# Carrying Loads. The Cost of Generating Muscular Force

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tentially hazardous situation for the patient.

The severity of this problem could have been significantly reduced by monitoring plasma colloid osmotic pressure, pulmonary arterial pressure, and systemic venous pressure and by providing therapy that would maintain these parameters within acceptable limits.

The use of colloids in this situation might have been more effective because a smaller total volume could have been given, thus minimizing the increases in pulmonary arterial pressure and systemic venous pressure during infusion. Also, plasma colloid osmotic pressure would not have been reduced by direct dilution. Along with colloid therapy, a pulmonary vasodilator could have been utilized to further lower pulmonary microvascular pressure.

Such circumstances require the careful monitoring of fluid therapy while making every effort to maintain pulmonary arterial pressure and systemic venous pressure as low as possible.

It should be obvious from the preceding discussion that basic physiological principles must be understood and applied when dealing with critically ill patients in order to optimize their chances for recovery.

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# Carrying Loads: The Cost of Generating Muscular Force

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**African women can carry loads of 20% of their body mass on their heads without measurable metabolic cost. In contrast, trained or untrained humans and animals increase their metabolism by 20% when they carry loads of this magnitude. Two possible mechanisms are proposed for the women's economic means of load carrying, based on considerations of the cost of generating muscular force during locomotion.**

### Economic load carrying by African women

Women of the Luo and Kikuyu tribes of East Africa frequently carry large loads for long distances. These loads may equal up to 70% of their body mass. The Luo women balance the loads on the tops of their heads, while the Kikuyu women support them by a strap across their foreheads (see Fig. 1). Both methods of carrying leave the hands free for other tasks, and it is not unusual to see a women nursing a baby suspended in a sling around her neck and knitting as she carries a load of firewood or water on her head. As these methods are learned as children, the women are extremely proficient.

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We have recently found that both the Luo and Kikuyu women can carry loads of up to 20% of their body mass without increasing their rate of oxygen consumption (2). This finding is surprising because it differs from results on trained men carrying packs and untrained men and women carrying loads on their heads or backs. Furthermore, a variety of animals carrying loads on their backs (4) also increase their rate of energy expenditure in direct proportion to the mass supported by the muscles when they walk at a given speed; that is, a load of 20% increases energy expenditure by 20%, a load of 30% by 30%, and so on. This simple direct proportionality suggests that it is the energetic cost of generating muscular force that determines cost of locomotion with or without a load.

Are the African women able to carry up to 20% of their body mass without increasing force generation by their muscles? Or have they hit on some way to reduce the cost of muscular force generation? Before attempting to answer this question, I will review the evidence that cost of force generation determines the costs of locomotion and of carrying loads.

### Energetic cost of generating muscular force during locomotion

Most attempts to explain the energetics of terrestrial locomotion have assumed that the major ener-


**FIGURE 1.** Women of the Luo tribe (*left*) and Kikuyu tribe (*right*) can often be seen carrying loads of wood, water, or other provisions supported by their heads. These loads normally represent up to 70% of the woman's body weight. Drawing by D. Njoroge. (From Maloiy et al. (2) reprinted by permission from *Nature Lond.*, vol. 319, p. 668–669. Copyright © 1986 Macmillan Journals Limited.)

getic cost occurs when muscles shorten and perform work, but recent studies of the mechanical work performed during locomotion as a function of speed and body size indicate that these assumptions are not justified (4). Metabolic cost of locomotion can vary by more than 10-fold with speed and size, yet these large differences are not reflected by parallel differences in the mechanical energy that the muscles supply to the limbs and body. For example, a 30-g mouse uses approximately 10 times as much energy as a 100-kg pony to move each gram of its body a given distance along the ground, but the mechanical work that the muscles must perform to keep each gram of the body moving at a constant speed is the same for the mouse and the pony. How does one explain this discrepancy?

Locomotion along the ground (with or without a load) is a regular cyclic process with the mechanical events repeated once during each stride. Active muscles are used for a variety of tasks: *1*) stabilization, when muscles generate force, but little or no shortening occurs and therefore little or no work is performed; *2*) when the muscles are alternately stretched and shortened while generating force, and therefore work is alternately performed on the muscles as they are stretched and then the muscles perform work when they shorten; and *3*) as machines for performing mechanical work when they shorten and perform work as they generate force.

In all these tasks the muscles generate force whether or not they perform mechanical work, and the hypothesis that the metabolic cost of generating force determines the cost of locomotion and the cost of carrying loads seemed reasonable. Then cost of generating force should change in a manner that accounts for the large differences in metabolic cost of locomotion observed with speed and body size. How does one test this hypothesis?

Experiments in which animals carried loads while metabolic energy consumption was measured provided a way of determining the cost of generating muscular force. The rate of oxygen consumption ($\dot{V}O_2$, a measure of metabolic rate) increased in direct proportion to the total mass ($m$) supported by the muscles at a given speed for small and large animals, including humans (Fig. 2), i.e.

$$\dot{V}O_2 = k\Delta m \qquad (1)$$

where $k$ is a proportionality constant.

