## **Life, Death and Energy: Nature Selects No Free Lunch**

Indrė Žliobaitė University of Helsinki, Finland indre.zliobaite@helsinki.fi

## **Abstract**

Brown et al. (2024) highlight that organisms invest a constant amount of energy into the production of viable offspring per unit of body mass per generation. This explains how diversity in life can exist. We interpret their result in relation to balancing offspring costs in real vs. physiological time.

In their recent article, Brown et al. (2024) highlight that life, no matter what the form, invests a constant amount of energy into the production of viable offspring per unit of its body mass. I salute the authors; the argument makes good sense and brings far-reaching  $implications - it explains how diversity in life can exist.$ 

As in mathematical optimization (Wolpert and Macready 1997), natural selection offers "no free lunch." The results of Braun et al. (2018,2024) imply that any two forms or ecological ways of life should be equivalent when their performance is averaged across all possible environments. There is a nuance, however.

The constancy of energy investment, 22.4 kJ/g per gram of offspring per generation, as estimated by Brown et al. (2018,2024), holds over a generation length, not in real-time. This estimate implies that in real-time, due to metabolic scaling (Kleiber 1932), larger organisms have lower investment costs in producing a viable offspring.

Brown et al. (2018) estimate the generation length to scale as  $3M^{0.25}$  (mass in g, generation length in years). If we divide the estimated energy investment per gram of offspring by the generation length, we get that energy investment into a gram of viable offspring in real-time, which is then  $0.02M^{-0.25}$ kJ/g per day. Brown et al. (2024) decouple the equal fitness paradigm from any particular scaling relations and tie it to the generation time. However, it still holds that all else being equal, larger organisms invest less energy into producing viable offspring in real time, even if they spend a constant amount of energy per lifetime. Thus, at equilibrium, when populations do not grow and do not decline, the energy spending is balanced over physiological Ime, and the equal fitness paradigm holds over physiological time, which ties to the generation time.

Competition for energy (Van Valen 1973), however, primarily happens in real time<sup>1</sup>, not in physiological time. A question might arise: why, then, do larger animals not gain a

<sup>1</sup> This is our interpretation; Van Valen was not explicit about real-time. However, he quantified expansive energy per unit of time (as rates). Van Valen (1973,1976,1980) highlighted that natural selection happens

competitive advantage due to their lower real-time investment into offspring? The answer is that the units that compete for energy are not grams of body mass, nor are they individuals, at least not primarily. The Red Queen's competition for energy (Van Valen 1973) is at the species level. And since the population density within a species scales as  $M^{-0.75}$  (Damuth 1981), at least within the same adaptive zone, the energy investment into offspring at the species level in real-time should scale as  $M^{-0.25}$ MM<sup>-0.75</sup> =  $M^{0}$ .

Beautifully, this holds at the equilibrium. However, what happens off the equilibrium, which is where selection operates? Expansive energy, which in the Red Queen's competition is "maximized unconditionally" (Van Valen 1980), is not the energy invested into offspring that replace parents, that is the energy invested into extra viable offspring that bring population growth. If expansive energy becomes available and the carrying capacity is unlimited, a shorter generation length of smaller-sized organisms would give an advantage to grow the population faster. In competitive circumstances, however, as we argued (Žliobaitė and Fortelius 2020), expansive energy is outcompeted from competitors so slowly in relation to the generation length that the advantage of a shorter generation length dilutes and disappears, and species of different ecological ways of life, even different life forms, can compete for expansive energy as potentially a priori equal competitors.

The Equal Fitness Paradigm thus balances out fitness at the cellular, individual, and species levels and explains the mechanism that allows "the spectacular diversity of living things" (Brown et al. 2024). A colleague and a game historian once said that one of the most difficult challenges in game design is to make a game balanced in such a way that no matter which strategy or weapon a player selects, the choice by itself does not give a competitive advantage. In all possible game worlds, it should be potentially possible to win using any strategy. Natural selection makes this happen naturally.

## **References**

Brown, J., Hall, Ch. and Sibly, R. (2018). Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nature Ecology and Evolution* 2(2): 262--268.

Brown, J., Hou, Ch., Hall, Ch. and Burger, J. (2024). Life, Death and Energy: What Does Nature Select? *Ecology Letters*.

Damuth, J. (1981). Population density and body size in mammals. *Nature* 290: 699--700.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia* 6(11): 315--335.

Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory* 1: 1--30.

at different time scales simultaneously, yet this does not imply a possibility of competition for resources happening at different time scales. Resources are available in real-time.

Van Valen, L. (1976). Evolution as a zero-sum game for energy. *Evolutionary Theory* 1: 179--229.

Van Valen, L. (1980). Evolution as a zero-sum game for energy. *Evolutionary Theory* 4: 289--300.

Wolpert, D. and Macready, W. (1997). No Free Lunch Theorems for Optimization. *IEEE Transactions on Evolutionary Computation* 1: 67--82.

Žliobaitė, I. and Fortelius, M. (2020). All sizes fit the Red Queen. Paleobiology 46 (4): 478-- 494.