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REVIEW

How low can you go? An adaptive energetic framework for interpreting basal metabolic rate variation in endotherms

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Abstract Adaptive explanations for both high and low body mass-independent basal metabolic rate (BMR) in endotherms are pervasive in evolutionary physiology, but arguments implying a direct adaptive benefit of high BMR are troublesome from an energetic standpoint. Here, we argue that conclusions about the adaptive benefit of BMR need to be interpreted, first and foremost, in terms of energetics, with particular attention to physiological traits on which natural selection is directly acting. We further argue from an energetic perspective that selection should always act to reduce BMR (i.e., maintenance costs) to the lowest level possible under prevailing environmental or ecological demands, so that high BMR per se is not directly adaptive. We emphasize the argument that high BMR arises as a correlated response to direct selection on other physiological traits associated with high ecological or environmental costs, such as daily energy expenditure (DEE) or capacities for activity or thermogenesis. High BMR thus represents elevated maintenance costs required to support energetically demanding lifestyles, including living in harsh environments. BMR is generally low under conditions of relaxed selection on energy demands for high metabolic capacities (e.g., thermoregulation, activity) or conditions promoting energy conservation. Under these conditions, we argue that selection can act directly to reduce BMR. We contend that, as a general rule, BMR should always be as low as environmental or ecological conditions permit, allowing energy to be allocated for other functions. Studies addressing relative reaction norms and response times to fluctuating environmental or ecological demands for BMR, DEE, and metabolic capacities and the fitness consequences of variation in BMR and other metabolic traits are needed to better delineate organismal metabolic responses to environmental or ecological selective forces.

Keywords Basal metabolic rate · Endotherms · Selection · Evolutionary physiology · Daily energy expenditure · Energetics

Introduction

Comparisons of energetic traits among endotherms across various environments and life history strategies require standardized measurements of metabolic rates, with basal metabolic rate (BMR) being by far the most commonly used metric for comparative analyses. Measurements of BMR have indeed been conducted for decades (e.g., Riddle et al. 1932; Scholander et al. 1950a; McKechnie 2008; McKechnie and Swanson 2010; Fristoe et al. 2015). BMR is defined as the minimum metabolic rate of a normothermic,

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resting endotherm, within the thermoneutral zone, and in the absence of digestive, circadian, or other increments in metabolic heat production (Benedict 1938; Kleiber 1961; Bligh and Johnson 1973; McNab 1997; McKechnie 2008). Because BMR is the lowest measurable rate of energy expenditure in a resting animal, it is widely considered as a measure of physiological maintenance costs. The strict definition of BMR also includes only non-growing, non-reproductive individuals (Benedict 1938; Kleiber 1961; Aschoff and Pohl 1970; McNab 1997), as growth and reproduction have energetic costs and thereby elevate metabolic rate above minimal levels (e.g., Vézina and Salvante 2010; Careau et al. 2013a). The conditions necessary to standardize metabolic measurements to conform with the definition of BMR are generally achievable only in laboratory studies, and likely do not reflect conditions that animals experience in their natural environment on a consistent basis. These standardized conditions do, however, allow for studying flexibility of energetic traits within individuals, with BMR varying with season (cold), migration, and other aspects of the annual cycle (reviewed by McKechnie 2008; McKechnie and Swanson 2010; Swanson 2010). We also suggest that growing and reproductive phases of life cycles similarly have minimum energetic costs and we suggest that these can be considered as BMR for these phases, thereby facilitating intraspecific comparisons of minimum metabolic costs among different phases of the annual cycle. Furthermore, dichotomous categorizations of reproductive and growth states are often difficult in practice, particularly for tropical and subtropical species in which the phenologies of breeding, growth, and processes, such as molt, are not strongly seasonal. Nevertheless, it remains critical that interspecific comparisons are based on data sets, where the reproductive and growth status of individuals are standardized as far as possible, which will usually require the exclusion of data collected during breeding seasons or periods of ontogenetic growth to avoid confounding variables. For this paper, we interpret BMR as the minimum maintenance energetic costs for any given stage of the life cycle of an organism, with the caveat that life stages (e.g., breeding vs. non-breeding, molting vs. non-molting, growing vs. non-growing) may sometimes be difficult to precisely delineate.

Correlations of BMR with other metabolic traits

Adaptive explanations for a high BMR are pervasive despite evidence that natural selection acts on field-active metabolic rates or maximal metabolic capacities (Hayes and O'Connor 1999; Rezende et al. 2004; Sears et al. 2006; Boratyński and Koteja 2009; Clavijo-Baquet and Bozinovic 2012; Zub et al. 2014; Pauli et al. 2016; Petit et al. 2017) rather than on BMR directly. Raichlen et al. (2010) articulated this idea, suggesting that "there may be adaptive reasons for relatively high or low BMR at a given body mass" (p. 302). Comparative studies of endotherm energetics often measure BMR as a proxy for overall energy turnover (more accurately defined by daily energy expenditure, DEE, or some similar metric), and then infer potential adaptive differences in energetics from patterns of variation in BMR. To complicate this issue further, evidence for the inferred link between BMR and DEE is inconsistent among studies (e.g., Ricklefs et al. 1996; White and Seymour 2004; Speakman et al. 2004; Speakman and Król 2011; Careau et al. 2013b; Welcker et al. 2015; Portugal et al. 2016), and, moreover, is mechanistically difficult to reconcile with the observations that different tissues are largely responsible for variation in BMR and DEE (Konarzewski and Diamond 1995; Chappell et al. 1999; Selman et al. 2001; Książek et al. 2009; Bacigalupe et al. 2010; but see; Green et al. 2013). Furthermore, the tissues influencing variation in BMR and DEE may vary from one life-history stage to another (Vézina and Williams 2003; Vézina et al. 2009). Similarly, evidence for phenotypic correlations between basal and maximal aerobic metabolic rates (either thermogenic or exercise maximal rates) is also often inconsistent. Such studies typically find positive correlations at the interspecific level (e.g., Hayes and Garland 1995; Dutenhoffer and Swanson 1996; Rezende et al. 2002, 2004; White and Seymour 2004; but see; Clavijo-Baquet and Bozinovic 2012), but variable relationships within species, with either positive correlations, positive correlations for raw, but not body mass-corrected values, or non-significant correlations (Boily 2002; Sadowska et al. 2005; Vézina et al. 2006; Gębczyński and Konarzewski 2009; Swanson et al. 2012). Speakman et al. (2004) also reviewed the functional significance of individual variation in BMR, examining the occurrence of high BMR as a means to support increased energy intake rates and sustained metabolic rates (SusMR; central limits hypothesis) or increased sustained activity levels (peripheral limits hypothesis), concluding that between-state comparisons (e.g., non-reproductive vs. lactating mice) of BMR were generally consistent with links between BMR and sustained maximal metabolic rates, but that these relationships disappeared at the individual level, at least after accounting for variation in body mass. The reasons for the differences between interspecific and intraspecific studies of these phenotypic correlations have not yet been resolved, but may involve different selective forces acting on BMR and DEE or MMR (maximal metabolic rate; see below), or may represent a statistical artifact associated with much lower levels of variation in body masses and metabolic rates for intraspecific than for interspecies studies. Supporting the idea of a phenotypic link between maximal and basal metabolic rates for interspecific comparisons, factorial aerobic scope (i.e., MMR/BMR) tends to remain fairly constant across vertebrate groups (Killen et al. 2016; Nespolo et al. 2017). For these reasons, we urge caution in developing adaptive explanations for BMR, either alone or as a proxy for overall endotherm energetics.

