

Metabolic Scope as a Proximate Constraint on Individual Behavioral Variation: Effects on Personality, Plasticity, and Predictability

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ABSTRACT: Behavioral ecologists have hypothesized that among-individual differences in resting metabolic rate (RMR) may predict consistent individual differences in mean values for costly behaviors or for behaviors that affect energy intake rate. This hypothesis has empirical support and presently attracts considerable attention, but, notably, it does not provide predictions for individual differences in (a) behavioral plasticity or (b) unexplained variation (residual variation from mean individual behavior, here termed predictability). We outline how consideration of aerobic maximum metabolic rate (MMR) and particularly aerobic scope (= MMR – RMR) can be used to simultaneously make predictions about mean and among- and within-individual variation in behavior. We predict that while RMR should be proportional to an individual's mean level of sustained behavioral activity (one aspect of its personality), individuals with greater aerobic scope will also have greater scope to express behavioral plasticity and/or greater unpredictability in behavior (= greater residual variation). As a first step toward testing these predictions, we analyze existing activity data from selectively bred lines of mice that differ in both daily activity and aerobic scope. We find that replicate high-scope mice are more active on average and show greater among-individual variation in activity, greater among-individual variation in plasticity, and greater unpredictability. These data provide some tentative first support for our hypothesis, suggesting that further research on this topic would be valuable.

Keywords: within-individual, residual, metabolism, behavior, consistent.

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Energetics as a Constraint on Behavioral Variation

The capacity for animals to generate and sustain energy output has recently attracted considerable interest from behavioral biologists because it has the potential to provide at least a partial proximate explanation for consistent among-individual differences in behavior, growth, and reproduction within animal populations (e.g., Biro and Stamps 2008; Burton et al. 2011; Careau and Garland 2012; Sadowska et al. 2013; Norin and Clark 2016). This is not surprising, given that energy is at the heart of all biological processes, fueling not only various behavioral activities, growth, and reproduction but also the maintenance of all body tissues. The idea that individuals differ in their capacity to generate and sustain high levels of energy output (Nespolo and Franco 2007; White et al. 2013) and that these differences may in turn be a predictor of levels of behavioral activity that are sustained over time has considerable intuitive appeal and both theoretical and empirical support (Metcalfe et al. 1995; Hammond and Diamond 1997; Hammond et al. 2000; Stamps 2007; Biro and Stamps 2008, 2010; Careau et al. 2008; Burton et al. 2011; Brzęk et al. 2016; Portugal et al. 2016).

Recent behavioral studies have focused on among-individual differences in average resting metabolic rate (RMR), as RMR is a major component of the total daily energy expenditure and also may be related to the capacity to engage in energetically costly physical activities that are sustained over time. These activities might include foraging, aggression, or parental care that need to be supported by concurrent energy intake (discussed and reviewed by Careau et al. 2008; Biro and Stamps 2010). RMR reflects, in large part, the energetic costs

of organs involved in the processing and conversion of food into usable energy (e.g., intestines, liver, kidneys, heart; Meerlo et al. 1997; Chappell et al. 1999; Moe et al. 2004; Gebczynski and Konarzewski 2009; Konarzewski and Ksiazek 2013; Sadowska et al. 2013). Correlations between RMR and size of these organs are perhaps not as common in ectotherms such as fish (Norin and Malte 2012; see also Metcalfe et al. 2016) but are evident in lizards (Garland 1984; Garland and Else 1987) and trout (Allen et al. 2016). Here, we use the term RMR for simplicity to define the minimum rate of energy expenditure while at rest, measured during periods of normal quiescence or sleep. We use this term for both endotherms and ectotherms, but note that RMR is temperature-specific in the latter.

The proximate energetic reasons for why animals (including humans) often display consistent individual differences in behavior and limited flexibility is presently a very active area of inquiry for both physiologists and behavioral biologists (reviewed and discussed by Careau et al. 2008; Biro and Stamps 2010; Careau et al. 2010; Burton et al. 2011; Careau and Garland 2012; Biro et al. 2016; Metcalfe et al. 2016). Existing theory on links between metabolic rate and behavior has focused exclusively on variation among individual average values, predicting generally positive correlations between individual mean-level activity and mean-level RMR (Stamps 2007; Biro and Stamps 2008, 2010; Careau et al. 2008; Wolf and McNamara 2012). However, whether or how metabolic rate might affect or constrain the expression of individual differences in behavioral variability (plasticity and/or predictability) is unclear.

Growing evidence indicates that individuals often consistently differ not only in their mean-level behavior over time in a given context or situation (an important aspect of animal personality) but often also in how they behaviorally respond to changes in internal and external stimuli (= plasticity; Stamps and Groothuis 2010; Mathot et al. 2012; Stamps 2016). In addition, individuals often differ in their behavioral predictability (an individual's residual variation after accounting for systematic variation; Stamps et al. 2012; Biro and Adriaenssens 2013; Briffa et al. 2013; Westneat et al. 2013). Individual variation in plasticity and predictability is an important aspect of behavioral variation and represents what is often assumed to be adaptive behavioral flexibility (Briffa 2013; Westneat et al. 2015). The key distinction between plasticity and predictability is that the former is explainable and attributed to some temporal or contextual gradient, whereas the latter is not (Stamps et al. 2012; Biro and Adriaenssens 2013; Mitchell et al. 2016). Note that these generally accepted terms in the behavioral literature differ from those referred to elsewhere as flexibility and stereotypy, respectively (Wainwright et al. 2008). We illustrate what we mean by personality, plasticity, and unpredictability in figure 1. Notably, frameworks to explain plasticity and unpredictability at a proximate level

