ENERGETICS OF LEGGED LOCOMOTION: WHY IS TOTAL METABOLIC COST PROPORTIONAL TO THE COST OF STANCE WORK?

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INTRODUCTION
What are the major contributors to the metabolic cost of legged locomotion? During the stance phase of a gait, energy is required to periodically redirect the velocity of the center of mass from down to up. This **"cost of stance"**, typically approximated by external work calculations, is a substantial fraction of the total metabolic cost. Another large fraction is the **"cost of swinging"**, relating to the energy required to swing the legs and other body parts faster than they would move passively.

In treadmill experiments [1], where an animal or a human runs at a number of speeds, researchers have found that the stance work (estimated by external work on the body) is approximately proportional to the total metabolic cost. And in a recent study, Marsh *et al* [2] showed that in running turkeys, over a range of speeds, the metabolic cost of swinging the leg is proportional to the metabolic cost of stance. While these two experimental results are consistent with each other, how can the proportionality be simply explained? We show that it can be explained by metabolic cost optimization.

METHODS
The total cost of locomotion, minus the resting metabolic cost, is modeled as the sum of the two terms – the cost of swing and the cost of stance. The magnitude of these terms will depend both on the speed v of locomotion and on the stride rate f, or equivalently, the step-length d. For example, keeping the speed constant and varying the stride rate, or vice versa, changes the magnitudes of the terms. In particular, while swing cost and stance cost do depend on the details of the muscular coordination, for simplicity, they can be assumed to be functions of only the speed and the stride rate. This assumption might be also interpreted as using the costs for the optimal muscular coordination for a given speed and stride rate.

For simple models of the animal's mechanics, and in experiments, the individual cost terms are relatively well-approximated by power laws (e.g., [2]). Typically, the stance cost per unit distance is of the form: $E_{stance} = c_1 v^m f^n$.

Assuming a metabolic cost proportional to work, maximum force, integral of force, or any other reasonable quantity, results in such a power law, in walking [3] and in running [5]. For much of the following discussion, however, how exactly the power law is derived is not important, but only that it be a power law.

The swing cost per unit distance is assumed to have the same functional form, $E_{swing} = c_2 v^p f^q$. This has also been verified by systematic experiments (e.g., [3]). In experiments and in models, for a given speed, E_{stance} decreases with increasing f, so $n<0$. E_{swing} increases with increasing f, so $q>0$. Other than these two conditions, the actual values of the various coefficients and exponents in these formulas are not important for obtaining the main result of the paper.

The total cost of locomotion is given by:
$$E_{total} = E_{stance} + E_{swing} = c_1 v^m f^n + c_2 v^p f^q. \qquad (1)$$

RESULTS AND DISCUSSION
It is well-established that, for a given velocity v, humans and animals pick the stride rate f_{opt} that minimizes their cost of locomotion (e.g., [6]). The optimal stride rate f_{opt} might be obtained by differentiating Eq.1 with respect to f, and setting it equal to zero. Substituting this expression for f_{opt} in the respective formulas for the costs, we get:

$$E_{stance} / E_{swing} = -q / n \qquad (2)$$

Thus, as experimentally determined by Marsh *et al* [2], our simple theory predicts that the ratio of the cost components is independent of the speed. Eq.2 also suggests that E_{stance} is proportional to the total metabolic cost, independent of speed. Assuming that the cost of stance E_{stance} is proportional to muscle work and that the elastic recovery is a constant fraction of the stance work, we predict that the metabolic cost is proportional to stance work alone, as observed by early investigators [1].

CONCLUSIONS
We have presented a simple way of understanding the apparently constant partitioning of the metabolic cost of legged locomotion observed in experiments, both old and new. More generally, the result provides a justification for the use of force plates as approximate ergometers [7], to estimate the total metabolic cost. The result is general in that it is independent of many details of the actual cost laws assumed. And it is likely to be applicable whenever the total metabolic cost of locomotion is modeled by sum of two terms, both of which are well-approximated by power laws.

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