

Review



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Physiology

Energetic mechanisms for coping with changes in resource availability

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Given current anthropogenic alterations to many ecosystems and communities, it is becoming increasingly important to consider whether and how organisms can cope with changing resources. Metabolic rate, because it represents the rate of energy expenditure, may play a key role in mediating the link between resource conditions and performance and thereby how well organisms can persist in the face of environmental change. Here, we focus on the role that energy metabolism plays in determining organismal responses to changes in food availability over both short-term ecological and longer-term evolutionary timescales. Using a meta-analytical approach encompassing multiple species, we find that individuals with a higher metabolic rate grow faster under high food levels but slower once food levels decline, suggesting that the association between metabolism and life-history traits shifts along resource gradients. We also find that organisms can cope with changing resource availability through both phenotypic plasticity and genetically based evolutionary adaptation in their rates of energy metabolism. However, the metabolic rates of individuals within a population and of species within a lineage do not all respond in the same manner to changes in food availability. This diversity of responses suggests that there are benefits but also costs to changes in metabolic rate. It also underscores the need to examine not just the energy budgets of organisms within the context of metabolic rate but also how energy metabolism changes alongside other physiological and behavioural traits in variable environments.

1. Introduction

Anthropogenic drivers such as climate change and habitat degradation are having a marked impact on resource availability for organisms in many biological communities. Shifts in food availability occur not only as a result of altered trophic interactions [1] but also via impacts on organismal physiology and behaviour that alter resource demands and foraging rates [2–4]. There is increasing evidence that these changes in resource availability can alter the structure and dynamics of populations [2,4] and, in some cases, lead to their decline and subsequent extinction [1]. In good times, abundant food sources provide sufficient energy for growth, reproduction and survival, but balancing energy intake with demand among these competing functions can present a formidable challenge when resources are limited [5–7]. Morphological, physiological and behavioural traits, such as organ size [5,8–10], body temperature [8,11] and activity levels [5,12], can respond to changes in food availability over both ecological and evolutionary timescales. Many of these strategies are facilitated by changes in energy acquisition and expenditure [13]. As such, shifts in the rate of energy metabolism may play a key role in mediating the link between population resilience and resource conditions, partly explaining how well organisms can persist in the face of environmental change.

Metabolic rate determines the energetic cost of living [14]. At the very minimum, organisms need energy to maintain the homeostatic mechanisms necessary for life [15,16]. This baseline or minimum rate of energy expenditure is termed standard metabolic rate in ectotherms and basal metabolic rate in endotherms and is typically measured as the rate of oxygen consumption of a post-absorptive, inactive, non-reproductive individual at a given temperature in ectotherms or within the thermoneutral zone of endotherms [17,18]. Above this baseline expenditure, aerobic power is needed to fuel important functions such as locomotion, digestion, thermoregulation, growth and reproduction. However, organisms are limited by their maximum metabolic rate, the upper bound to their aerobic capacity [19].

Shifts in metabolic rate may be an important mechanism for organisms to balance their energy budgets and thereby cope with changes in food availability over both ecological and evolutionary timescales. Indeed, metabolic rate is a plastic trait [20–22] that is also heritable [23] and known to evolve [24,25], but how it is expected to change in response to shifts in food availability is far from certain. The adaptive value of shifts in metabolic rate in response to changes in food availability will depend on how metabolic rate impacts fitness and whether that impact changes along gradients of resource availability. However, at present there are multiple mechanistic hypotheses for how metabolic rate should impact fitness and no apparent empirical support for any single hypothesis (see below). As such, it is difficult to make predictions for how metabolic rate may change in response to changes in food levels over both ecological and evolutionary timescales.

Here, we use a meta-analytical approach to examine links between metabolic rate and performance across gradients of food availability in multiple taxa. We focus on baseline rates of mass-independent metabolism, i.e. standard and basal metabolic rate (referred to more generally as resting metabolic rate hereafter), since they have received the greatest attention. We then use output from our meta-analysis to derive predictions for how resting metabolic rate may enable or constrain responses to changes in food conditions via phenotypic plasticity and evolutionary adaptation. Finally, we evaluate and discuss evidence for these predictions across a wide diversity of animal taxa.

