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Review

What causes intraspecific variation in resting metabolic rate and what are its ecological consequences?

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Individual differences in the energy cost of self-maintenance (resting metabolic rate, RMR) are substantial and the focus of an emerging research area. These differences may influence fitness because self-maintenance is considered as a life-history component along with growth and reproduction. In this review, we ask why do some individuals have two to three times the ‘maintenance costs’ of conspecifics, and what are the fitness consequences? Using evidence from a range of species, we demonstrate that diverse factors, such as genotypes, maternal effects, early developmental conditions and personality differences contribute to variation in individual RMR. We review evidence that RMR is linked with fitness, showing correlations with traits such as growth and survival. However, these relationships are modulated by environmental conditions (e.g. food supply), suggesting that the fitness consequences of a given RMR may be context-dependent. Then, using empirical examples, we discuss broad-scale reasons why variation in RMR might persist in natural populations, including the role of both spatial and temporal variation in selection pressures and trans-generational effects. To conclude, we discuss experimental approaches that will enable more rigorous examination of the causes and consequences of individual variation in this key physiological trait.

Keywords: standard metabolic rate; resting metabolic rate; basal metabolic rate; maternal effects; metabolism; energetics

1. INTRODUCTION

The energy cost of self-maintenance (when measured as minimal rates of energy metabolism) varies remarkably within species. It effectively forms a central component of life-history theory which concerns how individuals must allocate a finite-energy budget among the competing interests of growth, reproduction and self-maintenance [1]. Compulsory trade-offs among these functions mean that variation in the rate of using energy will probably have implications for life-history traits and hence fitness. Consequently, there is great contemporary interest in among-individual variation in minimal rates of energy metabolism. In this review, we address two issues: (i) why do some individuals consistently have two or three times the maintenance costs of conspecifics of the same size, age and sex; and (ii) what are the consequences for fitness? For our purposes, the ‘baseline’ measures of energy metabolism—basal, standard and resting metabolic rate (BMR, SMR and RMR, respectively) are most relevant. When measured on quiescent individuals, at a common temperature and corrected for body mass, these estimate the compulsory energy cost of self-maintenance that is central to life-history theory. The definitions of each vary slightly. SMR is the lowest rate of metabolism, measured at a

particular temperature, in an inactive and post-absorptive ectotherm [2]. BMR differs only because it is measured in endotherms and includes the cost of endothermy [2]. RMR also assumes a post-absorptive state, but is frequently applied to both endotherms and ectotherms and caters for low levels of spontaneous activity [3]. Since all three measures represent the minimal metabolism of an individual in a relatively quiescent state, we group them under the term RMR.

Variation in RMR between species is ubiquitous and mostly explained by body mass, temperature, phylogeny and a range of environmental factors (see [4–7] and references therein). These comparative studies have shown that RMR is a trait of ecological and evolutionary importance but are unable to identify causal mechanisms. Within-species studies are complementary in this respect because they can provide insights into the causal factors underlying variability in RMR. However, attempts at explaining intraspecific variation in RMR have in general been less successful than comparative studies. For example, even after correcting for body mass, temperature and other factors such as age [8], sex [9], season [10], dietary history [11] and reproductive state [12], threefold differences in RMR among post-absorptive individuals and even siblings remain unexplained [13–15].

Individual variation in RMR appears likely to have consequences for fitness because RMR can constitute

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up to 50 per cent of an individual's energy expenditure [15]. Moreover, RMR correlates with other important measures of metabolic demand [16] and a range of fitness-related behavioural traits [17]. Differences in RMR among individuals also appear to be permanent. For example, RMR is repeatable over periods of time ranging from days to years [18] even in individuals who have experienced a 20-fold increase in body mass between measurements [19]. Furthermore, individuals seem unable to compensate for periods of intense energy expenditure by lowering their RMR [20]. Thus, RMR has attracted considerable interest as an important ecological factor that can set rates of resource uptake and allocation to survival, growth and reproduction [21]. However, hypotheses that attempt to correlate variation in RMR with broad-scale ecological variables such as climate and diet are not supported unequivocally at the intraspecific level [11,22] and do not explain the variation in RMR that can occur among siblings.

