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ADDING FUEL TO THE "FIRE OF LIFE": ENERGY BUDGETS ACROSS LEVELS OF VARIATION IN ECTOTHERMS AND ENDOTHERMS

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INTRODUCTION

Energetics, within the realm of biology, is defined as *the study of the causes, mechanisms, and consequences of the acquisition, storage, and use of energy by biological organisms*. Energy metabolism – the "fire of life" – is the sum of the processes by which animals acquire energy, channel energy into useful functions, and dissipate energy from their bodies. Animals need energy to accomplish three main types of physiological work: biosynthesis (e.g., growth, lactation, gamete production), maintenance (e.g., circulation, respiration, tissue repair or turnover, nervous coordination), and generation of external work (e.g., locomotion). Kinetic energy (heat) is an inevitable by-product of this metabolism; the heat produced by an animal over an entire day, its *daily energy expenditure* (DEE; see Box 14.1 for definitions of bold terms), is a fundamental measure in biology because it provides quantitative information on how much food it needs, the total activity of all its physiological and behavioral mechanisms, and the energy it drains from its ecosystem (Speakman 2000).

Research initially concentrated on measurement of the *metabolic rate* (MR) of animals under standardized conditions to obtain a comparable measure of the minimal metabolic level required to maintain physiological homeostasis, such as *basal metabolic rate* (BMR), *resting metabolic rate* (RMR), *standard metabolic rate* (SMR), and *routine MR*. Physiologists have also quantified the MR of animals under challenging situations to estimate

maximal metabolic rate (MMR). A major advent was the invention of the doubly-labelled water technique to measure DEE in free-living subjects (Lifson *et al.* 1955). The wide application of this technique over the last 35 years yielded hundreds of DEE measurements in free-ranging animals (Speakman & Król 2010).

As of today, identifying and understanding the factors causing inter-specific variation in BMR, RMR, SMR, MMR, and DEE remains a major research line in the field of energetics, yet the focus is shifting toward understanding differences among individuals (Burton *et al.* 2011; Careau & Garland 2012). The hypotheses put forward to explain variation in DEE, BMR, SMR, and MMR have invoked a wide variation of factors, both intrinsic and environmental, that range from the subcellular to the habitat level (recently reviewed in Konarzewski & Ksiazek 2013; White & Kearney 2013).

Box 14.1. Definitions and Abbreviations of Key Terms

Metabolic rate (MR): the amount of energy consumed by an animal in a given period, as measured by heat produced, O_2 consumed, or CO_2 produced. It represents the rate at which an animal converts chemical energy to heat and mechanical work. Energy is measured in joules (J), and accordingly, the fundamental unit in which MR is expressed is the Watt (W; $= 1 \text{ J·s}^{-1}$).

Basal metabolic rate (BMR): the lowest MR of an adult endotherm, post-absorptive, nonreproductive, and inactive while in its thermal neutral zone and inactive phase of its daily cycle.

Resting metabolic rate (RMR): the lowest MR of an endotherm while resting in its thermal neutral zone, when one or more of the conditions required for measuring BMR cannot be met (e.g., adult, postabsorptive, nonreproductive, resting phase).

Standard metabolic (SMR): the lowest MR of an ectotherm, post-absorptive, nonreproductive, and inactive while in its resting phase, measured at a specified ambient temperature.

Routine metabolic rate (routine MR): in some aquatic animals, the MR of post-absorptive, undisturbed animals that also includes the costs of spontaneous activity and the maintenance of posture and equilibrium.

Maximum metabolic rate (MMR): the highest MR that can be sustained by an animal over a very short period of time (i.e., 1 to 10 min), usually elicited by forced exercise (e.g., running or swimming). Also termed $VO_{2\text{-max}}$ or peak metabolic rate (PMR). In endotherms, MMR can also be elicited by cold exposure, then termed summit metabolism. In fishes, the typical tests used to quantify MMR, such as the U_{crit} test, will force the animal to swim at a relatively sustainable (nonburst) level. Alternatively, MMR can be quantified over short period during recovery after complete exhaustion, sometimes yielding measures that differ from those obtained with U_{crit} tests.

