Energy metabolism and animal personality

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In this paper we show how animal personality could explain some of the large inter-individual variation in resting metabolic rate (MR) and explore methodological and functional linkages between personality and energetics. Personality will introduce variability in resting MR measures because individuals consistently differ in their stress response, exploration or activity levels, all of which influence MR measurements made with respirometry and the doubly-labelled water technique. Physiologists try to exclude these behavioural influences from resting MR measurements, but animal personality research indicates that these attempts are unlikely to be successful. For example, because reactive animals "freeze" when submitted to a stress, their MR could be classified as "resting" because of immobility when in fact they are highly stressed with an elevated MR. More importantly, recent research demonstrating that behavioural responses to novel and highly artificial stimuli are correlated with both behaviour and fitness under more natural circumstances calls into question the wisdom of excluding these behavioural influences on MR measurements. The reason that intra-specific variation in resting MR are so weakly correlated with daily energy expenditure (DEE) and fitness, may be that the latter two measures fully incorporate personality while the former partially excludes its influence. Because activity, exploration, boldness and aggressiveness are energetically costly, personality and metabolism should be correlated and physiological constraints may underlie behavioural syndromes. We show how physiological ecologists can better examine behavioural linkages between personality and metabolism, as required to better understand the physiological correlates of personality and the evolutionary consequences of metabolic variability.

Although inter-individual variation in phenotypic traits is omnipresent, it has historically been considered to be noise superimposed on the evolutionarily important signal, the population mean. Recently, however, researchers from a broad array of ecological sub-disciplines – population biology (Bolnick et al. 2003), epidemiology (Lloyd-Smith et al. 2005), endocrinology (Williams 2008), behavioural ecology (Wilson et al. 1994, Sih et al. 2004a, Réale et al. 2007), and physiology (Bennett 1987, this paper) – have begun to consider inter-individual variation as an important ecological and evolutionary characteristic of wild populations. The burgeoning field of animal personality seeks to explain the maintenance of variation in numerous behavioural traits, including exploration, boldness, activity and stress response among others, by examining their fitness in a variety of ecological, developmental, and demographic contexts. In this forum, we argue that personality may explain some of the large observed variation in rates of energy metabolism in animals and we explore potential synergies between personality and metabolism research.

Energy metabolism: the mystery of intra-specific variation

Energy is the common currency of life, as it fuels biological processes at every level of organization. Metabolic rate (MR) – the rate at which an animal oxidizes substrates to produce energy – is thus a fundamental measure in ecology and evolution (Brown et al. 2004). The MR of an animal while behaving normally in its natural habitat, averaged over the course of a day, is termed field MR or daily energy expenditure (DEE). DEE is usually measured using doubly-labelled water and, over the last several decades, has been measured on an expanding number of species (Speakman 1997, Anderson and Jetz 2005). To date, however, basal and resting MR are by far the most-studied aspects of energy metabolism in vertebrates (McNab 2002, Cruz-Neto and Bozinovic 2004). Differences between basal and resting MR refer to the laboratory conditions under which O_2-consumption or CO_2-production of an animal is measured by respirometry. Basal MR is the lowest measured MR of a post-absorptive, normothermic adult individual in

its thermoneutral zone during its inactive period (McNab 1997). Resting MR is a slightly less rigorous measure because it allows violation of some 'basal' conditions, such as post-absorptive state, while still requiring that the animal is resting in its thermoneutral zone (Speakman et al. 2004). Because the difference between basal and resting MR is generally small, the two terms are often used interchangeably in the literature. For this reason we will refer to both as resting MR to simplify terminology in this paper.

The rationale behind measuring the MR of an animal under standardized conditions is to obtain a repeatable (Nespolo and Franco 2007, but see Russell and Chappell 2007) measure of the minimal metabolic level required to maintain physiological homeostasis, or the minimal cost of living (Hulbert and Else 2004). In this view, resting MR is the 'idling cost' of the metabolic machinery required to support a given lifestyle or rate of DEE (Mueller and Diamond 2001). Inter-specific variation in resting MR reflects evolution of the metabolic machinery necessary to generate high MR during energetically demanding periods such as reproduction and sustained physical activity (Daan et al. 1990). 'Fast' species with lifestyles involving high DEE are forced to process more food and inevitably excrete more waste products at a faster rate, which presumably leads to an increase in the relative masses of organs involved in these processes, compared with 'slow' species. Even though heart and kidneys constitute a small fraction of an animal's lean body mass (M_b) they have very high mass-specific MR and contribute disproportionately to the whole-animal resting MR. For example, heart and kidney mass explain 50% of mass-corrected resting MR variation in 22 bird species (Daan et al. 1990). Resting MR usually represents 30–40% of DEE in free-living animals (Ricklefs et al. 1996, Speakman et al. 2003) and inter-specific comparisons show a positive correlation between resting MR and DEE, suggesting a functional link between the two (Daan et al. 1990, Nagy et al. 1999).

To date, resting MR has been measured for over 600 mammal and 300 bird species (McNab 2002, White and Seymour 2004, Speakman 2005). Body mass (M_b) is the main factor explaining inter-specific variation in resting MR, accounting for up to 95% of the variation (Fig. 1). Recent comparative studies have shown that factors such as phylogeny, climate, water accessibility, temperature, habitat productivity and diet explain some of the remaining 5% of inter-specific variation in resting MR (McNab 2002, Lovegrove 2003, Williams et al. 2004, Careau et al. 2007). These comparative studies show that resting MR is a physiological trait of ecological and evolutionary importance, since it can respond to selective pressures as species exploit different ecological conditions.

