The Metabolic Cost of Force Generation

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ABSTRACT
SIH, B. L., and J. H. STUHMILLER. The Metabolic Cost of Force Generation. Med. Sci. Sports Exerc., Vol. 35, No. 4, pp. 623–629, 2003. Introduction: The purpose of this study was to provide support, based on a review of existing data, for a general relationship between metabolic cost and force generated. There are confounding factors that can affect metabolic cost, including muscle contraction type (isometric, eccentric, or concentric), length, and speed as well as fiber type (e.g., fast or slow) and moment arm distances. Despite these factors, empirical relationships for metabolic cost have been found that transcend species and movements. Methods: We revisited the various equations that have been proposed to relate metabolic rate with mass, velocity, and step contact time during running and found that metabolic rate was proportional to the external force generated and the number of steps per unit time. This relationship was in agreement with a previously proposed hypothesis that the metabolic cost to generate a single application of a unit external force is a constant. Results: Data from the literature were collected for a number of different activities and species to support the hypothesis. Running quadrupedal and bipedal species, as well as human cycling, cross-country skiing, running (forward, backward, on an incline, and against a horizontal force), and arm activities (running, cycling, and ski poling), all had a constant metabolic cost per unit external force per application. Conclusion: The proportionality constant varied with activity, possibly reflecting differences in the aspects of muscular contraction, fiber types, or mechanical advantage in each activity. It is speculated that a more general relation could be obtained if biomechanical analyses to account for other factors, such as contraction length, were included. Key Words: METABOLIC RATE, MUSCLE, ENERGETICS, LOCOMOTION, RUNNING, CYCLING

Metabolic cost, measured by the amount of oxygen consumed, is often used as a method of quantifying energy expenditure during exercise. There are many benefits to being able to anticipate the metabolic cost from various human activities, including the ability to monitor performance, to make direct comparisons between different exercise protocols, to assess individual variability, and to design better equipment for load carriage. Even when important inroads in this subject have been made, knowledge of metabolic cost has not reached a level where we can accurately anticipate the effects of activity, equipment, and individual differences.

The diverse factors that affect metabolic cost of movement are well documented. Even when limited to aerobic movements, where pulmonary and circulatory limits are not reached, the dynamics of muscle and metabolic cost are complicated. At the muscle level, classic experiments have shown that contraction type (isometric, eccentric, or concentric), length, and speed as well as fiber type (e.g., fast or slow) and recruitment pattern influence force generation and, therefore, metabolic cost (1,3,14,19,20). In addition, species and individual differences in the effective mechanical advantage (EMA) of the muscles and bone (5) as well as fiber length (2) will affect both fiber recruitment and metabolic demand.

Despite the wide variation in metabolic cost and body design, empirical relationships have been found that appear to transcend species and movements. Remarkably, these include those relating metabolic cost to velocity, body mass, and step contact time for a wide range in quadrupedal species that run and hop (25,40) despite the vastly different muscular EMA and fiber lengths of the different species. Although it has been previously shown that these equations can be related to each other through additional allometric relations (39), we expect that metabolic cost is more closely related to the muscle force generated than body mass or velocity.

In this paper, we survey the widest range of activities possible, comparing empirical relationships of metabolic cost and allometry for various species and movements. We will find that a single metabolic cost relationship exists that is dependent only on the magnitude and frequency of force
generated. The coefficient relating the force parameters to metabolic cost differs, however, undoubtedly reflecting the effects of contraction length, type, speed, and recruitment pattern as well as moment arm, bone geometries, and fiber lengths.

In 1973, Gold (17) noted that the observed relationship between metabolic cost and body weight for swimming, flying, and running (36) could be explained by “the simple hypothesis that all animals require the same quantity of energy to carry a unit of their own body mass one “step”...” For quadrupedal running, Gold (17) estimated energy consumption to be approximately 0.13 J·N⁻¹·step⁻¹. Since that time, other correlations between metabolic cost and assorted variables have been found covering a wide range of species for running and running types of movements. In the seminal work by Taylor and his colleagues (40), metabolic experiments involving a large number of terrestrial animals established two additional trends. First, Taylor et al. (40) has shown that metabolic rate increases linearly with speed and body mass to the 0.7 power for nearly all animals that run. This relationship was found to hold for a variety of quadruped and biped species, covering a 4000-fold range in body mass. Second, Kram and Taylor (25) observed that the rate of energy consumption is proportional to body weight and inversely proportional to foot contact time for a variety of running quadrupeds. A single proportionality constant was found for five animal species ranging from 30 g (kangaroo rat) to 140 kg (pony). This relationship also appears to hold for bipeds (33) and a variety of human running movements (22,45), including cross-country skiing (4).