Daily energy expenditure (DEE): the total MR of an animal summed over 24 h, usually measured by metabolizable food intake and/or respirometry in captive animals, or heart rate monitoring and/or the doubly-labelled water technique in wild animals (then sometimes termed field metabolic rate (FMR).

Absolute aerobic scope (AAS=MMR-BMR or SMR): the absolute amount of energy (in Watts) available to an individual to cover the costs of various short-term, O_2-consuming, physiological functions (e.g., digestion, locomotion, thermoregulation).

> **Factorial aerobic scope (FAS=MMR/BMR or SMR):** the factor (in multiples of BMR or SMR) by which an individual can increase its metabolism above maintenance levels to cover the costs of various short-term, O_2-consuming, physiological functions (e.g., digestion, locomotion, thermoregulation).
>
> **Nonresting energy expenditure (NREE=DEE-BMR or SMR):** the total energy spent over 24 h to cover the costs of various sustainable, O_2-consuming, physiological functions (e.g., reproduction, growth, locomotion, thermoregulation).
>
> **Sustained metabolic scope (SusMS=DEE/BMR or SMR):** sustained levels of DEE expressed during periods long enough in duration that metabolism is powered by food intake rather than by transient depletion of energy reserves, expressed as a multiple of BMR or SMR.

INTRINSIC FACTORS THAT EXPLAIN VARIATION IN MR

Perhaps the most fundamental of intrinsic factors is body mass (M_b), since it accounts for over 90% of the inter-specific variation in BMR (White & Kearney 2013) and DEE (Speakman & Król 2010). However, the underlying cause of the strong effect of M_b on metabolism is still debated, as is the exact value of the allometric scaling exponent. There have been many attempts to find fundamental physiological or physical principles that can explain the relationship between M_b and metabolism (e.g., resource distribution theories such as the Metabolic Theory of Ecology (Brown *et al.* 2004), resource allocation theories such as Dynamic Energy Budgets (Nisbet *et al.* 2000), and physiological models based on constraints on cell size (Kozlowski *et al.* 2003) or heat dissipation (Speakman & Król 2010)). However, the current consensus is that the majority of these unifying principles are overly simplistic and that there is no single exponent that relates M_b to MR that can be applied across all animal groups or across the entire range of M_b (White & Kearney 2013). Instead it seems that different constraints take precedence at different M_bs, leading to complex exponents and nonlinear allometries (White & Kearney 2013). There is also evidence that environmental and ecological factors can modulate the effects of M_b on MR (Killen *et al.* 2010, Carey *et al.* 2013).

Even having controlled for the complex effect of M_b, there is still significant inter- and intra-specific variation in MR (Careau *et al.* 2008). Hulbert and Else (1999) highlighted the fact that the degree of phospholipid polyunsaturation of cell bilayer membranes affects the speed of key cellular processes and hence SMR or BMR (the "membrane pacemaker" hypothesis). Another important cellular mechanism is basal proton leakage across mitochondrial membranes: the greater the degree of leakage the less efficient are the mitochondria, resulting in a greater O_2 usage per unit of ATP produced. However, in light of the mixed empirical evidence, the general importance of both membrane pacemaker and mitochondrial functioning as unifying explanations for the variability in SMR and BMR is still debated (Polymeropoulos *et al.* 2012; Konarzewski and Ksiazek 2013).

Moving to a higher level of organization, it is commonly assumed that whole-animal MR should in some way be connected with body composition – and in particular with the relative size of organs presumed to have a high metabolic demand such as the intestine, liver, heart and kidneys. Broad support for this hypothesis comes from a range of studies relating variation in M_b-corrected BMR or SMR to relative organ size, but the details show inconsistency as organs identified as significant contributors to BMR or SMR differ widely among and even within studies (Russell & Chappell 2007). There are currently too few

studies aimed at determining the reason for this variation, let alone the effect of organs on DEE (Meerlo *et al.* 1997).