At the intra-specific level M_b has a far weaker – sometimes non-significant (Johnston et al. 2007a) – effect on resting MR (Fig. 2). Despite rigorous standardization of lab measurement conditions, there remains considerable inter-individual variation in resting MR (Speakman et al. 2004). Evolutionary physiologists recognize the importance of individual variation as the grist for evolution and adaptation at the population and species levels and frequently invoke this variability to explain intra-specific diversity in a variety of ecological variables such as competitive ability, parasite load, social rank, mate choice,
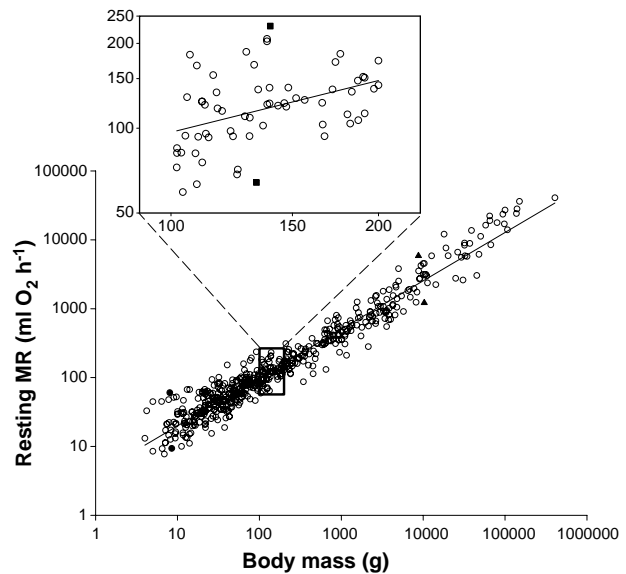

Fig. 1. Inter-specific variation in resting metabolic rate (MR) of 530 mammal species across a five-order-of-magnitude range in body mass (data from Lovegrove 2000). Although body mass explains 95% of the variation in resting MR observed across all mammals, within narrower ranges of body size variation mass accounts for a much smaller proportion of resting MR variation. For example, from 100 to 200 g (inset), mass accounts for only 17% of variation in MR which varies 3.6-fold between 133 g tenrecs *Hemicentetes semispinosus* (64 ml O_2 h^{-1}) and 139 g cotton rats *Sigmodon hispidus* (230 ml O_2 h^{-1}) (black squares). Large differences in resting MR of similar-sized mammals occurs at all body masses, including a 6.4-fold difference between the MR of 8.1 g shrews *Sorex araneus* (60.2 ml O_2 h^{-1}) and 8.5 g roundleaf bats *Hipposideros galeritus* (9.4 ml O_2 h^{-1}) (black circles) and a 4.8-fold difference between the resting MR of 8 kg wild dogs *Lycaon pictus* (5862 ml O_2 h^{-1}) and 10 kg echidnas *Zaglossus bruijni* (1215 ml O_2 h^{-1}) (black triangles).
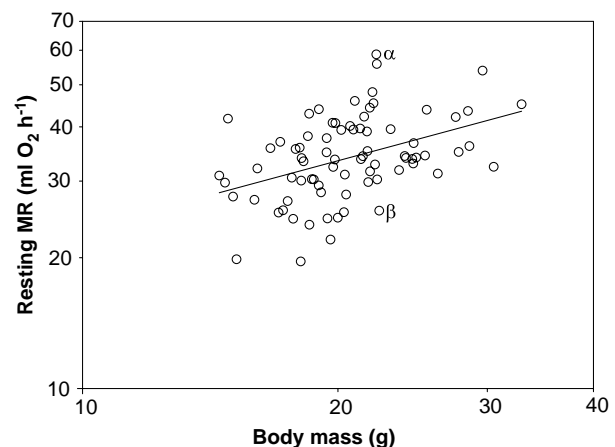

Fig. 2. Inter-individual variation in resting metabolic rate (MR) of 78 adult *Peromyscus maniculatus* held under lab conditions (V. Careau pers. comm). Body mass explains 18% of the variance in resting MR. Although individuals α and β have similar body mass, their resting MR varies from 25 to 59 ml O_2 h^{-1}, a 2.4-fold difference.

habitat selection or migratory patterns at the individual level (Townsend and Calow 1981, McNab 2002). Resting MR is supposedly subjected to selection, as it shows heritability values ranging from 10 to 40% (Dohm et al. 2001, Nespolo et al. 2003, Sadowska et al. 2005, Rønning et al. 2007). However, attempts at explaining intra-specific variation in resting MR continue to be much less successful than inter-specific comparisons (Geluso and Hayes 1999, Speakman et al. 2004, Vézina et al. 2006). Many studies of intra-specific variation focus on differences between populations (Thomas et al. 2001, Lahti et al. 2002, Careau et al. 2007), as though the mean (a population statistic) were inherently more important than variation around the mean (the individual measures). This focus on central tendencies was described 20 years ago as the "tyranny of the golden mean" by Bennett (1987). Although the analysis of inter-individual variation in resting MR offers the potential to link energy metabolism to other fields such as ecology, behaviour, evolution and genetics, it continues to receive insufficient attention in physiological studies (Hayes and Jenkins 1997). How else can we explain the fact that a difference as small as 10% (often less!) between the mean resting MR of two populations, groups, or treatments can be the subject of pages of discussion while variation as large as 200% in resting MR among individuals does not even merit mention (Meagher and O'Connor 2001, Thomas et al. 2001, Mathias et al. 2006, Scantlebury et al. 2007)? Many comparative eco-physiologists may implicitly assume that among-individual variation in resting MR is simply noise that has the undesirable effect of obscuring an underlying ecological or evolutionary signal. Williams (2008) has recently raised the same critique with regard to inter-individual variation in hormone levels.

Metabolic (and hormonal) measurements do indeed include noise, which may be partitioned into two main categories – measurement error (equipment and calculation error) vs biological variation which is an attribute of the individual being measured and may not be "error" at all. Measurement error in animal respirometry studies may originate from a variety of sources. Among others, these include drift in gas analyzers, errors in flow rate, incomplete scrubbing of gases, error in ambient or body temperature (T_b) measurements, and incorrect assumptions of respiratory quotient (Koteja 1996b, Witters 2001). However, due to refinements in equipment electronics, the increasing use of mass-flow controllers, and rigorous standardization and calibration of open-circuit respirometry systems equipment and calculation-based errors are typically small and likely amount to an error variance of about 5–10% of the measured value (Speakman et al. 2004). Indeed, repeatability studies suggest that little of the variation in resting MR can be attributed to analytical imprecision (Johnstone et al. 2005, Nespolo and Franco 2007). Visual inspection of plots of resting MR vs M_b in birds and mammals typically indicates up to six-fold inter-specific variation (Fig. 1) and two-fold intra-specific (Fig. 2) variation in the resting MR of similar-sized animals. Biological variation introduced by differences in the attributes of individuals thus seems to be far more important than measurement error.