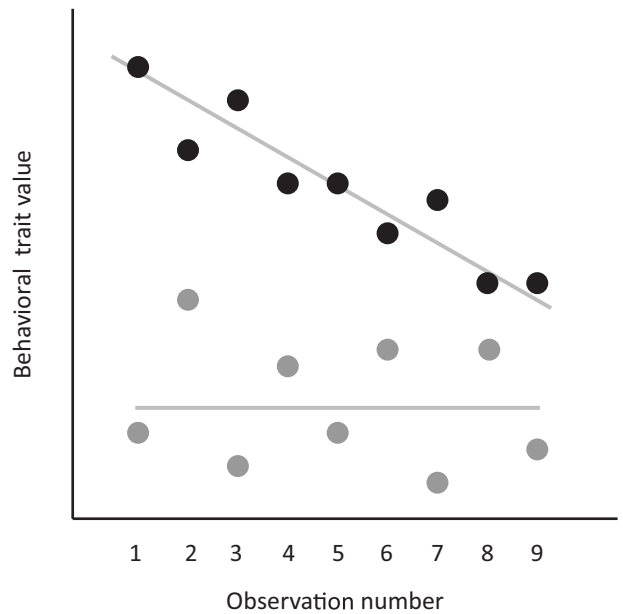


Figure 1: Mock-up illustration of what is meant by the terms personality, plasticity, and predictability. Shown are repeated measures of behavior for two hypothetical individuals sampled over time. Trend lines for each describe the temporal trajectory for each. The upper individual (black dots) has higher values on average than the lower individual (gray dots), and such differences are commonly referred to as differences in personality. In addition, the upper individual with higher scores on average also changes its behavior across observations and is thus plastic in its response over time, whereas the other individual is not; hence, these individuals differ in plasticity. Finally, the upper individual is more predictable (has lower residual variation about its trend line) than the highly variable lower individual. Differences in trend lines across successive observations could represent simply time-related change or change due to some contextual gradient that varies with each observation.

are currently lacking (Stamps 2016). Consequently, our aim here is to extend existing energetic hypotheses to additionally explain individual differences in plasticity and predictability and thus encompass all three levels of individual behavioral variation.

Individual differences in behavior are important to study because they provide the raw material on which natural and sexual selection can act. More broadly, behavior is a level of biological organization that has the most immediate effects on feeding, mating, and survival rates, making it one of the most important of all levels to study (e.g., see depictions and discussions in Careau and Garland 2012). Hence, an understanding of the energetic constraints underpinning behavioral variation at all three levels (as described above) is important for a mechanistic understanding of many ecological and evolutionary processes.

The Need to Consider Aerobic Scope

By contrast to the studies focusing on RMR, relatively few behavioral studies have considered relationships between individual behavior and maximum aerobic metabolic rate (hereafter MMR) or aerobic metabolic scope (= MMR – RMR; but see Jonas et al. 2010; Killen et al. 2014; Rupia et al. 2016). This is perhaps surprising, given that it could be argued that these are equally (or more) important measures of energetics in terms of their behavioral and ecological relevance. For example, several recent studies have examined both RMR and MMR together to understand individual differences in feeding capacity and responses to environmental change (Auer et al. 2015b; Holt and Jørgensen 2015; Killen et al. 2015; Norin and Clark 2016). MMR is the maximum rate of oxygen consumption, usually measured during forced exercise, where the speed is gradually increased every few minutes until the animal can no longer keep up and the rate of oxygen consumption has reached a plateau (e.g., Swallow et al. 1998). MMR may be a highly relevant energetic constraint, as the ability to sustain maximum or near-maximum aerobic energy expenditure may impinge on the capacity to patrol a home range, display to potential mates, fight rivals, and escape from predators in situations that involve prolonged pursuit (e.g., deer fleeing from a wolf pack). Aerobic metabolic scope represents the energetic bounds for aerobic work that is allocated to different demands, including behavioral activities, digestion, immune function, and cellular maintenance. Importantly, greater aerobic scope may represent a form of spare energetic capacity, which can be called on during periods of very high energy demand and also to speed recovery from activities that incur an oxygen debt, as discussed next.

Higher Aerobic Scope Can Provide Spare Capacity

Some studies indicate that larger aerobic scope may be a correlate of the capacity to regularly express high (but sub-MMR) output activities. For example, aggression leading to dominance was positively related to aerobic scope in fish, but the observed aggressive behavior did not require MMR, and so it was suggested that recovery from these activities may be faster for individuals with larger aerobic scope (Killen et al. 2014; Norin and Clark 2016). Indeed, recovery time from exhaustive exercise is faster for individual fish with larger scope (Marras et al. 2009). Similarly, selectively bred lines of rats with greater aerobic scope respond more to exercise training than do unselected lines, suggesting that greater aerobic scope may provide a reserve capacity that can be exploited when elevated activity is needed (Novak et al. 2009; Garton et al. 2016). Further, a fast-growing chicken strain possessed greater aerobic scope than a slow-growing strain (Konarzewski et al. 2000), and individual fish with larger scope have greater feeding capacity (Auer et al. 2015a). Together, these

studies and others like them suggest that greater aerobic scope might reflect past selection on capacities for high-output but not necessarily maximum-output activities that are frequently performed, thus leaving energetic scope for multiple energetic demands, including high costs of digestion (Auer et al. 2015a), growth, and reproduction.

Aerobic Metabolic Scope as a Constraint on Expression of Behavior

Aerobic metabolic scope is long established in the physiological literature as a constraint on individual locomotor performance (e.g., running endurance; Bennett et al. 1984), but aerobic scope has only relatively recently attracted empirical interest in the context of individual variation in behavior (e.g., aggression, activity; Jonas et al. 2010; Eliason et al. 2013; Killen et al. 2014, 2015; Baktoft et al. 2016; Metcalfe et al. 2016; Rupia et al. 2016). Note that here and elsewhere in the article we view performance as the “ability of an individual to conduct a task when maximally motivated” (Careau and Garland 2012).