A wide range of other individual factors can potentially generate variation in MR such as reproductive status (see Chapter 10, this volume), age (see Chapter 16, this volume), social rank, number of parasites, and "personality" (see Careau *et al.* 2008). As the list of potential factors continues to grow, it is becoming increasingly important to examine several factors simultaneously (including extrinsic factors, see next section) to estimate the *relative* importance of the contributors to BMR, SMR, MMR, and DEE, at both intra-specific (e.g., Fletcher *et al.* 2012; Careau *et al.* 2013b) and inter-specific levels (e.g., Anderson and Jetz 2005).

EXTRINSIC FACTORS THAT EXPLAIN VARIATION IN MR

Although some studies on ectotherms have found that species living at high latitude (cold environments) have higher SMR than species living at low latitudes (warm environments) when normalized to a common ambient temperature (T_a), the generality of this pattern remains very controversial (White *et al.* 2012). By contrast, in endotherms it is relatively well established that there is a positive interspecific correlation between latitude or T_a and BMR measured at thermoneutrality (Lovegrove 2000; Rezende *et al.* 2004). Interestingly, however, rodents that use torpor do not show this pattern, perhaps because they do not face the "problem" of maintaining body temperature (T_b) (Careau 2013). Endotherms must also avoid over-heating if living at high T_a, which selects for a reduction in relative BMR (Speakman & Król 2010; White & Kearney 2013). This has been achieved in tropical birds through reductions in organ size: they have relatively smaller hearts, liver, and flight muscles than their counterparts in temperate regions, leading to a lower total body metabolism (Wiersma *et al.* 2012). The relationship between MR and species range is discussed more fully by Bozinovic and Naya (Chapter 17, this volume).

It has been suggested that a high and temporally stable net primary productivity (NPP) allows the evolution of high MMR and DEE (since fuel is abundant) – and that it results indirectly in a high BMR or SMR because this reflects the metabolic cost of maintaining this high-performance metabolic machinery (Mueller & Diamond 2001; see also increased-intake model below). BMR has been found to be correlated with the NPP of the native habitat at both an inter-specific (Mueller & Diamond 2001) and intra-specific level (Bozinovic *et al.* 2009). However, NPP often correlates closely with other environmental factors (e.g., rainfall, T_a) that might affect MR and no such relationship between NPP and BMR was found in an inter-specific analysis of birds that occupied habitats covering a much wider range of primary productivities (White *et al.* 2007). The suggestion that diet itself may influence BMR (the "food-habits" hypothesis) has been much debated (Bozinovic & Sabat 2010), but it has proved difficult to tease apart effects of food quality versus quantity (or indeed NPP), and to separate cause and effect (which comes first – the diet or the MR?). Predation risk is another extrinsic factor that potentially interacts with NPP and food quality (Lovegrove 2000). Predators can significantly constrain the foraging ability of prey, which in turn can result in physiological changes (Lovegrove 2000; Handelsman *et al.* 2013).

The effect of intrinsic and extrinsic factors may vary according to whether analyses consider intraspecific or interspecific variation. For example, the effect of T_a on DEE was positive in a wild rodent population (Fletcher *et al.* 2012), which is opposite to the negative relationship found in inter-specific studies (Humphries *et al.* 2005). Links with

life history traits show similar contrasts: while rodent species with higher-than-average MMR have higher-than-average BMR (Rezende *et al.* 2004), there is mixed support for this relationship at the individual level (Careau *et al.* 2012). In mammals, a positive relationship between mass-adjusted DEE and BMR is widely supported at the inter-specific level (Ricklefs *et al.* 1996), but such a relationship was rarely found at the among-individual level (Careau *et al.* 2013b).

ENERGY BUDGETS

An animal can only start investing energy toward growth, reproduction, or activity when energy intake is above maintenance requirements. This can be achieved by either increasing food intake or reducing maintenance requirements. The first possibility is known as the "increased-intake" (or acquisition, or additive) model and the second as the "allocation" (or compensation) model.