Although these two running-related relations each correlate their own data sets, two questions can be raised. First, what is the common force element in the equations of Kram and Taylor (25) and Taylor et al. (40), which use different velocity- and mass-dependent quantities to predict metabolic cost? Second, how are these correlations related to the hypothesis proposed by Gold (17), which applies to other muscular movements and forces generated?

After examining the literature, we show that metabolic rate is proportional to the external force generated and the number of force applications per unit time, i.e., the equivalent energy per mass per “step” hypothesis proposed by Gold (17). We demonstrate that the Kram and Taylor (25) and the Taylor et al. (40) equations are both special cases of this, more fundamental, relationship. Published data for a wide range of activities, where metabolic rate, external force, and frequency of application can be calculated, follow a constant cost per force per application pattern. Like the Kram and Taylor hypothesis (25), higher order trends can be observed, indicating that metabolic rate may depend weakly on other factors. Nevertheless, the data presented agree with the cost per force per application hypothesis to first order, and is not in conflict with proposed theories of metabolic cost and muscle contraction rate.

METHODS

In a manner similar to the analysis of Taylor (39), we first show how the running equations of Taylor et al. (40) and Kram and Taylor (25) are related. Taylor et al. (40) derived an equation for the rate of oxygen consumption based on running speed and body mass from data for a variety of quadrupedal and bipedal runners (62 avian and mammalian species):

$$E = (10.7 \pm 2.6)M_b^{0.3}V$$

(1)

where $E$ (J·s⁻¹) is the increase in metabolic rate above resting, $M_b$ (kg) is body mass, and $V$ (m·s⁻¹) is running velocity. Kram and Taylor (25) developed a relationship between the rate of oxygen consumption, body weight, and time of foot contact for five quadruped species covering a wide range in body mass:

$$E = (0.18 \pm 0.04)M_b^{g}r^l$$

(2)

where $t_c$ (s) is the time a single foot applies force to the ground during a stride and $g$ (m·s⁻²) is the acceleration due to gravity. If we use the known relation between the distance traveled during a foot contact, $L_c$ (m), and body mass for quadrupeds (25),

$$L_c = 0.10(M_bg)^{0.3}$$

(3)

and the assumption of constant horizontal velocity,

$$V = L_c/t_c$$

(4)

then Equation 1 becomes:

$$E = (0.22\pm0.05)M_b^{g}(1/t_c)$$

(5)

Equation 5 is of the same form as Equation 2 and the range of proportionality constants overlap. Later, we show that the difference in constants is due mainly to combined quadruped and biped species of Taylor et al. (40), whereas Kram and Taylor (25) based Equation 2 strictly on quadruped data.

It is now possible to derive a cost per force per application relation from Equation 5, demonstrating how the Taylor et al. (40) and Kram and Taylor (25) running equations are in agreement with the Gold (17) hypothesis. The vertical forces during the time the feet are in contact with the ground must generate an impulse sufficient to support body weight during a stride. Because each leg contributes to the impulse,

$$n\cdot\bar{F}\cdot t_c = M_bg(t_c + t_a)$$

(6)

where $n$ is the number of legs, $\bar{F}$ (N) is the average vertical ground reaction force of a single leg during contact, and $t_a$ (s) is the time the leg is in the air. By definition, $t_c + t_a$ is stride time. Combining Equations 5 and 6 produces:

$$E = (0.22\pm0.05)\bar{F}w[1/(t_c + t_a)]$$

(7)

By definition, stride rate $S$ (strides·s⁻¹) is the inverse of the stride time,

$$S = 1/(t_c + t_a)$$

(8)

and step rate $N$ (steps·s⁻¹) is the product of stride rate and the number of legs,

$$N = St_c$$

(9)
Consequently, Equation 7 can be rewritten as

\[ E = (0.22 \pm 0.05) F \cdot N. \] (10)

Thus, we show that both relations found by Taylor and colleagues, which correlate the metabolic cost of running over a wide range of body masses and running speeds, are equivalent to the single relation that the rate is proportional to the magnitude of the external force generated by each leg and the number of times per second that the legs generate that force.

We, therefore, hypothesize that metabolic rate is proportional to the magnitude of the average external force generated and the number of applications per unit time,

\[ E = c F \cdot N. \] (11)

The proportionality constant \( c \), however, may depend on the movement.