Importantly, aerobic scope has seemingly not been considered as a constraint on behavior across its three levels of organization (i.e., individual mean, individual plasticity, and individual predictability), which is our focus here. Aerobic scope necessarily represents the aerobic energetic boundaries within which an individual must operate, and so individual variation in aerobic scope can constrain individual variation in behavioral variation. It can constrain expression of behavior because both RMR and MMR are repeatable traits, meaning that they are somewhat consistent over time within individuals (reviewed by Friedman et al. 1992; Dohm et al. 2001; Sadowska et al. 2005; Nespolo and Franco 2007; Gebczynski and Konarzewski 2009; Wone et al. 2009; White et al. 2013), even though RMR and MMR can also change over ontogeny or when conditions change (e.g., Swallow et al. 1998; Moe et al. 2004; Van Leeuwen et al. 2012; Auer et al. 2015b; Norin et al. 2016). Several studies and reviews have suggested that natural and artificial selection for increased MMR may also lead to increased RMR, or vice versa. Correlated evolution of RMR and MMR is likely due to the fact that some organs (e.g., heart, liver) and energy pathways (e.g., oxidative phosphorylation) contribute to aerobic respiration when individuals are performing at their maximum and when resting (Hayes and Garland 1995; Hammond and Diamond 1997; Meerlo et al. 1997; Dohm et al. 2001; Cutts et al. 2002; Arnott et al. 2006; Wone et al. 2011; Norin and Malte 2012; Auer et al. 2017; Gillooly et al. 2017; but see Gebczynski and Konarzewski 2009; Wone et al. 2015).

Regardless of the exact relationship between RMR and MMR within a species, an individual’s aerobic scope necessarily represents aerobic energetic boundaries within which individuals must operate and may be correlated with the sustained aerobic scope for submaximal activities as discussed below. Aerobic

scope is therefore a possible proximate cause of variation within species and a constraint on behavioral variation within individuals.

Here, we outline how individual (or genotypic) differences in aerobic scope within a given species may constrain the aerobic scope for individuals to express behavioral variation. This provides us with a means to make a priori predictions regarding (1) individual mean-level behavioral activity, (2) individual behavioral plasticity, and (3) individual predictability, all within a single conceptual framework.

Simply put, the key prediction we make is that greater aerobic scope should permit individuals the latitude to express greater behavioral variation (i.e., greater plasticity and greater unpredictability), whereas lesser scope should constrain the expression of behavior. Of course, because research on the among-individual relationships between metabolism and behavior is still not extensive, some of our predictions are necessarily based on empirical results for which clear and consistent trends are not yet apparent. Furthermore, because we are not aware of any existing study linking aerobic scope to individual variation in behavioral plasticity or predictability, we reanalyze a published data set (Eisenmann et al. 2009) on selectively bred lines of laboratory house mice that differ in aerobic scope and behavior to provide some first (tentative) data in support of our ideas.

How RMR Can Affect Individual Average Levels of Physical Activity

We begin by arguing that when individuals consistently differ in their mean RMR (after statistically removing effects of variation in body mass), as is often the case under controlled laboratory conditions and when food is ad lib. (reviewed by Nespolo and Franco 2007; Ksiazek et al. 2009; Wone et al. 2009; White et al. 2013), then those with higher RMR should (all else being equal) engage in consistently higher levels of physical activities that would serve to increase rates of food intake. Why? Because each day, during normal periods of activity, individuals must exhibit levels of behaviors that either directly (e.g., locomotor activity) or indirectly (e.g., boldness) affect intake rate sufficiently to at least pay the energy costs associated with maintaining the tissues of the body, as reflected by RMR. If this were not the case, then individuals would continually lose energetic condition each day (of course, some animals are adapted to feeding periodically and so would deviate from the more typical daily balancing of energy budgets). Thus, RMR may be directly proportional to minimum sustained levels of physical activity needed to acquire energy, representing a floor effect on sustained individual mean-level activity.

Indeed, individuals (or genotypes) with consistently higher RMR are often also more physically active on average with respect to locomotor activity, exploration, and aggression related to dominance (reviewed by Biro and Stamps 2010; see

also Cutts et al. 2001; Biro et al. 2006; Ksiazek et al. 2009; Novak et al. 2009; Careau et al. 2011; Allen et al. 2016; Metcalfe et al. 2016; Portugal et al. 2016). In turn, higher levels of activity and RMR are often also supported by higher intake rates (Selman et al. 2001; Ksiazek et al. 2004; Arnott et al. 2006; Biro et al. 2006; Gebczynski and Konarzewski 2009; Novak et al. 2009; Koch et al. 2011; Konarzewski and Ksiazek 2013; Sadowska et al. 2013; Allen et al. 2016; Brzęk et al. 2016). For example, among genotypes of rainbow trout, those with higher RMR also exhibit higher activity, boldness, and intake rates than those with lower RMR, both in the lab and in the field (Biro et al. 2006; Allen et al. 2016). It is likely that causal arrows operate in both directions and that these traits are pleiotropically and/or functionally related, but for our purposes the direction of causality between RMR and individual mean behavior is not important. We also note that although differences in food conversion efficiency could in principle offset some of the need for increased feeding-related activities (e.g., Allen et al. 2016), we are not aware of any empirical example showing that this would be sufficient to completely offset it.