Increased-Intake and Allocation Models

To ingest and process more food, an individual may need to increase the size of its alimentary tract, which may come with an increase in maintenance costs because organs such as gut, intestines, and liver are very active metabolically (see previous section). The increased-intake model therefore predicts a positive association between any energy-demanding activity and BMR or SMR (the "engine"). Individuals may differ in their capacity and willingness to acquire resources from their environment, yielding positive correlations between different components of the energy budget. By contrast, in the allocation model BMR is seen as the "competitor" because it monopolizes energy that becomes unavailable for other energy-demanding activities. Compensation may be achieved by behavioral modifications, choice of environment, and/or by physiological mechanisms (see Chapter 10, this volume). Energy allocation constraints should impose a trade-off between energy-demanding activities and BMR or SMR, hence generating negative relationships.

The increased-intake and allocation models have been widely used to interpret the relationship obtained between BMR and fitness, life-history, and behavioral traits. However, if reasonable arguments can be made to expect a positive and/or a negative relationship between BMR and energy-demanding activities, one may wonder whether these models are really helpful in making sense of the mixed results obtained and move the field forward. Or perhaps these models are simply convenient ways to "escape" the possibility that BMR and SMR do "not have as great an influence on life history and fitness traits as the current theoretical mindset would have us believe" (Schimpf *et al.* 2012)? Many studies on BMR and SMR have been framed as if they were testing or supporting the increased-intake vs. allocation principles as alternative hypotheses. This is absolutely correct, but what if no relationship at all was obtained because both processes are cancelling each other out (e.g., if a high BMR is associated with both high energy intake and high maintenance costs)?

Context-Dependence Hypothesis and the Y-model

In an attempt to reconcile the diversity of results obtained, the "context-dependence" hypothesis predicts that high-BMR individuals will have higher fitness when environmental conditions are productive, whereas low-BMR individuals will have higher fitness when environmental conditions are unproductive (Burton *et al.* 2011). The context-dependence
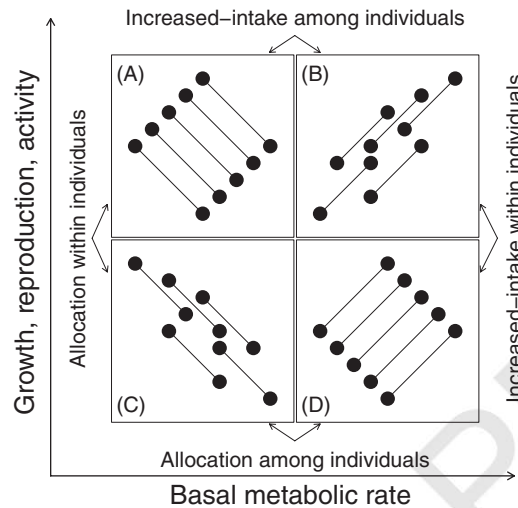
Figure 14.1. Schematic representations of among-individual correlations (r_{ind}) and within-individual correlations (r_e) between basal metabolic rate (BMR) and the energy invested in any energy-demanding activity (e.g., growth, reproduction, locomotion). Repeated pairs of measurements on each individual are represented by dots connected by a line. Panel A represents a scenario where the increased-intake principle applies among individuals (yielding a positive r_{ind}) and the allocation principle applies within individuals (yielding a negative r_e). The increased-intake principle may also apply within individuals (e.g., if increases in BMR allow a greater food intake, yielding a positive r_e; panel B). By contrast, the allocation principle may apply at both levels, yielding negative r_{ind} and r_e (panel C). Perhaps less intuitively, but still possible, would be the scenario in which high-BMR individuals have less energy available for other activities (negative r_{ind}), but when a given individual increases its intake it has more energy to invest into reproduction (positive r_e; panel D).

hypothesis can in fact be seen as a verbal representation of the Y-model envisioned by Van Noordwijk and de Jong (1986) applied to the case of BMR. Let's imagine that the increased-intake principle applies among individuals and the allocation principle applies within individuals (Figure 14.1A). Let's also imagine that as environmental productivity increases, variation in acquisition also *increases* to a point where there is relatively more variation in acquisition than allocation among individuals. This would generate a positive correlation between BMR and reproduction in productive environments, but a negative correlation in unproductive environments, as predicted by the context-dependence hypothesis (Burton *et al.* 2011).

