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-individuals 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 unrestrained 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].

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 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 forage 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?

The simple answer is no. Maintenance metabolic rates and total energy available and/or expended (e.g., DEE) can be related to one another in various ways. Below, we outline why the exact nature of the relationship (i.e., the energy management model) has profound consequences for the predicted relationship between MR and behavior.

Energy management models

BMR and DEE can be related to each other in one of three ways (Figure 1). (i) Under the 'allocation model', the total energy budget (DEE) is fixed and does not vary as a function of maintenance MR. Thus, to balance their energy budgets, individuals with higher RMR should have lower expression of energetically costly behaviors such as activity, aggression, and parental care. Since the total amount of energy required does not differ as a function of MR, there is no predicted relationship between MR and behaviors that bring in net energy such as foraging or foraging boldness. (ii) Under the 'independent model', variation in basic energy requirements neither reduce nor increase the amount of energy available for other processes (i.e., daily metabolic scope). Under this scenario, no relationship is predicted between measures of basal MR and the expression of energetically costly behaviors. However, because there remains an overall positive correlation between MR and DEE, positive correlations between MR and behaviors that bring in net energy gain are predicted. (iii) Under the 'performance model', higher MR reflects a greater capacity to mobilize energy (e.g., because individuals with relatively more digestive tissue have higher BMRs [14,15]). Higher MR is associated with both greater daily metabolic scope and higher DEE. Consequently, higher MR is predicted to be associated with higher expression of energetically costly behaviors as well as

behaviors that bring in net energy (e.g., foraging under predation risk, defense of feeding territory).

The importance of the energy management model for determining how among-individual differences in MR are predicted to correlate with among-individual differences in behavior has been highlighted previously [7,8]. However, our review of the literature suggests that, for most studies linking variation in MR to variation in behavior, the underlying relationships between MR, daily metabolic scope, and DEE remain untested assumptions or are evaluated only indirectly (Table 1). Interestingly, most studies testing relationships between MR and behavior assume that their system exhibits a performance energy management model (Table 1). Although this model is well supported at the interspecific level [14,16] (but see [17]), support is distinctly less clear at the among-individuals level. We compiled a review of intraspecific studies using keyword searches in the Institute for Scientific Information (ISI) database (Topic = 'basal metabolic rate' OR BMR OR 'resting metabolic rate' OR RMR) AND (Topic = 'daily energy expenditure' OR DEE or 'field metabolic rate' or FMR) and identified additional references from the literature cited in these papers. This non-exhaustive review indicates that more studies have reported nonsignificant relationships between MR and DEE than have reported positive relationships (Table 2).