MMR Sets an Upper Limit on Sustained, Aerobically Supported Physical Activity

By definition, the MMR (also known as maximal oxygen consumption or VO_{2max}) sets the maximum level of aerobic physical activity that can be sustained for relatively short intervals (minutes to hours, as opposed to days or weeks; Swallow et al. 1998). In broad phylogenetic comparisons (e.g., Gillooly et al. 2017), such as mammals (endotherms) versus lizards (ectotherms), differences in aerobic MMR go hand-in-hand with differences in daily movement distance and home range size (Garland and Albuquerque 2017), and among species of mammals aerobic MMR is positively correlated with home range size after removing correlations of both with body size (Albuquerque et al. 2015). Moving to the level of individuals within species, if individuals differ in aerobic MMR, then they must also differ in maximum possible levels of sustainable physical activity, thereby setting a ceiling effect on those activities. These activities might include searching for food or mates, sustained fighting of rivals or competitors, or migrating (as noted above). Similar to RMR, empirical studies in a wide variety of taxa show that individuals consistently differ in MMR; in other words, it is a repeatable (and heritable) trait (reviewed by Dohm et al. 2001; Nespolo and Franco 2007; Koch et al. 2011; Wone et al. 2011; White et al. 2013).

How Aerobic Metabolic Scope Constrains Variation in Behavior

If RMR can set a lower limit on sustained levels of activity (across days and weeks) and MMR sets the upper limit (across

minutes to hours), as outlined above, then by extension aerobic scope must constrain within-individual behavioral variation. Thus, given a group of individuals that differ in aerobic scope, we can predict plausible probability distributions for rates of energy expenditure among and within individuals. On that basis, we can in turn develop probability distributions for physical activity in light of those energetic constraints and thus make predictions about how within-individual scope for either plasticity or predictability can vary among individuals. We now address each component in turn.

Predicted Frequency Distributions for Individual Energy Expenditure

We begin by depicting among-individual differences in RMR and MMR and treat these values as though they were fixed means. We illustrate aerobic scope as increasing with increases in RMR among individuals or genotypes within a species (e.g., Wone et al. 2011; Pang et al. 2015; Rupia et al. 2016; Auer et al. 2017), but the basic arguments do not rely on this or any other particular among-individual relationship between RMR and MMR (fig. 2*a*; discussed below). Such a pattern of aerobic scope increasing with RMR has also been found across different species of fish with very different levels of activity (Killen et al. 2016) and particularly at within-species levels in a broad meta-analysis (Auer et al. 2017).

In any case, we can characterize the region between an individual's RMR and MMR as an envelope encompassing the probability distribution of hourly mass-corrected energy expenditure rates that represent normal daily activities (when not sleeping), over the course of days or weeks, and expect this distribution to be positively skewed, with a long, slim tail approaching MMR (fig. 2*a*; see also fig. 2 in Norin and Clark 2016). These normal daily activities include sustained physical activity (e.g., foraging, territory patrolling), less frequent activities such as chasing away rivals or pursuing potential mates that may reach maximal (MMR) or near-maximal levels of aerobic output, and of course, periods of rest.

The mode of this distribution obviously must be greater than the RMR (but well below MMR; Dlugosz et al. 2012; Norin and Clark 2016), given that physical activities are required to secure food that is needed not only to pay resting energy costs (RMR) but also to achieve a surplus for other essential purposes (fig. 2*a*). We further assume that individuals with different aerobic scope experience similar constraints on the proportion of available scope that can be exploited on a frequent basis (the thick portions of the distribution, here shown to be about half of the scope for illustration purposes; fig. 2*a*). Meta-analysis of the correlation between RMR and daily energy expenditure (arguably, a close correlate of the mode of the distributions in fig. 2*a*) indicates generally positive correlations among individuals for a range of different taxa (Auer et al. 2017).

Predicted Frequency Distributions for Individual Physical Activity

As we did for energy expenditure, we can similarly depict long-term physical activity of an individual as a probability distribution (excluding normal periods of sleep or extended rest), with the assumption that it is constrained by aerobic scope. So long as aerobic scope is relatively consistent over some time interval, so too will be the potential constraints on behavior that exist among individuals.

We begin by depicting among-individual variation in the minimum sustained levels of physical activity needed to gather resources to pay RMR costs (dashed blue line in fig. 2*b*). This, we assume, is directly proportional to RMR differences among individuals for reasons already explained above. If so, then the mode of the frequency distribution of physical activity should be higher than this minimum value (dashed gray line) and would represent an average level of sustained physical activity across days and weeks (see citations above showing correlations between RMR and individual mean levels of different behaviors and correlations between RMR and daily energy expenditure).

Next, we expect this frequency distribution to have long slim tails toward each extreme, extending from zero activity to the maximum aerobically sustainable level of activity defined by the MMR (fig. 2*b*). Long, slim tails are expected during normal periods of activity, because activity levels below the blue dashed line cannot be sustained without going into energy deficit (already discussed above) and by definition activity levels approaching MMR must be increasingly less likely to occur.

For species with sedentary lifestyles (e.g., sloths) and those that may feed infrequently (e.g., large-bodied pythons), we could expect RMR and activity distributions to be shifted toward much lower values, whereby the mode of the distribution might be quite close to zero activity. Indeed, among teleost fish, species with lower locomotor performance tend to have lower RMR, lower MMR, and reduced aerobic scope (Killen et al. 2016).