However, we currently know little on the relative changes in acquisition vs. allocation across environmental gradients. What if the variation in resource acquisition *decreases* as environmental productivity increases? Assuming the pattern in Figure 14.1A still holds, then one should expect a negative correlation between BMR and reproduction in productive environments. To add even more complexity, we can also imagine other scenarios whereby plastic changes in BMR within an individual follow the increased-intake principle (Figure 14.1B) or that compensation occurs among individuals (Figures 14.1C and D). If the same principles apply at both levels of variation (Figures 14.1B and C), then the phenotypic correlation (r_P) will be reflective of the principle governing energy budgets. However, if different principles apply among vs. within individuals (Figures 14.1A, B, C and D), then the r_P will not tell much about the nature of the association between

components of energy budgets and the processes that governs them as r_P depends on the relative amount of among- vs. within-individual variation (van Noordwijk & de Jong 1986). In the face of a nonsignificant r_P, for example, one could erroneously conclude that both increased-intake and allocation principles are not applicable, while both processes are occurring at the same time!

A r_P is shaped by correlations at the among-individual level (r_{ind}) and the within-individual level (r_e) (Dingemanse & Dochtermann 2013). Since repeatability of MR averages ~0.35 in fishes and wild mammals (White *et al.* 2013), r_P should be influenced 1.86x [i.e., $=(1-0.35)/0.35$] more strongly by r_e than r_{ind} in these taxa. By contrast, repeatability of MR in birds and reptiles appears to be relatively higher at 0.56 and 0.67 (White *et al.* 2013), respectively, and in these cases the influence of r_e on r_P should be 0.79x and 0.49x weaker than r_{ind}. All else being equal, differences in the sign and relative magnitude of r_{ind} and r_e can generate a range of values for r_P. Therefore, a better understanding of how the increased-intake and allocation models govern animals' energy budget can be reached by testing whether two components of the energy budget are correlated at the among- and within-individual levels (Dingemanse & Dochtermann 2013).

From Individuals to Species

The discrepancy between correlations obtained at the intra- and inter-specific levels of variation (see section 2) may be explained by the same logic as that described by van Noordwijk and de Jong (1986). One may be tempted to think that variation in allocation might be less important at the inter-specific level as this process is best thought of occurring within individuals. However, some species may need to allocate more energy to particular functions than others: in endotherms, those in colder environments may need to allocate more to heat production, iteroparous species presumably allocate less to reproductive tissue than semelparous species, those with poor quality diet (herbivores) may allocate more to digestion and so on (see also Chapter 18, this volume). In fact, some patterns of allocation may be more evident across species than within species, because there has been substantial time for selection to create larger relative differences in trait means.

A positive inter-specific correlation between maintenance costs and reproduction or activity may occur if species vary in total acquisition despite genetic tradeoffs that occur within species (Agrawal *et al.* 2010). To understand how processes occurring within species can determine patterns across species, we need information on the genetic variation in acquisition and allocation. Extending Van Noordwijk and de Jong's (1986) Y-model to genetic correlations, Houle (1991) showed theoretically that if there were more loci involved in resource acquisition than in allocation of that resource, the genetic correlation could be positive in spite of a fundamental allocation trade-off.

A positive genetic correlation between RMR and exploratory behavior in deer mice is concordant with a positive inter-specific correlation between the two traits among species of the Neotominae subfamily (Careau *et al.* 2011). As suggested by this and few other studies, genetic correlations may bias the direction of adaptive divergence across species along "genetic lines of least resistance" (Schluter 1996). These positive genetic and interspecific correlations between BMR and behavior do not imply that there is no energy allocation trade-off occurring, perhaps rather that Neotominae species have more energy to devote to both as they evolved toward higher energy budgets (Houle 1991, Mueller & Diamond 2001). Presumably, when selection or drift is strong enough the bias caused by genetic correlations can be broken, as for example the interspecific correlation between BMR and exploratory behavior is negative across a wider range of Muroid species (Careau *et al.* 2011).

