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The mechanical cost of transport of fast running animals



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HIGHLIGHTS

- At high speeds, mechanical cost of transport is proportional to ground forces ratio (F_x/F_y).
- Fast running requires maximizing (F_x/F_y) and minimizing ground contact time.
- At low speeds, animals choose (F_x/F_y) to be mechanically and metabolically efficient.

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ABSTRACT

Regarding running animals, algebraic expressions for the horizontal (ω_x) and vertical (ω_y) components of the mechanical cost of transport are deduced for a ground force pattern based on the Spring–mass model. Defining $\tilde{\mu}$ as the maximum ground forces ratio $\tilde{\mu} = \max(F_x)/\max(F_y)$, the analysis shows that the mechanical cost of transport $\omega_x + \omega_y$ for fast running animals is approximately proportional to $\tilde{\mu}$, and to the relative contact length, and positively correlated to the limb take-off angle and the collision angle. The vertical cost ω_y is shown to approximate to zero for fast running animals. Sustained top running speeds are predicted to require the largest possible values of $\tilde{\mu}$ and therefore relatively large horizontal propulsive forces, as well as a minimum possible ground contact time. The equations also show that animals running relatively slow would tend to prefer certain interval of values for parameter $\tilde{\mu}$, which would minimize both their mechanical cost of transport and their metabolic cost of transport. Very large animals are suspected to be less capable of developing large values of $\tilde{\mu}$, which possibly renders them incapable of developing great speeds.

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1. Introduction

In order to transport themselves, legged animals must invest energy. For instance, it is known that increased metabolic energy consumption is required by a moving animal with respect to a resting animal. Part of this additional energy investment is almost instantaneously lost as body heat, but part of it is usefully invested to accelerate the animal and swing the legs when they are not touching the ground. Another energy investment involves the fact that the center of mass (CoM) of the animal cyclically raises and falls during locomotion, and also experiences fluctuations in the horizontal and vertical speeds. This variation of the mechanical energy of the CoM, if considered during the time when the legs apply propulsive forces to the ground, is equivalent to the mechanical positive external work exerted on the CoM by the animal limbs. If we divide this work performed during one step, by the step length, and by the total mass of the animal, we obtain the mechanical cost of transport (hereafter the MCT), measured in

units of mechanical energy per unit of distance traveled, per unit of body mass (e.g. J/m/kg).

The metabolic efficiency (Alexander, 2005) of a moving animal has been defined as the ratio between the MCT and the metabolic cost of transport. The latter is measured in units of thermal energy consumed, per unit of distance traveled, per unit of mass. Therefore, the MCT has been calculated to compare it to the metabolic cost of transport in the assertion that gait parameters (stride frequency, speed, duty factor, type of gait, etc.) are selected by animals to minimize the MCT, which would also be translated into a minimization of the metabolic cost of transport (Alexander, 1992, 1989; Ruina et al., 2005). However, there are some difficulties in trying to link the metabolic cost of transport and the MCT. For instance, the metabolic cost of transport has been suggested to be affected by other activities (besides the MCT) such as the effort of exerting force independently of the existence of muscular mechanical work (Roberts et al., 1998; Kram and Taylor, 1990; Pontzer, 2007), and the work to swing the legs for repositioning them (Pontzer, 2007). To complicate matters, some part of the MCT is not completely provided by muscular work, given that the fluctuations of mechanical energy of the CoM can be elastically stored and released by the tendon work, not requiring the use of

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muscular contraction work to develop this part of the MCT (Biewener et al., 1998; Roberts et al., 1997).

In order to avoid the conundrum of the causes of the metabolic cost of transport, the present analysis suggests that the MCT can be firstly analyzed independently as a mechanical parameter that affects or reflects the running gait, forgetting for one moment about the analysis of the associated metabolic costs.

When it comes to high speeds, there is a motivation for not readily focusing on the metabolic efficiency analysis. Studying metabolic efficiency is justified in relatively slow speeds and gaits, which are compatible with endurance traveling, in which an excessive energy waste is undesirable. On the contrary, fast speeds are performed by animals in urgent situations, and mostly using anaerobic metabolism of muscles (Arsac and Locatelli, 2002). Very high speed efforts cannot be sustained aerobically for long periods of time and thus should not be necessarily expected to be metabolically efficient. Almost by definition, the variable to maximize during top speeds is the velocity of the animal, but not necessarily restricted by the metabolic or aerobic capacity. Therefore, it seems reasonable that the analysis of top speeds requires a better understanding of the MCT simply for what it is: a mechanical parameter.