Physiologists have long recognized that a variety of ecological factors can influence an individual's resting MR, such as diet composition (Cruz-Neto and Bozinovic 2004) local or seasonal acclimation (Broggi et al. 2007), and parasite load (Delahay et al. 1995, Scantlebury et al. 2007). Morphological attributes, such as lean M_b and the relative size of metabolically-active vs inactive tissues and organs (e.g. brain, liver, kidney, heart and digestive tract vs fat, bones, water, hair or feathers) introduce variation in O_2-consumption for an animal of a given M_b (Johnstone et al. 2005, Brzek et al. 2007, Russell and Chappell 2007). In mice, *Mus musculus,* for example, the liver alone can explain up to 33.5% of the residual variation in resting MR although it represents 5% of total tissue mass (Selman et al. 2001). However, there is little emerging consensus on the effects of organ size on resting MR, with several thorough studies explaining a relatively small proportion of observed intra-specific variation in metabolism (Konarzewski and Diamond 1995, Koteja 1996a, Krol et al. 2003). Furthermore, the organs identified as significant contributors to resting MR differ widely among studies (Speakman et al. 2004). Clearly, there are large inter-individual differences in resting MR still unaccounted for by ecological and morphological attributes.

Although rarely considered in metabolic studies, behavioural attributes can also introduce variation. For example, hyperactivity or an exaggerated stress response may cause certain individuals to maintain a higher activity level or simply greater muscle tonus during measurement of MR compared with calm, more relaxed individuals. If individuals vary randomly over time with regards to their activity or stress levels, then this variation can be viewed as noise. However, a variety of individual behavioural traits such as activity levels and the type or strength of a stress response are repeatable and intrinsic attributes of individuals that we now refer to as personality. Because systematic differences in personality between individuals appear to have a heritable basis and to be implicated in a large number of fitness-related traits and decisions, personality is receiving increasing attention from evolutionary ecologists (Wilson et al. 1994, Sih et al. 2004a, Réale et al. 2007). From the point of view of metabolism and animal energetics, however, personality has received surprisingly little attention. On one hand, personality may be perceived as introducing "error" into estimates by artificially inflating measures for one behavioural type relative to another, which might otherwise express the same MR if in the same relaxed state. On the other hand, differences in personality may also be related to true differences in resting MR and DEE and so be an important individual attribute that has been largely overlooked.

What is personality?

Variation around the "golden mean" has also been long-neglected by researchers in animal behaviour, and only recently has begun to receive more attention (Wilson et al. 1994, Sih et al. 2004a). Animal personality (also referred to as behavioural syndromes, coping styles, and temperament) offers a promising new and holistic perspective on animal behaviour (Sih et al. 2004b, Bell 2007). Personality refers to individual behavioural differences that are consistent – or largely maintained – over time and/or across situations

(Réale et al. 2007). Animal personality represents a fundamental shift in thinking because the "golden mean" becomes meaningless and individual differences become the essence (Wilson et al. 1993). That individuals often differ consistently in how they behave has been reported for a variety of mammals (including humans, Nettle 2006), birds, fish, reptiles, amphibians, insects, spiders and cephalopods (Gosling 2001). Individuals may consistently differ in one or more personality traits, such as boldness, aggressiveness, reactivity, sociability, exploration or activity levels (Réale et al. 2007). The so-called "laid back, relaxed, placid, or calm" vs "high-strung, restless, jumpy, or nervous" natural dispositions of animals referred to by physiologists (Mueller and Diamond 2001) actually represent personality traits. Personality is considered an intrinsic characteristic of the individual and thus should not be confused with non-repeatable variation in behaviours that may be determined by recent experience or environmental (extrinsic) conditions, as is the case for social status (Dingemanse and de Goede 2004).

Ecologists are increasingly interested in animal personality due to its ubiquity, its underlying physiological or neuroendocrine correlates, and its heritability and probable relation to fitness (Koolhaas et al. 1999, Réale et al. 2000, Dingemanse et al. 2002, Dingemanse and Réale 2005, Bell 2007). Differences in personality traits or combinations of traits have been shown to have consequences for individual fitness through their effect on predation rates (Réale and Festa-Bianchet 2003, Bell and Sih 2007), the form and outcome of competition for females and food (Dingemanse et al. 2004), or the response to social challenges (Dingemanse and Réale 2005, Sinn et al. 2006). The holistic nature of personality allows the identification of suites of correlated behaviours across contexts (Sih et al. 2004a, Bell 2007). Indeed, an individual's behaviour within one ecological context is often positively correlated with that individual's behaviour in other contexts. Individuals that are aggressive towards prey tend also to be aggressive in other contexts such as in interactions with conspecifics and predators. Aggressive individuals also tend to be bold and explorative while docile individuals tend to be shy and avoid novel situations (Sih et al. 2004a). It has recently been shown that the strength of correlations among behavioural traits (e.g. aggressiveness and boldness) can depend on environmental circumstances, such as the presence of predators (Bell and Sih 2007, Dingemanse et al. 2007).

Differences in the reaction of individuals to capture and handling may be indicative of differences in their personalities (Réale et al. 2000, 2007). Anyone who has captured and handled enough animals intuitively knows that their reactions towards handlers differ; some are hyperactive and aggressive while others freeze when handled. These simple observations represent differences in coping styles (Koolhaas et al. 1999). When submitted to a stress, 'proactive' individuals tend to actively manipulate the situation that causes the stress by avoidance or aggression (escape in this case), a response accompanied by a combination of neurophysiological mechanisms that increase heart rate, muscle tonus, O_2 and glucose consumption. At the opposite end of the stress response axis, 'reactive' individuals possess hormonal mechanisms that allow them adjust to stressful situations by immobility and passiveness (by freezing in this case). These behavioural differences have a genetic basis and are thought to be causally related to differences in the (re)activity of the vertebrate neuroendocrine system (Koolhaas et al. 1999). Studies on birds and mammals have suggested that proactive individuals are usually more active, explorative, aggressive and bold than reactive individuals (Koolhaas et al. 1999, Groothuis and Carere 2005). There is growing evidence that coping styles in vertebrates have been shaped by selection and form a general adaptive response to everyday challenges in natural habitats (Øverli et al. 2007). By being more explorative, aggressive and bold, proactive individuals may expend energy at higher rates than reactive individuals, thus generating a spectrum of metabolic rates within species, akin to the slow–fast metabolic continuum recognized among species (Lovegrove 2003).