METABOLIC SCOPES: A DIFFERENT KIND OF ENERGETIC BUDGETING

Acquisition and allocation processes deal with energy mainly as a quantity, but energy is absorbed or expended over a period of time (just as MR is measured in Watts; $J \cdot s^{-1}$); therefore, the most relevant way to conceptualize energy budgets is with the use of rate functions. Animals can only do so many things at once, and the ability to perform multiple O_2-consuming physiological tasks is limited by an animal's *absolute* or *factorial aerobic scopes* (AAS and FAS). Previous authors have argued that natural selection should act on the ability to maximize or optimize AAS (Fry 1975; Guderley & Pörtner 2010). In fact, the "energetic definition of fitness" is based on the principle of allocation (see section 3.1) and stipulates that natural selection should maximize the capacity to channel "residual energy" (i.e., energy in excess of maintenance, as represented by AAS) toward reproduction (Artacho & Nespolo 2009).

The boundaries of an animal's capacity to utilize energy aerobically are set by BMR or SMR (the metabolic "floor") and MMR (the "ceiling"). As these measures are made under contrasting circumstances, it is perhaps not surprising that the factors contributing to BMR (or SMR) and MMR can be somewhat different (i.e., the liver and kidney for BMR and musculature for MMR, Weibel *et al.* 2004, Wone *et al.* 2009). Analysing the difference between the two (AAS) or their ratio (FAS) may yield results otherwise undetectable from the individual analyses of the two components (see Boxes 14.2 and 14.3 for case studies).

Box 14.2. The Importance of FAS in Small Rodents

In a wild population of eastern chipmunks (*Tamias striatus*) FAS was not influenced by sex, age, or M_b, but significantly increased as the winter approached (Careau *et al.* 2012). Notably, FAS was strongly negatively correlated with the number of conspicuous botfly larvae that parasitize chipmunks, being the result of a differential effect of parasites on RMR (increase) and cold-induced MMR (decrease). Perhaps not coincidentally, botfly parasitism in this population negatively influences the likelihood of surviving winter (Careau *et al.* 2013a). Chipmunks survive winter by storing food in their burrow and using torpor, which simultaneously requires low maintenance costs (to conserve energy) and high thermogenic capacity (to warm up from a torpid state). Hence, parasitized chipmunks with low FAS may be doubly penalized as they have lower thermogenic capacity (cold-induced MMR) and higher maintenance costs (RMR). In fact, a comparative analysis of FAS in across rodent species reported a strong negative correlation between FAS and T_a, suggesting that torpor is an adaptation that entails a high FAS in cold climates (Careau 2013).

Box 14.3. The Importance of AAS in Young Marine Fish

Lumpfish (*Cyclopterus lumpus*) possess a ventral adhesive disc, which allows them to easily switch between actively swimming and remaining perfectly still even when exposed to wave action. Juveniles spend large amounts of time clinging to rocks and seaweed which probably reduces their predation risk, but also results in a 6–12% decrease in overall energetic costs. This decrease is modest, indicating that swimming at routine speeds while foraging is a relatively cheap activity. However, if individuals were to swim at speeds that would be most efficient, this activity alone would use approximately 46–70% of total AAS. This could restrict the ability to

> carry out other important aerobic processes while swimming, including growth, which is critical during this life-stage. Therefore, in addition to reducing overall energy expenditure, the behavioral flexibility to adjust locomotor strategies provides a means to save energy for other activities within a limited AAS (Killen *et al.* 2007a; Killen *et al.* 2007b).

