# Factors affecting the energy cost of level running at submaximal speed

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**Abstract** Metabolic measurement is still the criterion for investigation of the efficiency of mechanical work and for analysis of endurance performance in running. Metabolic demand may be expressed either as the energy spent per unit distance (energy cost of running, $C_r$) or as energy demand at a given running speed (running economy). Systematic studies showed a range of costs of about 20 % between runners. Factors affecting $C_r$ include body dimensions: body mass and leg architecture, mostly calcaneal tuberosity length, responsible for 60–80 % of the variability. Children show a higher $C_r$ than adults. Higher resting metabolism and lower leg length/stature ratio are the main putative factors responsible for the difference. Elastic energy storage and reuse also contribute to the variability of $C_r$. The increase in $C_r$ with increasing running speed due to increase in mechanical work is blunted till 6–7 m s$^{-1}$ by the increase in vertical stiffness and the decrease in ground contact time. Fatigue induced by prolonged or intense running is associated with up to 10 % increased $C_r$; the contribution of metabolic and biomechanical factors remains unclear. Women show a $C_r$ similar to men of similar body mass, despite differences in gait pattern. The superiority of black African runners is presumably related to their leg architecture and better elastic energy storage and reuse.

**Abbreviations**

| | |
|---|---|
| $C_r$ | Energy cost of running |
| COM | Center of mass |
| CV | Coefficient of variation |
| EMG | Electromyographic activity |
| $k_{leg}$ | Leg stiffness |
| $k_{vert}$ | Effective vertical stiffness |
| L | Leg length |
| L/S | Leg length-stature ratio |
| M | Body mass |
| RE | Running economy |
| RER | Respiratory exchange ratio |
| S | Stature |
| SF | Stride frequency |
| SL | Stride length |
| $t_c$ | Contact time |
| $T_{re}$ | Rectal temperature |
| $v_a$max | Maximal aerobic running speed |
| $\dot{V}E$ | Pulmonary ventilation |
| $\dot{V}O_2$ | Oxygen consumption |
| $\dot{V}O_{2max}$ | Maximal oxygen consumption |
| $v\dot{V}O_{2max}$ | Running speed sustained at $\dot{V}O_{2max}$ |
| $W_{EXT}$ | External work |
| $W_{INT}$ | Internal work |
| $W_{TOT}$ | Total work |

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## Introduction

Energy cost of running, symbolized by $C_r$ in the present review, is defined as the energy demand per unit distance normalized to body mass; it is expressed as ml $O_2$ kg$^{-1}$ m$^{-1}$ or J kg$^{-1}$ m$^{-1}$. This parameter was thoroughly reviewed by di Prampero (1986) as an aspect of human locomotion on land and was identified as one of the three factors contributing to aerobic performance, the other two being maximal oxygen consumption, $\dot{V}O_{2max}$, and $F$, the maximal fraction of $\dot{V}O_{2max}$ that can be sustained over a given distance. Systematic studies reviewed by Daniels (1985) showed a range of variation of 19–20 % in $C_r$. Variability of $C_r$ is still high in homogeneous cohorts: di Prampero et al. (1986) reported a range of variation (CV) of 9 % in a group of amateur endurance runners. A homogeneous cohort of top-level 5,000-m runners (Lacour et al. 1990) showed a CV of 4.3 %. In the two just cited groups, the $C_r$ and $\dot{V}O_{2max}$ variabilities were similar. As noted by Saibene and Minetti (2003), net metabolic power divided by the product of speed and body weight has the dimensions of power. As such, $C_r$ becomes dimensionless and can be viewed as the reciprocal of efficiency.

The purposes of this review are to assess the extent to which $C_r$ is really independent of body dimensions and running speed, and to provide an update on the biomechanical factors affecting this cost.

## The concept of energy cost of running

### Definition

Energy cost of running ($C_r$) is a specific application to running of the general concept of economy of transport expressing the specific power needed to propel a given body at a given velocity. As above discussed, relating energy expenditure to distance covered makes the cost dimensionless. In this respect, $C_r$ is different from Running Economy (RE) which was originally conceived as steady-state oxygen consumption (ml $O_2$ min$^{-1}$ kg$^{-1}$) for a given running speed. As such, RE is not dimensionless, since it restricts comparison to subjects running at a given speed. It so happens that most reviews have been devoted to running economy (Daniels 1985; Morgan et al. 1989; Saunders et al. 2004a; Foster and Lucia 2007). Furthermore, many studies covered by the present review reported oxygen uptake at a given running speed, i.e., running economy. RE is currently used as synonymous with oxygen cost of running or as general expression of oxygen demand with no specific unit. The present review will follow this attitude. In this respect, maximal aerobic velocity ($v_a$max) calculated by dividing $\dot{V}O_{2max}$ by $C_r$ and $v\dot{V}O_{2max}$ obtained by

prolonging the increase in RE with speed till $\dot{V}O_{2max}$ are considered as synonymous. RE will be specifically used when $O_2$ demand is related to a given speed.

### Measurement

Using treadmill measurements as an index of the energy cost of overground running, attention should be paid to several possible pitfalls. Fellin et al. (2010) observed no difference in the lower extremity of the kinematic curves between these two running conditions. Treadmill running is biomechanically equivalent to overground running if belt speed is constant (van Ingen Schenau 1980); however, this is not the case when belt speed is slowed down at each landing. Bergh et al. (1991) suggested that running at a given average speed on a resilient treadmill could be associated with lower oxygen uptake. In fact, the question has never been directly investigated, but progress in treadmill design in terms of engine power and regulation makes this pitfall less serious. Individual familiarization with treadmill running must also be taken into account: according to Brueckner et al. (1991), measurements are not reliable before an individual's third running bout on a treadmill. Finally, day-to-day variation must be taken into account. Well-controlled reliability studies indicate that intra-individual test–retest results are relatively stable, with mean CVs of 1.3 % (Morgan et al. 1991) or 1.5 % (Pereira and Freedson 1997). In contrast, Brisswalter and Legros (1994) found consistently higher day-to-day variation in $C_r$, with a mean CV of 4.65 ± 3.5 %. Shaw et al. (2013) reported typical errors in $C_r$ measurement ranging from 2.4 to 4.7 %, close to the $\dot{V}O_{2max}$ measurement reliability generally found using the Douglas bag method (Lacour et al. 2007). The between-test variability for oxygen cost may be greater when automatic systems are used, due in part to the possible non-linearity of the many transducers involved, but also to the problem that automated systems have in temporally matching gas flow and fractions (Macfarlane 2001). Overall, these data suggest that day-to-day variability in running mechanics plays little part in the variability of $C_r$.

### Baseline values

Assessment of the energy demand specific to running implies subtraction of resting energy consumption. This resting value, however, differs depending on whether it refers to lying quietly (resting metabolism, i.e., 3.5 ml $O_2$ min$^{-1}$ kg$^{-1}$), or standing (directly measured or estimated as 1.27 resting metabolism (Cavagna and Kaneko 1977), or 5 ml $O_2$ min$^{-1}$ kg$^{-1}$, the $y$-intercept of the regression line calculated from oxygen uptake measurement in subjects running at different speeds (Medbø et al. 1988).

The resting metabolism value of 3.5 ml $O_2$ $min^{-1}$ $kg^{-1}$ applies to normally active Caucasian adults, and is about 15 % lower in older subjects, due to their lower level of activity, and up to 15 % higher in athletes training 2 h a day (van Pelt et al. 2001); the standing value in athletes is thus very close to the 5 ml $O_2$ $min^{-1}$ $kg^{-1}$ obtained by Medbø et al. (1988). For the purposes of comparing active adults, these differences are negligible in relation to the oxygen demand of running. As discussed below, resting energy consumption must, however, be taken into account in calculating $C_r$ in children. It should be noted that the idea of subtracting the resting metabolism may be questionable, since it assumes that this resting metabolic demand remains unchanged during exercise. In cohorts of runners (Lacour et al. 1990; Padilla et al. 1992; Bourdin et al. 1993), whether gross or net values of cost of running are used does not consistently alter the relationship to running performance, confirming that the baseline values used to calculate the energy cost of running are still valid at maximal speeds. At all events, this doubt supports the current use of gross energy cost of running, calculated by simply dividing oxygen uptake by running speed. In the present review, unless otherwise stated, "energy cost of running", "running economy", "$O_2$ cost of running", and "oxygen demand" refer to gross values.