These expected distributions of possible activity levels (fig. 2*b*) lead us to the straightforward—but until now unexplored—prediction that individuals with greater aerobic scope should (*a*) be more physically active on average, (*b*) have the scope to express greater levels of plasticity for behaviors that are supported aerobically, and (*c*) have the scope to express greater levels of behavioral unpredictability (= greater individual residual variance). First, the difference between the floor (zero physical activity) and the ceiling (sustained activity at MMR) for activities is larger for individuals with larger aerobic scope, meaning greater latitude to express variation in behavior. Second, if the proportion of available aerobic scope that can be exploited on an ongoing basis is similar among individuals, then individuals with larger aerobic

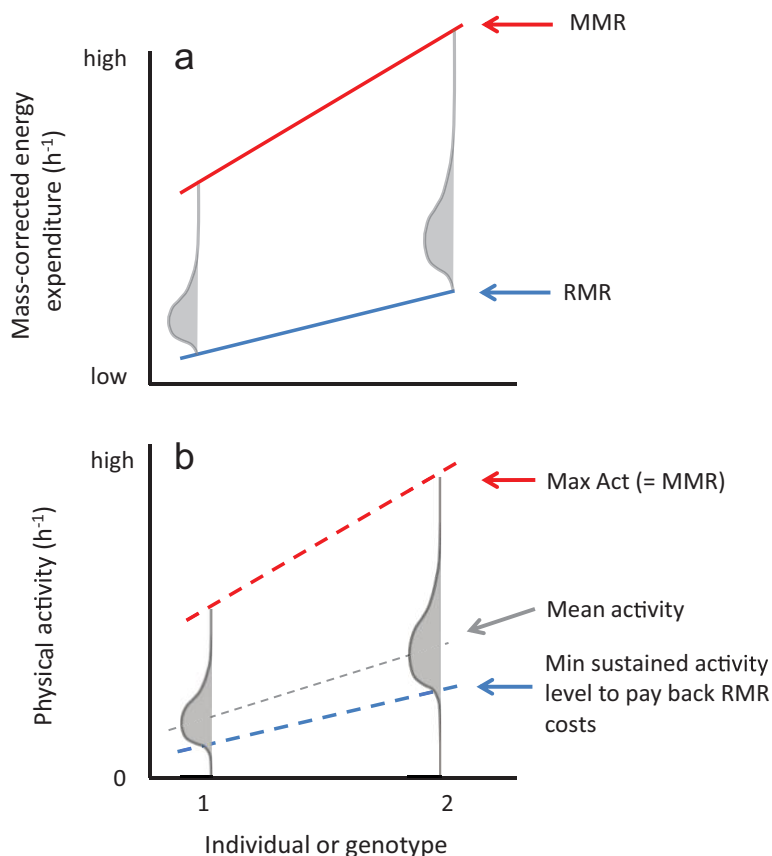


Figure 2: *a*, Illustration of individual variation in resting metabolic rate (RMR) and maximum aerobic metabolic rate (MMR), whereby we depict aerobic metabolic scope (= $MMR - RMR$) increasing with RMR across individuals (one of various possible patterns). The gray frequency distributions illustrate, for two individuals (or genotypes), their hourly rates of energy expenditure, accumulated across days and weeks during normal periods of activity. Although RMR and MMR can vary in relation to both internal physiological and external conditions, we depict them here as fixed (mean) values for each individual when measured under standardized conditions. Energy expenditure depicted in *a* represents mass-corrected values as residuals from a statistical model that accounts for mass effects on metabolism. *b*, Predicted individual variation in the scope for aerobic behavioral activities (during normal periods of activity) for the same two individuals as in *a*. Gray frequency distributions illustrate their expected hourly physical activity summed across days and weeks. By definition, MMR defines the upper limit on aerobic physical activity, and zero activity defines the lower bound on activity. We assume that minimum sustained activity (dashed blue line) and average activity (when not resting or sleeping) are directly proportional to RMR (for reasons outlined in the main text).

scope should also have greater scope to express variation in behavior in the range of values given by the broader (thick) portions of the frequency distribution (fig. 2*b*). In other words, individuals with greater aerobic scope have greater latitude for extreme levels of activity that can rarely be expressed and also for intermediate-level activities that can frequently be expressed.

These ideas share some similarity to those recently discussed in the context of among-species differences in teleost fishes—a literature review and analysis revealed that aerobic scope increases with RMR across species of fish and that those with greater aerobic scope (and higher RMR) tend to be more active species (see fig. 2*b* in Killen et al. 2016 and discussion therein). Similarly, at the within-species level, subpopulations of sockeye salmon that migrate to distant tribu-

taries of the Fraser River had greater metabolic scope than those migrating to nearby spawning tributaries (Eliason et al. 2013). Other behaviors that are not energetically costly themselves, such as boldness, may also be related to aerobic scope if boldness affects energy acquisition that in turn supports high-output activities and production of new biomass (Biro and Stamps 2010; Biro et al. 2014).

The preceding arguments do not imply that individuals with larger aerobic scope necessarily always exploit it to express greater behavioral variation—need and motivation may be lacking—but they have (if they choose), greater scope to express variation in behavior as either greater plasticity and/or greater unpredictability (our empirical example shows exactly this; see below). Greater plasticity may manifest as greater temporal plasticity (e.g., due to habituation, acclimation, or

some unknown factor that may vary over time; Bell and Peeke 2012; Dingemans et al. 2012), the more familiar contextual plasticity due to an environmental gradient (Pruitt et al. 2011; Briffa et al. 2013), or both (Westneat et al. 2011; Biro et al. 2014). Of course, quantitative predictions for behavioral variation will depend on the precise among-individual relationships between scope and RMR and MMR, which is variable and arguably understudied at the within-species level.

Implications of Variable Relationships between RMR and MMR

The relationship between RMR and MMR across individuals is likely to vary among species and lifestyles, and this will modify the predictions for variation in physical activity from those depicted in figure 1. For example, aerobic scope can be smaller for individuals with greater RMR (Hammond and Diamond 1997; Chappell et al. 1999; Cutts et al. 2002; Huang et al. 2013; Allen et al. 2016), and individuals (or genotypes) may differ in RMR but not MMR (e.g., Cutts et al. 2002; Arnott et al. 2006; Gebczynski and Konarzewski 2009). Either of these two kinds of scenarios would lead to reductions in aerobic scope for individuals with higher RMR. Thus, we predict that they should express higher average levels of activity but would be constrained to express lower levels of behavioral plasticity and lower unpredictability because the metabolic ceiling (MMR) is closer to the sustained minimum levels of activity needed to cover RMR costs and achieve a surplus for other purposes.