2. How does metabolic rate impact performance across resource gradients?

Given that energy is needed to persist in any environment, different mechanistic hypotheses have been put forward regarding how resting metabolic rate might impact organismal performance [26,27]. On the one hand, resting metabolic rate may reflect the maintenance costs of the metabolic machinery needed to maintain higher metabolic rates for activity, growth and/or reproduction [28–32], such that a higher resting metabolic rate facilitates higher energy intake, which is beneficial for fitness [26,33]. This ‘increased intake’ hypothesis predicts a positive relationship between resting metabolic rate and fitness. By contrast, the ‘allocation’ hypothesis proposes that a higher resting metabolic rate may limit metabolic power that could otherwise be devoted to other important functions, such that resting metabolic rate is negatively correlated with components of fitness [26,34]. A third hypothesis integrates both the allocation and increased

intake hypotheses but places them within the larger ecological context of varying food availability (figure 1a, [27]). Specifically, it proposes that, in the absence of food restriction, any fold-increase in whole-organism metabolic expenditure would be accompanied by a proportional increase in maintenance costs, activity levels and production rates (increased intake hypothesis), while under food restriction the available energy must be allocated to maintenance at the expense of activity, growth and/or reproduction (allocation hypothesis). As such, this ‘context-dependent’ hypothesis predicts that high resting metabolic rate will have a negative impact on performance under low food conditions but a positive impact on performance when food is readily available (figure 1a).

Numerous studies have examined the impact of resting metabolic rate on performance, but results are thus far equivocal. For example, some laboratory studies report a positive correlation between resting metabolic rate and growth [35], reproduction [36] and survival [37,38] while other studies report no correlation or a negative relationship with these same components of fitness (e.g. growth: [39], reproduction: [40], survival: [41]). Similar inconsistencies have been found in studies of wild populations [42,43]. These results have been interpreted to varying degrees as evidence for or against the increased intake and/or allocation hypotheses. However, the majority of studies are conducted under a single food level, so the role that food availability plays in determining these metabolic impacts and whether that varies across taxa or environments remains largely unexplored.

To address this question, we combed the literature for studies that examined the relationship between intra specific variation in mass-independent standard and basal metabolism and fitness-related traits. From those studies, we extracted the correlation coefficient (r) between metabolic rate and the fitness-related trait, and the temperature and food level used in each study. We then examined whether (1) effect sizes (z -scores) for the correlation differed from zero using an intercept-only model, and (2) food level (categorized as low or high per the authors description and included as a categorical predictor) and temperature (continuous covariate) had an impact on the magnitude and direction of the relationship between metabolic rate and components of fitness. Among studies that focused on metabolic impacts on somatic growth rate (i.e. change in body size over time; electronic supplementary material, table S1; $n = 27$ estimates from 14 ectotherm and 1 endotherm species), correlation coefficients (r) ranged from -0.53 to 0.76 and had a mean effect size ± 1 s.e. of 0.07 ± 0.08 , which did not differ from zero ($F_{1,27} = 0.64$, $p = 0.431$). However, effect sizes differed between food levels ($F_{1,25} = 14.76$, $p < 0.001$). Specifically, there was a significant positive effect size under high food conditions ($r = 0.25 \pm 0.08$, $t_{25} = 3.33$, $p = 0.003$) but a similar yet negative effect size ($r = -0.25 \pm 0.10$, $t_{25} = -2.49$, $p = 0.020$) under low food conditions (figure 1b,c). There was no effect of temperature on the correlation between metabolic rate and growth ($F_{1,25} = 0.31$, $p = 0.580$). We were unable to find any studies looking at the correlation between resting metabolic rate and reproduction under different food levels. Studies of metabolic impacts on survival were restricted to fishes and too few in number to warrant quantitative analysis, but results thus far were similar to those found for growth: there was a negative correlation between resting metabolic rate and survival under low food conditions, and a weak but positive correlation under high