Using recent evidence from both vertebrate and invertebrate taxa, we first discuss the diverse causes of variation in RMR. Second, we review evidence that RMR is linked with fitness. Third, we discuss recent suggestions that the benefits and costs of a relatively high or low RMR may depend on local environmental conditions and that selection on RMR may be constrained by trade-offs, thereby providing an explanation for the persistence of variation in RMR in natural populations and among siblings. We conclude by discussing experimental approaches that can evaluate this hypothesis and enable more rigorous examination of the causes and consequences of intraspecific variation in RMR.

2. INTRINSIC CAUSES OF INDIVIDUAL VARIATION IN RMR

(a) *Local adaptation, heritability and genetic determinants*

Broadly distributed species have been used to identify a genetic component to intraspecific variation in RMR that may reflect local adaptation. For example, using the widely distributed isopod *Porcellio laevis*, Lardies & Bozinovic [23] demonstrated inter-population differences in RMR among F₁ generation offspring that had been bred and reared in a common environment. Moreover, the observed differences in RMR correlated negatively with the latitude of the populations from which the parental generation were sourced [23]. Despite evidence of high within-individual repeatability and (possibly) local adaptation, breeding experiments have generally found the heritability (h^2) of RMR to be low [24–28], which is typical for traits related to fitness. However, exceptions do exist (e.g. [29,30]), and selective breeding experiments have shown that RMR can respond to selection [31], providing evidence for heritability. Such equivocal evidence has led to suggestions that the genetic architecture of RMR may be complex [32], or that maternal and environmental effects also influence RMR [25,33]. Indeed, different parental configurations of mitochondrial and nuclear DNA can interact with the thermal regime experienced during early development to shape whole-animal RMR [32].

(b) *Maternal effects*

Recent evidence suggests that maternal effects can exert a substantial influence on offspring RMR. A possible mechanism underlying such effects is the transfer of hormones from mother to embryo. In oviparous species, concentrations of egg hormones can vary considerably among- and within-clutches and can have significant effects on offspring phenotypes [34]. In relation to RMR, experimental elevation of testosterone levels in zebra finch (*Taeniopygia guttata*) eggs resulted in an increase in offspring RMR that persisted into adulthood [35,36]. Female three-spined sticklebacks (*Gasterosteus aculeatus*) exposed to the threat of predation produce eggs that have a higher concentration of cortisol and also higher RMR [37]. Likewise, elevation of cortisol in brown trout eggs increased embryonic RMR [38]. Further evidence of a link between hormone levels and RMR in older animals comes from positive correlations between endogenous levels of plasma hormones and RMR [15,39,40], or experiments that manipulate plasma hormone levels or induce stress and find changes in RMR [40,41]. Maternal effects on RMR are not necessarily restricted to hormonal pathways. Eggs laid by female clownfish (*Amphiprion melanopus*) on the periphery of the clutch had an RMR that was on average 24 per cent lower than that of eggs laid in the centre [42]. Although variation in maternal provisioning may account for this observation, it is also possible that gradients in dissolved oxygen content influence offspring RMR via their position within the clutch [42].

(c) *Biochemical, physiological and behavioural sources of intrinsic variation*

The interaction between an individual's genotype and the environment it experiences during ontogeny is likely to involve effects on a range of biochemical, physiological and behavioural factors that influence intrinsic metabolic demand. Resting individuals consume energy during fundamental processes, such as protein turnover, gluconeogenesis, enzyme activity, nitrogenous waste synthesis and proton transport across the membranes of mitochondria during energy metabolism [43]. However, the proportional contribution of these factors to metabolic demand is poorly understood, but may contribute to individual differences in RMR within species. For example, evidence from mice shows that intraspecific variation in the size of the intestines, liver, kidneys and heart accounts for more than 50 per cent of the variation in RMR, despite these organs making up a relatively small proportion (on average approx. 17%) of the total body mass [44]. Similarly, behavioural syndromes or differences in personality (e.g. bold versus shy phenotypes [45]) may influence individual daily energy expenditure (e.g. owing to differences in activity levels) and also RMR: more active individuals may have larger organs than less-active individuals, which allow for a higher peak metabolic output, but also need to be maintained at rest [17]. Behavioural differences among individuals may also affect estimates of RMR during respirometry. For example, some individuals are more 'reactive' than others when confined in respirometers, possibly leading to a higher estimate of RMR [4,46,47]. This indicates that some individuals may be more susceptible to stress than others, and in terms of

RMR, respond more acutely to a range of stimuli. Hence, the variation inherent in intraspecific studies of RMR may partially reflect the wide range of factors that contribute to individual RMR and are overlooked during analyses between species.