Finally, individuals may differ in MMR but not RMR, such that aerobic scope varies among individuals that possess the same (or similar) RMR—such is the case across lines of mice selected for high voluntary wheel-running behavior versus nonselected control lines (Swallow et al. 1998; Kane et al. 2008; Rezende et al. 2009). Thus, greater aerobic scope has evolved in that system as a response to selection that favors high sustained levels of activity (mean-level activity), without a corresponding increase in RMR. However, before one discounts the role of RMR completely in this empirical example, it is possible that mass-specific RMR is in fact higher in the high-selected lines if one were to account for the fact that they are leaner (Swallow et al. 2001; published analyses of their RMR do not account for body composition; Rezende et al. 2009).

Is There Any Evidence Consistent with Our Hypothesis?

To our knowledge, no previous study has investigated how behavioral variation at different hierarchical levels (as outlined above) varies with aerobic scope across individuals. Therefore, we took advantage of an existing data set on among- and within-individual variation in voluntary wheel running

of mice (Eisenmann et al. 2009)—this study used selectively bred lines of mice (sourced at generation 43) that differ in both propensity and ability for sustained, endurance-type activity, as well as aerobic MMR, but not in RMR (Swallow et al. 1998; Kane et al. 2008; Rezende et al. 2009). Therefore, high-runner lines have higher aerobic scope compared to controls. Replicate lines were bred for high levels of voluntary wheel running, which resulted in significantly higher MMR as measured during forced exercise but similar RMR: differences in MMR were already apparent in males at generation 10 (Swallow et al. 1998) and males (but not significantly higher for females) at generation 34 (Rezende et al. 2006*b*) and were significantly greater in females in generation 36 (Rezende et al. 2006*a*). Several subsequent studies have confirmed these differences in both sexes, but not every study conducted on these mice has included both sexes (e.g., Kolb et al. 2010; for females only at generation 45).

The data set used here (Eisenmann et al. 2009) contained estimates of daily running distance repeatedly measured for 20 consecutive days on a sample of 20 individual animals (10 males and 10 females per line) using one of the selected lines with high aerobic scope (lab designation = line 8) and one nonselected control line with lower aerobic scope (lab designation = line 2; total $N = 20 \times 2$ lines \times ca. 20 repeats per animal = 779 (Eisenmann et al. 2009). These data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.jn33140> (Biro et al. 2018). Data on metabolic rates of each individual are not available, and so we treat all individual mice from the selected line as replicate high-scope individuals and the control as replicate low-scope individuals. We predicted that high-scope mice would have greater scope to express both plasticity (greater among-individual variation) and unpredictability (= greater residual variance).

Statistical analyses. We tested for among-individual differences in plasticity (temporal reaction norms – individual trends in activity over time) and predictability (residual variation from the reaction norm) within each line and accounted for sex effects using a linear mixed effects model. Day, sex, and line were fixed effects, and we modeled individual differences in intercepts and slopes with respect to day as random intercept and random slope effects, respectively. These variances and the covariance between intercepts and slopes were fit separately for each line within the same model to give line-specific variance parameters. We also fit a separate residual variance parameter by line in that model to test whether predictability (residual variance) differed between lines. We used PROC GLIMMIX of the SAS statistical package.

In the laboratory, individual differences in temporal trend lines (indicated by random slope variance) might reflect differences in habituation or acclimation to some unknown factors (Bell and Peeke 2012), or short-term training effects, and these differences might be influenced (constrained) by aerobic scope (note that mice had access to running wheels

ca. 10 d prior to collecting data; Eisenmann et al. 2009). To avoid the inherent relationship between means and variances expected for lognormal data, we log transformed the activity data. We then followed this with standardization (z-transform) of the data (mean = 0, variance = 1) to permit better comparison of variance parameters and aid in model fitting. Together, these transformations reduce the likelihood of detecting any relationship between means and variances between the lines. We also log transformed day of observation because examination of the raw data indicated slight curvilinear increases in activity over time (this improved model fit as determined by corrected Akaike information criterion values, but using raw data produced near-identical results).

Results

As expected, mice from the selected line with greater aerobic scope had higher levels of activity on average (effect of line: $F_{1,30} = 14.9$, $P = .0005$), activity on average increased over time in both lines (effect of day: $F_{1,29} = 10.7$, $P = .0028$), and females were more active than males ($F_{1,36} = 6.4$, $P = .016$; the day \times line interaction was not significant, $P = .98$; app. A [degrees of freedom are rounded here for simplicity]). After accounting for these population mean-level trends due to day and sex (which are irrelevant to our predictions), our model revealed several important among-individual variance differences between the selected and the control line.

Among-individual variation in predicted mean values at the outset of the observations (day 1) was substantial, and this variation was more than twice as large in mice with high scope (var = 1.72, SE = 0.59) as compared to those with low scope (var = 0.81, SE = 0.30). This result indicates greater among-individual variation in motivation and/or ability to express activity in the high-scope mice (but see caveat in Discussion).