Because individuals with different personalities will react differently to the same treatment, personality is important for the design and interpretation of many experiments (Groothuis and Carere 2005). Ignoring personality traits may create serious methodological issues on measures considered important by ecologists. For example, because shy individuals are less frequently observed and are less trappable, differences in personality will introduce a bias in behavioural or capture–mark–recapture studies if not controlled for (Wilson et al. 1994). This is the trap-happy/trap-shy pattern well known to small animal trappers, especially those who use the doubly-labelled water (DLW) method to estimate DEE. This technique consists of injecting an animal with DLW, and taking an initial, post-equilibration blood sample, then releasing the animal for a multi-day sampling period, before trying to re-capture the animal for a second blood sample (Speakman 1997). The critical part of this method is the recapture because it must be done in a relatively short and fixed time window. Trap-shy individuals are – by definition – harder to catch and re-catch than trap-happy, which may create a bias in our sampling of DEE. The stress response to this relatively invasive technique (capture, handling, injection and bleeding), even though it may be relatively small in laboratory mice (Speakman et al. 1991), may also differ according to personality, hence introducing variation in estimates of DEE. There are reasons to believe that differences in personality may also affect the measurement of resting MR via respirometry (Hayes et al. 1992).

How is resting MR measured?

For decades, respirometry has been the standard technique in physiology laboratories for the measurement of resting MR. Typically, the technique requires measuring the extent to which O_2 is depleted or CO_2 accumulates in a restricted flow of air through either a low-volume metabolic chamber or a mask (Koteja 1996b, Witters 2001). Regardless whether measurements are made with chambers or masks, respirometry is likely to elicit a stress response. For analytical reasons, most chambers used to contain animals and air during respirometry trials are not much larger than the animal they contain (McNab 2006) and are usually devoid of bedding, water, food and any other form of

environmental enrichment. Researchers typically transfer animals from cages into chambers for a multi-hour respirometry run, then transfer animals back to their cages. Because T_b and M_b are important predictors of MR, researchers also frequently weigh and measure T_b before transferring animals into the respirometry chamber. All of these procedures require handling and restraint of animals in a new environment, which has the potential to induce significant stress. Presumably because of handling and the unfamiliar confines of a respirometry chamber, many animals are highly active during the first portion of a respirometry trial, exploring the chamber, scratching at the walls, and biting any exposed surfaces. Because researchers seek a precise, standardized, and comparable measure of resting MR this activity is viewed as a source of error. To minimize such error, usually only the portion of the respirometry trial characterized by the lowest and most stable MR is analysed as 'resting' (Fig. 3a). All other portions of the trial, characterized by higher MR and therefore presumed to be contaminated by behavioural activity, are discarded. In some cases, researchers monitor behavioural activity during respirometry runs via direct observation, video cameras, or motion detectors, but in most cases decisions about which portions of a respirometry trial are retained and which are discarded are based only on the nature of the gas composition trace. Because resting measurements may not be comparable when different trial lengths are used (Hayes et al. 1992), respirometry runs are usually standardised to a fixed length within studies.
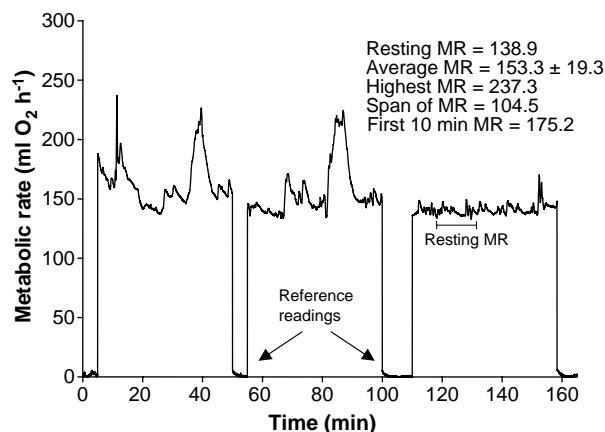

Fig. 3. Typical time course of O_2 consumption measured in a flow-through respirometry system. This trace refers to a wild-caught, 90 g eastern chipmunk. Trial begins by recording reference air entering the respirometry chamber. After 5 min the system switches to record air leaving the chamber, thus sampling the animal's metabolic rate (MR). Periodic reference readings are taken during the recording. The high peaks correspond to periods of activity whereas the low and stable portions of the curve correspond to resting periods. Resting MR is typically taken as the lowest MR during a 10-min period. We suggest that other measures, such as average MR throughout the trial and its standard deviation (mean $\pm$ SD), highest MR, span of MR (difference between highest and lowest MR), and average MR during the first 10 min of the trial may provide useful information related to personality.

Methodological linkages between personality and metabolism

Some observations arise out of the rapidly expanding literature on animal personality that we believe have particular pertinence to the measurement and interpretation of metabolic variability. In the following, we examine how consistent individual differences in personality may affect measurement of resting MR via respirometry and identify a series of predictions concerning the effect of personality in respirometry studies.

Individuals show consistent and marked differences in levels of activity and in their response to novel situations.

Whether animals freeze when placed in a respirometry chamber, settle down following a short burst of hyper-activity or remain hyper-active throughout even a multi-hour respirometry trial varies widely according to the general behavioural characteristics of the species and the personality of the individual under study. In most respirometry studies, if an individual never quiets sufficiently to generate a stable 'resting' MR during a trial of a fixed length, the run is rejected. Often, the individual is re-run on another day hoping for a more 'satisfactory' result or it may be excluded from the study altogether (Fig. 1 in Russell and Chappell 2007). Whether an individual is included or excluded from a respirometry study may thus depend on its personality. We expect that such exclusions are more common in studies of more active species where the proportion of 'restless' individuals is likely to be higher. If resting MR is positively correlated with activity level, then by excluding the most active individuals from the data set, researchers may bias their analyses, a bias that is linked to personality. Unfortunately, physiologists rarely indicate how many individuals were excluded from their study for causes of hyper-activity, so it is currently hard to evaluate the extent of this bias.

When introduced into a new environment or presented with a novel object, so-called 'fast-explorers' explore rapidly but superficially, whereas 'slow-explorers' explore slowly but thoroughly (Verbeek et al. 1994, Dingemanse et al. 2002). Because metabolic chambers can be considered a novel environment, different exploratory responses will influence measured metabolism. Even in confined spaces, such as cages and metabolic chambers, animals will differ in their degree of exploration. Some individuals will explore the same corner multiple times as they form an exploratory routine, thus remaining active for longer periods. Fast explorers may express high MR during the beginning of a respirometry run and then resort to resting whereas slow explorers may continue to slowly explore the chamber for longer, leading to a moderate and less variable MR over the entire run.