The way that aerobic scopes are conceptualized and applied varies among researchers working on different taxonomic groups. In endotherms, for example, aerobic scope is generally presumed to be most important over short temporal scales, for trade-offs between functions such as thermoregulation and locomotion. For ectotherms, however, aerobic scope also encompasses more protracted aerobic processes such as growth and reproduction (Guderley and Pörtner 2010), whereas in endotherm research these functions are usually studied from the perspective of *sustained metabolic scope* (SusMS) or *nonresting energy expenditure* (NREE). Ectotherms have a much lower AAS as compared to endotherms of similar size, and so over prolonged periods, small differences in activity level or any other source of metabolic loading can accumulate to cause trade-offs with growth or reproduction within an individual's aerobic scope (Guderley & Pörtner 2010). Endotherms have a much greater AAS as compared to similar-sized ectotherms, such that the long-term effects of locomotory activity on growth or reproduction are relatively trivial.

An examination of the proxies used for estimating aerobic scope in various taxa could be an effective means of inspiring new ways of thinking about research examining links between metabolic and behavioral traits. For example, for endotherms there has been considerable interest in the levels of DEE that can be sustained for long periods (Peterson *et al.* 1990). For endotherms, SusMS represents the upper boundary on the sum total of activities in which endotherms can engage over a prolonged period (Speakman 2000). This is the precise reason why researchers studying ectotherms have become interested in the potential effects of AAS on behavior and ecological phenomena (Killen *et al.* 2007b; Killen *et al.* 2012). Many of the same behavioral constraints and ecological effects stemming from a limited AAS in ecotherms could apply to SusMS in endotherms and vice-versa.

ENERGETIC CONSTRAINTS ON INDIVIDUAL BEHAVIOR

A large number of recent studies have examined co-variation in metabolic and behavioral traits among individuals (reviewed in Careau & Garland 2012; Krams *et al.* 2013). A general finding stemming from this body of work is that there is no single cause-and-effect mechanism driving these relationships, but that the direction of the effects is dynamic and shifts in different contexts and environments (Killen *et al.* 2013). However, the remarkable energetic differences between endotherms and ectotherms are an unexploited basis for achieving a further understanding of such relationships, as we now illustrate.

Spontaneous Activity

The effects of T_a pervade the behavioral and physiological differences observed between endotherms and ectotherms. Ectotherms tend to decrease activity at cooler T_a, while endotherms may either attempt to decrease energetic costs by entering torpor (Geiser 2004) or reducing activity (Humphries *et al.* 2005) or they may increase metabolic heat

production, either through shivering thermogenesis or via physical exercise. If the heat generated through activity can substitute for heat required for thermoregulation, then activity in cold environments may be energetically free for endotherms in some situations (Humphries & Careau 2011). Still, for endotherms, MR can increase as T_a becomes colder until animals approach MMR. This is in contrast to ectotherms, which tend to increase SMR as T_a becomes *warmer* until SMR is equal to MMR and AAS is equal to zero (Pörtner & Farrell 2008). A key difference is that the increase in MR with decreasing T_a in endotherms is due to increased thermoregulation and/or activity while the increase in MR in ectotherms with T_a is mainly due to increasing maintenance requirements, but the symmetry of these opposite responses is striking.

For both endotherms and ectotherms, the spontaneous activity of individuals will also affect the way that they experience environmental variation over short temporal scales. Exposure to different microhabitats might cause bold or active individuals to experience more variability in extrinsic factors (e.g., T_a, hypoxia, parasites). More active individuals may therefore require increased regulatory performance (Husak *et al.* 2009) to maintain activity and a high level of dynamic performance during acute exposure to a range of environmental conditions, or perhaps having a wider thermal performance breadth than individuals that are shier or less active. For endotherms, activity-thermoregulatory heat substitution (Humphries & Careau 2011) may allow individuals that are intrinsically more active to temporarily exploit colder environments that would be off-limits to more sedentary individuals.