**RESULTS**

To support the hypothesis that metabolic rate is proportional to the average force generated and the number of applications per unit time, we estimate the cost coefficient, \( c \), for a variety of activities using data published in the literature. Activities include human cycling and arm movements as well as various forms of running. We also calculate the cost coefficient for multiple species while running. Where necessary, human resting metabolic rate was estimated at 0.004 L O\(_2\) kg\(^{-1}\) min\(^{-1}\) (29) for studies where this value was missing.

Cycling is unique in that the cost coefficient can be calculated while varying the force magnitude and frequency independently. We consider those cycling experiments measuring metabolic rate in which the cadence and pedal forces were varied (7,9,11,12,15,23,26,37,38,43), allowing a direct calculation of the cost per unit force per application (i.e., the cost coefficient, \( c \)). The average force exerted on the pedal was calculated assuming a crank length of 17 cm and that each foot exerts force on the pedal during half a revolution. Ignoring low pedal forces (<20 N) where the metabolic cost of overcoming limb inertia may have been influencing the results, the coefficient was found to be 2.52 ± 0.42 J·N\(^{-1}\)·appl\(^{-1}\), nearly constant over a 14-fold range of pedal forces and a 4-fold range of cadences. See Figure 1.

The cost coefficient was estimated for a large number of running and hopping quadruped species, using the data from Kram and Taylor (25), Roberts et al. (32), and the quadrupedal subset of Taylor et al. (40). For Taylor et al. (40), the coefficient was calculated using Equation 3, the relation between step length and body mass for quadrupeds. Over the range of species and velocities tested, the cost coefficient was found to be 0.14 ± 0.04 J·N\(^{-1}\)·appl\(^{-1}\), see Figure 2. Note this value is comparable to the quadrupedal constant estimated by Gold (17).

The cost coefficient for avian and human bipeds while running can be estimated from a number of studies. First, we calculated the cost coefficient for the avian subset of the data presented by Taylor et al. (40) using the relationship for bipedal step length to body mass (33):

\[ L_s = 0.12 (M_b g)^{0.3}. \] (12)

Additional studies provided data for humans running on level ground (13,22,24,28,33,44,45), backward (45), simulated reduced gravity (13), and loaded lower extremity (27) running. The cost coefficient was 0.30 ± 0.05 J·N\(^{-1}\)·appl\(^{-1}\) for the range in biped species, masses, and velocities tested. See Figure 3. The cost coefficient was nearly twice the value of quadrupeds (0.14 ± 0.04 J·N\(^{-1}\)·appl\(^{-1}\)), which explains why the data set of Taylor et al. (40), which included both

![FIGURE 1—The metabolic cost coefficient for cycling at various pedal forces with cadences ranging from 30 to 120 rpm (7,9,11,12,15,23,26,37,38,43). Ignoring low pedal forces (<20 N) where the metabolic cost of overcoming limb inertia may have been influencing the results, the dashed line with error bars at the endpoints represent the total average value of 2.52 ± 0.42 J·N\(^{-1}\)·appl\(^{-1}\) over the range specified. Despite the almost 14-fold increase in pedal force and 4-fold increase in pedal rate, the cost coefficient remained nearly constant.

![FIGURE 2—The estimated metabolic cost coefficient for 56 species of quadrupeds while running. Filled diamonds (●) represent five species from Kram and Taylor (25), the filled square (■) is a group of dogs from Roberts et al. (32), and the plus signs (+) are 51 species from Taylor et al. (40). For species common to both Taylor et al. (40) and Kram and Taylor (25), only Kram and Taylor (25) values are shown as they represent a more direct measure of the cost coefficient. Data points are average values for a specific species and at a variety of speeds. Dashed line with error bars at the endpoints represent the total average value of 0.14 ± 0.04 J·N\(^{-1}\)·appl\(^{-1}\), similar across four orders of magnitude in mass.

![FIGURE 3—The estimated metabolic cost coefficient for 56 species of quadrupeds while running. Filled diamonds (●) represent five species from Kram and Taylor (25), the filled square (■) is a group of dogs from Roberts et al. (32), and the plus signs (+) are 51 species from Taylor et al. (40). For species common to both Taylor et al. (40) and Kram and Taylor (25), only Kram and Taylor (25) values are shown as they represent a more direct measure of the cost coefficient. Data points are average values for a specific species and at a variety of speeds. Dashed line with error bars at the endpoints represent the total average value of 0.14 ± 0.04 J·N\(^{-1}\)·appl\(^{-1}\), similar across four orders of magnitude in mass.
in almost direct proportion to the added load, whereas stride Taylor et al. (41) found that oxygen consumption increased load carrying dogs and horses provide data to support this. generated. Metabolic and biomechanical measurements of mass.

\[ 0.30 \pm 0.05 \text{ J N}^{-1} \text{ app l}^{-1} \]

The hypothesis also predicts that for a constant application rate \( N \), metabolic cost is proportional to average force generated. Metabolic and biomechanical measurements of load carrying dogs and horses provide data to support this. Taylor et al. (41) found that oxygen consumption increased in almost direct proportion to the added load, whereas stride frequency and time of foot contact did not change measurably.