Evaluating the energy management model

As outlined above, the energy management model is key for developing *a priori* predictions regarding the relationship between MR and behavior, and there are no rules of thumb for when to expect one energy management model over another (Table 2). Why then do so few empirical studies
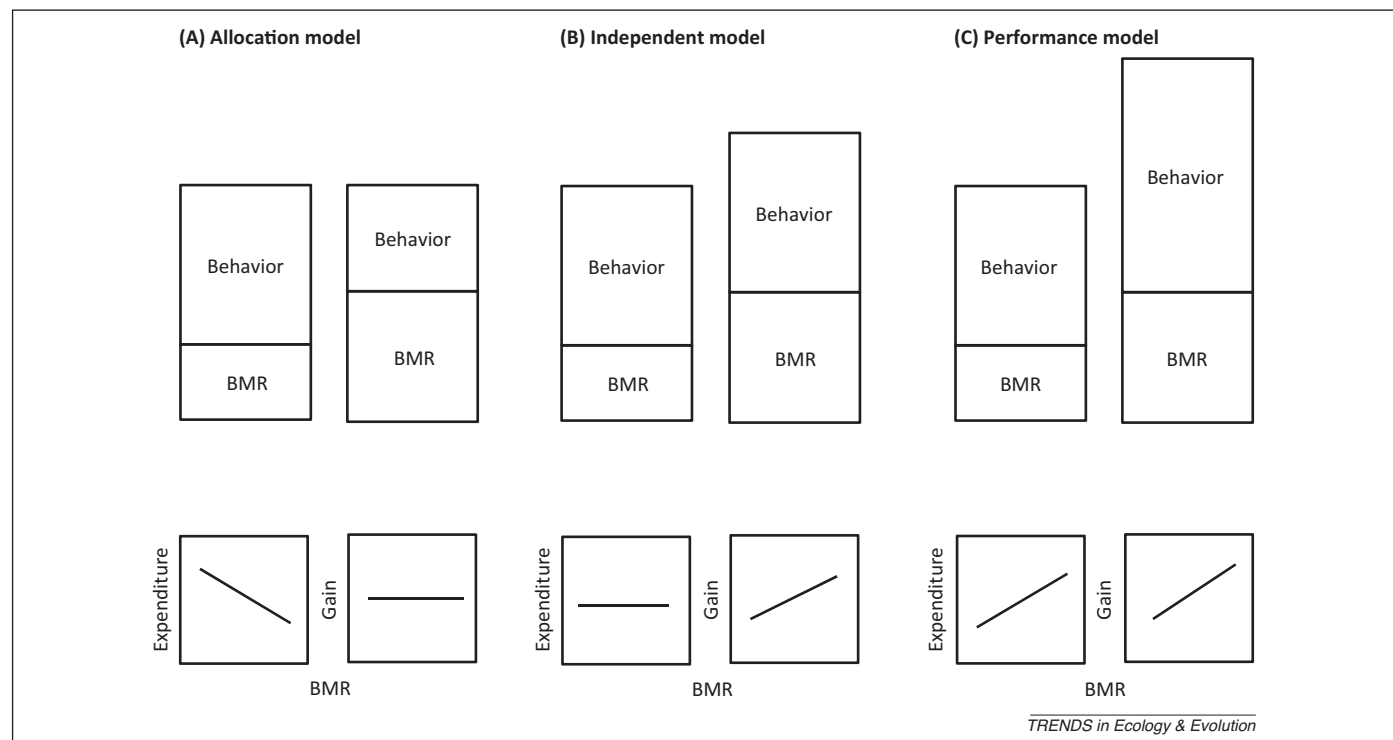
Figure 1. Illustration of alternative strategies for balancing energy budgets given variation in basal metabolic rate (BMR). The top panel shows how the energy available for behavior (i.e., daily metabolic scope) and total energy expenditure [daily energy expenditure (DEE), illustrated by the total height of the stack] vary as a function of BMR for different energy management models. The lower panel shows the predicted relationship between BMR and behaviors associated with energy expenditure versus energy gain.

Table 1. Review of studies testing among-individual relationships between energetic constraints and behavior, whether the energy management strategy was considered, and, if so, how it was determined

Species	Behavior	Correlation[a]	Energy management strategy[b]	Refs
Birds				
Chicken (*Gallus gallus*)	Dominance	−/NS (M/F)	P (assumed)	[26]
Dipper (*Cinclus cinclus*)	Dominance	+	None	[27]
Great tit (*Parus major*)	Exploration	NS/− (M/F)	P (assumed)	[28]
Great tit (*P. major*)	Risk taking	+/− (HD/LD)	P (inferred)	[29]
Junco (*Junco hyamalis*)	Dominance	NS	None	[30]
Zebra finch (*Taeniopygia guttata*)	Social foraging tactic	+	P/A (HF/LF)[c] (inferred)	[5]
Fish				
Arctic char (*Salvelinus arctitcus*)	Aggression	+	P (inferred)	[31]
Brook char (*Salvelinus fontinalis*)	Activity	NS	None	[32]
Carp (*Cyprinus carpio*)	Risk taking	+	P (assumed)	[33]
Salmon (*Salmo salar*)	Aggression	+	P (inferred)	[34]
Salmon (*S. salar*)	Dominance	+	P (assumed)	[35]
Salmon (*S. salar*)	Risk taking	+/NS (C/NC)	P (assumed)	[36]
Masu salmon (*Oncorhynchus masou*)	Dominance	+	P (inferred)	[37]
Salmon (*S. salar*)	Dominance	+	P (assumed)	[38]
Rainbow trout (*Oncorhynchus mykiss*)	Dominance	+	P (assumed)	[39]
Mammals				
House mouse (*Mus musculus*)	Activity	+	P (inferred)	[40]
House mouse (*M. musculus*)	Activity	+/− (M/F)	P (evaluated)	[44]
House mouse (*M. musculus*)	Running speed	NS/− (FB/VB)	P (assumed)	[45]
Bank vole (*Myodes glareolus*)	Dominance	NS	P (assumed)	[41]
Deer mouse (*Peromyscus maniculatus*)	Activity	+	None	[42]
Deer mouse (*P. maniculatus*)	Activity	+/NS (M/F)	None	[43]
Marmot (*Marmota flaviventris*)	Home range size	+	P (assumed)	[46]
Gerbil (*Meriones unguiculatus*)	Activity	NS	None	[47]
Root vole (*Microtus oeconomus*)	Exploration	+[d]	None	[48]
Meadow vole (*Microtus pennsylvanicus*)	Exploration	NS	P (assumed)	[49]
Deer mouse (*Peromyscus maniculatus*)	Exploration	+[e]	P (assumed)	[50]
Insects				
Cricket (*Gryllodes sigillatus*)	Calling	+	None	[51]
Mealworm beetle (*Tenebrio molitor*)	Risk taking	+	P (assumed)	[52,53]
Amphibians				
Ouachita dusky salamander (*Desmognathus brimleyorum*)	Exploration	NS	A (inferred)	[54]
Reptiles				
Common lizard (*Zootoca vivpara*)	Exploration	NS	P (assumed)	[55]