If BMR evolves as a correlated response to selection acting on other metabolic traits, such as DEE or maximal metabolic capacities for exercise or thermogenesis (summit metabolic rate, M_{sum}), then these traits should be heritable and the phenotypic correlation between them should also reflect underlying genetic correlations. A number of studies have used quantitative genetic analyses to examine such correlations in captive animals originating from both long-term laboratory-bred and wild populations, as well as narrow sense heritability (h^2 = the ratio of the additive genetic variance to the total phenotypic variance) of metabolic traits. In a review of heritabilities of metabolic traits in mammals, Konarzewski et al. (2005) found that support for significant heritability of metabolic traits was equivocal, with some studies showing very low and non-significant heritability, but others showing high and significant heritabilities. Subsequent mammalian studies have also supported this conclusion, as some show significant heritabilities of metabolic traits (Sadowska et al. 2005; Nespolo et al. 2005; Wone et al. 2009; Boratyński et al. 2013), but others do not (Nespolo et al. 2005; Boratyński et al. 2013). There are relatively few studies of heritability of avian metabolic traits, but Rønning et al. (2007) and Tieleman et al. (2009) found significant heritability for BMR in zebra finches (*Taeniopygia guttata*) and stonechats (*Saxicola* spp.), respectively. Moreover, heritabilities may differ between BMR and other metabolic traits (exercise MMR, M_{sum}, SusMR) (Dohm et al. 2001; Bacigalupe et al. 2004; Nespolo et al. 2005).

Positive genetic correlations of BMR with other metabolic traits, such as exercise MMR, M_{sum}, or SusMR, or with other traits (e.g., locomotor movements, growth rates, and litter size) potentially related to metabolic capacities, occur in some endotherms (Dohm et al. 2001; Sadowska et al. 2005, 2009; Wone et al. 2009, 2015; Careau et al. 2011; Boratyński et al. 2013). In contrast, non-significant correlations of BMR with other metabolic traits also occur in endotherms (Książek et al. 2004; Nespolo et al. 2005; Sadowska et al. 2005; Gębczyński and Konarzewski 2009). Thus, although these studies collectively provide some support for the idea that metabolic traits are heritable and that BMR and other metabolic traits are genetically correlated, support for this hypothesis is far from universal. Further studies are needed to illuminate the genetic architecture underlying metabolic traits.

BMR and thermal conditions

Many endotherms, especially small species inhabiting temperate or polar climates, have lower critical temperatures (T_{lc} = the temperature below which regulatory thermogenesis must occur to balance heat loss, and, therefore, the lower limit of the thermoneutral zone) that are substantially higher than the environmental temperatures they typically encounter (Rubner 1883; Scholander et al. 1950b; Schmidt-Nielsen 1984; Porter and Kearney 2009). As a consequence, these animals should almost always be outside of their thermoneutral zones under natural conditions (Fig. 1), so rarely does metabolic rate in the wild reach levels approximating BMR. However, we emphasize that few data directly address the proportion of time endotherms spent inside or outside of their thermoneutral zones in natural thermal environments, which encompass all avenues of heat exchange between the animal and the environment (but see Liwanag et al. 2009). Behavioral mechanisms, such as basking or huddling, may mollify thermal demands to some extent (Maldonado et al. 2009). Nevertheless, small endotherms likely still operate outside of their thermoneutral zones under most natural environmental conditions, although even very small species can substantially modify roost temperatures by occupying thermally buffered microsites and/or using communal roosting (see Walsberg 1990 for an example). Larger endotherms, because of their lower surface area to volume ratios, thicker pelages

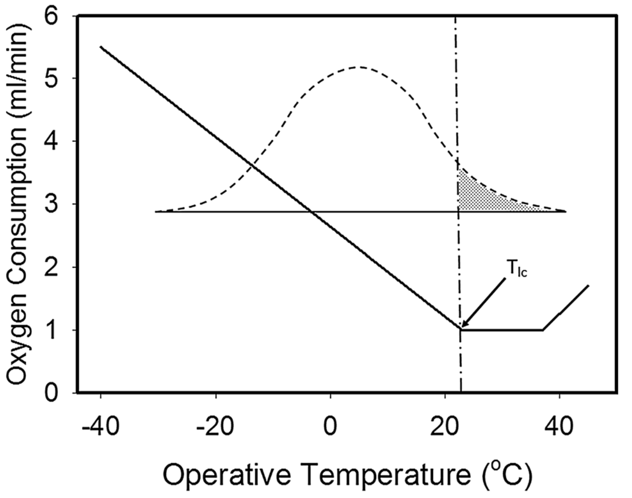

Fig. 1 Relationship between metabolic rate (*solid line* measured as oxygen consumption) and environmental operative temperature for a hypothetical small endotherm from a temperate-zone environment. The lower critical temperature (T_{lc}), below which regulatory thermogenesis is required, occurs at 23 °C. The *dashed line* represents the hypothetical distribution of operative temperatures encountered by this animal over the entire annual cycle. Note that only a small percentage of these temperatures (filled area of the *curve*) occur within the thermoneutral zone of this animal

or plumages, and consequent lower thermal conductances, more often encounter thermal conditions within their thermoneutral zones, so metabolic rates may more frequently approach BMR compared to the situation in smaller endotherms (Rubner 1883; Schmidt-Nielsen 1984; Porter and Kearney 2009; Liwanag et al. 2009). If endotherms only rarely experience thermoneutral conditions, it is difficult to envision natural selection acting directly on BMR, which by definition is associated with these temperatures. Activity also increases metabolic rates above BMR, with DEE usually averaging two to fourfold higher than BMR (Ricklefs et al. 1996; Piersma and van Gils 2011; Careau et al. 2013b). Therefore, because animals are most often not simply "idling" during their activity periods, it again becomes difficult to envision selection acting directly on BMR under conditions necessitating metabolic rates elevated above basal levels.

These issues raise a fundamental question pertinent to comparative energetic studies of endotherms: Does BMR, especially a high BMR, possess direct adaptive value? Dawson and Marsh (1989) and Dawson and O'Connor (1996) raised this issue directly in considering BMR flexibility in small birds wintering in cold climates, stating that the "… adaptive value [of a high BMR] … is not immediately obvious" and "… at first glance … [a high BMR is] a needless encumbrance," respectively. Rezende and Bacigalupe (2015, p. 719) echoed this sentiment, noting that for endotherms, in general, "the adaptive significance of higher BMR per se remains unclear."