The two observations raised above will come as no surprise to researchers who regularly use respirometry. They recognize that just as some species are difficult to measure due to hyperactivity, some individuals also refuse to settle down in metabolic chambers. The widespread recognition

of individual variation in activity and exploration and its major effects on metabolic measurements is – of course – the primary reason why researchers have been so careful to define and measure metabolic traits in a manner that excludes as much of this behavioural variation as possible. It has also led some researchers to run individuals over multiple trials to habituate them to the procedure, before making actual measurements.

Some intense behavioural responses to novel situations and handling do not manifest themselves as easily observed motor activity responses, and these non-motor responses can persist for much longer than motor responses

Not only do individuals differ in the threshold at which they respond to a given stress stimulus, but they also differ in the time required to restore normal behaviour after a stress (Øverli et al. 2007). For example, Carere and van Oers (2004) showed that T_b (an important determinant of MR) of 'shy' individuals takes longer to return to a normal level after handling. Individuals that express a reactive coping style and remain motionless may give the false impression of resting when they are in fact exhibiting a strong and lengthy stress response to a novel situation. By excluding periods of activity from respirometry trials, researchers may think that they are eliminating the stress response from their metabolic measures when in fact they preferentially retain data which include elevated MR for reactive personality types. This is in part due to the necessarily subjective way in which resting MR is estimated from respirometry trials. It is easy to recognize periods of 'low' MR when they follow periods of 'high' MR (as in Fig. 3), but it is difficult to know whether a relatively flat trace is 'high' or 'low'.

The degree to which the influence of stress can be eliminated from respirometry estimates of MR will vary among individuals and species according to the form and extent of stress response that is expressed. These considerations are extremely important for respirometry because it suggests that the influence of personality is variably and incompletely eliminated from usual 'resting' MR measures. If some of the variance in estimates of resting MR reflects differences in the extent to which the animal relaxed during bouts of inactivity, then personality should leave a signal in intra- and inter-specific variability in resting MR. For example, because proactive individuals react actively to stress, they may evacuate the stress effectively and their following period of inactivity may be not influenced by stress, generating a low estimate of resting MR. It is possible that – contrary to intuition – individuals that are least active in the chamber are most likely to generate stress-inflated resting MR estimates because it is these individuals that are more likely to be characterized by long-lasting, non-motor stress responses. If this is true, we predict a negative correlation between frequency and intensity of activity bouts in chamber and resting MR estimate. In other words, proactive individuals get the stress out of their system by responding actively to a stress (leading to a low resting MR), whereas reactive individuals remain anxious for longer (leading to a higher MR, which is erroneously considered as resting). If stress is ineffectively eliminated from usual resting MR estimates, then we predict significant correlations between personality traits and usual resting MR measures. Habituation should have the effect of decreasing the measured resting MR over multiple respirometry trials.

Individual responses to novel situations are correlated with behavioural responses expressed under more natural circumstances

For great tits, *Parus major*, exploratory behaviour in laboratory conditions is related to both dispersal and the ability to monopolize clumped food in the wild (Dingemanse et al. 2003, Dingemanse and de Goede 2004). Thus, how an animal responds in one situation may well be indicative of its response in another often very different situation. This carry-over of behavioural responses between situations, termed the behavioural syndrome (Sih et al. 2004a), has interesting implications for metabolic studies because the response to handling and restraint in a metabolic chamber may inform us of its behaviour when returned to the wild. We do not yet know whether an animal that expresses high levels of activity and exploration in a metabolic chamber will also express high levels of activity and exploration in the wild, but the behavioural syndrome framework suggests that this may be the case. If behaviour in the laboratory and in the field prove to be correlated, this will have intriguing consequences for metabolic studies. Researchers may gain more insight into how traits such as DEE, home range size, or reproductive success correlate with resting MR by accepting and incorporating the variability that personality traits generate than by attempting to minimize or eliminate it. Like any field that goes to great methodological efforts to isolate a trait of interest from additional interacting traits, it is sometimes worth stepping back to consider what additional insights could be gained by also studying the trait when fully imbedded in its multifactorial complexity.

Regardless of whether the influence of personality is fully or only partially removed from estimates of resting MR, it may prove that by even partially removing the effect of personality from metabolic measures we have lost an important biological signal. Eco-physiologists question why intra-specific variation in resting MR is at best weakly correlated with DEE (Meerlo et al. 1997, Fyhn et al. 2001, Speakman et al. 2003) and fitness (Johnston et al. 2007b) when both are subject to selection and are logically related. Field measures of DEE and fitness, however, necessarily incorporate the effects of personality while lab measures of resting MR attempt to exclude them. We suggest that lab measures of MR may be more strongly correlated with DEE or fitness when they include some of the variability that personality necessarily generates. The intensity and frequency of activity bouts expressed in the respirometry chamber may prove to be correlated with DEE- and fitness-determining behaviours in the field.

A methodological framework for incorporating personality in metabolic measurements

Here we suggest how we might evaluate whether different responses to stress and/or novelty (different personalities) need to be taken into account when measuring, interpreting, and comparing metabolic traits. The principal questions are: "does the response to a novel environment (the metabolic chamber) affect or otherwise bias estimates of resting MR" and "does the effect/bias vary between personality types". To better evaluate the first question, we need more tests of whether habituation causes estimated resting MR to decline over repeated respirometry trials. If so, we need to know by how much and over how many runs resting MR estimates continue to decline. To answer the second question, one could measure behavioural responses to other novel situations prior to the first respirometry trial. Open field, hole board, and novel object tests (Réale et al. 2007) all allow researchers to quantify differences in how animals explore new environments (Verbeek et al. 1994, Dingemanse et al. 2002). Exploration intensity declines with the number of times the test is repeated in open field tests (Archer 1973, Dingemanse et al. 2002) and novel object tests (Mettke-Hofmann et al. 2006) as animals become habituated. However, individuals may not only differ in their original response to novelty, but also in the speed with which they habituate (but see Martin and Réale 2008a). Comparing the results of these standardized personality assays to the pattern of habituation observed across respirometry trials, would evaluate both the extent to which responses to novel environments bias estimates of MR and how this bias differs among individuals and personality types. At this effect, a reaction norm or random regression approach that allows to compare individual rate of habituation may be useful (Nussey et al. 2007, Réale et al. 2007).