[a]Observed correlation: +, positive; −, negative; NS, nonsignificant. Parentheses detail categories of comparison: M/F, male/female; H/L, high danger/low danger; C/NC, cover/no cover; F/V, forced behavior/voluntary behavior; NF only, nonreproductive females only.

[b]Energy management strategy in a given study: A (allocation), P (performance), or none (not explicitly mentioned). Parentheses indicate whether the energy management strategy was assumed based on previous studies, inferred based on indirect evidence (food intake or growth), or directly evaluated in that study with measures of DEE.

[c]HF/LF, high food/low food.

[d]Correlation observed in nonreproductive females only.

[e]Correlation significant at the genotypic level but not at the phenotypic level.

explicitly evaluate energy management models? One likely explanation is the logistical challenges associated with available methods for estimating DEE. For example, the doubly labeled water method, the most common method for estimated DEE, requires capture and recapture of animals [18]. Recapturing individuals is not feasible in many study systems. However, even in systems where recapture is possible, recaptured individuals might represent a non-random subset of the overall population (e.g., trap-happy versus trap-shy animals), which is particularly problematic if recaptures biases are correlated with the behavioral trait of interest [19]. Additionally, the doubly labeled water method is not suitable for estimating the energy demands of aquatic exothermic animals (e.g., fish, amphibians,

aquatic insects) [18,20]. In these systems, alternative methods for estimating DEE should be used, such as quantification of the costs of various activities using indirect calorimetry combined with detailed observations of activity budgets or heart rate monitoring [20,21]. However, the former approach typically comes with large measurement error, while the latter requires time-consuming calibrations. Alternatively, radiotracer techniques can be used to estimate field MRs in aquatic organisms (e.g., [22]).

Despite potential logistical challenges, we urge empiricists to take up the challenge of simultaneously measuring maintenance MR (being careful to exclude behavioral influences) and DEE in studies investigating links between MR and behavior [7]. However, we argue that the common

Table 2. Review of intraspecific studies reporting correlations between BMR, (RMR, SMR, or routine MR and total energy expenditure (DEE or (FMR)

Species	Correlation?[a]	Context	N	Refs
Birds				
Zebra finch (*Taeniopygia guttata*)	Positive/NS	Nonreproductive/reproductive	24/24	[56]
Black-legged kittiwake (*Rissa tridactyla*)	NS	Early chick rearing	27	[57]
	NS	Incubation and chick rearing	32	[58]
Thick-billed murre (*Uria lomvia*)	NS	Incubation and chick rearing	52	[58]
House wren (*Troglodytes aedon*)	Positive	Chick rearing	27	[59]
Marsh tit (*Parus palustris*)	Positive	Chick rearing	6	[60]
Reptiles				
Garter snake (*Thamnophis sirtalis*)	NS	Reproductive	78	[61]
Mammals				
Field vole (*Microtis agrestis*)	NS[b]	Nonreproductive	75	[62]
	NS[c]	Mix of reproductive and nonreproductive	21	[63]
House mouse (*Mus musculus*)	Positive		96	[44]
Eastern chipmunk (*Tamias striatus*)	Positive/NS	Reproductive/nonreproductive	22/17	[64]

[a]Estimated correlation between maintenance MR and DEE. NS, non-significant; Positive, significant positive correlation.