## Metabolic factors affecting energy cost of running

Respiratory exchange ratio

When measurements are conducted at speeds <75–85 % of the speed corresponding to $\dot{V}O_{2max}$ ($v\dot{V}O_{2max}$ or $v_a max$), the absence of non-metabolic $CO_2$ output makes it possible to assess substrate metabolism from the respiratory exchange ratio (RER), and thus to convert $\dot{V}O_2$ into energy output. $C_r$ may thus be expressed as either oxygen cost (ml $O_2$ $kg^{-1}$) or energy cost (J $kg^{-1}$) per unit of distance (Shaw et al. 2013). As discussed below, the latter takes better account of the changes in metabolic demand when changes in running speed or duration induce shifts toward carbohydrate or fatty acid oxidation associated with changes in $O_2$ energy equivalent.

Relationship of energy cost of running to $\dot{V}O_{2max}$

The direct respective influence of $\dot{V}O_{2max}$ and $C_r$ on running performance is obscured by the positive relationship between these two variables. This correlation was first reported by Mayhew (1977) and confirmed by Lacour et al. (1990), Padilla et al. (1992), Pate et al. (1992), and Fletcher et al. (2009). This relationship is presumably spurious: besides the fact that $C_r$ and $\dot{V}O_{2max}$ are both inversely

related with body mass (M), the cross-sectional investigation designs may have involved a subject selection bias, since the homogeneous groups of runners were selected on the basis of endurance running performance, which is directly related to $v_a max$: to be included, runners with lower $\dot{V}O_{2max}$ had to compensate by having a lower $C_r$ and those with a high cost by having high $\dot{V}O_{2max}$.

## Biomechanical factors affecting energy cost of running

The biomechanical factors affecting $C_r$ were reviewed by Williams and Cavanagh (1987), Morgan et al. (1989), Kaneko (1990), Martin et al. (1993), Anderson (1996), Kyröläinen et al. (2001) and Nummela et al. (2007). The complex movement of running can be described by the simple model of a spring (Cavagna et al. 1965). The purpose of this section is to discuss the models still used to describe elastic energy storage and reuse, focusing on factors which directly or indirectly account for this mechanism.

Models

### Center of mass model

Because of the large number of body segments involved in running and the possible energy transfers between segments, the complex movements occurring in running can be better understood using the simple model proposed by Fenn (1930) and modified by Cavagna and Kaneko (1977), according to which $W_{TOT}$, the work done to move the body during running, is the sum of the absolute values of external work ($W_{EXT}$) [the work done to raise and accelerate the body center of mass (COM)] and internal work ($W_{INT}$) (the work done to accelerate limb segments around the total body COM). $W_{EXT}$ may be calculated from data obtained with a force plate or by video analysis; $W_{INT}$ may be calculated from data obtained by video analysis only. According to Cavagna and Kaneko (1977), $W_{EXT}$ constitutes 60–75 % of $W_{TOT}$, the percentage decreasing with increasing running speed. The difference between the apparent efficiency of $W_{EXT}$ (i.e., $W_{EXT}/\dot{V}O_2$ ratio) and 25 %, the maximal efficiency of the transformation of chemical energy into positive mechanical work, indicates the contribution of elastic energy. This contribution of muscle–tendon elasticity was first hypothesized by Cavagna et al. (1965). Norman and Komi (1979) demonstrated that muscle is active during the lengthening phase. A combination of eccentric and concentric action forms the stretch–shortening muscle function. Bourdin et al. (1995) demonstrated a significant negative correlation between the energy cost of running and the eccentric-to-concentric ratio for integrated leg extensor muscle EMG activity; the correlation accounted

for 50 % of the variance. Abe et al. (2007) confirmed both the negative correlation between energy cost of running and the eccentric-to-concentric ratio for vastus lateralis muscle integrated EMG activity and the 50 % contribution to variance. The combination of contraction of the pre-activated muscle and lengthening of the series elastic tendon units results in elastic energy storage associated with small changes in muscle–tendon length.

$W_{EXT}$ is difficult to assess. Arampatzis et al. (2000) compared mechanical power over a wide range of velocities, using data from force plates or video analysis: although mechanical power correlated strongly with running speed whichever the method used, results were significantly different; this impairs calculation of running efficiency and hence of elastic energy contribution.

*The Bouncing ball model*

The bouncing ball model, proposed by Cavagna et al. (1964) and developed by McMahon and Cheng (1990), consists in modeling the runner as a bouncing ball, the mass representing the total body mass and the spring, considered as linear, the behavior of the support leg. By reference to the relationship between the deformation of a spring and the force applied to it, the ratio between the stretching force applied to muscle tendon units and their lengthening is referred to as stiffness ($kN\ m^{-1}$). The stiffness of the spring can be described in two ways. (1) The stiffness coefficient, $k_{leg}$, associated with leg spring deformation, calculated as the quotient of maximum ground reaction and leg deformation: besides its effects on the impact stress of the step, an increase in $k_{leg}$ corresponds to greater involvement of the stretch–shortening cycle in muscle–tendon elastic energy storage and reuse. However, due to difficulties in directly measuring leg spring compression, there is some uncertainty as to the real value of $k_{leg}$; moreover, in some studies, data for effective vertical stiffness are presented as representing $k_{leg}$ (Serpell et al. 2012). (2) Effective vertical stiffness, $k_{vert}$, which is the quotient of maximum ground reaction force and COM vertical displacement. According to this model, the body presents a resonance frequency, corresponding to the natural frequency of the mass spring system, at which

the energy necessary to maintain running oscillation is minimal. This system quickly adapts to changes in running surface (Ferris et al. 1999). $k_{vert}$ is directly related to the resonance frequency of the body. The relations between $k_{vert}$ and energy cost of running at a given speed were clearly demonstrated in transversal studies. Dalleau et al. (1998) found a negative correlation between $k_{vert}$ (presented as $k_{leg}$) and $C_r$ at a given speed in middle-distance athletes running at 90 % $v_a$max. This was confirmed by Heise and Martin. (1998), Fletcher et al. (2013), Lazzer et al. (2014) and by a longitudinal study made by Barnes et al. (2014). Arampatzis et al. (2006) found that more economical runners showed greater plantar flexor muscle strength and greater tendon-aponeurosis stiffness in the triceps surae. The negative relationship between energy cost of running and lower-limb and trunk flexibility, reported by Craib et al. (1996), Jones (2002) and Hunter et al. (2011), deserves attention. Two mechanisms may account for this relation: (1) stiffer musculo-tendinous structures may induce greater elastic energy return during the shortening phase of the stretch–shortening cycle; (2) Arampatzis et al. (2011) suggested that joint inflexibility and increased tendon stiffness increase the resonance frequency of the oscillating body during running. The bouncing ball model takes account of many factors:

## Anthropometrical factors

Body mass and size

The following discussions refer to the retrospective analysis of data collected from the "reference group" of 129 endurance-trained athletes of national rank, comprising two cohorts: 41 women and 88 men, with competitive distances ranging from 800 m to 100 km. Measurements were made after obtaining informed consent, using procedures complying with French legislation regarding the testing of elite athletes. The main characteristics of the two cohorts are listed in Table 1.