Some personality tests could be incorporated into respirometry trials without inordinately complicating logistics. Tests could be as simple as recording whether the animal shows a 'fright response' to handling, since docility or stress coping styles are likely to explain part of the variation in MR during metabolic runs (Hayes et al. 1992). Urination and defecation behaviour following introduction into metabolic chambers can be considered as measures of personality or activity of the sympathetic nervous system in response to stress stimuli (Archer 1973, Walsh and Cummins 1976). Respirometry trials invariably include a measure of M_b and physiologists know that some individuals are harder to weigh than others because they never sit quietly on the scale, so recording the time it takes to weigh accurately an animal could be another indication of its docility and stress coping style. Docility scores assigned to each individual at capture and based on the response to handling have been shown to be related to cortisol hair concentration (Martin and Réale 2008b) and fitness in wild (Réale et al. 2000, Boon et al. 2007). During respirometry trials, one could measure more behavioural traits than just movement, including ventilation rate, heart rate, T_b, and even cortisol concentrations in hair samples. Video monitoring during MR measurements and subsequent analysis in terms of proactive vs reactive behaviours could reveal a link between metabolism and coping styles. Proactive individuals may be more likely to actively search to escape from the metabolic chamber (Koolhaas et al. 1999). In rodents, for instance, gnawing or scratching at physical structures of the metabolic chamber represents an attempt to escape (Lewis and Hurst 2004), which could be related to a proactive coping style. Finally, concurrent respirometry and physiological measures could elucidate interesting metabolic consequences of different stress responses. For example, measuring circulating cortisol level immediately at the end of a respirometry run (i.e. within 2–4 min after the opening of the metabolic chamber) will provide information on how stress influence MR measurements (Wikelski et al. 1999).

Interest in incorporating personality into measures of MR might motivate eco-physiologists to have a second look at old respirometry runs. For example, in addition to measures of resting MR based on standard criteria, one might also extract other features that measure the influence of activity on MR. These might include trends in activity and MR over the course of respirometry runs, highest spontaneous MR, the span of MR measured by the difference between lowest and highest MR, and the average MR throughout the trial and its variance (Fig. 3a–b). In other words, we invite physiologists to stop discarding so much potentially informative data!

However, rigorous evaluation of links between personality and resting MR must start with documentation of the repeatability of behavioural assays, metabolic measurements, and correlations between behaviour and metabolism. Researchers must be careful to investigate and report potentially confounding variables that may underlie correlations between personality and metabolism. Extrapolating personality-metabolism correlations observed in captivity to the wild requires comparisons of metabolic and personality measures obtained in captivity with those observed under more natural, free-ranging conditions. Free-ranging personality measures could include dispersal, home range size, general activity level, trappability (number of times trapped vs trap hour), agonistic interactions over food patch, reactions to predators, etc. Free-ranging metabolic measures could include estimates of DEE based on the DLW method or heart-rate monitoring (Butler et al. 2004).

Functional linkages between personality and metabolism

We argue that studies focusing on the ecological context and evolution of MR, whether resting MR or DEE, will benefit from the inclusion of personality. Activity and aggressiveness are personality traits that have long interested eco-physiologists because they should affect DEE, the establishment of dominance relationships, acquisition and defence of mates, food resources, space and, ultimately, the fitness of individuals. Considering the number of studies of resting MR and DEE, it is surprising how little we know about how activity and aggressiveness affect energy metabolism (Speakman and Selman 2003). Two competing models (termed performance and allocation models; Fig. 4)

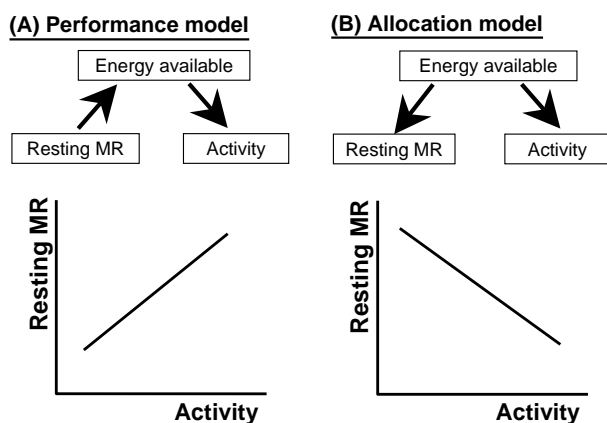## (A) Performance model

(B) Allocation model

Fig. 4. Hypothetical relationships between resting metabolic rate (MR) and activity. According to the performance model (A) resting MR determines the total energy available to an individual; individuals with higher resting MR are able to collect, process, and invest more energy in activity. In the allocation model (B), an animal must allocate a fixed amount of energy between competing processes such, as resting MR or activity. Animals with higher resting MR have less energy to spend in activity. Note that these models can be generalised to other energy-demanding personality traits or reproductive output (Speakman 1997, p. 25).

predict opposite relationships between MR and activity or aggressiveness. The performance model predicts a positive relationship between resting MR and activity or aggressiveness (Fig. 4a) because resting MR reflects the size of the digestive and metabolic machinery needed to capture, ingest, extract, and mobilize energy. Since active or aggressive individuals sustain high levels of energy throughput, they should require larger-than-average organ size for food and energy processing and hence higher-than-average maintenance costs (Daan et al. 1990). In contrast, the allocation model predicts a negative relationship between resting MR and activity or aggressiveness (Fig. 4b). Free-living animals often have access to limited amounts of food, resulting in a tradeoff between competing energy pathways. Energy spent in activity or aggressive behaviours necessarily limits the energy that can be allocated to resting MR.

The literature provides support for both models. Many studies on fish support the performance model by showing that more aggressive individuals have higher standard MR (the term 'standard' is specific for ectotherms because they have no thermoneutral zone, so is generally measured at a specified T_b). This relationship was found both within (Cutts et al. 1998, 1999) and among (Lahti et al. 2002) salmonid populations. Recently, Vaanholt et al (2007) supported the allocation model when they experimentally manipulated the amount of wheel running activity required for lab mice to obtain a food reward. The most active mice (those who had to run the most to obtain food) decreased their resting MR the most (by $\sim 50\%$), an effect that has been shown in several other studies manipulating workload (Table 4 in Wiersma and Verhulst 2005). Another example of a compensatory allocation between activity and resting MR comes from bird studies, where increasing the energy invested in activity (stimulated by elevated levels of testosterone or workload) resulted in a reduced resting MR (Deerenberg et al. 1998, Wikelski et al. 1999). Although these latter studies support the allocation model,

activity levels were dictated by a forced change in the environment rather than personality. Overall, activity and aggressiveness are certainly linked to resting MR, but the direction of the link and the underlying mechanisms are not yet well resolved.