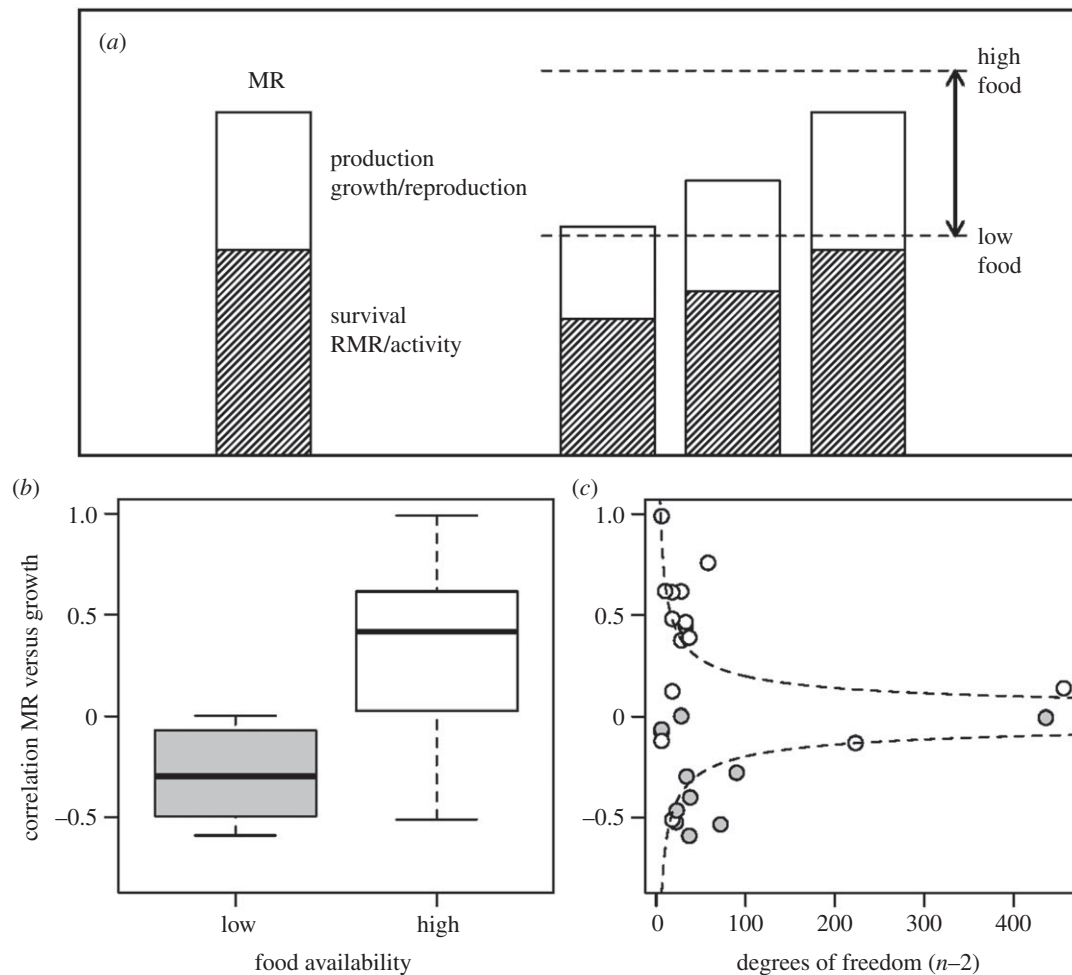


Figure 1. Context-dependent hypothesis (a) and mean effect sizes for low and high food conditions (b,c). (a) Whole-organism metabolic rate (MR) can be partitioned into survival costs (i.e. ‘the costs of living’, which include the costs of maintenance (as measured by resting metabolic rate (RMR) and activity) and production of new tissue (i.e. metabolic power allocated to growth or reproduction). In the absence of food restriction (high food), any fold-increase in MR would be accompanied by a proportional increase in both maintenance costs and production rates, while under food restriction (low food) the available energy must be allocated to maintenance at the expense of production. (b) Average intra-specific correlation between metabolism (MR) and growth rates obtained under low and high food. (c) Correlations reported in different studies plotted against their sample sizes (symbol colours as in b). In both (b) and (c), Pearson correlation coefficients r were transformed to z effects following Fisher’s transformation to comply with assumptions of normality and homogeneity of variance. Dashed lines show the z -transformed critical values for a two-tailed hypothesis; hence values outside these boundaries are statistically significant, with $p < 0.05$.