Since Williams et al. (1987) first demonstrated an inverse relationship between body size and RE in homogeneous groups of trained adult runners, the possible relationships

**Table 1** Main characteristics of the reference group

| | Female ($n = 41$) | Male ($n = 88$) | |
|---|---|---|---|
| Age (years) | $26.5 \pm 8.6$ | $26.4 \pm 7.8$ | NS |
| Body mass (kg) | $53.2 \pm 5.5$ | $64.5 \pm 5.5$ | $p < 0.0001$ |
| Stature (m) | $1.65 \pm 0.06$ | $1.76 \pm 0.06$ | $p < 0.0001$ |
| $\dot{V}O_{2max}$ (ml $O_2$ $kg^{-1}$ $min^{-1}$) | $60.3 \pm 5.1$ | $67.0 \pm 5.4$ | $p < 0.0001$ |
| Gross cost of running (ml $O_2$ $kg^{-1}$ $km^{-1}$) | $198 \pm 9$ | $195 \pm 10$ | $p = 0.03$ |
| Gross cost of running (ml $kg^{-0.87}$ $km^{-1}$) | $0.332 \pm 0.015$ | $0.334 \pm 0.016$ | NS |
| Size-Independent Cost (ml $O_2$ $kg^{-1}$ $S^{-1}$) | $0.326 \pm 0.015$ | $0.342 \pm 0.016$ | $p < 0.0001$ |

between these two variables have been debated and normalizations proposed. Body mass (M, kg) and stature (S, m) are closely linked ($r = 0.83$; $p < 0.0001$ in the reference group), making it difficult to distinguish their respective influence. In the reference group, $C_r$ correlated similarly with both S and M. Other studies (Bourdin et al. 1993; Pate et al. 1992) reported similar or slightly closer relationships with M: Dissociating M from S, by extra-loading the trunk, results in a further decrease in $C_r$ in relation to total mass (Thorstensson 1986; Bourdin et al. 1995). This suggests that $C_r$ is directly related to M, not to S. In the reference group, a 1 kg difference in M induced a cost difference of 0.6 ml kg$^{-1}$ km$^{-1}$ in both cohorts (Fig. 1).

Removing the influence of body mass

Influence of body mass on energy cost of running has long been conceived in dimensional terms. According to this theory, $C_r$ is proportional to the linear dimension, S, raised to the 2/3 (0.67) power, in line with the relations between $\dot{V}O_{2max}$ and M investigated by von Döbeln (1956). Based on calculated limitations imposed by the elastic components of biological material, or a greater proportion of proximal leg muscle mass in relation to M (Nevill 1994), metabolic rates have been suggested to be proportional to the ¾ power of M. In line with these speculations, Bergh et al. (1991) proposed systematically relating oxygen demand during running to M$^{0.75}$ rather than to M. It so happens, however, that the 0.75 exponent was specific only to male runners, and was 0.83 in females; it was different in other cohorts. Moreover, the exponents relating oxygen demand and $\dot{V}O_{2max}$ to M were systematically different among groups; speed running performance, i.e., $\dot{V}O_{2max}$ should thus be raised to a third exponent. In a large population of 172 runners with competitive distances ranging from 800 m to marathon, Shaw et al. (2014) calculated exponents of 0.90 and 0.88 in males and females, respectively, close to the present values of 0.87 in males and females. This raises doubt as to whether a 0.75 exponent is the appropriate means to remove the influence of M, since it results in a positive relationship between M and energy cost of running (Fig. 1), thus replacing one confounding effect with its opposite. McCann and Adams (2003) derived the Size-Independent Cost of locomotion ($VO_2$ M$^{-1}$). S$^{-1}$, expressed as (ml kg$^{-1}$) S$^{-1}$, where M is body mass (kg) and S is stature (m), defined as the net amount of oxygen used to move a mass of 1 kg a distance equal to stature, in agreement with the constraints of biological similarity. However, M$^{-1}$ S$^{-1}$ again relates $VO_2$ to M$^{0.67}$, which is too low an exponent, as discussed above.

Why does energy cost of running decrease with increasing M? The relations between body dimensions and $C_r$ presumably take account of leg extensor muscle stretching in the ground contact phase. Scholz et al. (2008) suggested
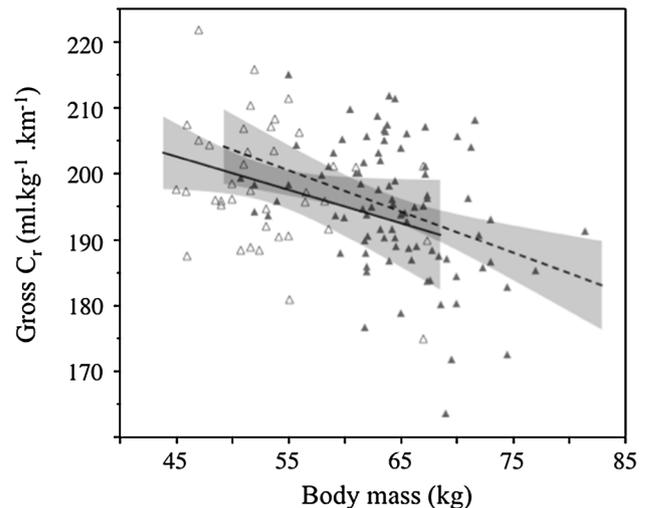


**Fig. 1** Gross $O_2$ cost of running (gross $C_r$) as a function of body mass (M; kg) for female and male competitive runners in the reference group: regression and 95 % confidence intervals of the fit are presented using solid and dotted lines, respectively. *Dotted line*, *solid triangle* male, $n = 88$; gross $C_r = 231.2 - 0.56$ M; $r^2 = 0.1$; $p < 0.03$. *Solid line*, *open triangle* female, $n = 41$; gross $C_r = 230.3 - 0.61$ M; $r^2 = 0.36$; $p < 0.02$

that an increase in dorsiflexion at foot-strike with increasing body mass could contribute to a decrease in $C_r$: the larger the angle, the greater the energy stored in the Achilles tendon and reused during propulsion; shank angle at foot-strike was identified by Williams and Cavanagh (1987) and by Santos-Concejero et al. (2014) as a factor of $C_r$. Instead of expressing geometrical similarity, the effect of M on $C_r$ may thus be a general consequence of the effects of the stretch–shortening cycle on the storage and reuse of elastic energy. In contrast, Taboga et al. (2012) found no decrease in $C_r$ according to M in a cohort of subjects including normal-weight and obese individuals, with M ranging from 52 to 172 kg. These results disagree with the previously cited findings. The authors suggested that progressive adaptation to extra fat mass made the obese subjects able to maintain the same motor strategies as adopted by normal-weight subjects by maintaining the same mass-specific work to raise and accelerate the body COM. An alternative hypothesis would be that, once the maximum shank angle is reached, any further increase in M cannot induce further energy storage in elastic structures.

Lower body dimensions

*Leg length/stature ratio (L/S)*

It is widely accepted that leg length (L) and leg length/stature ratio (L/S) show no correlation with $C_r$: none of the

studies measuring both variables (Cavanagh and Williams 1982; Williams and Cavanagh 1987; Williams et al. 1987; Morgan et al. 1994; Dalleau et al. 1998) found a relation with $C_r$; nor is L related to optimal stride length (Cavanagh and Williams 1982; Morgan et al. 1994). Steudel-Numbers et al. (2007), however, found a strong correlation between L/S and RE at 9.5 km h$^{-1}$ in a cohort of subjects selected as having longer or shorter lower-limb lengths than predicted from their M. The relationship between L/S and changes in $C_r$ during growth is discussed below.

### Moment arm of the Achilles tendon

One factor related to elastic energy storage has emerged recently: Scholz et al. (2008) demonstrated a strong inverse correlation between RE at a running speed of 16 km h$^{-1}$ and the moment arm of the Achilles tendon (mean distance of the tendon to the medial and lateral malleoli, which is directly related to calcaneal tuberosity length); this was confirmed by Raichlen et al. (2011) and Barnes et al. (2015). The shorter the moment arm, the greater is the force stretching the Achilles tendon on landing, increasing the amount of energy stored in the tendon, reutilization of which reduces energy demand in running. The important feature is that, in the three cited studies, moment arm accounted for 58–81 % of O$_2$ cost variance, more than any other factor. Another important feature is that the moment arm of the Achilles tendon is positively related to lower-leg volume and lower-leg moment of inertia (Scholz et al. 2008). These findings suggest that the main variable accounting for inter-individual differences in $C_r$ is the energy stored in the triceps surae muscle–tendon units at foot-strike, which in turn is related to calcaneal tuberosity length. In the three above-cited studies, the ranges of variation of RE from the shorter to the longer moment arm were about 30 %. Some other mechanisms might contribute to the decrease in RE. Barnes et al. (2015) obtained a strong relationship between leg stiffness and the moment arm of the Achilles tendon. Besides its pure mechanical effects, the greater stretching of the triceps surae muscle tendon structure thus activates the whole leg extensor system.

