

Energetics and behavior: many paths to understanding

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In a recent Opinion, Mathot and Dingemans [1] draw attention to a claimed major assumption of studies linking animal personality and energetics: ‘that the selected measure of [metabolism] is a valid proxy for energetic constraints.’ They argue that unless this assumption is tested, results from many studies are uninterpretable. We would like to argue that the definition of energetic constraints they propose would make it difficult if not impossible to test this assumption.

Problems with the redefinition of energetic constraints

The allocation principle goes back to Fisher [2] and is based on the idea that energetic (or time or space) constraints can generate trade-offs (i.e., a situation in which one trait or function cannot increase unless another decreases [3]). Yet, the adopted definition of ‘energetic constraints’ is problematic. Energy requirements in and of themselves are not constraints. Otherwise, if constraints equate to energy requirements, and energy requirements are ‘more directly related to the total energy expenditure’, an organism sustaining high levels of daily energy expenditure (DEE) when it has unlimited access to food would be considered more ‘constrained’ than an organism with lower DEE during periods of low food abundance. As a sensible way to view constraints, one might, for example, compare the energy required for a bat to survive winter with the energy available as fat stores [4].

Neither common nor flawed practice

In our reading of the literature, we would dispute that it is common practice to test for a relationship between resting metabolic rate (RMR) and DEE to distinguish between alternative models of energy management. The word ‘allocst’ is mentioned in seven of ten studies in Mathot and Dingemans’s Table 2, but in every case allocation was discussed in relation to additional components of the energy budget such as workload, activity level, parental care, growth, or immune function. Thus, we would argue it is not the case that nonsignificant correlations between RMR and DEE are often assumed to support the allocation model. When both DEE and RMR are measured in free-living animals, it is highly informative to look at the relationship between the two *per se*, without any need to invoke energy management models. This is what was done in the cited vole [5] and chipmunk [6] studies. We agree

that the slope between DEE and RMR should always be provided, but it could be misleading to distinguish among energy management models based on that information alone (Box 1).

RMR versus basal metabolic rate (BMR)

Mathot and Dingemans [1] state that the ‘trend to measure RMR has probably arisen in part because of the difficulty of obtaining post-absorptive measures...; for example, in small mammals...there is a fine line between being post-absorptive and metabolizing energy stores.’ We question this statement in terms of both animal energetics and the history of the field. By definition, a post-absorptive animal needs to metabolize energy stores, so there can be no fine line between the two. RMR was introduced because two or more criteria for measuring BMR are sometimes mutually exclusive. Some rodents and insectivores, for example, become hyperactive or enter torpor when deprived of food [7]. It is also interesting to measure the RMR of growing juveniles or lactating females, so ecophysiologicalists felt the need to free themselves from the overly restrictive criteria for measuring BMR. When intentionally violating one criterion due to logistic constraints (or for biological reasons), precautions are usually taken to standardize measurements across individuals. When animals cannot all be fasted, for example, they should be housed individually and provided with an equal amount of food before testing.

Causality or coadaptation?

Mathot and Dingemans [1] focus on how consistent individual differences in metabolism can drive behavior. This is somewhat understandable, because many models recently developed in behavioral ecology attempt to explain the existence of animal personalities by linking behavior with a state variable inherently less flexible than behavior, such as body size, condition, life-history stage, or metabolism [8]. Yet, available data do not support the idea that metabolism is less flexible than behavior. Although the average repeatability of behavior has been estimated as 0.37 [9], the value for maintenance metabolism (after conditioning on body mass) is only slightly higher at 0.42 [10]. Even if metabolism were truly more repeatable than – and driving variability in – behavior, the question becomes ‘what drives individual differences in metabolism?’, which leaves us no closer to understanding mechanism in the strict sense [11]. Because metabolic and personality traits are labile, the question becomes what explains consistent individual covariance in these complex phenotypes and whether they are part of coadaptations to heterogeneous and variable environmental conditions.

