0.25 \pm 0.04^*$	(Rønning et al., 2007)
Blue tit <i>Cyanistes caeruleus</i>	RMR	0.59 ± 0.25	(Nilsson et al., 2009)
Stonechat <i>Saxicola torquata rubicola</i>	BMR _{residual}	0.48 ± 0.16	(Tieleman et al., 2009b)
Stonechat <i>Saxicola torquata axillaris</i>	BMR _{residual}	0.20 ± 0.35	(Tieleman et al., 2009b)
Stonechat <i>Saxicola torquata maura</i>	BMR (g^{-1})	0.37 ± 0.47	(Tieleman et al., 2009b)
Laboratory mouse <i>Mus musculus</i>	BMR _{residual}	$0.19 \pm 0.07^*$	(Wone et al., 2009)
	$\dot{V}O_{2\max\text{residual}}$	$0.16 \pm 0.06^*$	(Wone et al., 2009)
Pied Flycatcher <i>Ficedula hypoleuca</i>	RMR	$0.43 \pm 0.17^*$	(Bushuev et al., 2011)
Deer mouse <i>Peromyscus maniculatus</i>	RMR _{residual}	0.39 ± 0.20	(Careau et al., 2011)

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1673 Table 6. Broad-sense (H^2) and narrow sense (h^2) heritability of metabolic rate in ectothermic animals
 1674 (* $p < 0.05$, *** $p < 0.001$).
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Species	Measurement	Heritability $\pm$ SE	Reference
Garter snake <i>Thamnophis sirtalis</i>	Maximum	$H^2 = 0.88^{***}$	(Garland and Bennett, 1990)
<i>Drosophila melanogaster</i>			
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 <i>Gryllus firmus</i>	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 <i>Gryllodes sigillatus</i>	Resting	$h^2 = 0.142 \pm 0.187$	(Ketola and Kotiaho, 2009)
	Exercise	$h^2 = 0.718^* \pm 0.313$	(Ketola and Kotiaho, 2009)

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1678 Table 7. Additive genetic correlations between metabolic rate and body mass in animals, shown $\pm$
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Species	MR level	Correlation	Reference
Zebra finch <i>Taeniopygia guttata</i>	BMR	0.914 ± 0.081	(Rønning et al., 2007)
Blue tit <i>Cyanistes caeruleus</i>	RMR	1.178 ± 0.456	(Nilsson et al., 2009)
Stonechat <i>Saxicola torquata rubicola</i>	BMR	0.400 ± 0.349	(Tieleman et al., 2009b)
Stonechat <i>Saxicola torquata axillaris</i>	BMR	0.780 ± 0.360	(Tieleman et al., 2009b)
Deer mouse <i>Peromyscus maniculatus</i>	BMR	0.72 ± 0.23	(Careau et al., 2011)

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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 ($= \text{AIC} - \text{minimum AIC}$); 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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