Minimal waste production is a fundamental law for animal locomotion

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Is there a unifying principle underpinning animal locomotion in its rich diversity? A thermodynamic analysis performed by a Skoltech professor and his French collaborators at Université Paris Diderot, Université Paris

Saclay, and the Muséum national d'Histoire Naturelle, shows why and how waste minimization prevails on efficiency or power maximization when it comes to free locomotion irrespective of the available mode and gaits. The research is published in the *Physical Review Letters*.

"Locomotion is a hallmark of animal life," says Skoltech professor Henni Ouerdane, "and that is why it has fascinated thinkers since at least Aristotle's time." Prof. Ouerdane adds that "in the late 19th century Eadweard Muybridge's invention, the zoopraxiscope, a precursor of the motion picture, mesmerized crowds witnessing the beautiful complexity of biomechanics; and that detailed comparisons between living and man-made machines naturally followed, but with very limited success to explain life."

For the man-made machines, maximization of energy conversion efficiency is a must to save resources, but does this apply to animals when they freely move about? Answering this question poses a formidable challenge considering the multiform character of animal life and habitats. Power maximization is the obvious target under stressful contexts, prey chasing or flight; but no clear principle, if any, seemed to apply to free locomotion. In fact, the detailed interplay between energy management and locomotion, and in particular the optimization of energy expenditure across gaits, had always remained elusive.

Prof. Ouerdane and his main collaborator, Prof. Christophe Goupil, had previously extensively studied the nonequilibrium thermodynamics of energy converters, but the leap to the physics of life was a daunting prospect. Indeed, the formulation of a generic compact model of locomotion of highly complex systems such as living organisms seemed out of reach. "Of course, the literature on the topic is rich and abundant, but many models rely on large sets of fitting parameters to reproduce part of the observed energetics of muscle action, which somehow hinders a clear vision of the thermodynamic processes at work. Further, the basic muscle model derives from original works using dead, dissected muscles, while one wants to understand the chemical-to-mechanical energy conversion in living organisms," says Prof. Goupil.

The first step to a thermodynamic model of locomotion was a proper model of metabolic energy conversion in actual, living muscles. This work, published in the *New Journal of Physics* in 2019, by Prof. Ouerdane and his collaborators, emphasized the necessity to consider rigorously the particular boundary conditions to which a living muscle under load is subjected, and their feedback effects related to the metabolic intensity. Their work thus bridged an outstanding gap between inert muscle models and live muscle put to work by an actual animal.

"In our latest work, introducing the energy cost of efforts, we unraveled a fundamental extremal principle of the nonequilibrium thermodynamics of animal locomotion: free locomotion entails minimization of metabolic waste production. We used published experimental data for walk, trot, and gallop, each gait representing different biomechanical working conditions. We recovered the trends with our model, and provided new insights into animal locomotion, hence reaching beyond our case study," says Prof. Ouerdane.

This research contributes to significant progress in the understanding of locomotion in any environment (terrestrial, aerial, aquatic) independently of the phylogeny. Interestingly, it also sheds light on a natural principle that can drive the innovative design of future man-made waste-efficient machines, and it may also feed bioinspired robotics for problems related to, e.g., proprioception and variable mechanical impedance of actuators, which in turn could advance the development of physics-based theories of life.

More information: E. Herbert et al, Thermodynamics of Animal Locomotion, *Physical Review Letters* (2020). DOI:

10.1103/PhysRevLett.125.228102 Thermodynamics of metabolic energy conversion under muscle load

Christophe Goupil et al. Thermodynamics of metabolic energy conversion under muscle load. *New Journal of Physics*, Published 28 February 2019. Volume 21, 1 February 2019

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