3. EXTRINSIC CAUSES OF INDIVIDUAL VARIATION IN RMR

(a) *Physical and biological environment*

The expression of RMR can also be affected by environmental conditions experienced during and after development. For example, developmental temperature is known to be a strong determinant of later life RMR [48,49]. Furthermore, challenges to the immune system and levels of conspecific density experienced during early development can also influence later life RMR. For example, juvenile and adult RMR in birds can be influenced by brood density during early development [33,50]. In eastern chipmunks (*Tamias striatus*), juvenile parasite load was a significant determinant of adult (non-parasitized) RMR when measured a year later [51]. This effect on RMR probably results from upregulated immune function, as challenges to the immune system elicit a temporary increase in RMR [52,53], which is similar to that observed in parasite-infected individuals [51,54].

RMR in adulthood may also be affected by early growth conditions. Growth compensation in juvenile zebra finches (following a temporary reduction in dietary protein content) resulted in an elevated RMR once those birds became adults [55]. This suggests that the long-term energy costs of a higher RMR may be outweighed by the immediate benefits of catching up in body size (reduced predation risk, for example). Supportive evidence from biomedical and epidemiological studies shows that poor quality nutrition during early development can have irreversible effects on traits likely to affect RMR such as organ size, nutrient metabolism and enzyme physiology [56]. Conversely, a reduction in diet quantity (calorie restriction) during development can reduce RMR [57–62]. However, this reduction is reversible once conditions improve [59,63], suggesting that it may be a mechanism that conserves energy when food is limiting [58–61].

RMR is also known to fluctuate over short periods of time in response to both physical and social stimuli. Juvenile Atlantic salmon (*Salmo salar*) without access to overhead shelter can incur 30 per cent higher resting metabolic costs than those with a shelter, even if the shelter is not used [64,65]. The presence of conspecifics can also affect individual RMR. For example, in juvenile Atlantic salmon, the close proximity of a smaller conspecific was found to cause a 40 per cent reduction in RMR, whereas the presence of a slightly larger fish caused RMR to nearly double. This divergence in RMR occurred in the absence of activity and the presence of a transparent barrier that prevented physical interactions between the fish [66]. A similar deviation in RMR between dominant and subordinate individuals has been reported in other species. Sloman *et al.* [67] measured the RMR of individual brown trout before and after size-matched pairs were allowed to establish a social hierarchy. After pairing, the RMR of subordinate fish increased by

nearly 30 per cent, whereas that of the dominant decreased by 10 per cent.

4. DOES RMR AFFECT FITNESS? EVIDENCE FOR CONTEXT-DEPENDENT EFFECTS AND TRADE-OFFS

Studies that have investigated links between RMR and fitness have used a range of proxies including growth, reproductive output (number and size of propagules), reproductive fitness (number of surviving offspring), senescence and survival/lifespan. However, predicting the direction of the relationship between RMR and fitness is difficult because logical arguments can be made for both negative and positive trends [68]. The ‘compensation’ hypothesis proposes that individuals with a low RMR will have higher fitness because they have lower self-maintenance costs and can devote more energy to growth and reproduction. Conversely, the ‘increased intake’ hypothesis (for explanations of each see [68] and references therein) predicts that individuals with a high RMR will have higher fitness than low-RMR individuals because they generally have larger internal organs [16] and higher maximum metabolic rates [16,17]. This greater ‘metabolic machinery’ [17] might allow for higher sustained energy throughput, thus enabling greater assimilation of energy for growth and reproduction [69].