Selective forces acting on metabolic rates

Burton et al. (2011) developed three hypotheses explaining the persistence of variable BMR in natural populations, which collectively provide adaptive explanations for low, high, and variable BMR. The compensation hypothesis posits that low BMR increases fitness, because individuals can devote more energy to processes other than maintenance (e.g., growth and reproduction). The increased intake hypothesis suggests that high BMR increases fitness, because individuals will have larger internal organs capable of supporting higher activity or thermoregulatory capacities. Finally, the context-dependent hypothesis states that interactions between resource availability, environmental conditions, and BMR are such that high BMR is favored in some conditions and low BMR is favored in others. This latter hypothesis is akin to a stabilizing selection hypothesis (Nespolo et al. 2017), where fluctuating environmental conditions favor high metabolic capacities (and thereby high maintenance costs) in some years and low metabolic capacities others (Nilsson and Nilsson 2016). Such fluctuating selection might produce an optimum BMR which functions well over a wide range of environmental and ecological conditions. Although these hypotheses do help explain why BMR variation might persist among populations, we argue here that natural selection acts directly on BMR only to reduce it. Such a selective pattern is consistent with predictions of the compensation hypothesis and the low end of the context-dependent hypothesis, particularly for conditions, where selection on activity or thermoregulatory capacities is relaxed. For the increased energy intake and the high end of the context-dependent hypotheses, we argue that natural selection is operating directly on other traits (e.g., activity or thermoregulatory capacities) and that BMR merely tags along as a correlated response. Thus, our hypothesis is that, from an energetic standpoint, natural selection should always act to minimize BMR while still meeting maintenance requirements for a given set of environmental or ecological demands.

Is a high BMR adaptive?

A few scenarios exist where a high BMR has been hypothesized to have direct adaptive value. These include a reduction in the lower critical temperature, protection of the tissues against cold temperatures, or a correlated response resulting in an increased general metabolic level (Dawson and Marsh 1989; Dawson and O'Connor 1996; Fristoe et al. 2015). In the first scenario, the argument is that an elevation in BMR would reduce $T_{lc,}$ so that regulatory thermogenesis is postponed until lower temperatures (e.g., Fristoe et al. 2015). From an energetic standpoint, this argument fails, because energy is merely redistributed to BMR (i.e., maintenance costs) rather than to regulatory thermogenesis. Whether metabolic rate is elevated due to higher BMR, regulatory thermogenesis, or other factors that may substitute for thermoregulatory heat production, such as activity or the heat increment of feeding (e.g., Hindle et al. 2003; Enstipp et al. 2008; Humphries and Careau 2011), the overall energetic cost of maintaining body temperature would remain the same. A higher BMR and subsequent reductions in T_{lc} would delay the onset of shivering, but active shivering, even at relatively high intensities, does not seem to be injurious to muscle (Swanson and Thomas 2007), so we see little selective advantage to this strategy. In theory, if the upper limit to thermogenesis (summit metabolism, M_{sum}) was a fixed, invariant multiple of BMR, and conductance remained constant, then increases in BMR could directly lead to improved cold tolerance by reducing the minimum environmental temperature at which a body temperature setpoint can be regulated. However, empirical studies of seasonal changes in BMR, $M_{sum,}$ and metabolic expansibility (i.e., M_{sum}/BMR) do not support the idea of metabolic expansibility remaining sufficiently constant for BMR to directly influence cold tolerance in this way (Swanson

2010; Petit et al. 2013). Finally, the adaptive advantage of such a scenario still directly results from an increase in M_{sum}, rather than BMR.

The protective response to cold idea is also not a particularly appealing explanation, as such protection is precisely why regulatory thermogenesis exists—to increase metabolic heat production in the face of declining temperatures to maintain a high, stable body temperature. This leaves us with the correlated response suggestion, where selection acts to increase BMR with a correlated increase in general metabolic level. We argue, however, that the reverse, selection acting on maximal or sustained maximal capacities for activity or thermoregulation, with BMR increasing as a correlated response, is far more likely than selection to increase BMR, with a correlated response in metabolic capacities. Indeed, the former scenario was the basis for the aerobic capacity model for the evolution of endothermy (Bennett and Ruben 1979). In such a scenario, BMR is not a direct target of selection. Thus, none of these ideas for why natural selection should act to increase BMR directly seems obviously adaptive.

Potential adaptive explanations for a high BMR

To further explore this issue, we will examine some environmental or ecological conditions, where BMR is typically high and consider the selective factors that could be driving these high levels of BMR. Environmental temperature is a strong predictor of BMR, with endotherms living in cold environments typically having higher BMR than those living in warm climates (White and Seymour 2004; Wiersma et al. 2007; Jetz et al. 2008; Naya et al. 2013; Fristoe et al. 2015; Luna et al. 2017; but see also; Londoño et al. 2015). In addition, BMR is often elevated in winter relative to summer for birds wintering in cold climates or for cold acclimated relative to warm-acclimated birds (McKechnie 2008; McKechnie and Swanson 2010). This pattern of winter or cold-induced increments in BMR is also characteristic of several winter-active small mammals (e.g., Heldmaier and Steinlechner 1981; Li and Wang 2005) and of intermediate-sized (100–1000 g) mammals in general (Lovegrove 2005). In contrast, for endotherms from tropical or subtropical climates, lesser seasonal temperature variation and warmer winter temperatures than in cold-temperate and polar climates result in low energy demands in winter. Under such conditions, energetic demands during summer associated with reproductive workloads are greater than in winter, so BMR may be greater in summer than in winter if BMR is positively correlated with energy demands (Wells and Schaeffer 2012; McKechnie et al. 2015). Moreover, subtropical sites may show differential seasonal patterns of temperature variation, with some sites showing colder winters than summers and some sites with less seasonal variation (van de Ven et al. 2013; McKechnie et al. 2015; Noakes et al. 2017). Consequently, seasonal patterns of thermoregulatory costs may vary among subtropical sites, which may lead to variation in seasonal metabolic patterns (McKechnie et al. 2015; Noakes et al. 2017). In addition, lower latitudes may present a greater diversity of metabolic niches (Londoño et al. 2015), whereas higher latitudes with cold winters produce much greater thermoregulatory demands in winter than in summer, thereby producing common seasonal patterns of metabolic variation, with higher metabolic rates in winter than in summer (Swanson 2010). Londoño et al. (2015) also found no correlation between temperature and BMR in a large comparative study of birds from the New World tropics, suggesting that tropical birds are more variable in their responses to temperature than birds from higher latitudes.

Identifying latitudinal patterns in the seasonal BMR adjustments of mammals is significantly complicated by the more widespread occurrence of torpor and hibernation in mammals compared to birds. The most recent analysis of which we are aware (Lovegrove 2005) revealed that the magnitude and direction of mammalian seasonal metabolic adjustments are strongly size-dependent. Among small mammals (<100 g), metabolic rates generally decrease in winter, a process driven both by body mass reductions as well as reductions in mass-specific BMR. In the Lovegrove (2005) analysis, neither winter body mass nor BMR reductions were correlated with latitude and predictions concerning the possible existence of latitudinal gradients in the variability of seasonal BMR adjustments were not tested. However, none of the figures in this paper give any cause to suspect a similar trend as occurs in birds, whereby patterns of seasonal adjustments are more variable in subtropical or tropical regions compared to high latitudes (McKechnie et al. 2015).