food conditions [44,45]. These results provide strong evidence for the context-dependent hypothesis, particularly for growth, in that a high resting metabolic rate is advantageous under high food conditions, and conversely, that a low metabolic rate is beneficial when food is scarce.

Given that the impact of resting metabolic rate on these different metrics of performance depends on food availability, we might therefore make the following predictions with respect to how metabolic rate may respond in an adaptive manner to changing food levels:

Prediction 1: Under short-term changes in food availability, phenotypic plasticity in metabolic rate will be advantageous such that selection favours those individuals that upregulate their metabolic rate when food levels increase and downregulate their metabolic rate when food levels decrease.

Prediction 2: Over longer timescales, organisms will evolve higher metabolic rates in more productive environments, while populations and species living in less productive environments will evolve a lower metabolic rate. We would therefore expect a positive relationship between metabolic rate and food availability across populations and species.

3. Metabolic responses to short-term changes in food availability

Phenotypic plasticity of standard and basal metabolic rate in response to changing food availability is found across a wide variety of taxa including invertebrates [20,46] and all major vertebrate classes such as fish [12,21,47,48], amphibians [49], reptiles [22,50], birds [51–54] and mammals [55,56]. Changes in energy metabolism occur over timescales ranging from days to weeks [47,57] and differ considerably among individuals [12,21,48,57]. For example, the magnitude of shifts in metabolic rate can differ by up to 10-fold among individuals in the same population [21]. Species also show variation in their metabolic responses to changes in food availability but are more difficult to compare owing to differences in experimental design and treatments across studies [5]. However, on average, organisms typically upregulate their resting metabolic rate when food levels increase and downregulate their metabolism when food becomes scarce [5]. These shifts in metabolic rate are thought to reflect underlying changes in organ mass and associated digestive and assimilative processes [9], mitochondrial number and/or efficiency [58], and respiratory substrate use [5].

Metabolic responses to changes in food availability may reflect adaptive strategies for meeting energy demands, but studies of the fitness consequences of metabolic plasticity are currently few in number and thus far focus exclusively on growth impacts in fishes [12,21]. Collectively, these laboratory food manipulation studies demonstrate that individuals that upregulate their resting metabolic rate to a greater extent in response to increasing food levels grow at a faster rate compared with individuals whose metabolic rates are less flexible [21,59,60]. By contrast, when food levels decline, those individuals that downregulate their metabolic rate to a greater extent grow at faster rates or lose less body mass than less flexible individuals [12,21,59,60]. These studies support Prediction 1 and provide evidence that plasticity in metabolic rate in response to changes in food availability can be advantageous, but more research across a wider diversity of taxa is needed to evaluate the impacts of metabolic flexibility on growth and other fitness-related traits such as reproduction and survival.

Why individuals within a population differ in their metabolic flexibility is also not clear given the beneficial impacts observed for growth. Reduced metabolic plasticity may be maladaptive, but differences among individuals in their metabolic plasticity may also reflect alternative strategies for maximizing fitness under changing food levels. One alternative strategy is the reduction of activity levels rather than metabolic rate *per se* under low food conditions. For example, in brown trout (*Salmo trutta*), some individuals reduce their rates of mass loss by downregulating their metabolism while other individuals in the same population do so by reducing their activity in response to food deprivation [12]. Changes in habitat use may also represent an alternative strategy for coping with changes in food availability. For instance, Atlantic salmon (*Salmo salar*) individuals with higher standard metabolic rates shift from foraging in pools to faster-flowing but more profitable riffle habitats when food availability declines [61]. Similarly, in environments with high spatial or temporal thermal variability, the selection of cooler microclimates can result in substantial energy savings by behavioural means without major changes in physiological machinery (e.g. [62,63]).