However, high rates of resting metabolism may also carry a cost in terms of increased mitochondrial production of reactive oxygen species (ROS) that cause damage to important biological molecules (e.g. proteins, lipids and nucleic acids), accelerating cellular senescence and ultimately death. On this basis, a higher RMR has been assumed to decrease lifespan through an increased production of ROS—the ‘free radical’ hypothesis of ageing [70]. However, comparative studies show that this hypothesis is too simplistic, as a high RMR does not necessarily result in either greater ROS production or reduced lifespan [71]. Only one study, to our knowledge, has investigated the relationship between RMR and lifespan at an intraspecific level and it revealed that individual mice with a higher RMR tend to survive longer [72]. This was attributed to higher levels of uncoupling proteins in the mitochondria, which increase the conductance of protons across the mitochondrial inner membrane. Such ‘uncoupled’ mitochondria require more oxygen per unit of ATP produced, but produce fewer ROS. Hence, greater mitochondrial uncoupling is thought to increase overall energy consumption (and so mass-specific RMR) but generate less oxidative stress, resulting in an inverse relationship between RMR and lifespan [72].

Relationships between RMR and growth, reproductive output, reproductive fitness and reproductive senescence have been subject to greater scrutiny and are summarized in table 1. Laboratory studies that use ad libitum levels of food have failed to find any relationship between RMR and reproductive output, leading to speculation that there is no direct physiological link between the two traits [77]. However, this is consistent with life-history theory because unlimited access to energy is unlikely to cause trade-offs in allocation among self-maintenance, growth and reproductive processes. In this respect, a positive relationship between RMR and reproductive output

Table 1. Representative summary of relationships between RMR and fitness-related traits obtained in laboratory (L), semi-natural (S) and field conditions (F). (Positive (+ve), negative (−ve) and non-significant (n.s.) relationships between RMR and each trait are shown. Also indicated (in the case of laboratory experiments), are whether ad libitum (AL) or restricted (R) rations were employed. Ration level is denoted as being not applicable (n.a.) in field experiments.)

trait	species	setting	food ration	relationship	references
growth	Atlantic salmon (<i>Salmo salar</i>)	L	AL	+ve	[19]
	masu salmon (<i>Oncorhynchus masou</i>)	L	AL	+ve	[73]
	brown trout (<i>Salmo trutta</i>)	L	AL	+ve	[74]
	snapping turtle (<i>Chelydra serpentina</i>)	L	AL	−ve	[75]
	zebra finch (<i>Taeniopygia guttata</i>)	L	AL and R	n.s. under R ration +ve under AL	[76]
	brown trout (<i>S. trutta</i>)	F	n.a.	n.s. in two streams −ve in two streams	[74]
reproductive output	laboratory mice (<i>Mus domesticus</i>)	L	AL	n.s.	[13,77,78]
	cotton rat (<i>Sigmodon hispidus</i>)	L	AL	n.s.	[79]
	house sparrow (<i>Passer domesticus</i>)	F	n.a.	+ve	[39]
reproductive fitness	bank vole (<i>Myodes glareolus</i>)	F	n.a.	+ve	[68]
senescence	great tit (<i>Parus major</i>)	F	n.a.	n.s.	[80]
survival	radiated shanny (<i>Ulvaria subbifurcata</i>)	L	AL and R	−ve under R ration n.s. under AL	[81]
	bank vole (<i>M. glareolus</i>)	S	n.a.	dependent on sex and season	[82,83]
	garden snail (<i>Helix aspersa</i>)	S	n.a.	−ve	[84]
	brown trout (<i>S. trutta</i>)	F	n.a.	−ve	[74]
	red squirrel (<i>Tamiasciurus hudsonicus</i>)	F	n.a.	−ve	[85]
	short-tailed field vole (<i>Microtus agrestis</i>)	F	n.a.	+ve	[86]

has been demonstrated in natural conditions (table 1), where food levels and other important factors may be more variable.

When considering growth as a measure of fitness, there is evidence for and against both the ‘compensation’ and ‘increased intake’ hypotheses. The majority of laboratory studies use ad libitum levels of food and reveal that high-RMR individuals show faster rates of growth, supporting the latter hypothesis (table 1). However, where food is restricted, high-RMR individuals do not grow any faster than those with lower RMRs, and can lose mass faster than low-RMR individuals when completely deprived of food [46]. Similarly, brown trout with high RMRs had higher growth rates when fed ad libitum in captivity, but not when they were released in four natural streams. No correlation was found between RMR and growth in two of the streams, whereas in the other two, growth and RMR were negatively correlated [74], lending support to the ‘compensation’ hypothesis.

