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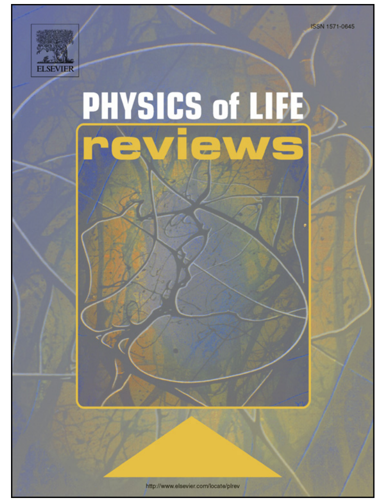

The universality and the future prospects of physiological energetics

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The universality and the future prospects of physiological energetics
Reply to comments on "Physics of metabolic organization"

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Abstract

In response to the comments on review "Physics of metabolic organization", we discuss the universality and the future prospects of physiological energetics. The topics range from the role of entropy in modeling living organisms to the apparent ubiquity of the von Bertalanffy curve, and the potential applications of the theory in yet unexplored domains. Tradeoffs in outreach to non-specialists are also briefly considered.

Keywords: entropy, DEB theory, homeostasis, von Bertalanffy curve, metabolic acceleration

We would like to begin this reply by expressing our sincere gratitude to all the commentators for providing insightful and challenging comments. We are painfully aware that replies to many of the topics brought forward by the commentators could easily match the size of the original review [1], but do our best to provide concise and informative answers and notes. The fact that there is so much to discuss goes a long way in showing how much physics can inform biology—and vice-versa—in a quest to understand the links between metabolic processes and levels of biological organization ranging from molecules to individuals to ecosystems [2]. Commentators generally expressed their views on (i) the universality of physical principles on which to build full life-cycle, bioenergetic models for individual organisms [3, 4, 5, 6], as well as on (ii) the potential for future developments in this field [7, 8, 9, 10, 11]. Other, more specialized topics include (iii) the importance of tracking the maturity level of individuals [12], (iv) the difficulties of parameter estimation in relatively large phase spaces [13], and (v) a need for more approachable expositions of theoretical foundations if a broad acceptance among non-specialists is to be achieved [14]. For a reader interested in a succinct, yet remarkably thorough overview of the current state of affairs in the field, there is hardly a better resource than [15].

Criticizing the very fundamentals of [1], Martyushev [3] proposed an intriguing hypothesis that organisms should be viewed as maximizers of entropy production. We believe that a skeptical mind can neither discard this hypothesis lightly, nor accept it at face value without a deeper consideration. As it is seen from Eq. (8) in [1], a mere exchange of materials and energy with the environment for the purpose of accumulating reserve, building structure, and performing the necessary maintenance, demands that entropy is produced. Thus, we are in complete agreement with Schrödinger [16] in that organisms avoid decay by producing entropy and by freeing themselves from this entropy in some way. As explained in Section 5.4 of [1], heterotrophic aerobes get rid of entropy by dissipating heat, i.e., $T\sigma = -\dot{Q}$ (the need for a minus sign in this equation was nicely spotted and explained in [13]). In fact, we are also in agreement with Emden [17] in that the law of energy conservation provides us with little more than a means for bookkeeping, i.e., balancing inputs and outputs; the law indeed tells us nothing about *why* organisms do what they do. To answer the question *why*, Martyushev [3] invokes the principle of maximal entropy production.

The exposition in [1] steers clear of the question *why* and takes a more pragmatic approach of accounting for what organisms are readily observed to do. The two most fundamental observations on which we base our theoretical developments are very precisely stated in [4]: organisms change their chemical composition in response to the nutritional status and possess metabolic memory in the sense of provisioning for life stages (e.g.,

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