For species wintering in cold climates, the winter- or cold-induced increases in BMR are accompanied by increases in thermogenic capacity via shivering and non-shivering thermogenesis. In fact, for both mammals and birds, such cold-induced increases in thermogenic capacity are more commonly detected than increases in BMR (see Rezende et al. 2004; McKechnie and Swanson 2010; Swanson 2010 for reviews). Thus, the strong effect of cold temperatures on endotherm BMR appears mediated by thermoregulatory demands, with selection acting to increase thermogenic capacity, and BMR increasing as a correlated response to support life in the cold. One exception to this general rule, however, involves mammals wintering in cold climates with scarce food resources, many of which enter torpor and/or hibernation. Such mammals may differ from other endotherms in seasonal patterns of cold acclimation or winter acclimatization, as they often show a reduction in BMR, which is usually interpreted as a mechanism of energy conservation at a time when food resources are low (e.g., Geiser and Baudinette 1987; Boratyński et al. 2016). Birds also use torpor, but the mean latitude for birds using daily torpor is 23°, with a 95% confidence interval extending from 19° to 27° (Ruf and Geiser 2015). Thus, heterothermic birds generally do not inhabit very cold winter climates, at least compared to heterothermic mammals, so selection for winter energy conservation is likely lower than for mammals wintering in cold climates with marked reductions in resource availability. Interestingly, minimum environmental temperatures are negatively correlated with M_{sum}, but not with BMR, in heterothermic rodents, suggesting a decoupling of any phenotypic correlation between M_{sum} and BMR in these rodents where selection forces may act to conserve energy during torpor but maintain high M_{sum} for arousal during inter-torpor bouts (Careau 2013). Such decoupling may be mediated through large contributions to arousal metabolic rates of non-shivering thermogenesis by brown adipose tissue by torpid rodents, rather than primary reliance on muscular shivering (e.g., Jefimow et al. 2004; Oelkrug et al. 2011).

If selection acts directly to increase BMR under conditions of high energy demand, such as thermoregulation in cold environments, then BMR should be correlated with fitness components to a greater degree than other metabolic traits. The relationship of BMR to fitness has been examined for several birds and mammals, but correlations between BMR and reproductive output or survival are variable, with positive, negative, or no correlations detected (see Rønning et al. 2016 for review). Such variability could result from non-directional (e.g., stabilizing, fluctuating, and disruptive) selection (Nilsson and Nilsson 2016; Rønning et al. 2016). Alternatively, variability in the direction and strength of correlations between BMR and fitness could result from selection acting directly on other physiological traits, such as DEE or activity or thermogenic capacities, rather than BMR, as we argue here. In this case, correlations between BMR and fitness traits may differ from the corresponding correlations for physiological traits under direct selection. In support of the idea that selection acts directly to promote phenotypic flexibility of thermogenic performance in cold environments, rather than on BMR, Petit et al. (2017) found that black-capped chickadees from eastern Canada with a winter M_{sum} above a threshold level showed improved winter survival, whereas BMR variation did not similarly impact survival (Fig. 2; but see Nilsson and Nilsson 2016). In this specific system, mass-independent M_{sum} increased by 34% between summer and winter, but mass-independent BMR only changed by 6%, and variations in M_{sum} and BMR were not temporally matched (Petit et al. 2013). These results suggest that these traits could reflect different body components responding to different demands associated with the winter season. Barceló et al. (2017) subsequently tested the uncoupling of BMR and M_{sum} in captive white-throated sparrows (*Zonotrichia albicollis*) using a combination of experimental diets and temperature treatments. Both BMR (15%) and M_{sum} (19%) increased in the cold (−8 °C) relative to the warm (28 °C) treatment. However, although both traits varied with lean body mass and were correlated, the components of lean mass that exerted the greatest influence on BMR variation were the digestive and excretory organs through the influence on food intake. In this specific experiment, temperature did not influence muscle size per se, but cold acclimated individuals with larger hearts and skeletal muscles also had higher thermogenic capacity. These observations, therefore, support the thesis that BMR reflects support

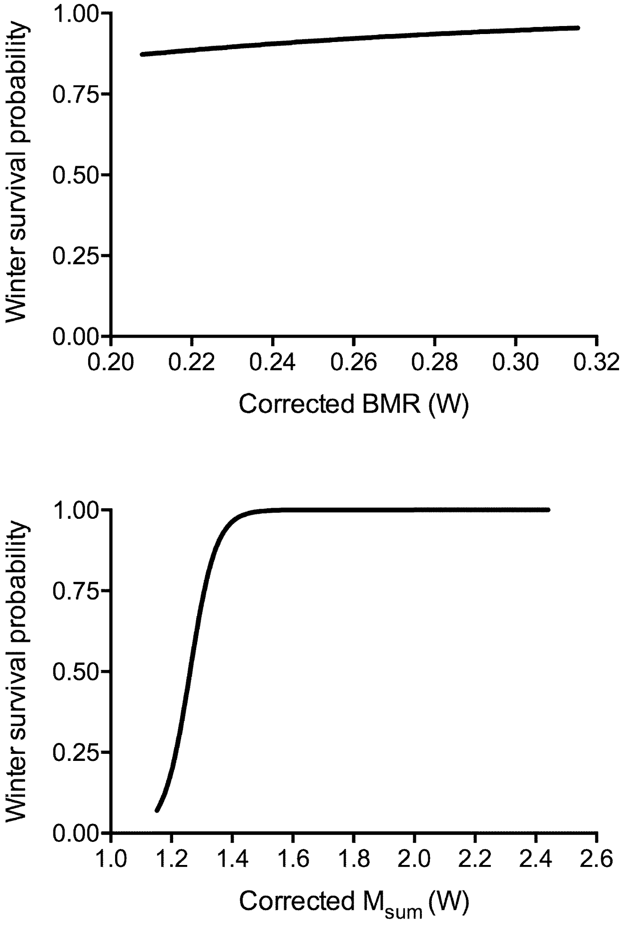

Fig. 2 Winter survival probability of *black*-capped chickadees (*Poecile atricapillus*) as a function of BMR (*top*) and M_{sum} (*bottom*). BMR was not significantly related to overwinter survival, but M_{sum} was significantly and asymptotically associated with survival, with the asymptote occurring above 1.4 W. BMR values are corrected for the effect of body mass, while M_{sum} values are corrected for the effects of date of capture and measurement and body mass (see Petit et al. 2017 for details)

functions (energy acquisition) in a thermal acclimation context and that fitness consequences stem primarily from direct selection on other metabolic traits.

Another factor often correlated with BMR is personality or social status, which in turn may be related to "pace of life" along a fast-slow continuum. A fast pace of life is characterized by high reproductive output, high activity, and relatively short life spans. These features tend to be positively correlated with BMR, such that a high BMR is an associated characteristic of the fast lifestyle (e.g., Wiersma et al. 2007; Williams et al. 2010; Versteegh et al. 2012; but see; Speakman 2005). Regarding personality traits, high levels of exploratory behaviors and social dominance are typical of fast lifestyles and are often (Careau et al. 2008; Møller 2009; Careau and Garland 2012; Maldonado et al. 2012; Mathot et al. 2015), but not always (Lewden et al. 2012), positively correlated with BMR. Behaviors and activities associated with fast lifestyles may involve higher support costs, such as larger reproductive or other organs (Wiersma et al. 2012), which, in turn, may result in higher BMR relative to individuals on the slow end of the pace of life continuum. Therefore, a high BMR would allow a fast pace of life, which may be adaptive in variable environments by allowing rapid exploitation of resources when they become available. As we see it, however, these arguments are ambiguous with respect to causation—does high BMR drive a fast pace of life or does a fast pace of life result in a high BMR (e.g., Glazier 2015)? We suspect that the latter scenario is more likely, as natural selection should act directly on personality traits that may relate to fitness, such as aggression or exploratory behavior, with BMR reflecting higher maintenance costs associated with the exploitative lifestyle (Réale et al. 2010).