The presence of alternative strategies suggests that there are costs to plasticity that differ among individuals [64]. One potentially important cost is the impact of an increase in resting metabolic rate on absolute aerobic scope, the metabolic power available to the organism after meeting its baseline energetic demands [65]. Evidence thus far is limited but suggests that, in contrast to the flexibility observed in resting metabolic rates, maximum rates of metabolism are immutable under changing food levels [66]. As a result, allocation of metabolic power to *maintain* important functions (resting metabolic rate) comes at a cost to the amount of power allocated to *drive* those same functions (aerobic scope; [65,67]). Given this trade-off between resting metabolic rate and aerobic scope, we might therefore expect that individuals with a low maximum aerobic capacity would be less likely to increase their resting metabolic rates when food levels increase and more likely to decrease them when food levels decline. It is also possible that metabolism affects life-history traits in multiple ways—e.g. under low food conditions, a lower metabolism is beneficial for growth but could also come at a cost to an organism's ability to compete with other individuals or escape from predators—resulting in

trade-offs that give rise to different strategies. However, the costs, benefits and limitations of metabolic flexibility versus alternative behavioural strategies require further research.

4. Evolution of metabolic rate along resource gradients

Metabolic rates are heritable [23,68–70], subject to selection [45,71,72], and known to evolve in both laboratory [24,25,73] and wild [72,74] populations. However, at large spatial and temporal scales, it is unclear how metabolic responses to different levels of food availability translate into variation across populations, species or lineages. Studies thus far have looked at population- or species-specific metabolic rates and whether they covary with environmental factors such as productivity [74–77] and climate [76,78–81] that are thought to reflect food availability, but evidence is thus far mixed. For example, many studies report a positive correlation [74–77,81] as proposed in our Prediction 2, but others find a correlation with some but not all [78,82] indices of food availability.

Equivocality of results may arise in part because factors such as productivity and climate are often highly correlated in space and time (e.g. [78]) but also due to the breadth of adaptive responses that lineages can exhibit to cope with decreased food availability. For example, strategies such as torpor or hibernation in endotherms constitute classic examples of evolutionary responses that have been favoured to a large degree as an energy saving strategy [83–85], and heterothermy has been suggested as an important attribute for avoiding extinction [86]. In ectothermic organisms, aestivation is often employed to cope with the combined challenge posed by high temperatures and low food or water supply [85]. However, in light of the predominant role of temperature in shaping metabolic variation at multiple timescales (from minutes up to millions of years), it remains to be seen whether general responses to different levels of food availability exist across ectotherms.

Another confounding factor in interspecific studies of metabolic diversity is body size. Because energy balance is inherently linked with body size, a thorough understanding of how metabolism evolves in response to food availability must also take body size evolution into consideration. Plastic or evolutionary responses such as Dehnel's phenomenon, where certain species decrease in size in anticipation of periods of scarcity [87], or insular dwarfism [88], may reflect strategies to cope with restricted resource availability and yet, from a strictly energetic perspective, similar reductions in energy expenditure could have been attained at a constant body size by decreasing mass-specific metabolism. The fundamental issue, analytically, is to disentangle how variation in resource availability translates into metabolic responses at the whole-organism level, which include scaling effects with their own degree of uncertainty, and responses that are independent of size (figure 2*a,b*). Importantly, other factors that vary with body size, such as life-history traits or thermoregulatory performance, are also under selection during the evolution of different lineages, adding layers of complexity that are neglected here for sake of clarity.