It has been shown by Full (1989) and Full and Tu (1991) that the MCT has an apparently invariant value of 1.07 J/kg/m (average) for a compilation of animals of different sizes, ranging from insects to mammals. Observations made by Heglund et al. (1982) on birds and mammals led them to obtain a value of 0.7 J/kg/m for the average MCT. Alexander (2005) theorized that the MCT of differently sized animals should be independent of body size, provided a dynamically similar gait in the compared animals. Alexander (1977, 2003) theorized that the MCT for a fast running biped

should be proportional to the duty factor multiplied by the relative stride or step length, a product that is numerically similar to the *relative contact length*, RCL, which is defined as the contact length divided by the leg length or the hip height. It has been assumed that the RCL remains more or less constant at different speeds (Alexander, 2003; McMahon and Greene, 1979), but there is no confirmation of this idea for fast speeds. On the contrary, some studies show that the RCL indeed increases with speed (Hoyt et al., 2000; Gatesy and Biewener, 1991).

A collisional model of locomotion (Lee et al., 2011) concluded that the MCT is approximately equivalent to the overall collision angle. Another collisional model (Ruina et al., 2005) theoretically predicted that the MCT diminishes to half its value when the collision angle diminishes to half its value by doubling the quantity of collisions during one stride (a conclusion that would benefit animals with more legs, possibly making them more economical). Thus, the MCT has been suggested to be proportional to the collision angle.

A problematic aspect of the understanding of the MCT is that the experimental and theoretical research has provided little, if any, information on the MCT of animals running very fast. Another problematic aspect of the MCT at faster speeds is that it depends more strongly on the work of horizontal ground forces rather than vertical ground forces, but horizontal ground forces have not been studied or considered as important as vertical ground forces (Chang and Kram, 1999). Therefore, the present study focuses on the characteristics of horizontal ground forces.

Another problem with the MCT is that the apparent historical body-size invariance for the reported values of MCT has exceptions. For instance, Genin et al. (2010) found a “strikingly” small MCT of about 0.2 J/kg/m for Asian elephants running at moderate

Table 1
Symbols, definitions and units.

Symbol	Units	Description
MCT	J/kg/m	The mechanical cost of transport. $MCT = \omega_x + \omega_y$
ω_y	J/kg/m	Vertical mechanical cost of transport
ω_x	J/kg/m	Horizontal mechanical cost of transport
m	kg	The mass of the animal
L	m	Step length, the distance between two successive ground contact instances
W	J	Mechanical cost per step. $W = W_x + W_y$
W_y	J	Vertical mechanical cost per step. $\omega_y = W_y/L/m$
W_x	J	Horizontal mechanical cost per step. $\omega_x = W_x/L/m$
CoM	Dimensionless	Acronym for the center of mass of the animal
T	s	Step period or duration
V	m/s	Overall speed of the running animal
g	m/s ²	Gravity acceleration on Earth's surface
$F_y(t)$	N	Vertical ground force of the supporting leg (upwards normal force)
$F_x(t)$	N	Horizontal ground force of the supporting leg (traction force)
t	s	Temporal variable. $t = 0$ for the instant of the beginning of the propulsive phase
ϕ_y	N	Maximum value of $F_y(t)$ during the propulsive phase. $\phi_y = \max(F_y)$
ϕ_x	N	Maximum value of $F_x(t)$ during the propulsive phase. $\phi_x = \max(F_x)$
$\tilde{\mu}$	Non-dim.	Parameter representing the ground maximum forces ratio. $\tilde{\mu} = \phi_x/\phi_y$
θ	s	Contact time duration
$\theta/2$	s	Propulsive phase duration
τ	Non-dim.	Duty factor parameter: the fraction of the total time that any foot is in contact with the ground. $\tau = \theta/T$
$x(t)$	m	The horizontal location of the CoM. $x = 0$ for $t = 0$
d	m	Horizontal distance traveled by the CoM towards the end of the propulsive phase
V_{Ax}	m/s	Horizontal speed of the CoM during the aerial phase, i.e. after the propulsive phase
kV_{Ax}	m/s	Horizontal speed of the CoM when $t = 0$, i.e. before the propulsive phase
k	Non-dim.	The horizontal speed fluctuation parameter
V_{Ay}	m/s	Vertical speed of the CoM after the propulsive phase, i.e. at the take-off
$y(t)$	m	Vertical location of the CoM. $y = 0$ for $t = 0$
Δy	m	Vertical displacement of the CoM at the end of the propulsive phase. $\Delta y = y(\theta/2)$
h	m	Average height of the CoM counted from the ground level, approximately equivalent to the leg length or the hip height
$A = 0.561$	Non-dim	Normalizing dimensionless constant that permits the parameter ϕ_x to effectively be the maximum value of force $F_x(t)$
β	Non-dim.	The take-off angle of the leg, $\beta = a \tan(d/h)$. See Fig. 2
RCL	Non-dim.	Relative contact length, $RCL = 2d/h \approx \theta L/h$
φ	Non-dim.	Collision angle at the take-off. See Fig. 2
α	Non-dim.	Angle of the velocity vector with respect to horizontal level line, at the take-off

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