One candidate for explaining links between certain personality traits and metabolism is the hypothalamic-pituitary-adrenal (HPA) axis which is involved in the regulation of both energy metabolism and the stress response (Jacobson 2005). Corticosteroids and insulin have reciprocal effects on energy storage and together they may constitute at least part of a multi-hormonal system that regulates overall energy balance (Dallman et al. 1995). Proactive and reactive individuals have been shown to differ in HPA axis reactivity, sympathetic and parasympathetic reactivity, as well as testosterone activity (Koolhaas et al. 1999). In house sparrows, *Passer domesticus*, basal MR is positively correlated with plasma levels of thyroid hormone and testosterone (Buchanan et al. 2001, Chastel et al. 2003), the latter being strongly linked to aggression. In humans, cortisol infusion increases resting MR (Brillon et al. 1995) while Tyrka et al. (2006) showed an inverse relationship between cortisol and exploration. Martin and Réale (2008b) recently showed a positive correlation between summer hair cortisol concentration and docility as measured by response to handling in wild eastern chipmunks, *Tamias striatus*.

It could be argued that resting MR and personality traits are not causally related, but rather show a correlation because that they share common hormonal basis. In this view, once the effects of hormone levels on resting MR are controlled for, personality would not explain any of the residual variation. While this is possible, it does not provide a valid reason for ignoring the correlation between MR and personality, whether causal or not. Indeed, there are several reasons to continue to focus on personality. First, physiology and behaviour are influenced by complex interactions between numerous hormones, only a few of which can be assayed accurately. Endrocrinology is a complex, methodologically challenging field of study, and it is unlikely that assaying concentrations of one or a few hormones in one or a few substrates (e.g. blood, feces, hair) will explain all correlated variation in both personality and metabolism. Although endocrinologists have had some success in relating behavioural variation to hormonal variation, they are still far away from explaining the causes and consequences of inter-individual variation in hormone levels (Williams 2008). Second, the expression of both personality and metabolism are influenced by many factors other than endocrine status (e.g. age, nutrition, predation risk). Therefore, some of the residual variation in metabolism and personality (i.e. after hormonal effects have been removed) could remain correlated simply because these traits are much more than emergent expression of circulating hormone levels. Finally, the direction of causality in any correlations among hormones, behaviour, and metabolism would be unclear. For example, correlations could arise if hormonal status independently affected personality and metabolism, or if hormonal status affected personality, which in turn affected metabolism (Wikelski et al. 1999). Therefore, one may not want to 'remove' the confounding effects of hormonal status to examine the underlying

relationships between resting MR and personality, but rather attempt to untangle cause and effect relationships among all three traits using approaches such as structural equations and path analyses (Shipley 1999).

Even if endocrine status emerges as an important covariate with metabolism and personality, there is another reason to not neglect personality-metabolism correlations. The nature of the causal links between hormones, personality and metabolism is an important question to physiologists. However, from an evolutionary point of view the important question is the degree of (genetic) correlation between traits that could explain the evolution of each trait and the pattern of coevolution of suites of traits under particular selection pressures. The primary target of selection is phenotypic variation in traits linked to personality (such as exploration, aggressiveness, risk-taking) and traits linked to metabolism (e.g. thermoregulation, cold tolerance, fasting endurance, burst speed, reproductive investment), rather than phenotypic variation in hormones per se. Thus, if a limited suite of hormones jointly determined personality traits and metabolic levels, the result would be correlated selection on personality and metabolic traits. For example, evolution of increased aerobic scope should also lead to evolution of altered personality traits, if both have a shared hormonal basis. Thus, understanding the evolution of either animal metabolism or animal personality would require understanding the direction, strength and genetic basis of the correlations between these traits.

A conceptual framework for functional linkages between metabolism and personality

Two fundamental questions in the study of animal personalities are: why do populations harbour more than one personality type? Why do animals exhibit behavioural consistency? In the following, we show why incorporating energy metabolism into theoretical and empirical studies of personality may give further insights of why individuals behave consistently over time and across contexts.

Physiological constraints may underlie behavioural consistency through time and/or across situations

According to the performance model (Fig. 4a), energetic constraints may underlie consistent behavioural variation over time and across contexts. We use a classic example of a behavioural syndrome (Fig. 5) to show how physiology can constrain phenotypic plasticity in behaviour. In this hypothetical example, the optimal level of activity (represented by stars) differs between two environments because predation risk is low in A and high in B. The optimum level of activity is high in A because active animals are able to find and gather large quantities of food or mates without the risk of predation; however, this entails a sustained energy expenditure resulting in a high resting MR and DEE (Daan et al. 1990, Hammond and Diamond 1997). The metabolic traits that allow an active individual (line α) to perform well and have high fitness in environment A where predation risk is low become a disadvantage in environment
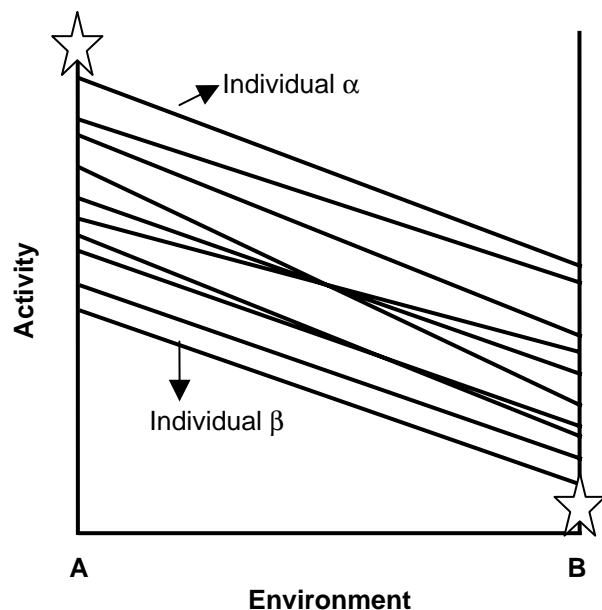

Fig. 5. Graphical representation of a behavioural syndrome by means of a plasticity plot (modified from Sih et al. 2004b). Each line represents a different individual and how it changes activity (and consequently energy expenditure) between two different environments (A without predators; B with predators). Stars indicate the optimal level of activity for each environment (high in A and low in B). The behavioural syndrome occurs when plasticity lines tend to be parallel – the most active individuals in A are also the most active in B, maintaining their ranks across environments. Because individual α (fast metabolism) has a physiology adapted to perform well in environment A, it will carry over this high energy demand to environment B where it has lower fitness (being forced to maintain a high level of activity to meet its basic daily energetic requirements). Alternatively, individual β will perform better in situation B, where its slow metabolism will allow it to conserve energy and remain inactive for longer, but once in situation A this individual cannot sustain the high rates of energy throughput needed for optimal activity levels.