The inclusion of body size complicates analyses based on energy balance because of the impact body size has on metabolic rates (i.e. energetic costs) but also other factors such as home range area, starvation resistance and foraging efficiency

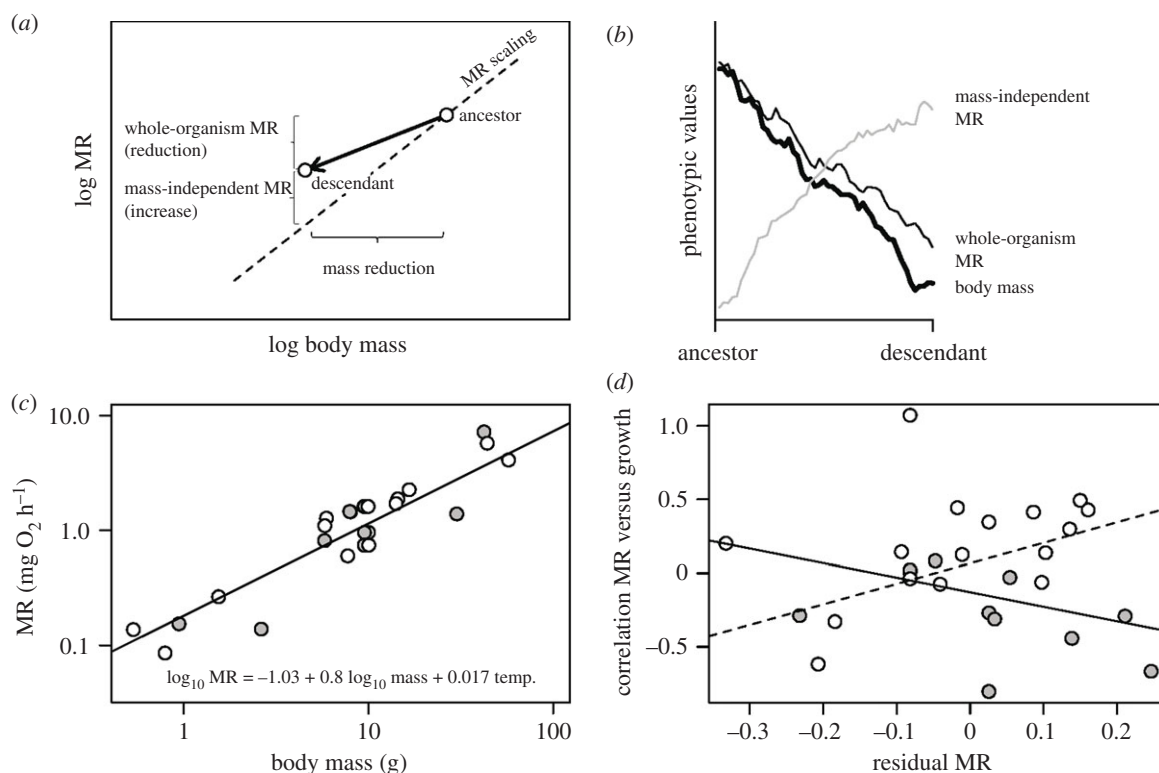


Figure 2. Energy allocation with varying body size. (a) Interspecific metabolic variation is analysed including body size as an independent variable, but size can also vary in response to resource availability. Therefore, the evolution of metabolic rates (MR) and size must be studied in tandem. The scheme shows how an evolutionary shift in both traits deviating from the scaling relationship may be interpreted as selection either for reduced whole-organismal MR or for increased mass-corrected MR. (b) Schematic evolutionary trajectories of these traits with simulated body mass and MR data. (c) Scaling of MR for ectothermic organisms with low and high food reviewed here (*P. darwini* was not included), also accounting for the effects of temperature ($R^2 = 0.914$). (d) Metabolic levels removing scaling and temperature effects predict the strength of the association (z-scores) between MR and growth, but this effect varies in sign in high (white circles, dashed line) versus low food (grey circles, solid line) and suggests that resource availability can alter the evolutionary trajectory of these traits, everything else being equal.