The accelerations of the center of mass ($a$) of the loaded and unloaded

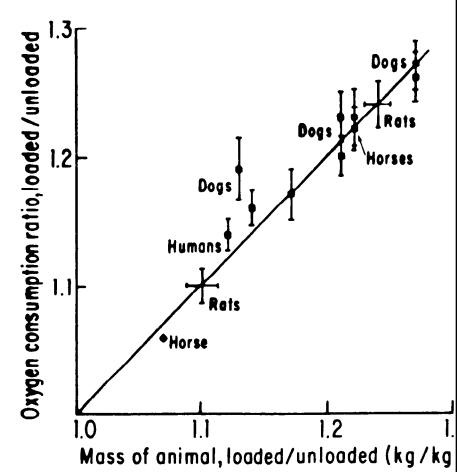


**FIGURE 2.** Oxygen consumption increases in direct proportion to the mass of a load carried by large and small animals irrespective of speeds of locomotion. (From Taylor et al. (4).)

animals were found to be the same, and most (>90%) of the force ($F$) generated by the muscles was used to maintain the forward speed and height of the center of mass constant from stride to stride. With the use of Newton's law

$$F = ma,\ a = k' \quad (2)$$

$$\Delta F = k'\Delta m \quad (3)$$

and combining *Eqs. 1* and *3*

$$\Delta F = k''\dot{V}O_2 \quad (4)$$

An important consequence of this direct proportionality is that cost of supporting each gram of load should increase both with speed and with decreasing body size in the same manner as cost of locomotion, i.e., it can cost an animal 10 times as much to generate one Newton of force at a high speed as at a low speed, and it costs a small 30-g mouse 10 times as much as the 100-kg pony to generate one Newton of force when the animals move at the same speed.

## Why does cost of carrying loads change with speed and body size?

The large differences in cost of carrying loads and cost of locomotion with speed and size can be understood by considering the properties of the force generators, the muscles. The maximum force per cross-sectional area (stress) exerted by a mammalian muscle is independent of body size (~300–400 kN/$m^2$ cross section of muscle fiber) because of the basic similarity in the structures of the contractile proteins, actin and myosin.

Muscle stresses during locomotion are the same for large and small animals at equivalent speeds (e.g., gait transitions, preferred speeds within a gait, top speed, etc.). However, the regular cyclic muscular activities of locomotion occur at higher frequencies in smaller animals. These higher frequencies require faster rates of cross-bridge cycling between actin and myosin (the energy-consuming step in force generation) because the forces must be generated and decay more rapidly. They also require more frequent activation-deactivation of the muscle, an event that involves actively pumping calcium and also consumes energy. Dividing the cost of generating a given force (by using an equivalent speed) by the frequency of the cyclic muscular event (stride frequency) yields a constant cost per cycle (Table 1).

**TABLE 1.** Costs of carrying loads and of locomotion

| $m_b$, kg | $\dot{V}O_2/m_b$ at Trot-Gallop Transition, ml $O_2 \cdot s^{-1} \cdot kg^{-1}$ | Stride-Frequency at Trot-Gallop Transition, stride/s | Cost/Stride at Trot-Gallop Transition, ml $O_2 \cdot stride^{-1} \cdot kg^{-1}$ |
|---|---|---|---|
| 0.1 | 2.38 | 8.54 | 0.28 |
| 1.0 | 1.12 | 4.48 | 0.25 |
| 100 | 0.65 | 2.35 | 0.28 |

Energetic cost of supporting each kilogram of mass during each stride is the same for animals of different size at speeds where muscle stress (force/cross-sectional area) is the same (3). $\dot{V}O_2$, rate of oxygen consumption; $m_b$, body mass.

Thus it appears that the higher frequencies of the complex muscular events occurring during locomotion determine the higher cost for force generation in small animals. Similar considerations may also explain the higher costs of force generation at higher speeds. Although the average vertical force integrated over a number of strides will equal the weight of the animal plus any load it carries, this force will be exerted over a shorter portion of each stride. The peak force exerted will increase, and time of generation and decay will decrease with speed. These changes will require faster rates of cross-bridge cycling and higher cost for force generation.

## How do African women carry their loads more economically?

At least two possibilities might explain how African women can carry loads up to 20% of the body mass without any measurable metabolic cost. Perhaps an anatomic change has occurred as a result of carrying large loads since childhood that allows these women to support small loads using nonmuscular (i.e., nonmetabolizing) structural elements. Another possibility would be an adjustment of the time course of force generation so that slower and more economic muscle fibers are used for generating the force. It would be interesting to measure the magnitude and time course of forces applied to the ground by these women and to try to find out exactly how they do it.

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