Running pattern effects

### Kinematic parameters

Williams and Cavanagh (1987), Svedenhag and Sjödin (1994), Kyröläinen et al. (2001) and Arampatzis et al. (2006) demonstrated that, in homogeneous groups of runners, differences in $C_r$ are poorly or not at all related to kinematic parameters. On the other hand, Högberg (1952) reported that, at all running speeds, an optimal combination of stride length (SL) and stride frequency (SF),

minimizing oxygen uptake, was freely chosen by runners. This was partially confirmed by Cavanagh and Williams (1982) in a cohort of recreational runners: the freely chosen step length was 1.7 % longer than the optimal SL corresponding to minimum oxygen uptake, resulting in slightly (0.4 %) higher oxygen consumption. Whilst the first studies focused on the relation between SL and the contraction patterns of the muscles involved in running, the key factor in SL–SF combinations is presumably SF in relation to the natural oscillation frequency. The variability of self-selected SF is low (de Ruiter et al. 2014). At sub-maximal speeds, increases in running speed are achieved by similar increases in SL and SF, associated with increasing $k_{vert}$ (McMahon and Cheng 1990) and, to a smaller extent, $k_{leg}$ (Arampatzis et al. 1999). The self-selected combination of SL and SF appears to be precisely regulated. Snyder et al. (2012) observed that response time to return to self-selected SF after various kinds of disturbance was fast (1.47 ± 0.05 s), and suggested that the processes underlying such fast adjustment represent fundamental strategies for minimizing energy cost in running. The relationship between $C_r$ and step variability in running (Belli et al. 1995) supports this hypothesis.

### Ground contact: contact time ($t_c$)

Roberts et al. (1998) found that, in humans like in many mammal species, changes in metabolic rate showed close inverse correlation with ground contact time ($t_c^{-1}$). This is in line with Kram and Taylor's (1990) hypothesis that the energy used by each gram of active muscle in running is proportional to the time available to produce force in each step, measured as $t_c$: the shorter $t_c$ at a given speed, the faster and therefore the more costly the rate of force generation. Nummela et al. (2007), however, reported significant negative correlations between energy cost at high running speeds and $t_c^{-1}$. Morin et al. (2007) demonstrated that $t_c$ was strongly correlated with $k_{leg}$: the shorter $t_c$, the greater $k_{leg}$. The relations between $C_r$ and $t_c$ are thus not univocal since, in contrast to the costly increase in rate of force generation, $t_c$ shortening reduces $C_r$ by shortening the time for the braking force to decelerate forward motion of the body whilst the increase in $k_{leg}$ associated with shorter $t_c$ accounts for a greater storage and reuse of elastic energy.

### Trajectory of the center of pressure

Lazzer et al. (2014) observed the cost of running to be related to the footprint index, i.e., the area (cm$^2$) between the foot axis and the trajectory of the center of pressure; the lower the index, the lower is the cost. The footprint index is a global evaluation of the mediolateral displacement during the whole stance phase. A low footprint index accounts

for a better ankle stability and allows better elastic energy absorption along the foot axis. This index is strongly related to $k_{vert}$ and to the stiffness of Achilles tendon.

### Limb muscle mechanical advantage

Given that $C_r$ is related to muscle force generation requirements, Biewener et al. (2004) hypothesized that differences in the $C_r$ are affected by differences in limb extensor muscle effective mechanical advantage defined as the ratio of the weighted mean extensor muscle moment arm to the moment arm of the ground reaction force: the greater the effective mechanical advantage, the lower is the energy cost. The extensor moments include the hip, knee and ankle joints, with knee joint moment being the greatest in running. Changes in running posture alter effective mechanical advantage and hence energy cost of running by moving the ground reaction force application point.

### Muscle fiber type distribution

Contractile structures may have some importance in $C_r$. With the metabolic cost being lower in type II than type I muscle fibers (Hunter et al. 2001), $C_r$ may be expected to be affected by muscle fiber distribution. Bosco et al. (1987) found a positive correlation between type II fibers and RE at a running speed of 3.3 m s$^{-1}$. Most reports, however, were contrasting: Williams and Cavanagh (1987) found a non-significant relation between percentage type I fibers and RE at 3.6 m s$^{-1}$; Kyröläinen et al. (2003) found an inverse correlation between energy expenditure at a running speed of 7 m s$^{-1}$ and both the amount of MHC II and the percentage of type II fibers; Iaia et al. (2009) reported speed training to result in decreased energy expenditure during running, associated with an increased percentage of FTx fibers. Whether this paradoxical difference is due to the respective metabolic efficiency of slow- versus fast-twitch fibers according to speed or to their different contributions to elastic energy storage is still unclear. Nor should the role played by the greater strength development by type II muscle fibers be disregarded: Arampatzis et al. (2006) reported that the most economical runners showed greater triceps surae contractile strength, but could not ascertain whether this was due to contractile strength itself or to the greater tendon stiffness associated with the greater contractile strength of the triceps surae muscle.

### Environmental factors

### Aerodynamic resistance

Pugh (1970) demonstrated that a certain fraction of $C_r$, known as the energy cost against aerodynamic forces,

increased with the square of wind velocity. Bassett et al. (1985), however, found no difference between the oxygen requirements of overground and treadmill running at speeds under 4.33 m s$^{-1}$, in line with Jones and Doust (1996) who reported the relationship of $\dot{V}O_2$ to running speed to be linear under 5 m s$^{-1}$ and not a cubic function of velocity. These findings are in agreement with the observation by Pugh (1970) that the relationship could be adequately described by a linear function between 2.92 and 6.11 m s$^{-1}$. According to the Pugh's equations, the energy demand of overcoming air resistance for a man (1.75 m, 70 kg) running at 5.0 m s$^{-1}$ amounts to about 6.5 % of total cost. Measurement reliability and intra-subject variability make this theoretical increase compatible with the measured constant costs just cited. These values apply for sea-level conditions. Besides running speed and body dimensions, aerodynamic energy demand depends on air density, which is a function of barometric pressure. East African runners live and train at moderate altitudes of 2,000–2,600 m, and some high-level endurance runners complete their winter season training at these altitudes. At 2,300 m, barometric pressure is around 540 mmHg; aerodynamic resistance is thus reduced by 30 %, resulting in a 2.5 % decrease in the total energy cost of running at 5.0–5.5 m s$^{-1}$, whilst $\dot{V}O_{2max}$ is decreased by 12 % (Capelli and di Prampero 1995). Training intensity similar to that sustained at sea-level thus requires a decrease of approximately 10 % in running speed. To compensate for air resistance cost, some authors measure $C_r$ in subjects running against a 1 % treadmill gradient, as proposed by Jones and Doust (1996). According to their study, costs during running on road or treadmill against a 1 % gradient were similar at speeds ranging from 2.92 to 5.0 m s$^{-1}$, and both were 5 % higher than during level treadmill running.

### Effects of surface stiffness and footwear

Running may be performed on a variety of terrains, differing in stiffness. Compressible shoe soles and compliant surfaces add springs in series to the runner's spring mass system. Leg stiffness should adjust so as to achieve similar running on different surfaces. Tarmac and concrete are not compliant, but track surfaces are designed to be compliant, with stiffness ranging from 100 to 875 kN m$^{-1}$ (McMahon and Greene 1979). Ferris et al. (1998) measured $k_{leg}$ and $k_{vert}$ during running at a given speed on different surfaces. Runners were able to keep $k_{vert}$ constant by increasing $k_{leg}$ with increased surface compliance. The authors suggested two complementary explanations for enhanced running performance on compliant track: (1) The runner's stiffer leg compresses less; running with a straighter leg should improve the limb's mechanical advantage, reducing recruited muscle volume and the force required to support

body weight. (2) Compliant elastic surfaces passively store energy and return it with each step, reducing the mechanical work performed by the muscles. These hypotheses were tested by Kerdok et al. (2002), who measured change in metabolic data, ground reaction force and kinematic data in response to running over surfaces of differing stiffness, from 75 to 945 kN m$^{-1}$; the 12.5-fold decrease in surface stiffness resulted in a 29 % increase in $k_{leg}$ whilst $k_{vert}$ remained constant, maintaining total leg-plus-track stiffness nearly constant. Metabolic rate decreased by 12 %, mostly due to enhanced energy return from the compliant platform and, to a very slight extent, to improvement in the limb's mechanical advantage. Some team sports or cross-country imply running on grass, the surface stiffness of which is about 90 kN m$^{-1}$. This soft surface is not elastic; the increased compliance results in an increase of about 15 % in the energy cost of running (Pinnington and Dawson 2001a, b).