Potential adaptive explanations for a low BMR

We argue here that, as a general rule, natural selection does not act directly to increase BMR. Because BMR typically comprises about 30–50% of total energy expenditure for endotherms (Raichlen et al. 2010; Burton et al. 2011), it represents a significant component of the overall energy budget. Energetically, it would, therefore, make sense to reduce BMR to the lowest level possible, while still effectively supporting overall metabolic demands, to minimize energy expended on maintenance functions. As such, cases where BMR does seem directly adaptive are scenarios where selection acts to reduce BMR. These include scenarios where animals live in warm climates or scenarios involving conditions that promote energy (or water) conservation, such as hot deserts, sedentary lifestyles, low food resources, torpor use, or low-risk behavioral strategies (Møller 2009; McNab 2012; Pauli et al. 2016). All of these cases should favor maintaining maintenance energy expenditures, and, therefore, BMR, at the lowest feasible levels. To examine this idea further, we will briefly review examples of where selection on high energy demands is relaxed, which could allow direct selection for reduction of BMR.

Food habits are related to BMR variation in endotherms (McNab 1988, 2008; Cruz-Neto and Bozinovic 2004; Bozinovic and Sabat 2010; Sabat et al. 2010; Naya et al. 2013). The general mechanistic explanation for this relationship is that animals on low-energy diets adopt an energy conserving lifestyle, including low BMR, to deal with low dietary energy intake or low availability of food resources (see McNab 2008; Bozinovic and Sabat 2010 for reviews). Endotherms with more abundant, better-quality, and/or more predictable food can adopt a more energetically expensive lifestyle, since they are less constrained by the requirement for energy conservation. Again, however, we emphasize that direct selection on BMR occurs only to drive BMR downward in the low resource situation. When food is readily available, we contend that selection likely acts on field metabolic rates, activity, or thermogenic capacities, with BMR increasing as a correlated response.

Related to both abiotic factors (e.g., aridity) and food resources, environmental productivity has also been postulated to influence BMR. This correlation is thought to be driven by reduced food availability in environments where productivity is low, thereby promoting an energy-conservation strategy for lifestyle and energetics (Bozinovic et al. 2009). The well-known trend of lower BMR in desert endotherms than in those from more mesic environments (e.g., Lovegrove 2003; Tieleman et al. 2003; McNab 2012) supports this idea. Reduced maintenance energetic costs also have the added benefit of reducing respiratory evaporative water loss and, thereby, water requirements in arid environments, which is especially advantageous in hot deserts where evaporative cooling for thermoregulation is particularly crucial (McNab 2012). Indeed, rodents from hot deserts tend to have lower BMR than allometrically predicted, but rodents from cold deserts tend to have higher BMR than allometrically predicted (Rezende et al. 2004). Camelids also have a low BMR for mammals and are associated with arid environments with low food resources (Dittmann et al. 2014). Positive correlations between net primary productivity and BMR occur for several intraspecific studies of endotherms (Mueller and Diamond 2001; Bozinovic et al. 2009). Nevertheless, net primary productivity is often not a prominent factor associated with high BMR in broad comparative multivariate analyses (White et al. 2007; Jetz et al. 2008; Naya et al. 2013; Luna et al. 2017; but see; Tieleman et al. 2003; Rezende et al. 2004). In these studies, variation in abiotic factors, especially temperature, tends to swamp effects of habitat productivity or precipitation on BMR, suggesting that temperature acting on thermoregulatory capacities and their associated support costs is generally a more important driver of metabolic variation. The trends of low BMR in desert environments, where energy conservation is a priority, and the primary importance of temperature as a driver of metabolic variation, with BMR elevated in the cold in support of higher energy requirements, collectively fit the idea that natural selection serves to drive BMR to the lowest levels that environmental or ecological circumstances permit.

Another factor potentially selecting for a low BMR is the heat produced during daily activities, for example, the metabolic heat production associated with breeding activities in warm climates, which must be dissipated. This factor forms the basis for the heat dissipation limit hypothesis for upper limits to energy expenditure in endotherms (Speakman and Król 2010). Under many (perhaps most) environmental conditions, with the possible exception of small endotherms breeding in cold climates, a downregulation of maintenance functions during activity would be selectively advantageous, as it would reduce the overall heat load needing to be dissipated. For small endotherms in cold climates, a high BMR might be required to support energetically expensive breeding activities or thermoregulation, but if energy availability is not limiting, selection to reduce BMR to lower the amount of heat dissipation required may be relaxed. Even under these conditions, however, a high BMR would necessitate increased energy intake and, thereby, increased foraging efforts, which might expose animals to increased ecological risks from predation or competition. Thus, even under conditions when energy is not limiting, we argue that selection may be expected to reduce BMR to the lowest level possible.

Some of the most convincing evidence for selection for low BMR and consequent energy conservation comes from endothermic taxa in which the capacity of individuals to effectively thermoregulate in the absence of thermally buffered microsites and/or communal roosting with conspecifics has apparently been lost. The classic mammalian example is the naked mole rat (*Heterocephalus glaber*, Buffenstein and Yahav 1991). This species lives in subterranean burrows with warm stable temperatures and practices behaviors, such as huddling, that limit thermoregulatory demands (Yahav and Buffenstein 1991). Consequently, thermogenic ability is downregulated along with maintenance costs (Hislop and Buffenstein 1994; Woodley and Buffenstein 2002). A broadly analogous avian example involves mousebirds (Coliiformes). Mousebirds are highly sociable birds that exhibit well-developed communal roosting behavior in which groups form tight clusters while clinging to branches. In addition to leading to substantial energy savings (Prinzinger 1988; McKechnie and Lovegrove 2001), the clustering behavior of mousebirds provides the basis for the defense of a normothermic body temperature setpoint; individuals prevented from clustering with conspecifics exhibit labile body temperature that decreases during the night (McKechnie and Lovegrove 2001; McKechnie et al. 2006). Moreover, the fact that mousebirds have long been viewed as a highly heterothermic taxon that routinely uses torpor (Bartholomew and Trost 1970; Prinzinger et al. 1981; Finke et al. 1995) appears to largely represent an artifact of studies investigating thermoregulation in individual birds without the presence of conspecifics. Data collected under laboratory and free-ranging conditions suggest that torpor is very rare in clustering mousebirds (McKechnie and Lovegrove 2001; McKechnie et al. 2004, 2006). Although McKechnie and Lovegrove (2001) argued that the thermoregulatory characteristics of mousebirds reflect a plesiomorphic trait linked to their ancient phylogenetic position, this argument was based on the placement of the Coliiformes in the phylogeny proposed by Sibley and Ahlquist (1990). More recent work suggests that the mousebirds belong to a more-recently derived clade (Hackett et al. 2008; Prum et al. 2015), supporting the idea that the thermal physiology of this group arose from selection for energy conservation acting on maintenance energy costs.

Functional correlates of BMR

We are proposing here that selection acts generally to reduce BMR, which begs the question of the mechanisms by which such a reduction might occur. In the following, we review several mechanisms potentially available to endotherms for mediating variation in BMR.