[b]Positive relationship between RMR and DEE found among individuals only when not controlling for population of origin.

[c]Positive relationship between RMR and DEE found among individuals only when not controlling for body mass.

practice of testing for a significant relationship between MR and DEE (or a proxy for DEE) is insufficient to distinguish between alternative energy management models. A significant relationship between MR and DEE can allow one to exclude or not the allocation model as the likely energy management strategy of the study system. However, precise information on the magnitude of the relationship between MR and DEE provides a greater opportunity to evaluate the likelihood of each of the three alternative energy management models (see worked example in Box 1). We therefore


Box 1. Assessing the energy management model: a worked example

To date, very few studies have directly tested correlations between MR and DEE at the intraspecific level (see Table 2 in main text and main text), and each of these studies has focused on whether correlations between maintenance MR were significantly different from zero. Nonsignificant correlations are often assumed to support the allocation model, while significant correlations are assumed to support the performance model. Here we show using worked examples why this approach is flawed and can lead to erroneous conclusions.

From Figure 1 in main text, it follows that different energy management strategies will result in different relationships between maintenance MR and DEE. Under the allocation model, among-individual variation in DEE is independent of variation in maintenance MR and the predicted correlation between the two is zero. Under the independent model, it is the daily metabolic scope that is independent of maintenance MR. Since DEE is the sum of maintenance MR and daily metabolic scope, even when there is no functional relationship between MR and daily metabolic scope (i.e., the independent model), part-whole correlations will generate a positive relationship between maintenance MR and DEE with a slope equal to 1 [where maintenance MR is the predictor (x) variable and DEE the response (y) variable]. Under the performance model, daily metabolic scope increases with increasing maintenance MR, resulting in a positive regression of MR on DEE with a slope >1. Thus, demonstrating that a slope differs from zero allows the allocation model to be eliminated as a candidate energy management strategy but is not sufficient to distinguish between independent versus performance models [which requires distinguishing between an effect size of 1 (independent) and of >1 (performance)]. Similarly, nonsignificant relationships might or might not exclude the independent or performance model, depending on the magnitude of the estimated effect. Consequently, we advocate presenting effects sizes (i.e., slopes) and their confidence intervals to facilitate evaluation of the level of support for alternative energy management models [23].

To illustrate, we highlight two studies both of which reported nonsignificant relationships between RMR and DEE [62,64]. Relying strictly on significance levels, both results would appear to provide support for the allocation model because we cannot reject the null hypothesis of no effect of maintenance MR on DEE. However, when considering the estimated effect of RMR on DEE and the associated confidence in that estimate, it is clear that only one of these studies [62] provides strong support for the allocation model, while the other is consistent with all three energy management models [64] (Figure I).
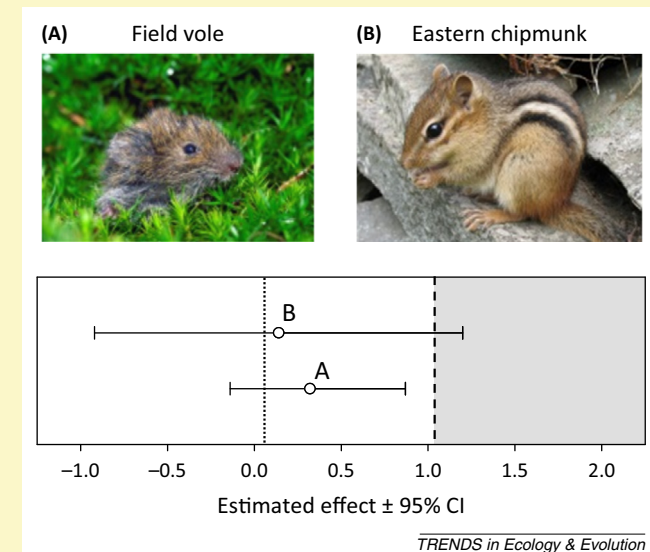
Figure I. Illustration of how significance values for correlations can provide misleading support (or lack of support) for a given energy management model. The allocation model predicts an effect of resting metabolic rate (RMR) on daily energy expenditure (DEE) of zero (vertical dotted line), the independent model predicts an effect of 1 (vertical broken line), and the performance model predicts an effect >1 (grey shaded area). Both of the estimates and 95% confidence intervals presented above are derived from studies reporting statistically nonsignificant relationships between RMR and DEE. However, the nonsignificant relationship estimated in field voles **(A)** provides unambiguous support for the allocation model [62], while the nonsignificant relationship estimated in eastern chipmunks **(B)** cannot exclude any of the three energy management models [64]. Photographs from Wikimedia Commons.

recommend that future studies reporting relationships between maintenance MR and DEE provide direct estimates of the slope of the relationship and its confidence interval [23], rather than simply reporting a correlation coefficient and a *P* value.