The high-scope mice also displayed much greater levels of variation in plasticity with respect to time-related change in activity (some individuals increased activity rapidly over time, others much less so; var = 0.13, SE = 0.04) compared to low-scope mice (var = 0.04, SE = 0.01). With greater intercept and slope variance for high-scope mice, it was not surprising that the observed negative covariance between individual intercepts and slopes was larger for high-scope mice (correlation = -0.83) than for low-scope mice (correlation = -0.48 ; see also app. A). Negative covariance indicates that individuals with higher than average activity (within a given line) on day 1 tended to have the smallest increases in activity over time (i.e., their temporal trend line was relatively high and flat). Residual variance was also higher in the high-scope mice, thus indicating that individuals were more variable on a day-to-day basis (var = 0.15, SE = 0.01) than the low-scope mice (var = 0.09, SE = 0.007), as is clearly evident in figure 3.

Including these line-specific random effects improved model fit substantially and was supported by significant likelihood-ratio tests. Although a random intercept model, fit separately by line, did not improve fit over one with only a single random intercept effect ($\chi^2_1 < 1$, $P > .05$), a random intercepts and slopes (and covariance) by line did improve fit over one with random intercepts by line ($\chi^2_4 = 206$, $P < .01$); adding a separate residual variance by line improved fit even more ($\chi^2_1 = 23.5$, $P < .01$). For full model output, see appendix A. By comparison, analysis of the raw activity data in the same way produced much larger differences in variances between lines, as we would expect for lognormal data, but would have violated model assumptions.

Discussion

Interestingly, our results on voluntary wheel-running behavior in mice are in agreement with the main predictions

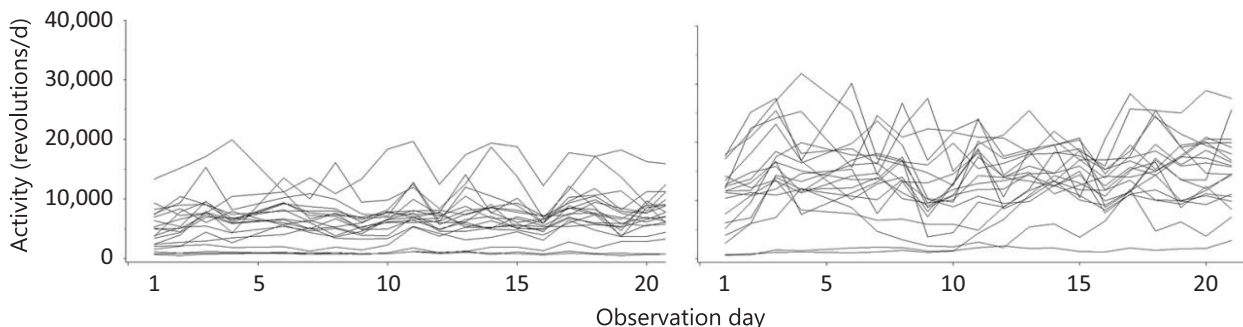


Figure 3: Activity rates for 20 individual mice recorded over 20 consecutive days originating from each of low-scope (*left*) and high-scope (*right*) genotypes. Lines join the successive observations for each mouse to illustrate the greater among-individual differences in average activity and within-individual variation in activity in the high- compared to low-scope mice. Shown are the raw activity data; however, analysis was performed on transformed data.

stemming from our energetic hypothesis: we observed higher individual mean levels of activity, greater temporal plasticity (individuals differed more in their temporal trends), and higher residual variance in the mouse line with higher aerobic scope. As already mentioned, we predict that individuals or genotypes with greater aerobic scope have the energetic latitude to express greater levels of plasticity and/or greater residual variance, not that they always take advantage of this. Indeed, some individuals were highly plastic in their activity trends over time and others were not, and high-scope mice showed greater among-individual variability in temporal plasticity and greater residual variation (and thus were less predictable in their behavior at any point in time). Given that the two mouse lines differ in MMR but not in RMR (Swallow et al. 1998; Kane et al. 2008; Rezende et al. 2009), it is either aerobic scope or MMR per se that constrains not only mean levels of sustained activity but also behavioral plasticity and predictability (individual residual variance). However, it is possible that mass-specific RMR is in fact significantly higher in the high-selected line if one were to account for the fact that they are leaner (Swallow et al. 2001; Rezende et al. 2009).

Our hypothesis and empirical data consistent with it indicate that aerobic scope may act as a proximate constraint on behavioral plasticity and predictability. Given that the data were not designed to test this hypothesis, this empirical evidence is tentative and further study is needed. We suggest that future studies begin with straightforward but time-intensive longitudinal studies of RMR and MMR among individuals or genotypes, along with measures of ecologically relevant behaviors (e.g., general physical activity, foraging), under relatively constant conditions. In particular, it is necessary to gather repeated measures of both RMR and MMR to estimate scope that is based on individual means, not single estimates as is often done. Estimating scope with a single estimate of RMR and MMR per individual, as is often done, will likely lead to highly imprecise estimates of individual scope, given that both are labile traits (Wolak et al. 2012). Several recent articles offer a discussion of the nuances and data requirements for estimating trait repeatability and individual means of labile traits with precision (van de Pol 2012; Wolak et al. 2012; Biro and Stamps 2015; Cleasby et al. 2015; Mitchell et al. 2016). With modern multiarena tracking software and multichannel respirometry equipment, it is now feasible to get many repeated measures of individuals for behavior and metabolism over reasonable time intervals to address these sampling considerations head-on.

Extending predictions to include changing conditions. We clarify here that our predictions are valid so long as among-individual variation in metabolic rate is consistent over the time frame during which measurements of behavioral variation are being made. As already outlined above, RMR and MMR are statistically consistent over time frames ranging from days to weeks or more in a great variety of taxa (White et al. 2013). This is why we suggest that future studies begin with systems where conditions are held constant. A valuable next step would be to study how changes in environmental conditions might affect changes in aerobic scope and therefore also behavior.