Frederick et al. (1984) were the first to quantify the differences in aerobic demand between barefoot and shod running. The authors reported that oxygen demand increased across a range of running speeds by 1 % for each 100 g mass added to each shoe. However, as reviewed by Franz et al. (2012), further studies provided inconsistent results, suggesting that factors other than shoe mass play an important role in determining the metabolic cost of barefoot versus shod running. By measuring the metabolic effects of adding mass to the feet in subjects controlled for barefoot running experience and foot-strike pattern, the authors confirmed the 1 % $\dot{V}O_2$ increase per 100 g added per foot, whether barefoot or shod. On the other hand, for footwear conditions of equal mass, shod running had 3–4 % lower $\dot{V}O_2$ demand than barefoot running. This is related to differences in running biomechanics. Boyer and Nigg (2004) found a strong correlation between quadriceps pre-activation intensity and impact loading rate. The increased SF, $k_{leg}$ and $k_{vert}$ described by Divert et al. (2008) in barefoot running may be related to increased leg extensor muscle pre-activation. The cushioning system of a running shoe is designed to provide a protective layer between foot and ground, attenuating impact shock and distributing force over a larger area of the plantar surface. Some of the work performed is dissipated as heat overcoming viscous resistance, while some becomes strain energy stored in the elastically deformed material. To what extent is it possible to increase this reuse? According to Shorten's (1993) review, the cushioning and energy storage functions imply conflicting sole designs, suggesting that "differences between running shoes of modern design are too small to have a direct effect on energy expenditure". The metabolic and mechanical aspects of foot-strike pattern were investigated by Ardigò et al. (1995). In the 2.50–4.17 m s$^{-1}$ range, there was no difference in $C_r$ between rearfoot and forefoot landing types, as confirmed by Perl et al. (2012). According to Ardigò et al. (1995), forefoot striking is, however, associated with an increase in work performed against both gravitational and inertial forces. The authors found that forefoot striking was associated with shorter contact and acceleration times.

## Effects of running speed

Margaria et al. (1963), who were the first to address the question, did not observe any increase in $C_r$ between 8 and 20 km h$^{-1}$; this was confirmed by di Prampero (1986) and Saibene and Minetti (2003), and is now widely accepted (di Prampero et al. 2009). The data of the literature are, however, inconsistent in this regard. Helgerud (1994), Fletcher et al. (2009), Helgerud et al. (2010), Tam et al. (2012) and Shaw et al. (2014) reported $C_r$ to be independent of running speed. A single study (Iaia et al. 2009) reported a decrease with speed. In contrast, a slight increase in $C_r$ with running speed was found in many studies in male or female runners (Costill et al. 1971; Bransford and Howley 1977; Daniels et al. 1977, 1986; Davies and Thompson 1979; Conley and Krahenbuhl 1980; Svedenhag and Sjödin 1994; Saltin et al. 1995; Jones and Doust 1996). The increases, ranging from 2 % (Daniels et al. 1977) to 10 % (Jones and Doust 1996), were similar in trained and untrained subjects of both sexes. Elite distance runners may also show this increase: Derek Clayton, who had the world's best marathon performance for years, showed a 6.5 % increase in RE between 12 and 21 km h$^{-1}$ (Costill et al. 1971). In this respect, performance may be more reliably predicted from $C_r$ measured at high relative velocity. Increase in metabolic demand induces a progressive shift of RER toward 1.00, associated with an increase in O$_2$ energy equivalent. Fletcher et al. (2009, 2010) and Shaw et al. (2014), who reported constant oxygen cost with increasing running speed, calculated a progressive increase in energy cost expressed as J kg$^{-1}$ m$^{-1}$ when the shift in O$_2$ energy equivalent was taken into account. The difference was not negligible, since an RER shift from 0.85 (in jogging) to 1.00 (at $v_a$max) is associated with a 3.5 % increase in O$_2$ energy equivalent. The moderate increases in oxygen demand with speed reported by many studies are thus associated with greater increases in energy demand. Taking account of the contribution of anaerobic glycolysis to total energy production, by converting the increase in blood lactate concentration during testing into energy expenditure; an increase equivalent to 3 ml O$_2$ kg$^{-1}$ per mmol l$^{-1}$ is generally assumed (di Prampero and Ferretti 1999). Kyröläinen et al. (2001, 2003) observed that, when the energy equivalent of blood lactate concentration was included, total energy expenditure increased fairly

linearly with increasing running speed up to $v\dot{V}O_{2max}$, instead of progressively leveling off.

Increased running speed is associated with an increased mechanical work. Kyröläinen et al. (2001) and Nummela et al. (2007) measured kinematics, kinetics and muscle activity at different running speeds in endurance runners: from 4.0 to 7.0 m s$^{-1}$, step frequency (SF) and step length (SL) increased in similar proportions, up to 40 %. These changes imply a consistent increase in the kinematic work performed at each step. At the same time, the hip extended with a larger angle, while the EMG activity of the biceps femoris muscle increased, in relation with the increase in energy expenditure. Cavagna et al. (1988) described the alteration of the bouncing system at running speeds above 3.6 m s$^{-1}$, with adoption of an asymmetric rebound. The aerial phase became longer than the contact phase, and SF thus became progressively lower than the natural frequency. This loss of match between chosen and optimal frequencies resulted in a progressive increase in $W_{EXT}$. Horizontal and vertical ground reaction forces also increase with increasing speed (Kyröläinen et al. 2001). Taken together these data are consistent with the 17 % increase in $W_{TOT}$ with increasing running speed from 3.9 to 6.4 m s$^{-1}$ reported by Luhtanen and Komi (1978). It is still an open question why this increase in $C_r$ with increasing speed is so slight. The small increase in $C_r$ results from the blunted increase in $W_{TOT}$, associated with increased work efficiency; combination of the two factors may vary among individuals. The small increase in $W_{TOT}$ is accounted for by the progressive decrease in the COM oscillation amplitude (Luhtanen and Komi 1978). Efficiency was described as either increasing from 52 to 63 % between 3 and 6 m s$^{-1}$ (Cavagna and Kaneko 1977) or close to 55 % but relatively constant (Ito et al. 1983). As discussed above, inaccuracy in assessing COM movements makes it difficult to calculate their efficiency, and interpretation needs to be cautious.

Many factors plead in favor of an increased efficiency. A major role may be played by the greater involvement of the stretch–shortening mechanisms, which result in increased elastic energy storage and reuse. Ito et al. (1983) observed a progressive increase in the elastic energy stored in a step with speed, associated with shortened coupling time, resulting in a better reuse during the concentric phase. These changes are related to neural activation of the leg extensor muscles during the eccentric phase of ground contact, as demonstrated by the electromyographic measurements made by Mero and Komi (1986) and Kyröläinen et al. (2001). The increase in neural activation comprises increases in both pre-activation before ground contact and short stretch reflex latency (Ishikawa and Komi 2007), resulting in a progressive increase in leg stiffness. However, there was some discrepancy between studies with respect to change in leg stiffness with running speed. He et al. (1991) and Farley and González (1996), assessing leg length change indirectly, found $k_{vert}$ to increase with speed whilst $k_{leg}$ was independent of running speed. Arampatzis et al. (1999), using change in COM position according to the point of force application, observed increases in both vertical and leg stiffness, but to differing degrees: an increase in running speed from 2.5 to 6.5 m s$^{-1}$ was associated with a $k_{leg}$ increase of about 50 % whilst the increase in $k_{vert}$ was 300 %. The increase in $k_{leg}$ may be related to the observed changes in ankle and knee joint stiffness, accounted for by reduced angular displacement during the contact phase. Knee extensor-flexor muscle coactivation, described by Kyröläinen et al. (2001), may contribute to this increased stiffness: Heise et al. (1996) observed that the most economical runners displayed longer bursts of agonist–antagonist coactivation during stance. A further consequence of the narrower range of joint motion is to maintain the working range of sarcomere length close to the plateau region of the force–length relation. This contributes to increasing the efficiency of force production of cross-bridge formation (Ishikawa and Komi 2007). Other factors related to the increase in leg and vertical stiffness are also involved in the small increase in $C_r$. The first kinematic consequence is a decrease of more than 20 % in the amplitude of the vertical oscillation of the center of gravity with increasing running speed, described by Luhtanen and Komi (1978) and Cavagna et al. (1988), counterbalancing the increase in stride frequency and resulting constant potential energy output. A second consequence is a gradual shortening of ground contact time, by 35–40 % from 3.25 to 6.25 m s$^{-1}$ (Kyröläinen et al. 2001; Nummela et al. 2007), shortening the time for the braking force to decelerate the forward motion of the body.

