

# Energetics and behavior: unrequited needs and new directions

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**The number of studies investigating links between among-individual differences in metabolic rate (MR) and behavior has grown dramatically in the past several years. A major and often untested assumption of these studies is that the selected measure of MR is a valid proxy for energetic constraints. We argue that without explicitly testing this assumption, observed patterns between MR and behavior are uninterpretable. We provide guidelines for evaluating how a given measure of MR relates to constraints on the acquisition or expenditure of energy. The approach we advocate will allow researchers to develop and test *a priori* predictions relating energy metabolism and behavior. We conclude by highlighting several exciting directions for future work in this rapidly growing field.**

## Energetics and behavior

Behavioral ecologists have a long tradition of considering how energetic constraints shape animal behavior. For example, how do increasing energy demands (e.g., due to decreasing temperature and higher costs of thermoregulation) affect patch departure decisions [1], foraging group sizes [2], and habitat selection [3]? How does food deprivation influence predator inspection behavior [4] and how does food availability influence social foraging behavior [5]? These types of studies have shown that within-individual changes in energetic constraints are associated with within-individual changes in behavior.

More recently, behavioral ecologists have become interested in the potential role of consistent among-individual differences in energetic constraints as a driver of consistent among-individual differences in behavior (i.e., animal personality) [6–8], motivated in part by the observation that MRs often differ consistently among individuals [9]. The number of studies investigating links between individual differences in energetic constraints (inferred from MR) and behavior has grown dramatically in the past several years (reviewed in [6,7]). In this Opinion, we begin by describing

the typical study design that has been used to this end. We then outline why we believe that this approach is unlikely to further our understanding of how among-individual differences in energetic constraints shape among-individual differences in behavior. We focus our discussion on problems associated with the proxies for energetic constraints that are typically used in such studies. We provide guidelines for the types of measure that are needed to allow empiricists to develop and test *a priori* predictions relating energy metabolism and behavior and conclude with a discussion of what we believe are exciting directions for future work in this burgeoning field of research.

## Glossary

**Allocation model:** a model of energy management where variation in maintenance MR does not reflect variation in the size of organs that mobilize energy (e.g., digestive organs, muscle); differences in RMR are therefore not associated with differences in energy budgets (DEE). Individuals with higher maintenance MR have less energy available to allocate to energetically costly behaviors and so are predicted to have lower expression of such traits [8].

**Basal metabolic rate (BMR):** the lowest metabolic rate of an adult endotherm that is at rest during its normal period of inactivity, post-absorptive, nonreproductive, and within its thermoneutral zone. Often viewed as the minimum energy required for self-maintenance [11].

**Daily energy expenditure (DEE):** the total energy expenditure of an unrestained animal over the course of 24 h. Sometimes also called field MR (FMR) [24].

**Daily metabolic scope:** the amount of energy available to fuel behavior (i.e., DEE minus maintenance costs).

**Energetic constraints:** energy requirements for a given period of time. All else being equal, animals with higher total energy requirements face greater constraints in meeting their daily energy budgets.

**Independent allocation model:** a model of energy management where the amount of energy available above basic maintenance costs is independent of maintenance MR. Higher maintenance MR is associated with higher DEE and thus with higher expression of behaviors related to energy acquisition, but not with variation in behaviors associated with energy expenditure.

**Performance model:** a model of energy management where variation in maintenance MR reflects variation in the size of organs that mobilize energy (e.g., digestive organs, muscle). Individuals with higher maintenance MR are able to maintain higher levels of energy output (i.e., have higher DEE) and so are predicted to show higher expression of energetically costly behaviors and behaviors related to energy acquisition [8].

**Resting metabolic rate (RMR):** the lowest metabolic rate of an endotherm that is at rest and thermoneutral, but where one or more of the criteria required for BMR is not met (i.e., adult, normal period of inactivity, post-absorptive, nonreproductive) [11].

**Routine metabolic rate (routine MR):** the lowest metabolic rate of a post-absorptive, undisturbed ectotherm, allowing for some spontaneous activity (e.g., ventilation of gills) and maintenance of body posture [13].

**Standard metabolic rate (SMR):** the lowest metabolic rate of an ectotherm that is at rest during its normal period of inactivity, post-absorptive, and nonreproductive at a specified ambient temperature [25].

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## Measuring energetic constraints independent of behavior

Energetic constraints arise because animals are limited by the total amount of energy that can be expended and/or the amount of energy that can be assimilated during a given period of time (see [Glossary](#)) [10]. Empiricists interested in understanding whether among-individual differences in energetic constraints shape among-individual differences in behavior face a chicken-and-egg problem. All behavior consumes energy (to varying degrees) and some behaviors facilitate energy acquisition. Consequently, the behavior of animals is intimately linked to their overall energy budgets (energy expenditures and energy gains). How can individual differences in energetic constraints and behavior be teased apart? One way around this issue has been to focus on measures of energetic requirements that are assumed to be largely independent of behavior: basal MR (BMR), resting MR (RMR), standard MR (SMR), and routine MR. Here we critically evaluate the assumption that these MR measures are indeed independent of behavior.