With regard to the association between RMR and survival, positive, negative and variable relationships have been reported, with the latter differing among sexes and seasons (table 1). Information on the relationships between RMR and reproductive performance is scarce. Directional selection on RMR varied between sexes and among seasons in a study of free-living bank voles (*Myodes glareolus*), but overall reproductive fitness was positively correlated with RMR [68]. Conversely, an analysis of cross-sectional data on a population of wild great tits showed no relationship between RMR and rates of reproductive senescence [80]. Currently, few

studies have considered RMR in the context of sexual selection. However, positive relationships have been demonstrated between RMR and secondary sexual characters, such as the duration and rate of acoustic calls and the production of olfactory attractants [87–89].

The influence of food availability on the relationship between RMR and growth in laboratory experiments, and the absence of a general trend between RMR and survival in natural settings (where food levels and other important environmental factors may vary) indicate that a single optimal RMR may not exist. It is unlikely that either a high or a low RMR will be favoured in all conditions and at all times when natural environments can be so variable. Indeed, the strength and direction of selection on RMR are known to operate differently according to sex and season [68,82]. Some authors have also speculated that selection on RMR may be modulated by environmental factors, such as the availability of resources [15,74], which can fluctuate substantially in space and time. Thus, the relationship between RMR and fitness may depend, at least partly, upon the quality of environmental conditions—what we propose to call the ‘context dependence’ hypothesis that links RMR and fitness. High-RMR individuals are likely to have relatively high fitness when environmental conditions are favourable and vice versa when they are poor (food supply being the most obvious factor, but gradients in other environmental variables may be applicable). In comparison, low-RMR individuals may be somewhat buffered against the environment owing to their lower costs of maintenance. We predict that low-RMR individuals will have

relatively high fitness in such conditions but lower fitness than high-RMR individuals in favourable environments. The 'context dependence' hypothesis is perhaps best understood when considering how resource availability (i.e. food supply) can interact with individual RMR to influence growth rate.

Growth is dependent on both access to food and the ability to convert ingested food into new tissue. Relatively high-RMR individuals tend to be more aggressive and dominant over those with low RMRs [17], giving them preferential access to food [14]. Where resources are abundant or predictable, individuals with relatively high RMRs can therefore exhibit faster growth rates than low-RMR individuals (table 1). They may also have a greater physiological capacity for growth, as they can digest and process meals faster [90] and have higher digestive efficiency [31,91]. This may be advantageous in highly seasonal environments (e.g. high latitudes) where conditions can be favourable for growth only for a limited period of time. Evidence from the Atlantic silverside *Menidia menidia*, a broadly distributed species of marine fish, shows that individuals from high-latitude populations tend to have higher RMRs and a larger specific dynamic action (i.e. investment of energy in food digestion). They also consume more food and have higher food-conversion efficiencies than those from low-latitude populations (see [92] and references therein). Likewise, selective breeding of mice for high RMR results in a higher rate of food consumption and assimilation of new tissue [31]. Furthermore, when exposed to a sudden and unpredictable decrease in ambient temperature, mice selectively bred for high RMR are less likely to enter a negative energy balance because they can consume and digest more food, if it is freely available [91]. The advantages of a high RMR, such as rapid growth potential, may however, be realized only in environmental conditions that can offset the higher costs of routine maintenance, for example where food is abundant, accessible, predictable or defensible by aggression. If these conditions are not satisfied, individuals with high RMRs may not benefit from any growth advantage or may even experience lower rates of growth and/or survival (table 1). Thus, low-RMR individuals may be more resilient in adverse conditions owing to their lower maintenance requirements. Such effects need not only relate to food supply: juvenile Atlantic salmon lost energy reserves over the winter faster when no in-stream cover was available. However, this energy loss was least in fish with a relatively low RMR [93]. Also, only individuals with relatively low RMR may be able to use habitats where foraging costs are relatively high, as in the case of salmonid fishes feeding on invertebrates carried in stream currents [94]. Furthermore, individuals with high RMR are also known to engage in riskier behaviour [46,95]. Thus, the benefits of a high RMR (e.g. high social status and growth capacity) might be traded off against costs, such as an increased predation risk. Thus, we propose that variation in RMR might be maintained for the following reasons. First, selection on RMR is unlikely to remain static in space and time (alternatively, organisms may only encounter brief episodes of selection on RMR). Second, trade-offs may constrain the directional evolution of RMR. And third, individual RMR may be shaped by maternal effects (which could be influenced

by the environment experienced by the mother), early developmental conditions or an interaction between the genotype and either the current or the parental environment.