Importantly, measures of DEE cannot replace measures of maintenance MR in understanding how energetic constraints shape behavior, because it is the relationship between the two that provides critical information on whether among-individual differences in energetic constraints arise because of differences in the need to acquire and assimilate energy, the potential daily metabolic scope, or both (Figure 1).

What can we learn by measuring MR and behavior?

We argue that without explicitly addressing the energy management model of the study system, correlations between MR and behavior will provide little insight into how among-individual differences in energetic constraints shape behavior. This is because a single measure of MR (e.g., BMR, DEE) is insufficient to infer the energetic constraints that individuals face (e.g., differences in the need to acquire and assimilate energy, in daily metabolic scope, or both). Yet, if we know the energy management model of the system, and we measure meaningful behaviors (i.e., whose consequences for energy gain and/or expenditure are known), correlations between energy metabolism and behavior must necessarily exist – so what do we stand to learn?

Given variation in MR, all three energy management models predict associations between MR and certain types of behavior (e.g., behaviors associated with energy expenditure, energy gain, or both). However, the predictions are extremely general. For example, under the allocation model, higher maintenance MR should be associated with lower expression of energetically demanding behaviors. Does this mean that all behaviors should be downregulated equally or should only certain behaviors be downregulated? This will undoubtedly depend on the overall costs and benefits of exhibiting particular behavioral actions, of which energetic cost is only one component. For example, if the fitness costs of decreasing provisioning effort are greater than the fitness costs of decreasing aggressiveness, individuals with a lower metabolic scope might balance their energy budgets by downregulating aggression but not provisioning effort.

This possibility that animals adaptively adjust only a subset of all possible behaviors to balance their energy budgets is not trivial because it implies that null results cannot be taken as evidence that among-individual differences in energetic constraints do not shape among-individual differences in behavior generally, but only for the specific behavior in question. However, we believe that the potential for animals to make countless different decisions about how to allocate energy to different behaviors provides exciting opportunities to develop and test new ideas about the factors constraining the expression of behavior (Box 2). We hope that the points raised in this Opinion will prove useful for guiding future empirical work in this burgeoning field of research.

Box 2. Outstanding questions

- What factors determine the energy management strategy of a given species? Presently, there are too few studies documenting variation in measures of maintenance metabolism and DEE (see Table 2 in main text) to infer any general patterns. However, knowledge of any such patterns would provide insights into the role of ecology in shaping energetic constraints. For example, does the prevalent energy management strategy differ across taxa (e.g., birds versus mammals) or depending on the ecological context (e.g., reproductive versus nonreproductive animals)?
- Are certain behaviors more likely to covary with metabolic rate than others? For example, foraging rate, foraging boldness, social dominance, and territory defense might all increase access to resources. Do individuals with higher DEE have higher expression of all of these behaviors or are some behaviors affected more than others? Do the types of behavior that covary most strongly with MR differ depending on, for example, the energy management strategy or the ecology of the system?
- Do patterns vary across hierarchical levels? Do energy management models differ across hierarchical levels (e.g., within- versus among-individuals, among populations)? Do energetic constraints influence the same suites of behaviors at different hierarchical levels?
- What is the causal relationship between MR and behavior? Throughout this Opinion, we have emphasized the potential for variation in energetic constraints to drive variation in behavior, but among-individual differences in energetic constraints can also be the outcome of among-individual differences in behavior. Studies measuring MR, DEE, and behavior repeatedly in the same individuals are needed to quantify feedbacks between state and behavior and elucidate causal relationships [65].
- Are correlations between MR and behavior developing over ecological or evolutionary timescales? Does selection favor among-individual correlations between MR by means of adaptive phenotypic plasticity (e.g., [66]) or the evolution of genetic correlations (e.g., [67])? Do energy management strategies differ across life history stages?

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