BMR, RMR, SMR, and routine MR are all measured under fairly strict conditions. BMR and RMR are both measures of maintenance metabolism for endotherms. BMR is meant to provide a measure of the minimum energy requirement for self-maintenance and so is measured under conditions that attempt to eliminate all other energetic costs. BMR is measured in nonreproductive, non-growing, post-absorptive (i.e., not expending energy processing food) animals during their normal period of rest (i.e., not expending energy on executing behavior) within their thermoneutral zone (i.e., not expending energy maintaining body temperature). RMR is a slightly less rigorous measure in that one of the first three conditions (nonreproductive, non-growing, post-absorptive) need not be met [11]. The trend to measure RMR has probably arisen in part because of the difficulty of obtaining post-absorptive measures in some animals; for example, in small mammals where there is a fine line between being post-absorptive and metabolizing energy stores or in ruminants, which take a long time to evacuate their gut.

BMR and RMR are often used interchangeably (e.g., [6,8]); however, the seemingly small differences in the conditions under which they are measured provide scope for among-individual differences in RMR to become conflated with among-individual differences in behavior. Among-individual differences in RMR can arise from various unmeasured variables that might themselves be outcomes of the among-individual behavioral variation that the study aims to explain. For example, animals that are able to monopolize food resources (e.g., because they display more resource-defense behavior) or animals that forage more intensively are less likely to be post-absorptive during any given measurement than individuals that are less competitively dominant for food or that forages less. In this type of case, competitively dominant individuals might have higher RMRs on average because, for these individuals, RMR measures will often include the energetic costs of food processing, while for animals that are competitively inferior the energetic costs of processing food are less likely to be included in RMR measures when care is not taken to control for the absorptive status of individuals. Thus, apparent

among-individual differences in MR might be the outcome of behavioral variation rather than the driver of behavioral variation. Although among-individual differences in BMR in principle should exclude behavioral effects, they might also be confounded by behavioral variation (see discussion in [8]).

The difficulty of removing potential behavioral influences from measures of SMR and routine MR are perhaps more widely appreciated [12]. SMR and routine MR are both measured in ectotherms. Because ectotherms do not thermoregulate, SMR and routine MR measurements are reported at a specified ambient temperature (in contrast with endotherms, where BMR and RMR are measured within the thermoneutral zone of the organism). Although achieving truly 'at-rest' measures of metabolism is challenging in any organism, the problem is even more pronounced in aquatic animals that must move to ventilate their gills [12]. In some cases, researchers accept that some random activity will be included in MR measures, and these measures are referred to as routine MR (e.g., [13]). However, among-individual differences in the propensity to display baseline levels of activity can result in apparent relationships between routine MR and behavior. Another way of attempting to exclude behavioral influences in MR measures is to measure MR at different forced levels of activity (e.g., swim velocity) and extrapolate relationships back to zero velocity to estimate SMR [12]. However, this method can result in overestimation of SMR; for example, when swimming at high speeds imposes additional maneuvering costs. Alternatively, this method can result in underestimation of SMR if active individuals suppress metabolism in organs that should normally be included in measures of SMR [12]. If the magnitude of over- or underestimation of SMR varies as a function of the behavioral profile of the animal, these types of estimation errors can generate spurious among-individual relationships between estimated SMR and behavior (or mask relationships).

## Are BMR, RMR, SMR, and routine MR valid proxies for energetic constraints?

Besides the assumption that maintenance MRs can be measured independent of behavior, another major assumption of studies investigating relationships between MR and behavior is that the MR measure used is a valid proxy for energetic constraints; in other words, that the chosen MR measure reflects among-individual differences in the amount of energy that can be expended and/or assimilated in a given time period. However, the need to acquire and assimilate energy is more directly related to the total energy expenditure of an organism [e.g., daily energy expenditure (DEE) for animals with balanced energy budgets] as opposed to the subset of energy requirements required for self-maintenance (e.g., BMR, RMR, SMR, routine MR). Similarly, the energy available to fuel behavior is not directly determined by the maintenance MR but rather by the difference between the total energy budget (e.g., DEE) and the energy allocated to behavior. We refer to the portion of the daily energy budget in excess of basic maintenance costs as daily metabolic scope (i.e., maintenance MR + daily metabolic scope = DEE). Do measures of maintenance MR reliably predict DEE and daily metabolic scope?

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