(i.e. potential benefits). Neglecting this issue, as well as the dichotomy between whole-organism versus mass-independent metabolism, will inevitably lead to an incomplete understanding of the set of circumstances underlying the evolution of animal size and energetic strategies. For instance, analyses testing whether mass-independent metabolic rates vary as a function of food availability are not conclusive [89], partly because what is meant by availability varies with size. As recent studies on size evolution in whales [90] and endothermy in birds [91] suggest, larger sizes, as well as higher mass-independent metabolic rates, can be favoured by selection and explained on energetic grounds. While larger whales are more efficient foragers, the emergence of birds from their ectothermic theropod ancestors involved a consistent reduction in body size that seems to have offset the costs of elevated mass-specific metabolic rates typical of endotherms (figure 2a,b).

Selective pressures aside, the multivariate genetic and phenotypic nature of these traits makes it difficult to predict long-term evolutionary trends. For instance, the impact of food availability on phenotypic correlations between metabolism and growth rates (electronic supplementary material, table S1) should result in different responses to selection in any of these traits, assuming that growth rates will have an impact on adult body size. Similarly, the presence of central or peripheral limitations in energy and nutrient turnover may impose a limit on the amount of resources that can be allocated to growth or reproduction (figure 1), suggesting that organisms with high metabolism may be differentially affected by food

restriction. Accordingly, after removing scaling and temperature effects on resting metabolism (figure 2c), effect sizes for the intraspecific correlation between growth and resting metabolic rates (electronic supplementary material, table S1) were affected by food availability primarily in animals with high metabolic levels, as evidenced by a significant interaction between mass-independent metabolic rate and food availability ($t_{22} = 2.32$, $p = 0.029$) in a regression weighted for the correlation sample size (figure 2d). In summary, not only will the nature of selection associated with food availability vary with size, the trajectory of the response to this selective pressure may also be contingent on many other factors. Spatial and temporal variation in temperature and food availability complicate things further, as some strategies such as selecting cooler microhabitats (ectotherms) or entering torpor or hibernation (endotherms) may reduce overall energy expenditure below metabolic estimates standardized for comparative purposes, such as standard metabolism at a specific temperature or basal metabolic rates. Consequently, it is not surprising that the general expectation that lineages should reduce their total energy expenditure by decreasing size [92] and/or mass-independent metabolic rates [75,76] under restricted food availability is not always supported [78].

5. Conclusion and future directions

Balancing energy intake with demand among competing functions in the face of changing resource levels is requisite

for persisting in variable environments. Given increasing anthropogenic impacts on communities and ecosystems [93,94], understanding whether and how organisms cope with changes in resource availability will be key to predicting the fitness of individuals and the abundance, distribution and evolutionary trajectories of species now and in the future. Our meta-analysis provides evidence that the impacts of baseline metabolic rate on performance depend on environmental conditions. In addition, our review highlights the mutability of metabolic rate; resting metabolic rate can increase or decrease in response to shifts in food availability through both phenotypic plasticity and genetically based evolutionary adaptation. The direction of these changes is generally in line with our predictions for adaptive responses at the individual and species level: (1) performance is higher among individuals that upregulate their baseline metabolic rate when food levels increase and that downregulate their metabolism when resources decline, and (2) many populations and species evolve a higher baseline metabolic rate in more productive environments. However, the metabolic rates of individuals within a population and of species within a lineage do not all respond in the same manner to changes in food availability.

This diversity of responses underscores the need to examine not just the energy budgets of organisms within the

context of metabolic rate but also how energy metabolism changes alongside other physiological and behavioural traits in variable environments. We highlight evidence for strategies at the individual (e.g. shifts in activity rates or microhabitat use) and species (e.g. evolution of smaller body size) levels that may interact with and influence how whole-organism as well as mass-independent metabolism respond to environmental change. However, more integrative research is needed to better understand the costs and benefits of these and other strategies and thereby how they evolve across environmental gradients.

Data accessibility. Data used in the meta-analysis are available in electronic supplementary material, table S1.

Authors' contributions. S.K.A., J.R.S. and S.R. searched the literature and collected data for the meta-analysis. S.K.A. and E.L.R. analysed the data and drafted the manuscript. All authors contributed to manuscript revisions and approved the final version.

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