## Effects of growth and maturation; aging

There is substantial evidence that oxygen demand of running is higher in children than in adults. Davies (1980) found $\dot{V}O_2$ measured in 11–13 year-old boys at speeds ranging from 9 to 16 km h$^{-1}$ to be higher by about 25 % than that expected from previous data in adults. Two direct adult-child comparisons in 9–13 year-old boys and adults (Rowland et al. 1987; Thorstensson 1986) found 24 and 20 % differences, respectively. In females, Rowland and Green (1988) found a 16 % difference between 8.4–12.6 year-old premenarcheal girls and adults. The differences are not specific to running. Turley and Wilmore (1997) found the energy costs of both cycling and running to be higher in similar proportions in 7–9 year-old children than in adults.

Longitudinal studies demonstrate continuously decreasing costs of running in children: Daniels et al. (1978) observed a decrease from 55 to 42.2 ml kg$^{-1}$ min$^{-1}$ in O$_2$ uptake measured in boys aged 10–18 years at the same running speed of 3.37 m s$^{-1}$. Krahenbuhl and Williams (1992) found that long-term running training did not greatly enhance the natural improvement in $C_r$ with age. Likewise, Sjödin and Svedenhag (1992) reported a similar decrease in $C_r$ with age in trained and untrained boys, although the cost was systematically lower in the trained boys; this was confirmed by Mayers and Gutin (1979). Whether these differences were due to selection or to training was not clear.

Change in $C_r$ with age is associated with change in body dimensions. The longitudinal studies by Daniels and Oldridge (1971) and Ariëns et al. (1997) demonstrated that most of the decrease in cost of running (expressed as ml O$_2$ min$^{-1}$ kg$^{-1}$) occurred during the period of maximal growth. Various attempts were made to remove the influence of M. Scaling body mass by a factor of 0.75 gave a constant $C_r$ over age in two groups of boys studied by Sjödin and Svedenhag (1992). McCann and Adams (2003) calculated similar Size-Independent Costs in children and adults, but not in adolescents. The limitations of these normalizations were discussed above. In any case, lower M is not the only factor responsible for the higher $C_r$ in children: Bourdin et al. (1993) observed a higher $C_r$ in male and female adolescent basketball players than in middle-distance runners of similar M. Allor et al. (2000), comparing groups of adolescents (13.3 years) and young women matched for height and body mass, found that the girls showed 12 % greater aerobic demand than the adult women.

The higher cost observed in children may be due to several underlying mechanisms. Whether it is due to incomplete maturation of the mechanisms governing elastic energy storage and reuse, to differences in resting metabolism or differences in the relative dimensions of body segments is still not completely elucidated. The role played by incomplete maturation has never been directly addressed in running. Comparing performance in squat jump and counter-movement jump, Harrison and Gaffney (2001) found that 6-year-old children were as much able as adults to reuse the energy stored during counter movement. The extent to which similar mechanisms operate during running remains to be investigated. Schepens et al. (2001) found similar $W_{EXT}$ efficiency in children and adults, suggesting that elastic energy storage and reuse are the same. This is in agreement with Thorstensson's (1986) findings that 10-year-old boys were as much able as adults to reduce their oxygen demand relative to the total mass moved in response to external loading.

The role played by differences in resting metabolism must not be neglected. After peaking around the age of 6 years, at 125 % the adult value according to body area, resting metabolism remained 10 % higher at 15 years of age (Kleiber 1961). However, subtracting the standing metabolic rate, calculated as 1.27 times the resting rate (Cavagna and Kaneko 1977), did not abolish the differences between children and adults; moreover, the difference increased with increasing treadmill speed (Turley and Wilmore 1997). L/S has been incriminated as a putative factor of changes in $C_r$. Schepens et al. (2001) explored the mechanics of running in groups of boys aged 3–12 years and suggested that, at running speeds higher than 13 km h$^{-1}$, lower L/S results in a larger angle of contact with the ground (i.e., greater plantar flexion) due to lower COM, resulting in greater forward deceleration of the COM at each step, increasing mass-specific power output. This explanation, however, was specific to the highest running speeds. Re-analyzing the force-platform records of Schepens' study, Legramandi et al. (2013) demonstrated that the L/S changes involved more complex mechanisms. Due to their smaller stature and lower L/S, younger subjects show higher step frequency, associated with higher $k_{vert}$ and higher impact peak. The greater vertical deceleration lengthens both leg muscle and tendons. The muscle's decreased ability to reuse stored energy results in lower efficiency and longer work duration during propulsion. The brake/push duration ratio is thus low in children. The growth-related lower step frequency results in longer brake duration, associated with greater tendon energy storage. This improvement in elastic energy storage and reuse contributes to more efficient running, accounted for by a shorter relative duration of push. The running bounce tends to be more symmetrical. According to the authors, optimal similarity to an elastic bounce is attained at about 16 years of age.

Aging

Participation of older subjects of both sexes in running competitions has increased over the recent decades. Jokl et al. (2004) reported that while participation in the New York City Marathon increased by 119 % over the 1983–1999 period, the age groups older than 60 years showed the largest relative increase in participation and the greatest improvement in performance. In this respect, investigating the possible alterations of $C_r$ with age and the underlying mechanisms is of growing interest. A few studies were devoted to this topic; most reported $C_r$ to be similar in small groups of young and older experienced runners, in level running (Allen et al. 1985; Quinn et al. 2011) or in uphill running (Wells et al. 1992). Sultana et al. (2012) measured a higher $C_r$ in older triathletes. Actually this studied group was small and the difference of little magnitude: 8.0 %. It is worth noting that the older groups included subjects of

40–70 years; the picture might be different in the nonagenarian subjects who are more and more present in running competitions. Actually this quasi-constancy of $C_r$ with aging accounts for opposite contributions, as analyzed by Arampatzis et al. (2011). Type II fibers in animal are more compliant than type I; atrophy of type II fibers with aging should increase the muscle stiffness; on the other hand, the reduction of tendon stiffness with age will counteract the effects of increased muscle stiffness, thus maintaining the apparent vertical stiffness, and hence the natural frequency of the oscillating body during running unchanged (Cavagna et al. 2008). Another conflicting contribution is relative to running kinematics: Cavagna et al. (2008) reported subjects aged $73.6 \pm 5.5$ years to demonstrate higher SF and reduced amplitude of the oscillation of the centre of mass, compared to subjects aged $20.8 \pm 1.6$ yrs, the increase in internal work compensating for the decrease in external work. Taken together, these data suggest that under 70 years, there is no contribution of $C_r$ alteration to the decrease in running performance with aging.

## Effects of training

Margaria et al. (1963) were the first to demonstrate a difference in $O_2$ cost of running between trained runners and untrained subjects. The latter presented 6 % greater $O_2$ consumption at any sustained running speed. Differences in performance and training volume between trained runners may be associated with differences in $C_r$: Cavanagh et al. (1977) reported a 6 % difference between good and elite distance runners. A 24 % difference between novice and competitive runners was reported by de Ruiter et al. (2014). Scrimgeour et al. (1986) compared groups of endurance-trained runners having different weekly training volumes, from less than 60 km to more than 100 km per week; those training more than 100 km per week had a 20 % lower $C_r$ than the other groups. Daniels et al. (1986) reported a 6 % lower $C_r$ in elite female middle- and long-distance compared to sub-elite runners. Morgan et al. (1995) made a detailed retrospective analysis of 79 male runners, stratified in three categories from elite to good, compared to active subjects not engaged in run training; $C_r$ was lower in distance runners than in non-runners, and the higher the performance level the greater the difference, with a maximum difference of 11 % between the elite group and the non-runners. Of interest are the observation that (1) differences between groups of runners as distinct from non-runners were not significant, even between the elite and good groups; (2) differences in performances were associated with differences in M: the higher the performance the lighter the subjects, this may have blunted the differences in $C_r$; (3) variability within groups was great: in each

category, the range of economy between the most and the least economical runners averaged $20 \pm 2$ %. This may explain why Pereira and Freedson (1997) and Slawinski and Billat (2004) found no difference between smaller cohorts of highly trained and occasional runners.