5. FUTURE DIRECTIONS: TESTING HYPOTHESES REGARDING THE CAUSES AND CONSEQUENCES OF INDIVIDUAL VARIATION IN RMR

The causes of intraspecific variation in RMR, on both proximate and ultimate levels, are poorly understood and require further investigation. Maternal effects and environmental factors operating during early ontogeny offer a proximate mechanism needing greater scrutiny. Moreover, the interaction between environment and genotype during this period may also be critical [32]. On a broader level, the mechanisms maintaining intraspecific variation in RMR remain speculative. Environmental heterogeneity has attracted attention as a candidate factor ([15,74,94], this review), and both observational and experimental studies may contribute to the evaluation of this hypothesis. In the case of the former, the scale of individual variability in RMR among natural populations (as opposed to mean differences) that are exposed to different environmental conditions has not been measured. When measured in a common environment, one might predict that variability in RMR would be higher among individuals originating from populations that inhabit stochastic rather than stable environments. Alternatively, experimental tests of this hypothesis might involve longitudinal studies that monitor the growth and survival of individuals with known RMRs in semi-natural conditions where environmental conditions such as food availability and habitat complexity can be manipulated.

While RMR can sometimes be associated with components of fitness in free-living animals, the causal mechanism underlying these associations is usually unclear. This occurs because most studies rely on natural variation in RMR and so the relationships could be driven by a third, unidentified, factor. Ideally, RMR should be manipulated independently of other trait(s) that may influence performance. Selective breeding for high and low RMRs is a useful approach [31]. However, selection experiments are time-consuming and can be performed in controlled conditions only where other selective forces are largely absent. Additionally, the genetic architecture of metabolic traits may be complex [32]. Thus, it could be difficult to select for RMR alone and not for correlated traits that also influence fitness. A promising approach would be to manipulate RMR during early ontogeny in the laboratory and then monitor the performance of the animals in semi-natural or natural conditions. Recent studies suggest that this can be achieved by hormonal manipulation of the developing embryo or by altering competitor density or protein intake during ontogeny [33,35,50,55]. However, it is currently unclear whether these experimental manipulations affect other traits that may also influence fitness.

A major obstacle confronting researchers interested in individual variation in RMR is separating cause from effect. For example, RMR is often correlated with levels of plasma hormones [15,40,60], and manipulation of plasma hormone levels can affect RMR [40], suggesting causality. However, both RMR and plasma hormone

levels can also correlate with organ size [15]. Thus, the causal factor in these relationships is obscure—do large organs and/or high hormone levels cause a high RMR, or do large organs or high hormone levels result from high RMR?

We also emphasize the value of longitudinal studies where RMR and related traits are measured repeatedly within the same individual, as these may reveal information that is not observed in short-term or cross-sectional studies. Biro & Stamps [17] suggested that longitudinal studies are necessary to reveal if correlations between RMR and behaviour are temporally consistent. This suggestion is applicable to other phenotypic traits and also studies investigating the causes of individual variation in RMR. Maternal effects and environmental factors experienced during early development can affect the expression of RMR [33,35–38,42,48–51,55], but most of these studies made a single measurement of RMR (usually in early life), neglecting measurements during later life stages and thus the repeatability of any effect. Longitudinal studies that have examined individual variation in RMR in relation to performance in free-living animals have also revealed important information regarding the strength and direction of selection on RMR [68,82,83]. Estimates of lifetime reproductive success in relation to RMR are however absent and, with the exception of studies on a single species of fish [74] and snail [84], current knowledge of the fitness consequences of variation in RMR in free-living animals is restricted to investigations conducted on short-lived mammals overwintering at high latitudes. Data from other study systems, for example, species with longer life expectancies and different thermoregulatory strategies that inhabit lower latitudes, are required to evaluate the generality of conclusions drawn from the currently narrow range of study systems.

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