Body size and BMR

Body size is the greatest determinant of metabolic rate variation in animals (Schmidt-Nielsen 1984; McNab 2012). Consequently, adjustment of body size represents one potential mechanism for adjustment of BMR to varying environmental or ecological demands, although variation in body size will have opposite effects on mass-specific and whole-organism metabolic rates. A decrease in body size, for example, will result in a reduction in overall metabolic costs, but an increase in mass-specific metabolic rates, so selection could act on either whole-organism or mass-specific rates, with different selective forces potentially focusing on one or the other of these metabolic traits. One example of how body size might be adjusted to environmental demands is Bergmann's rule. Bergmann's rule codifies a general relationship between body size and climate for endotherms, with body size expected to increase in colder climates as a function of lower surface areas for heat loss (Bergmann 1847). Whether Bergmann's rule is valid for endotherms is a contentious issue, with some studies of endotherms supporting the rule (e.g., Ashton et al. 2000; Ashton 2002; Meiri and Dayan 2003; Blackburn and Hawkins 2004; Olson et al. 2009), but others not (e.g., Geist 1987; Fristoe et al. 2015), and some studies finding support in cold climates, but not in warmer climates (Rodríguez et al. 2006, 2008). Nevertheless, the general reasoning behind Bergmann's rule serves as the basis for recent suggestions that reductions in body size may serve as a general response of endotherms and other vertebrate animals to climate warming (Gardner et al. 2011; Sheridan and Bickford 2011; Goodman et al. 2012). Thus, adjustment of body size in response to changing environmental or ecological demands may be one mechanism for adaptive adjustment of BMR, although such adjustment is likely to be accompanied by variation in body composition (e.g., Piersma and van Gils 2011) and the direction of adjustment may vary depending on the selective forces involved.

Body temperature and BMR

Another potential mechanism for adjusting BMR is to increase or decrease body temperature (T_b). Because resting metabolic rates in endotherms have Q_{10} values (i.e., the change in metabolic rate for a 10 °C change in T_b) ranging from about 2–3 (Clarke et al. 2010), a relatively small change in the T_b setpoint could impact metabolic rates. As such, a reduction in normothermic T_b might serve as an effective mechanism to reduce BMR generally. Substantial variation in T_b occurs among different endotherm taxa; among extant mammals, T_b varies by approximately 10 °C (Lovegrove 2012). Clarke and Rothery (2008) argued that T_b may be influenced by ecology but constrained by physiology, suggesting that selection may adjust BMR through T_b variation or, alternatively, that T_b differences are a consequence of selection on BMR or other metabolic traits. Because metabolic rates during thermoregulation or activity are equivalent to maintenance costs plus an increment due to thermoregulatory or activity costs, higher maintenance costs would elevate the metabolic rate for thermoregulation or activity generally if costs for these actions were purely additive (e.g., no substitution of heat produced by BMR for thermoregulation). Under such conditions, if thermal conductance and environmental temperatures were kept constant, the higher BMR should result in a higher T_b, so an elevated BMR could help to maintain elevated T_b (as suggested by the thermoregulatory model for the evolution of endothermy; Crompton et al. 1978; McNab 1978). For example, Clarke et al. (2010) modeled T_b in mammals as functions of body mass and average ambient temperature (T_a) within the animals' range and found that T_a was inversely related to T_b, such that T_b increased by 1 °C for every 13 °C decrease in temperature. Thus, a polar animal at an average annual T_a of −13 °C would be predicted to have a T_b 2.7 °C higher than that of a tropical mammal living at an average annual T_a of 25 °C (Clarke et al. 2010). Such an increase in T_b should result in higher BMR for endotherms from cold climates than from warm climates, which is indeed the case (e.g., Weathers 1979; Rezende et al. 2004; Wiersma et al. 2007), although the precise contribution of T_b variation to the relationship of BMR to climate in endotherms is not known. From an energetic standpoint, however, the level of BMR should not affect the overall cost for thermoregulation, because absolute heat production is the same whether it is BMR or regulatory thermogenesis that results in the higher metabolic heat production. Thus, from an energetic standpoint, increasing T_b to elevate BMR for thermoregulation seems unnecessary.

Organ masses and BMR

BMR is primarily thought to be functionally derived from the metabolism of central organs and brain, with high maintenance activities at rest reflecting costs for protein turnover, gluconeogenesis, ion pumping, enzyme activities, nitrogenous waste synthesis, and mitochondrial membrane proton transport (Rolfe and Brown 1997; Burton et al. 2011; Nespolo et al. 2011). Elia (1992) estimated contributions of various organs and tissues to BMR for humans, with central organs (liver, kidney, heart, and "other," including the gut) accounting for 56%, brain accounting for 20% and skeletal muscles accounting for 16–22% of organismal BMR. Rolfe and Brown (1997) also estimated contribution of organs and tissues to BMR for humans, with central organs (liver, gut, kidney, heart, and lung) accounting for 48%, brain for 20%, and skeletal muscles for 20% of organismal BMR. Similar values for rats (*Rattus norvegicus*) were 36% for central organs (liver, gut, kidney, heart, and lung), 3% for brain, and 30% for skeletal muscles (Rolfe and Brown 1997). Many studies also reveal positive correlations between the masses of central organs and variation in BMR (see Swanson 2010; Williams et al. 2010; Burton et al. 2011; Wiersma et al. 2012; Careau et al. 2014 for reviews), although such positive correlations are not necessarily universal among all selective forces. For example, Williams et al. (2001) found that marine carnivores had substantially higher BMRs than carnivorous terrestrial mammals, and these elevated BMRs were associated with large digestive tracts, which were necessary for supporting the energetic demands and varied diet of the marine lifestyle. In addition, increasing energy demands associated with winter, acclimation to cold or short photoperiod, and lactation or endurance training in mammals result in BMR variation that is often positively associated with changes in some or all central organ masses (i.e., digestive tract, liver, kidney, heart) (Hammond and Kristan 2000; Nespolo et al.

2002; Zhu et al. 2012). In contrast, an inverse relationship between BMR and intestine mass occurred for South American field mouse (*Abrothrix andinus*, Bozinovic et al. 1990), masses of small intestine, liver, kidney, and heart were not significantly correlated with BMR in leaf-eared mice (*Phyllotis darwini*, Bacigalupe et al. 2010), and masses of heart, lungs, gut, liver, and kidney were not significantly correlated with altitude-induced BMR variation in deer mice (*Peromyscus maniculatus*, Hammond et al. 1999).

Another approach to studying the relationship between BMR and organ masses and other functional correlates in mammals is artificial selection experiments, which have focused primarily on laboratory mice. Genetic lines selected for high BMR or high food intake tend to produce increases in BMR (Konarzewski and Diamond 1995; Selman et al. 2001; Książek et al. 2004; Brzęk et al. 2007). Genetic lines selected for high wheel running activity or high running endurance increase energy expenditure relative to control lines and often increase maximum metabolic rates, but do not necessarily increase BMR. Nevertheless, such artificial selection treatments can alter central organ masses which might affect BMR. For example, masses for some or all central organs (intestine, liver, heart, and kidney) increase in mice lines selected for high BMR (Książek et al. 2004; Brzęk et al. 2007). Inbred mice strains with high BMR showed higher liver, small intestine, kidney, and heart masses relative to strains with low BMR (Konarzewski and Diamond 1995). Mice lines selected for high food intake resulted in increased BMR and increased liver, but not digestive tract, mass (Selman et al. 2001). In contrast, mice lines selected for high wheel-running activity increased maximum metabolic rates, but not BMR, and masses of gastrocnemius muscle, heart, and liver also did not vary with selection for wheel-running behavior (Swallow et al. 2005; Kane et al. 2008). Finally, mice lines selected for high aerobic capacity (increased endurance) exhibited higher maximum metabolic rates, but not BMR, relative to control lines, and these changes were accompanied by increases in masses of gastrocnemius muscle and heart, but not gut, liver, or kidney (Gębczyński and Konarzewski 2009). Collectively, these artificial selection studies provide general support for the idea that central organ masses are positively correlated with BMR, but such a correlation is not inviolate.