Additional metabolic cost is generated by running on an incline (24, 28) or against a horizontal force (10). We relate the increased cost to the additional force that must be overcome (via the externally applied horizontal force or gravity from the slope for incline running). The cost coefficient is similar for the two types of running (Fig. 4). Excluding the cases when the aiding forces are so large (\( > -50 \) N) that the running mechanics may have changed, the cost coefficient is constant (2.95 ± 0.45 J N\(^{-1}\) app l\(^{-1}\)).

Cross-country leg-only skiing also supports a constant horizontal cost coefficient. Bellizzi et al. (4) found metabolic rate related to body weight and the time of the propulsive phase, \( t_p \), for a leg through

\[ E = c_{ski} M_{ski} N (1/t_p) \]

where \( c_{ski} \) is a proportionality constant. To correlate this to the cost coefficient, we first assumed the horizontal friction due to the skis, \( F_{ski} \), is related to the normal force through a coefficient of friction, \( \mu_{ski} \), and body weight,

\[ F_{ski} = \mu_{ski} N. \]

Second, in a method analogous to calculating vertical impulse (Equation 6), the horizontal impulse during propulsion by the legs is equal the external friction force multiplied by the total stride time, \( t_p + t_{np} \),

\[ n \cdot F_{np} = F_{ski}(t_p + t_{np}) \]

where \( t_{np} \) is the nonpropulsive time. In addition, from Equation 8 and 9,

\[ N = n(t_p + t_{np}) \]

Combining, we obtain

\[ E = (c_{ski}/\mu_{ski}) \cdot F \cdot N. \]

Therefore, we find a constant cost coefficient while generating horizontal skiing forces for a nearly twofold range in speed and threefold range in cadence tested.

The cost coefficient can be calculated for a variety of repetitive arm movements, including arm running (16), arm cycling (23, 30, 42), and arm ski poling (4). Ignoring low pedal forces (<20 N), consistent with our treatment of leg cycling, arm pedaling was also constant with wide variability (3.61 ± 1.06 J N\(^{-1}\) app l\(^{-1}\)) for a sixfold range in pedal force (Fig. 5). The type of equipment (i.e., asynchronous/synchronous tricycle arm pedaling or arm erector) appears to influence the coefficient value and account for some of the variability. In arm ski poling (4), we assumed that the reported load is per arm. Ski poling values collected over a twofold range in velocity were comparable to arm cycling (4.06 ± 0.08 J N\(^{-1}\) app l\(^{-1}\)). See Figure 5. For arm running, we observed a cost coefficient of 0.96 ± 0.04 J N\(^{-1}\) app l\(^{-1}\) for a wide range in supported force and running speed (1.5–3.0 m s\(^{-1}\)). See Figure 6.
DISCUSSION

After reiterating that previously proposed correlations of metabolic cost to running can be unified, we have shown that this leads naturally to the hypothesis that the cost is proportional to the force applied and the number of repetitive applications of the force, a theory first proposed by Gold (17) in 1973. Published data since that time continue to support a constant metabolic cost per force per application for a wide range of forces, species, body weights, and rates of application, although the proportionality constant varies between activities (Fig. 7).

We note that there is a certain amount of variability in the data, that in some instances the cost coefficient is not constant, and that under carefully controlled conditions, other, more subtle, trends may be observed. For example, there is a small metabolic dependence on velocity and both the cost coefficient and step length appear to increase slightly with speed (21,33,45). It is also well established that there is an optimum cadence that minimizes metabolic cost at a given speed for movements such as running (8) and cycling (12). Our results, however, show that the resulting change in metabolic cost per unit force per application is small over a wide range of cadences. In addition, we note that the reported cost coefficient for cycling is dependent on our assumption of applying force during half a revolution. If the natural tendency is to apply force during a different proportion of the pedal stroke, the coefficient mean would change but continue to be independent of both speed and duration. Therefore, we conclude that the dominant effect is that metabolic cost is proportional to the external force magnitude and the number of applications over a wide range of species and repetitive movements.

