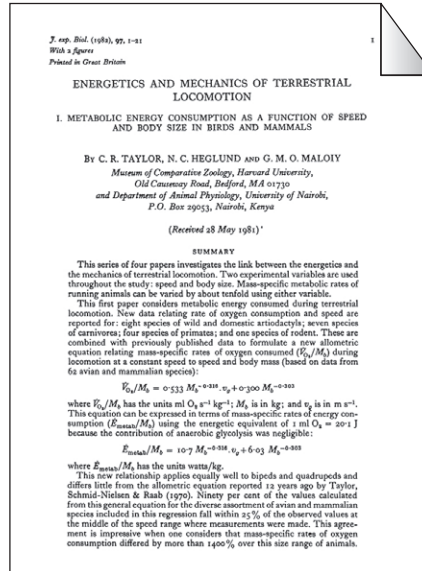


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JEB CLASSICS

TAYLOR'S TREADMILL MENAGERIE



Rodger Kram discusses the series of four papers published by C. Richard Taylor and colleagues, which addressed the energetics and biomechanics of terrestrial locomotion.

Copies of the papers can be obtained from <http://jeb.biologists.org/content/97/1.toc>

A series of four papers in JEB in 1982, masterminded by C. Richard Taylor, asked two deceptively simple questions: why does running faster consume metabolic energy at a faster rate, and why do larger animals require less energy to transport each gram of tissue? The audacious goal of these experiments was to link the energetics and biomechanics of terrestrial locomotion. These were not the first studies to quantify how the energetics of locomotion change with speed and size, but they were the first to comprehensively explore why. Many of us are still working to answer those same questions, trying to follow the large footprints left by this *magnum opus*.

The first paper in the series (Taylor et al., 1982) presented new locomotion energetics data for a diverse assortment of 20 wild and domestic mammal species, from the aptly named dwarf mongoose to behemoth bovines. Measuring locomotion energetics does not involve staid, bench-top pipetting. Rather, depending on the animal's temperament, it can require the combined skills of a rodeo clown, an animal psychologist and a circus sanitation worker. Indeed, the first step in this study was to cajole and train the animals to walk and run on a motorized treadmill without them fighting, fidgeting or fatiguing. The smaller animals were enclosed in respirometry

chambers that fitted over the treadmills whereas the larger beasts wore loose-fitting face masks from which the expired air was captured using the open flow method of respirometry recently perfected by Taylor's group (Fedak et al., 1981). Note: not mentioned in the methods sections is the fact that the masks were custom-made for each species, cobbled together from plastic laundry detergent bottles, Velcro and the ubiquitous duct tape.

The team combined their new data for 20 species with literature data for 42 other species of mammals and birds. Taylor was a co-author on almost all of those studies too. Body mass ranged from 15 g in mice to 254 kg in zebu cattle, a nearly 17,000-fold span. As expected, metabolic rate increased linearly with speed in all but a few of the animals studied. To analyze across body size, Taylor and colleagues calculated the cost of transport (Joules of energy required to move a kilogram of body mass 1 m forward) and then used allometry. Most comparative physiology students first meet allometry *via* Max Kleiber's mouse-to-elephant line for resting metabolism (Kleiber, 1932). Allometry quantifies how structures or functions scale with body mass using equations of the form $Y=aM^b$, where Y is the quantity of interest, a is the coefficient, M is body mass and b is the exponent (Schmidt-Nielsen, 1984). Usually, the exponent, representing the slope, is most informative and is called the primary allometric signal (Fig. 1). Taylor's team found that the mass-specific cost of transport scaled with mass to the -0.316 power. Translating that exponent to something more familiar, a mouse uses approximately 12 times more energy than a human to move each gram of its body. The obvious first tentative explanation was that smaller animals perform more mechanical work (per kilogram body mass) when they walk or run.