B where predation risk is high. High energy requirements, manifested as high hunger levels, will motivate individual α to leave protecting cover to resume foraging (i.e. take greater risks). In contrast, a less active individual (line β) with lower energy requirements will be motivated to take fewer risks and so have higher fitness in environment B. If the physiological traits that result in a low MR and low activity level for individual β in B also limit its maximum performance in A, then it will have a comparatively low fitness in B. For both individuals, the activity levels and supporting metabolic traits that allow for high performance in one environment handicap performance in the other. We should therefore expect a coevolution between activity, resource acquisition and MR. Behavioural syndromes such as this explain why more than one personality type (and metabolic strategy) persists in environments that are heterogeneous in space or time.

Behavioural correlations across contexts may disappear when the behaviour performed in one context is constrained by a metabolic ceiling. For example, boldness in fishing spiders, *Dolomedes triton,* can be measured by the time an individual remains submerged (and breathing in an air capsule) as an anti-predator response. Female spiders

displayed highly repeatable responses across time and contexts, except when carrying an egg sac (Johnson and Sih 2007). In this case, the behavioural syndrome did not extend to the parental care context probably because O_2 requirements (total MR) increase when females are carrying an egg sac. High O_2-requirements constrain the time that females can remain submerged on a fixed air supply. Physiological constraints on behavioural syndromes may also be important to consider with regards to aggressiveness, since contests are known to be energetically costly and the outcome of a fight depend on an individual's capacity to devote energy in the contest (Briffa and Sneddon 2007). Overall, one might expect no behavioural correlation across two contexts when the behaviour in one of the context is constrained by a metabolic ceiling, thereby reflecting physical and aerobic capacity rather than personality per se. Physiological constraints on behavioural syndromes may vary according to their importance in terms of energy costs and their effects on the costs and benefits of a behavioural type in one or more contexts.

The personality–metabolism link is likely to create fitness tradeoffs

Since natural selection acts on whole organisms, physiology and behaviour are coupled in evolution, thus creating fitness tradeoffs. For example, the energetic costs and benefits of different coping styles may differ among circumstances. Because proactive individuals are usually aggressive, dominant, and bold, they are more likely to engage in energetically costly behaviour, which increases DEE. Proactives also grow faster and have higher energy requirements, which they can afford by higher rates of energy acquisition (Stamps 2007). When food is abundant, proactive individuals with higher resting MR than reactive individuals may perform best (Mueller and Diamond 2001, Bouwhuis et al. 2006). However, when food is scarce, reactive individuals who are generally docile, submissive, and shy may perform better due to their lower DEE and resting MR. Recent studies on fish suggest that the link between aggression and energy metabolism is likely to create fitness tradeoffs as the energy expenditure costs and energy acquisition benefits vary with food abundance and competition (Lahti et al. 2002). Because food abundance and competition often vary from year to year, balancing selection may explain the evolution and maintenance of differences in personality (Penke et al. 2007) and MR. Not surprisingly, behavioural ecologists already invoke energetic cost–benefit arguments to explain differential fitness benefits of personalities in different years (Dingemanse et al. 2004, Boon et al. 2007). Understanding and, more importantly, measuring the energetic consequences of personality differences is likely to help us understand how balancing selection operates to maintain more than one personality phenotype in wild populations.

Personality and metabolism may well be integrated into life-history theory

Stamps (2007) suggested that the evolution of personality traits may be easier to understand if we consider the functional connections between those traits and physiological processes like metabolism that support growth, maintenance, and reproduction. The fact that personality traits are correlated with life-history traits (Réale et al. 2000, Boon et al. 2007) suggests that personality can be considered as just another facet of broad life-history strategies (Stamps 2007, Wolf et al. 2007). This is intriguingly similar to the notion that variation in multiple correlated physiological traits may be related to alternate life-history strategies, such as the slow–fast metabolic continuum (Ricklefs and Wikelski 2002, Lovegrove 2003). How animals grow, survive, and reproduce under a given set of environmental conditions depends on physiological and behavioural systems that have been shaped together through evolution. Although no theoretical framework linking personality, slow–fast metabolic continuum, and life-history yet exists, we believe that it will develop rapidly. As an example, since tropical bird species present slow life-history strategies and also are at the slow end of the slow–fast metabolic continuum (Wiersma et al. 2007), under the metabolism–personality framework, one would expect tropical birds to also have more reactive personalities (i.e. shy, low activity, less aggressive, etc.). Linking energy metabolism and personality will be yet another step towards a more integrative biology where behaviour, morphology, and physiology are called upon to explain why coexisting life-strategies persist in natural populations (Ricklefs and Wikelski 2002, Bartholomew 2005, Gilmour et al. 2005, Stamps 2007, Wolf et al. 2007).

Conclusion

Most physiological mechanisms. including energy flow, can be modulated by behavioural responses. This is why physiology and behaviour have long been viewed as complementary in the fields of ecology and evolution (Bartholomew 1964, Cabanac 1996). Physiologists readily acknowledge that behaviour is a powerful way to cope with environmental challenges, while behavioural ecologists have long recognized the importance of energetics in the context of behavioural decisions and the evolution of life-history strategies. Indeed, the energetic approach lies at the very basis of the optimal foraging and life-history allocation theories. However, because it is easy to invoke an energetic explanation for a given behaviour but hard to actually measure it in the field, energetic explanations too often remain untested assumptions or hypotheses (Speakman 1997). The revolution that the concept of personality brings to behavioural ecology must be accompanied by energetic measurements.

There are reasons to expect that personality and energy metabolism are linked at both proximate and ultimate levels, making the overlap between these two fields a promising area of research. From the physiologist's point of view, personality is an emerging field that could greatly contribute to explain part of the variation in energy metabolism. Whether variation in resting MR is related to personality as 'error' due to a reaction to novelty or stress or whether it is the result of selection on suites of traits that optimise performance is certainly worthy of attention. From the behavioural ecologist's point of view, knowing the

energetic consequences of different behavioural types and coping strategies will help us understand the evolution of personality. The holistic point of view introduced by personality coupled with energetics could shed light on fundamental aspects of behavioural variation among individuals.

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