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Box 1. Assessing the energy management model: more than just DEE and RMR

Mathot and Dingemanse [1] proposed to distinguish among the allocation, independent, and performance models using the slope of the regression of DEE on RMR. We agree that a slope of 0 indicates that reallocation is occurring within the energy budget, but it does not demonstrate which components are involved nor whether the trade-off occurs at the among- or within-individual level or both [12]. Obviously, one needs to quantify more components of the energy budget to be able to identify trade-offs, constraints, or even allocation as an underlying process. Moreover, allocation can still occur within

individuals even if the slope of the relationship between DEE and BMR is >1 . In Figure 1A, the slope of the least-squares linear regression is significantly >1 (estimate \pm SE = 2.54 ± 0.57), which would eliminate the allocation model. In Figure 1B, however, allocation is occurring within individuals: as BMR varies, DEE does not, so other components of the budget must be changing in a compensatory fashion. However, this allocation is masked in Figure 1A by greater variability in DEE and RMR among than within individuals [12].

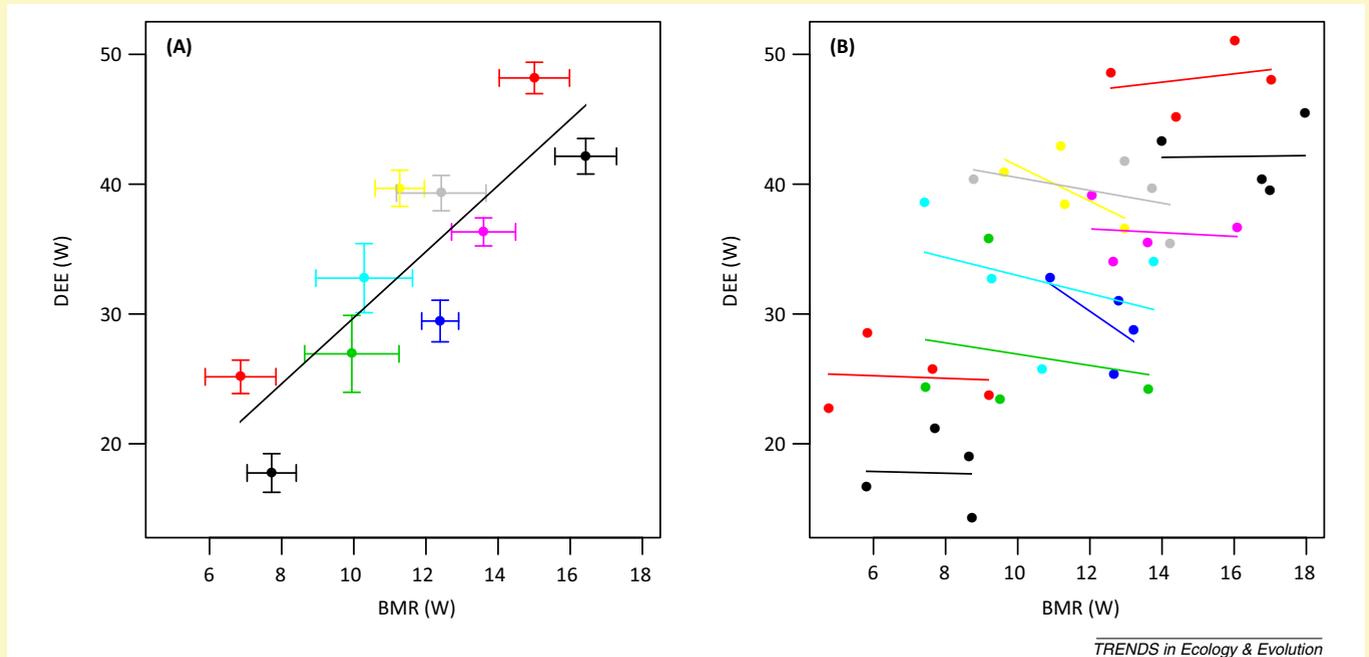


Figure 1. (A) The average daily energy expenditure (DEE) and basal metabolic rate (BMR) in ten hypothetical individuals. (B) DEE and BMR in the same individuals, this time showing the regression lines fitted for the four repeated measures of each individual.

Concluding remarks

Studies linking animal personality and energetics have flourished in the past 10 years, attesting to the topic's importance. Although we applaud Mathot and Dingemanse's [1] attempt to further elaborate concepts of energy management, we emphasize that more correlative studies will offer limited insight on how personality and metabolism are coadapted. Instead, we need more experimental studies, including both phenotypic manipulations and selection experiments [11].

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