Birds also show generally positive relationships between central organ masses and BMR, although as for mammals, this relationship is not inviolate (see Swanson 2010; Wiersma et al. 2012 for reviews) and may vary depending on the predominant selective forces. For example, Tieleman et al. (2003) found that BMR was reduced in lark species from arid environments compared to those from mesic environments, but central organ masses did not vary with aridity. Larks from both arid and mesic environments, however, increased BMR and central organ masses in response to cold acclimation (Williams and Tieleman 2000; Tieleman et al. 2003). Skeletal muscle is generally thought to be less important than central organs as an effector of BMR, since it demonstrates low metabolic rates at rest. However, because skeletal muscle makes up a large percentage of body mass in most endotherms, perhaps especially birds, it may nevertheless be an important determinant of BMR (Elia 1992; Weber and Piersma 1996; Chappell et al. 1999; Vézina and Williams 2003; Raichlen et al. 2010; Petit et al. 2014). Several recent studies, however, highlight the variability of the relationships between central organ masses, skeletal muscle masses, and BMR in birds. Petit et al. (2014) studied seasonally acclimatized black-capped chickadees (*Poecile atricapillus*) from Quebec, Canada, finding that BMR increased during winter and that BMR was positively correlated with skeletal muscle, liver, and kidney masses, but not digestive tract mass, with skeletal muscle mass being the strongest predictor of BMR. Liang et al. (2015) exposed Chinese bulbuls (*Pycnonotus sinensis*) to short-term (7-day) food restriction, resulting in a reduction in BMR which was accompanied by reductions in liver and heart masses, but not kidney and digestive tract masses. Bai et al. (2016) examined three species of Chinese passerines in spring, including both migrants and residents, and found that BMR was positively correlated only with total digestive tract mass, whereas pectoralis muscle, heart, liver, kidney, gizzard, and small intestine masses were not significantly correlated with BMR. Finally, Barceló et al. (2017) exposed white-throated sparrows (*Zonotrichia albicollis*) to experimental cold and high fiber diet treatments. BMR in these sparrows increased during cold exposure, as did heart, digestive tract, liver, and kidney, but not pectoralis muscle, masses (Barceló et al. 2017). Thus, various central organ masses may often be positively correlated with BMR variation in birds, but this is not always the case and pectoralis muscle mass may or may not be positively associated with BMR in birds.

Cellular metabolic intensity and BMR

In addition to the overall size of organs, cellular metabolic rates, especially in central organs with high maintenance activities, could also influence BMR. Maximal activities of key aerobic regulatory enzymes (citrate synthase [CS] or cytochrome C oxidase [COX]) in various tissues are often used as indices of cellular metabolic intensities, but these are more effective measures of maximal cellular metabolic capacity, rather than rates occurring at BMR. Mitochondrial volume density, basal cellular metabolic rates in isolated cells, or State 4 respiration in isolated mitochondria (an index of resting mitochondrial respiration rates) might be more appropriate measures for studying effectors of BMR variation, since these may be better measures of resting cellular aerobic flux. Several mammalian studies document positive associations between either BMR or conditions that increase energy demand (e.g., winter acclimatization, cold acclimation, or endurance training), which might be expected to increase BMR, and/or CS or COX activities, state 4 respiration or mitochondrial density in liver, brown adipose tissue, or skeletal muscle (Wickler 1981; Hoppeler et al. 1995; Li et al. 2001; Liu et al. 2009). In contrast, some mammalian studies fail to detect positive correlations between BMR and these variables in liver, skeletal muscle, or brown adipose tissue under conditions of increased energy demand (Li et al. 2001; Villarin et al. 2003). To complicate the issue further, indices of cellular metabolic intensity sometimes show variable relationships with BMR. Mineo et al. (2012) found that CS activities in skeletal muscle and brown adipose tissue increased with cold acclimation, but State 4 respiration did not. Artificial selection experiments in mice and rats have focused mainly on cellular metabolic intensity of hindlimb muscle and heart in lines selected for high running activity and generally show increased CS and/or COX activities in these tissues (Houle-Leroy et al. 2000; Koch and Britton 2005; Kelly et al. 2017). These cellular changes, however, may not be positively correlated with BMR changes (Kane et al. 2008). Finally, BMR in humans was not correlated with skeletal muscle mitochondrial density or CS activity, but was positively correlated with mitochondrial oxygen affinity, which, in turn, was mediated in part by COX activity (Larsen et al. 2011). Thus, variation in cellular metabolic intensity in various tissues may contribute to BMR variation in mammals, but such variation is far from universal.

A similar situation exists for birds, where pectoralis muscle activities of key aerobic enzymes are often, although not always, positively correlated with maximal metabolic capacities (Swanson 2010; Liknes and Swanson 2011; Price et al. 2011), but whether correlations also exist for BMR is less studied. In addition, cellular metabolic intensities of central organs are likely to be important to BMR variation. Avian aerobic enzyme activities are substantially higher in skeletal muscle and heart than for central organs, such as liver and kidney (Weber and Piersma 1996; Vézina and Williams 2005), but, as mentioned before, these activities provide measures of maximal flux through these pathways, so a better measure of resting cellular metabolic intensity is State 4 mitochondrial respiration. Correlations of BMR with both aerobic enzyme activities and State 4 mitochondrial respiration have been examined for a number of bird species under conditions differing in energy demands and results generally fall into two patterns: positive correlations with BMR or no relationship with BMR. Positive correlations of BMR with CS, COX, and/or State 4 mitochondrial respiration in pectoralis and/or liver occur for a number of bird species under conditions of winter acclimatization, cold acclimation, geographic temperature variation, or photoperiod variation (Liu et al. 2008; Zheng et al. 2008a, b, 2010, 2013, 2014a, b; Peña-Villalobos et al. 2014; Bai et al. 2016; Zhou et al. 2016; Hu et al. 2017), although not all indices of cellular metabolic intensity in all organs produced significant correlations with BMR in these studies. In contrast, BMR was not correlated with CS activity in pectoralis, kidney, heart, or liver in breeding European starlings (*Sturnus vulgaris*, Vézina and Williams 2005). In addition, cellular metabolic rates of temperate birds are higher than for tropical birds, consistent with broad BMR differences between these groups (Jimenez et al. 2014). Thus, for birds, variation in cellular metabolic intensities in different tissues often covary with BMR, but such relationships are not universal for birds in all tissues or under all selective regimes.