From studies too numerous to list, we were unable to utilize data that may have supported a constant cost coefficient because metabolic rate and force were not both measured simultaneously. For some experiments, there was no means of estimating average force. This was especially true for human running, where there is a plethora of studies relating metabolic rate to biomechanical factors and running conditions. However, without the appropriate gait timing measures such as \( t_c \) to estimate average vertical force, we were unable to calculate the cost coefficient for these studies. In other experiments, the primary focus was to describe the biomechanics of a movement, and oxygen consumption was not measured. We also ignored investigations of anaerobic effort where the metabolic rate would not be accurately reflected in oxygen uptake measurements. And finally, although there are a large number of studies analyzing the energetics and biomechanics of human walking, we were unable to find a study with sufficient information to estimate metabolic rate and average vertical force, primarily because double support makes calculating the average force per leg from \( t_c \) indeterminate.
The cost coefficient appears constant for a given movement, suggesting that the contraction parameters identified in the introductory section do not change appreciably despite changes in force magnitude and frequency. Conversely, the variation in the cost coefficient between activities undoubtedly reflects the effects of different contraction parameters. We follow with a more detailed discussion of some of the potential factors influencing the cost coefficient value.

The results show a constant cost coefficient for running quadrupeds (or bipeds) that is interspecific, and the relationship between muscle fiber length and EMA may be a factor. Taylor (39) has previously shown that allometric differences in muscle fiber length and EMA for quadrupeds cancel each other, resulting in similar volumes of muscle per body mass active during running and explaining why metabolic comparisons across species are possible. In addition, both the cost coefficient and the ratio of muscle fiber length to EMA appear to depend on the number of legs. A comparison of fiber length and EMA between dogs and turkeys (32) supports a hypothesis that a large part of the difference in bipedal-quadrupedal metabolic cost per force per application can be accounted for by differences in the fiber length to EMA ratio.

It is likely that the EMA also influences the cost coefficient for other movements as our analysis is based on the total external force observed, whereas metabolic cost is primarily due to muscle activation. Activities such as running have more skeletal support than generating horizontal forces and some arm movements. This results in an increased EMA (5) where the external force is largely supported by the skeletal structure rather than the muscle. It can be hypothesized that external force is not representative of muscular force and that the coefficient will be more nearly constant across various movements if the muscular force alone is used.

We can also derive the cost per application hypothesis from observations of ATP consumption at the fiber level, providing a direct link between the molecular properties of muscle and whole-body energetics as well as further insight into the cost coefficient. Bottinelli and Reggiani (6) note that recent studies found similar peak “fiber” efficiencies (mechanical power generated/rate of energy expended) for fast and slow fibers for both rat (31) and human (18) when contracting at a fiber’s most efficient velocity. Because power is the product of force and velocity, this implies

\[ E_i = kF_i/V_i \]  

where \( F_i \) and \( V_i \) are force and most efficient velocity, respectively, for a contracting fiber of type \( i \), and \( k \) is a fiber type-independent efficiency constant. Studies indicate that muscles have evolved to maximize efficiency by utilizing the appropriate fiber type for a given speed (34,35) and Bottinelli and Reggiani (6) expect that the in vivo fiber efficiency to remain a constant. If a contraction occurs over a fixed length \( l_c \) for a given movement, then the number of contractions per unit time is the shortening velocity divided by the contraction length.

\[ N_e = V/\dot{l}_c \]

Combining Equations 18 and 19 gives:

\[ E_e = (k\dot{l}_c)F_i/V_i \]

which is the same form as Equation 11. Thus, the empirical relationship between force generated and metabolic cost may be a consequence of an underlying fiber type recruitment and efficiency characteristic of muscle. Moreover, Equation 20 suggests that the cost coefficient \( c \) varies depending on contraction length.

Like the proposed effect of EMA, a cost coefficient that varies with contraction length is consistent with the observation of different coefficients for various movements. For example, it is reasonable to assume that running has nearly isometric contractions (39) and, therefore, the smallest contraction length and cost coefficient, whereas cycling and assorted arm movements have larger contraction lengths and correspondingly larger coefficients. Thus, both EMA and contraction length may be important factors in determining a cost coefficient that is invariant across movement and species. See Figure 7.

This work demonstrates that a single relation between metabolic cost and the magnitude and frequency of applied force exists for many activities. This observation should assist in the ability to assess the metabolic cost of various human activities such as exercise and load carriage. If biomechanics can estimate the muscular component of force and more detailed parameters such as contraction length for each activity, then a single cost coefficient might emerge that would allow composite activities to be estimated.

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