Thus, in the following papers in the series (Fedak et al., 1982; Heglund et al., 1982a; Heglund et al., 1982b), the team attempted to measure the mechanical work performed by the muscles during terrestrial locomotion. Total work is comprised of the internal work required to swing the legs and the external work required to lift and accelerate the center of mass. The team found that the total mechanical work rate increased curvilinearly with speed, not linearly like metabolic rate. Further, they found that the sum of the internal and external work required to move a given distance (the mechanical cost of transport) was nearly constant in small, medium and large animals. This meant that on a per gram basis, the small animals used a lot more metabolic energy to perform the same

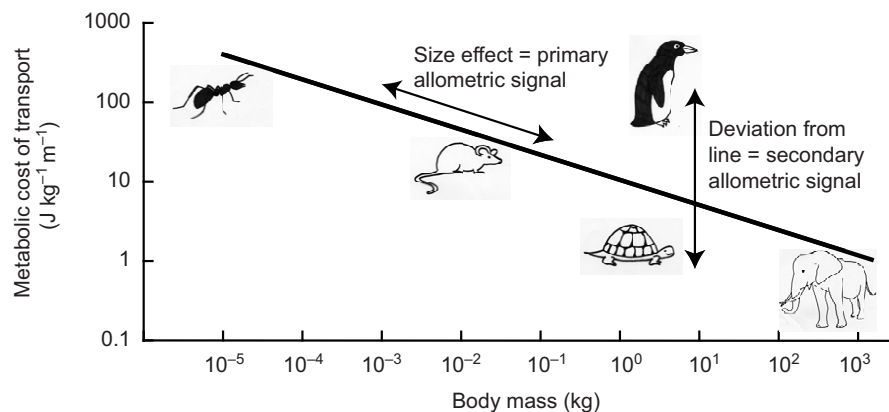


Fig. 1. From ants to elephants, the mass-specific metabolic cost of transport for terrestrial legged locomotion decreases with increasing body mass in a systematic manner (primary allometric signal). Yet at each body size, one finds species with energetic costs of transport that are much greater or less than expected (secondary allometric signal). Animal figure drawings by Helen J. Huang, PhD.

amount of work as the large animals. In the last paper in the series (Heglund et al., 1982b), the team had to conclude that, assuming a constant muscle efficiency, mechanical work during locomotion could not explain either the linear increase in metabolic rate with speed or the regular change in cost of locomotion with body size. After years of effort, this result must have been incredibly frustrating. However, the final paper in the series (Heglund et al., 1982b) offered several ideas that have proven prescient.

One beguiling idea was that small and large animals appeared to consume nearly the same amount of metabolic energy per gram, per stride when compared at physiologically equivalent speeds. Norm Heglund and Taylor followed up on that idea a few years later (Heglund and Taylor, 1988), but they found that within each species, the cost per stride did not remain constant across speed. Fortunately, the final sentence of Heglund et al. (Heglund et al., 1982b) pointed to another idea: ‘It seems likely that the energetic costs involved in generating force and activating the muscles may provide a simple explanation [for the linear increase in metabolic rate with speed and the regular change in cost of locomotion with body size].’ Indeed, Taylor and I (Kram and Taylor, 1990) eventually recognized just such a simple explanation by focusing on the time available for generating force on the ground. The concept of the cost of generating force has persisted as a well-accepted, simple explanation for the energetic cost of running.

Even a classic paper is not perfect. Taylor’s team made no distinction between walking and running gaits although they have fundamentally different biomechanics. By sorting Taylor et al.’s metabolic data into walking and running gaits, Jonas Rubenson and colleagues found that the energetic costs of walking and running scale differently (Rubenson et al., 2007). Another shortcoming of Taylor et al.’s approach was that they measured as few as two individuals for many of the species studied. But, thanks to the power of allometry, such quibbles do not affect the overall conclusions.

The four papers that are the focus of this article are classics in several senses. The allometric equation (‘the line’) established by Taylor et al. (Taylor et al., 1982) remains the standard by which the locomotion energetics of newly measured species are judged. Knut Schmidt-Nielsen defined deviation from the line as the secondary allometric signal (Fig. 1) (Schmidt-Nielsen, 1984). For example, penguins consume an inordinately large amount of metabolic energy to waddle on foot (Pinshow et al., 1977) whereas turtles walk with exceptional economy (Zani and Kram, 2008). Scientists in my laboratory and many others still use the biomechanics techniques pioneered in the four-paper series to better understand the unusual energetics of such creatures (Griffin and Kram, 2000; Zani et al., 2005). Finally, since 1982, the cost of terrestrial locomotion has been quantified in a diverse assortment of other vertebrate and invertebrate taxa, extended down in size to

ants (e.g. Moll et al., 2012) and up in size to elephants (Langman et al., 1995). Taylor et al.’s (Taylor et al., 1982) equation has quantitatively predicted these findings with uncanny accuracy. Any equation that can predict out 30 years of research and three or four orders of magnitude in animal size is, by my definition, a classic.

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