An unexpected food shortage, for instance, may encourage a reduction in RMR over time, leading to a prediction that in the first instance mean-level activities should also be reduced; expectations for behavioral variation under this scenario would then depend on whether and how MMR also responds to food shortage. In short, we would predict that any changes that could affect metabolism will in turn lead to a corresponding change on the constraints on behavior as outlined in our hypothesis. Thus, our hypothesis provides a mechanistic basis from which to make predictions about behavioral variation under constant or varying energetic conditions, to the extent that we have knowledge of aerobic scope across situations.

Again, we suggest here a longitudinal approach in which individuals are tracked over time under one set of conditions, and then conditions are varied to examine how individuals changed relative to one another (e.g., Norin et al. 2016). In a field setting, this might be achieved by comparing across seasons with marked individuals or by manipulating food abundance. In the laboratory, taking advantage of existing lines of animals that have been bred for differential levels of metabolism or behavior, as done here, may represent a productive and powerful way forward (see, e.g., Smyers et al. 2015).

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APPENDIX

Table A1: Detailed model output of mouse wheel-running data (from Eisenmann et al. 2009), including line-specific random effects, as analyzed in SAS PROC MIXED

| Effect | bsex | Line | Estimate | SE | df | <i>t</i> | <i>P</i> > <i>t</i> |
|---|--------------|----------------|----------|---------------------|-----------------------|----------|-----------------------|
| Solutions for fixed effects: | | | | | | | |
| Intercept | | | -.5154 | .3384 | 23.16 | -1.52 | .1414 |
| bsex | 0 | | .6941 | .274 | 35.76 | 2.53 | .0158 |
| bsex | 1 | | 0 | ... | ... | ... | ... |
| Line | | Low | -.9493 | .3694 | 30.27 | -2.57 | .0153 |
| Line | | High | 0 | ... | ... | ... | ... |
| logday | | | .1664 | .08807 | 18 | 1.89 | .075 |
| logday × line | | 2 | -.00185 | .1014 | 28.74 | -0.02 | .9855 |
| logday × line | | 8 | 0 | ... | ... | ... | ... |
| | Numerator df | Denominator df | <i>F</i> | <i>P</i> > <i>F</i> | | | |
| Type III tests of fixed effects: | | | | | | | |
| bsex | 1 | 35.76 | 6.42 | .0158 | | | |
| Line | 1 | 30.27 | 6.6 | .0153 | | | |
| logday | 1 | 28.74 | 10.66 | .0028 | | | |
| logday × line | 1 | 28.74 | 0 | .9855 | | | |
| | Estimate | SE | df | <i>t</i> | <i>P</i> > <i>t</i> | | |
| Least squares means: | | | | | | | |
| Low | -.7575 | .1773 | 16.74 | -4.27 | .0005 | | |
| High | .1958 | .1804 | 17.05 | 1.09 | .2929 | | |
| Female | .0662 | .1838 | 37.1 | .36 | .7207 | | |
| Male | -.6279 | .1891 | 37.11 | -3.32 | .002 | | |
| Cov parameter | Subject | Group | Estimate | SE | | | |
| Random effects variances and covariances: | | | | | | | |
| UN(1,1) | id | Low | .8152 | .303 | | | |
| UN(2,1) | id | Low | -.09122 | .05471 | | | |
| UN(2,2) | id | Low | .04343 | .01637 | | | |
| UN(1,1) | id | High | 1.7167 | .5948 | | | |
| UN(2,1) | id | High | -.4012 | .1581 | | | |
| UN(2,2) | id | High | .1355 | .04913 | | | |
| Residual (VC) | id | Low | .0916 | .006827 | | | |
| Residual (VC) | id | High | .1544 | .01182 | | | |

Note: We used the Kenward-Roger method to determine the (denominator) df for fixed effects, yielding noninteger values.

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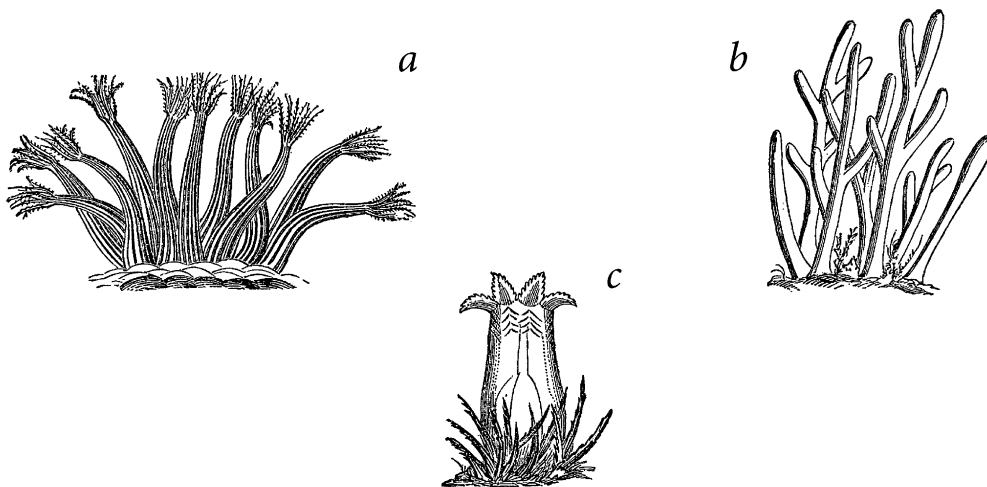
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“An excellent summary of the class of ‘Cnidaria,’ or Polyps, precedes the account of new species.” Figured: a, “*Anthella lineata* Stimps. . . . from Hong Kong”; b, “*Telesto ramiculosa* V. . . . polyp-colony . . . from the same locality”; c, “*Acanthogorgia coccinea* V. . . . from Hong Kong.” From the review of *The Polyps and Corals of the North Pacific Exploring Expedition* (*The American Naturalist*, 1870, 4:488–491).