Foraging

An interesting example of how energetic constraints affect foraging is the differential responses of endotherms and ectotherms to spatial variation in prey density (Helfman 1990; Killen *et al.* 2007b). In many species individuals switch between alternate foraging strategies that differ in the level of energetic investment (e.g., active searching vs. sit and wait ambush). Curiously, individual endotherms and ectotherms choose opposite strategies in relation to prey density. Endotherms switch to the more costly foraging strategy only at relatively high prey densities (Rudolph 1982) while ectotherms switch to the more expensive strategy when prey densities decrease (Killen *et al.* 2007b). The explanation is that while endotherms maximize energy intake to satisfy high BMR and activity costs, ectotherms need only meet some minimal rate of energy intake. A promising area for future research will be to examine how foraging strategies may vary among individuals of the same species in relation to metabolic traits. At certain prey densities some individuals may become more active and susceptible to predation as a function of intrinsic physiological traits such as metabolic demand or AAS.

An important constraint for ectotherms stemming from foraging is the proportion of AAS that must be directed toward digestion and assimilation of food and the resulting trade-offs with other physiological functions. In some reptiles and fishes, MR measured after feeding can be substantial and exceed that measured during peak exercise (Fu *et al.* 2008). Endotherms also require aerobic capacity to be re-routed while processing a meal, but the trade-offs with other physiological functions are much less severe (e.g., Nespolo *et al.* 2003). It is also important to note that in endotherms the heat generated through digestion can substitute for heat production required for thermoregulation (Lovvorn 2007). As a result, individual variability in the energetic costs and efficiency of digestion may be a much less important factor constraining the behavior of endotherms as compared to ectotherms, where it can be significant (Dupont-Prinet *et al.* 2009).

Habitat Selection

Although the capacity for performance in endotherms can be affected by abiotic factors such as T_a, mainly due to effects on muscular activity stemming from regional homeothermy, these effects are much more pronounced for ectotherms (Angilletta *et al.* 2010). It is therefore possible that, compared to ectotherms, habitat selection in individual endotherms might be less driven by abiotic environmental factors and instead primarily affected by factors such as food availability or predation. Individual endotherms with decreased thermosensitivity could have a wider range of microhabitat options, but will still be bound to habitats that can satisfy the demand of an elevated BMR. For individual endotherms, a major benefit of a reduced BMR could be continued activity and foraging in relatively cold habitats with a higher threshold for starvation tolerance before either torpor or thermal conformity become necessary.

Habitat selection for ectotherms will also be affected by food availability and safety, but for them abiotic characteristics of environment itself may have a much stronger effect on the performance capacity of individuals (Claireaux *et al.* 2000). An interesting possibility which has not been investigated is that among individual ectotherms, bolder or more active individuals might select conditions (e.g warmer T_a) that maximize AAS and facilitate an active lifestyle; shy individuals might prefer conditions (e.g., cooler T_a) that minimize energetic costs. For ectotherms more so than endotherms, the environment itself could facilitate the expression of behavioral phenotypes or even cause bold and shy individuals to have different priorities when selecting habitats.

CONCLUSIONS AND FUTURE PERSPECTIVES

As energy is quantifiable and comparable across many levels of or biological organization (cells, organs, individuals, population, species), the field of energetics lends itself to integrative studies linking patterns and processes at multiple levels. Although it is well known that variation in MR is determined by several intrinsic and extrinsic factors, few studies have evaluated the relative importance of many factors simultaneously, let alone the causal relationships between them. As many studies on the increased-intake and allocation processes were conducted at the phenotypic level, we still do not have a clear picture of how these processes govern energy budgets of animal. Together, changes in the relative importance of these two processes may produce contrasting correlations across levels of variation (e.g., within individuals, among individuals, among species) and potentially underlie the context-dependence nature of the relationship between maintenance costs and fitness or behavior. Our attempt to compare and integrate differences in the energy budgets of ectotherms and endotherms yielded interesting possibilities as to how the relative magnitude of individual variability should differ in these taxa, with implications on ecologically relevant aspects such as spontaneous activity, foraging patterns, and habitat selection.

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Queries in Chapter 14

Q1.   We have shortened the running head. Please check and advice