The above-cited transversal studies do not allow assessment of the extent to which improvement in $C_r$ is due to training or to predisposition: longitudinal studies confirm both contributions. Beginners may demonstrate consistent improvement: Moore et al. (2012) reported an 8.8 % improvement in $C_r$ in adult women participating in a 10-week running program for beginners. Daniels (1974) reported the effects of retraining in the Olympic middle-distance runner Jim Ryun after a year of inactivity: RE at 4.77 m s$^{-1}$ decreased by 7 % within 3 months in spite of 5 kg (6 %) weight loss. Similarly, Conley et al. (1981) reported that, in a champion long-distance runner, 10 weeks' retraining after 2 years' inactivity resulted in a 13 % decrease in $C_r$ in spite of a 6 % decrease in M. These improvements were obtained with training consisting mainly in distance running; speed training and interval training sessions during the following weeks did not result in consistent further improvement.

The literature contains many studies of partial replacement of endurance training by sessions involving more intense muscle activity. On the whole, apart from a few studies (Lake and Cavanagh 1996; Ferrauti et al. 2010), 6–14 weeks' interval high speed or uphill running (Franch et al. 1998; Billat et al. 1999; Helgerud et al. 2007; Iaia et al. 2009; Ferley et al. 2013), heavy resistance training, explosive or plyometric training (Johnston et al. 1997; Millet et al. 2002; Spurrs et al. 2003; Turner et al. 2003; Saunders et al. 2006; Støren et al. 2008; Taipale et al. 2010; Barnes et al. 2013) were reported to decrease $C_r$ by 2–7 % in endurance runners, whatever their training background. Paavolainen et al. (1999b) reported a decrease in $C_r$ by about 7.5 % after 9 weeks' explosive training consisting of sprints, jumps and resistance exercises with high movement velocity, associated with reduced endurance running mileage. Most of the improvement was obtained within the first weeks. Race performance, however, improved inconsistently: performance over 3,000 m (Spurrs et al. 2003) or 5,000 m (Paavolainen et al. 1999b) or time to exhaustion at submaximal speed (Franch et al. 1998; Støren et al. 2008; Taipale et al. 2013) improved, but performance on a 10,000 m time trial (Iaia et al. 2009) or time to exhaustion at $\dot{V}O_{2max}$ (Billat et al. 1999) was unchanged.

Jones (1998, 2006) provided the only description of progressive decrease in $C_r$ over a long period, in the 12-year follow-up study of Paula Radcliffe, the women's marathon world record holder for many years. Paula had been studied since the age of 17. $C_r$ decreased steadily by 14.5 %, from 205 ml $O_2$ kg$^{-1}$ km$^{-1}$ in 1991, when she was already

a promising junior, to 175 ml $O_2$ $kg^{-1}$ $km^{-1}$ in 2003, while M was relatively constant between 51 and 54 kg. An even lower value of 165 ml $O_2$ $kg^{-1}$ $km^{-1}$ was obtained a few years later. Her training program consisted mainly in running. Over the 12 years' follow-up, mileage increased from 40–45 km to about 220 km per week at running speeds representing about 75 % $v\dot{V}O_{2max}$ (which increased from 20.5 to 23.5 km $h^{-1}$). Running series at speeds ranging from 85 to 100 % $v\dot{V}O_{2max}$ and strength training were progressively added to steady running sessions. Much of her training was performed at altitude. This case study thus illustrates the effects of long-lasting training on an athlete who showed a rather high $C_r$ at 17 years of age: in our reference group, the average $C_r$ of a woman weighing 51.3 kg, as she did, was around 199 ml $O_2$ $kg^{-1}$ $km^{-1}$. Predisposition may only be ascribed to her outstanding ability to sustain such training loads for so many years. Other long-term studies of outstanding athletes that could confirm these impressive data are lacking.

Some of the mechanisms underlying the decrease in $C_r$ remain poorly understood. Respiratory and metabolic factors have been proposed. Franch et al. (1998) found a tight correlation between individual decrements in pulmonary ventilation ($\dot{V}E$) and decrease in $C_r$. The authors reported a 0.11 l.$min^{-1}$ decrease in the total $O_2$ demand at the 10th minute of exercise, associated with an average 11 l $min^{-1}$ decrement in $\dot{V}E$. They postulated that the latter could account for 25–70 % of the decrease in $O_2$ demand. In moderate exercise, a 20 $l_{BTP}$ $min^{-1}$ increase in $\dot{V}E$ is usually associated with a 1 $l_{STPD}$ $min^{-1}$ increase in $\dot{V}O_2$ (Aaron et al. 1992), the cost of which is included in the whole energy cost of running. According to this relationship, the 0.11 l $min^{-1}$ decrease in $\dot{V}O_2$ obtained by Franch et al. (1998) should correspond to a 2 l $min^{-1}$ $\dot{V}E$ decrement. The 11 l.$min^{-1}$ decrement in $\dot{V}E$ is much higher than expected. The difference of about 9 l $min^{-1}$ is thus a specific effect of training on ventilatory output. Taking into account the ratio of 1.5–2.0 ml $min^{-1}$ $\dot{V}O_2$ per l $min^{-1}$ of hyperpnea calculated by Aaron et al. (1992), a 9 l $min^{-1}$ difference in $\dot{V}E$ should correspond to 15 ml $O_2$ $min^{-1}$, a 15 % contribution to the 0.11 l $min^{-1}$ decrease in $\dot{V}O_2$. Iaia et al. (2009) assessed this proportion to be 8 % for similar decrements. Possible relationships between improvement in oxygen demand and increased mitochondrial efficiency due to reduced uncoupled respiration were investigated by Iaia et al. (2009). The hypothesis was not confirmed; furthermore, improvement in $C_r$ with change in training was associated with higher protein expression of skeletal muscle UCP3.

Improvement in $C_r$ must mainly be ascribed to changes in biomechanical parameters. Moore et al. (2012) demonstrated that 3 kinematic variables explained 94.3 % of the variance in the 8 % decrease in $C_r$ in beginner runners with a 10-week training program. Interestingly, these 3 variables concerned ankle behavior at touchdown and during stance and knee extension at toe-off, all related to better elastic energy storage during the ground contact phase. In line with the better elastic storage, de Ruiter et al. (2014) compared competitive versus novice runners. The mean difference between self-selected and optimal SF was greater in novices than in the trained group: 8 and 3 % ($p < 0.05$), respectively. Contrastingly, studies of experienced runners did not demonstrate consistent change in kinematic parameters with training. Specific training may, however, optimize SL: Morgan et al. (1994) attempted SL (and hence SF) optimization in recreational runners selected on the basis of a freely chosen SL differing by about 10 % leg length from the optimal value. Training consisted in combined audio and visual feedback matching optimal SL; 15 sessions resulted in a decrease in the difference between freely chosen and optimal SL, from 10 to 2.5 % leg length, and a 3.7 % decrease in $\dot{V}O_2$ at similar running speed; no information was provided as to the long-term impact of this gait optimization. Ground contact time, when measured, was shown to shorten with decreased $C_r$ (Paavolainen et al. 1999b; Millet et al. 2002). Likewise, Spurrs et al. (2003) reported a relation between decrease in $C_r$ and increase in lower-leg musculo-tendinous stiffness.