An additional potential mechanism for increasing cellular metabolic intensity could involve elevated plasma levels or turnover of triiodothyronine (T_3), which are generally positively correlated with BMR in endotherms (e.g., Kim 2008), although the cause–effect relationship between T_3 and BMR is not known (see Hulbert and Else 2004 for review). Plasma T_3 levels are positively correlated with BMR under conditions of varying energy demand in both birds (Liu et al. 2006; Zheng et al. 2008b; 2010, 2013; but see; Welcker et al. 2013) and mammals (e.g., Seidel et al. 1988; Li et al. 2001; Liu et al. 2009; Brinkmann et al. 2016; Rimbach et al. 2017). Modifications of plasma membrane fatty acids can also influence cellular metabolic intensity and BMR, generally with increasing levels of unsaturation leading to increasing permeability of membranes to ions and increased costs of maintaining ionic gradients (Rolfe and Brown 1997; Hulbert and Else 2000). Indeed, this relationship underlies the membrane pacemaker hypothesis for the connection between metabolic rates and life history in endotherms (Hulbert and Else 1999, 2000). Membrane fatty acid unsaturation is also mechanistically associated with the metabolic rate–body size relationship in endotherms, with smaller animals having a generally greater degree of unsaturation and higher mass-specific metabolic rates (Hulbert and Else 2004). A number of endotherm studies offer variable support for the membrane pacemaker hypothesis, with some endotherms showing unsaturation of membrane fatty acids in various tissues positively correlated with BMR or MMR, but others not, and correlations of different fatty acids in different tissues with either BMR or MMR in different organisms (Guglielmo et al. 2002; Pierce et al. 2005; Brzęk et al. 2007; Haggerty et al. 2008; Wone et al. 2013). Thus, membrane fatty acid composition can influence BMR or MMR, although not in a particularly consistent manner across all organisms or all selective forces.

Because BMR and MMR are largely products of different tissues (see “Organ masses and BMR”) and selection on BMR (reduction) and MMR (elevation in many cases) may be operating in different directions, a dissociation of the phenotypic correlation between these traits might be expected under current selective regimes (Fig. 3). According to the aerobic capacity model for the evolution of endothermy (Bennett and Ruben 1979), both traits increased during the evolution of endothermy, as sustained activity capacities and concomitant support costs both increased. Such selective trends might not continue to operate under present-day conditions, as selection on MMR may now represent stabilizing selection instead of selection for further increases (Swanson and Garland 2009; Raichlen et al. 2010; Swanson and Bozinovic 2011; Nilsson and Nilsson 2016; Nespolo et al. 2017), while selection should act to minimize BMR, as long as maintenance costs are covered. In other words, the selective advantage of low BMR, as long as necessary support costs are met, stays consistent through evolutionary time, but selection on high sustained activity does not. This could dissociate selective trends on the two traits under current conditions (Fig. 3). In summary, adjustments of body size, body temperature, and organ masses and/or cellular metabolic intensities in endotherms, especially adjustments associated with central organs, are likely to influence BMR. However, we emphasize that such adjustments promoting increases in BMR arise from selection for activity or maximal aerobic metabolic rates (MMR) rather than for high BMR directly.

Summary

In conclusion, we contend that BMR can be subject to directional selection for reduction under conditions favoring energy conservation and a low BMR can, therefore, be directly adaptive. High BMR, however, seems unlikely to be directly adaptive and instead appears to be largely a correlated response to selection on physiological traits associated with increased capacities for activity or thermoregulation. We postulate that the selection for maintaining BMR as low as possible is a general selective feature for BMR in endotherms. We further contend that variation in endotherm energetics arises from selection on other traits and that these other factors promote higher maintenance costs (i.e., higher BMR) under energetically demanding conditions. Nevertheless, even under energetically demanding conditions, BMR should always be as low as possible under existing environmental or ecological constraints. Otherwise, the animal is “wasting” energy (i.e., the “needless encumbrance” of Dawson and O’Connor 1996). Studies examining concurrent variation in BMR and DEE (or activity or thermoregulatory capacities) and their mechanistic underpinnings (e.g., organ masses, cellular metabolic capacities, variation in transcriptomes, proteomes, or metabolomes) in response to natural or experimentally manipulated energetic demands should help to resolve how these metabolic traits are adjusted (perhaps differentially) to changing energy demands. In addition, studies of the relative timing of such variation will be important in delineating selective actions on these traits. In addition,

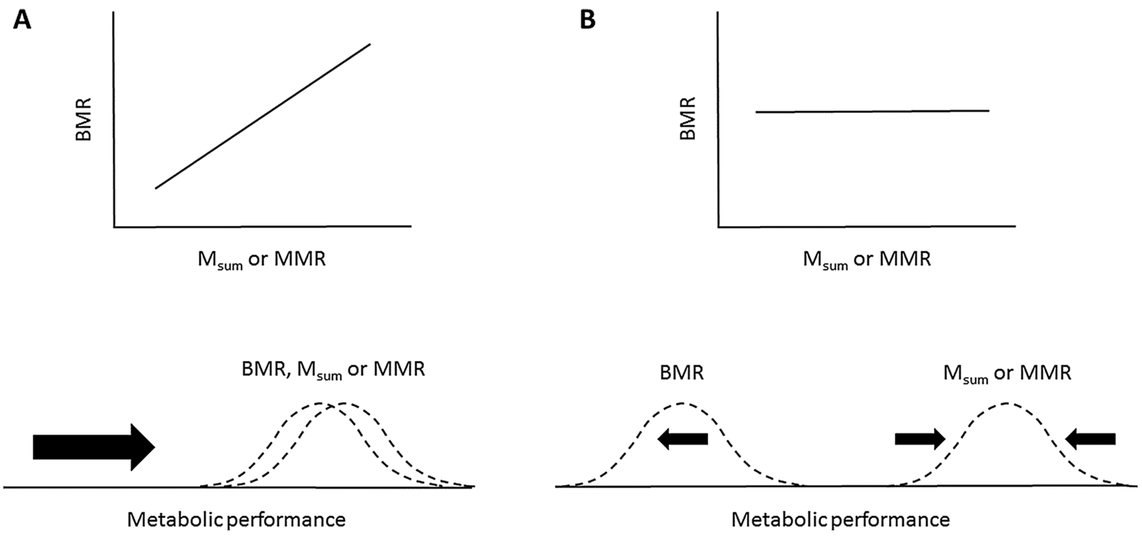

Fig. 3 Graphical representation for how erosion of the phenotypic correlation between basal and maximal metabolic rates might occur. The aerobic capacity model for the evolution of endothermy posits that both basal and maximal metabolic rates increased in parallel, leading to a positive relationship between these variables (**a**). Selection patterns for maximal metabolic rates, however, may now be stabilizing instead of directional selection for further increases, while selection should act to minimize BMR, as long as maintenance costs are met, potentially leading to dissociation of the phenotypic correlation between BMR and metabolic capacities (**b**)

studies examining relative fitness consequences of BMR and DEE or activity or thermogenic capacities (e.g., Petit et al. 2017) are needed to determine whether fitness is more closely associated with BMR or with other physiological traits. Finally, experimental manipulation of BMR, perhaps through thyroid hormone treatment or other mechanisms, without changing DEE or metabolic capacities (Bishop et al. 1995; Burger and Denver 2002; Liu et al. 2006; Welcker et al. 2013; King and Swanson 2013), followed by measurement of fitness consequences under conditions of variable energy demand could reveal whether, and under what conditions, selection acts directly on BMR or on other metabolic traits.

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