Thickening of the triceps surae tendon could contribute to the effect of sprint- or strength-training on $C_r$. Arampatzis et al. (2007) reported increased triceps surae tendon thickness in response to sprint training, whilst Hansen et al. (2003) reported that 9 months' endurance training did not result in any change in the mechanical properties of the triceps surae tendon-aponeurosis complex. In a transversal study of experienced runners, Arampatzis et al. (2006) found that more economical runners showed greater plantar flexor muscle strength and greater triceps surae tendon-aponeurosis stiffness; this was confirmed by Fletcher et al. (2010). Albracht and Arampatzis (2013) found significant changes in both $C_r$ and triceps surae tendon stiffness in a cohort of recreational runners in response to 14 weeks' isometric training. Increased stiffness, associated with higher triceps surae force, improved elastic energy storage during the early stance phase, thus decreasing work related to fascicle shortening during propulsion.

The quadriceps femoris is also involved in improvement in $C_r$. According to Biewener et al. (2004) and Arampatzis et al. (2006), work performed by the quadriceps femoris accounts for at least 40 % of total energy expenditure during running. Training makes the quadriceps tendon and aponeurosis more compliant. Increased elongation of the series elastic element during the braking phase reduces the shortening velocity of the contractile elements during the subsequent contraction. The volume of active muscle corresponding to a given force generation is reduced, decreasing

the cost of force production. Albracht and Arampatzis (2013) analyzed the combined effects of increased triceps surae muscle–tendon stiffness and increased quadriceps tendon compliance; after training, muscle fascicle length and the elongation of the elastic elements of the triceps surae were unchanged during the braking phase when running at a given speed. Greater force was required to induce the same elongation of the elastic elements, the stiffness of which had increased, resulting in greater energy storage. Ground contact force being presumably unchanged, the increased force can be presumed to result from increased lateral ankle-joint moment associated with an anterior shift of the point of ground force application, enhancing mechanical advantage for the knee joint and leading to reduced force in the knee extensor muscles (Biewener et al. 2004). Although partially counteracted by the effects of decreased mechanical advantage in the hip and ankle, the reduced knee extensor muscle energy demand results in decreased $C_r$. This is a long-term effect superimposed on the short-term changes in nervous control of muscle stiffness.

Warne and Warrington (2014) reported that 4 weeks' habituation to simulated barefoot running (i.e., running with minimal cushioning) decreased $C_r$ by about 7 %. This improvement was associated with increased SF (2.6 %) and a trend toward forefoot striking. The decrease in $C_r$ may thus be interpreted as an effect of improved limb muscle mechanical advantage. Foot-arch stiffness was not investigated. The post-habituation improvement in $C_r$ disappeared when subjects were wearing shoes, and was attributed to learned pre-activation of the extensor leg muscles to attenuate impact, as a result of proprioceptive feedback from the foot. It would be of interest to investigate whether longer habituation to barefoot running might improve the cost of shod running.

Mention should be made of Saunders et al.'s (2004b) specific findings of decreased $C_r$ by 3.3 % after 20 nights sleeping at simulated 2,000–3,100 m altitude during training at 600 m. Effects on performance were not addressed, and the underlying mechanisms were not elucidated; specifically, the improvement could not be explained by any metabolic alteration: neither $\dot{V}E$ nor heart rate decreased with the reduced metabolic demand. Running mechanics were not investigated. It is noteworthy that the 3.3 % improvement lies within the limits of measurement error. According to a thorough review by Lundby et al. (2007), there is nothing to support the hypothesis that $C_r$ changes with acclimatization to altitude.

Taken together, these data provide a general picture of similar small improvements in $C_r$ obtained whatever the type of training or the runners' training background. The improvements, which were obtained within a few weeks and the durability of which was not investigated, were inconsistently related to improvement in maximal performance. When measured, an increase in mechanical stiffness was associated with decreased $C_r$. The relations between running kinematics and leg stiffness are precisely regulated (Morin et al. 2007). The fact that Dalleau et al. (1998), in line with Morgan et al. (1994), found SF to be systematically less than optimal suggests that the self-optimization process governing running mechanics is systematically regulated toward a mechanical stiffness less than that corresponding to the lowest $C_r$, responding to mechanical input, including lower extremity impact loading, of which the runner is precisely aware (Lake and Lafortune 1998), rather than to energy saving, to which the runner is not directly sensitive. Long-term intense training, and hence predisposition to sustaining such loading, may be mandatory to altering this setting.

## Response to prolonged exercise: fatigue effects

Since Davies and Thompson (1986) first described an increase in oxygen demand over time in highly trained ultramarathon athletes, the upward drift in $\dot{V}O_2$ during exhaustive running has been confirmed in all but one studies of running durations ranging from 60 min to 24 h and for relative running speeds ranging from 34 to 100 % $v\dot{V}O_{2max}$. This increase, however, is not systematic during intense exercises of shorter duration: Dick and Cavanagh (1987), Morgan et al. (1990, 1996), Billat et al. (1998a, b) and Rabita et al. (2011) found no change in $C_r$ after completion of exhaustive running bouts. The drift is lower in running than cycling requiring initially similar $\dot{V}O_2$ (Jones and McConnell 1999).

A major feature is the variability between studies, average variations in cost ranging from 0 to 18 %. Running duration is not a consistent factor of variation since the two above-cited extreme values were obtained in long-distance races of similar intensities: Place et al. (2004), 18 % increase in 5 h; Millet et al. (2000) no increase in 6 h. Most studies relate the increase in $C_r$ to intensity (%$\dot{V}O_{2max}$) in long-distance and short-lasting exhaustive running (Xu and Montgomery 1995; Sproule 1998; Millet et al. 2000; Gimenez et al. 2013; Bernard et al. 1998). Contrastingly, two 10 min running bouts at 95 % $\dot{V}O_{2max}$ were reported to result in either a 10.5 % increase in $C_r$ (Borrani et al. 2003) or no increase (Rabita et al. 2011). This variability between studies is mainly due to the inter-subject variability pointed out by Brueckner et al. (1991), who reported that increases in $C_r$ over a marathon ranged from 0.06 to 0.19 % per km in an homogeneous group of marathon runners. Training status was pointed out: Carter et al. (2000b) reported 6 weeks' endurance training to reduce the $\dot{V}O_2$ drift measured over a 6-min exercise by 35 %. The effects of training

status on the $\dot{V}O_2$ drift in long-distance running were not investigated till now.

Putative mechanisms for increased $C_r$ over time include metabolic factors, mechanical factors specific to running, and changes in muscle recruitment. Metabolic events partially contribute to the upward drift in $\dot{V}O_2$. In long-distance running, progressive RER decrement is due to a shift to fatty acid oxidation. A 0.05 decrease in RER would be compensated for by an increase in $\dot{V}O_2$ of about 1 %. Kyröläinen et al. (2000) and Brueckner et al. (1991) reported 0.07 reduction in RER over a marathon, accounting for a 1.4 % $\dot{V}O_2$ increase (about 40 % of the total $\dot{V}O_2$ increase reported in these studies). In intense exercise, the progressive shift of RER toward 1.0, due to greater reliance on carbohydrates, results in an opposite effect on $\dot{V}O_2$. In heavy running exercises performed at intensities lying between the so-called lactate threshold and $v\dot{V}O_{2}max$, the increase in $C_r$ has been supposed to be due to a slow component related to lactate oxidation, supplementing the primary exponential response and causing $\dot{V}O_2$ to increase. This component is calculated by fitting the time course of the breath-by-breath $\dot{V}O_2$ response after exercise onset with an exponential function (Barstow and Molé 1991). Lactate is no longer thought to stimulate $O_2$ demand (Carter et al. 2000a); the metabolic factors mostly frequently considered as putative factors of the slow component of oxygen uptake in heavy exercise may thus also be responsible for the $O_2$ drift in long-distance running. As discussed by Westerlind et al. (1992), increased rectal temperature ($T_{re}$), as an indicator of core temperature in relation with muscle heat production, may contribute to the $\dot{V}O_2$ drift. This is keeping with the $Q_{10}$ effect, linking increased temperature to increased mitochondrial respiration. The extent to which the increase in $T_{re}$ contributes to the $\dot{V}O_2$ drift is, however, not established: Davies and Thompson (1986) and Westerlind et al. (1992) reported a discrepancy between $T_{re}$ increases and $\dot{V}O_2$ drift. Also, the contribution of increased $\dot{V}E$ is controversial: $\dot{V}O_2$ increases ranging from 80 to 170 ml min$^{-1}$ are associated with $\dot{V}E$ changes up to 22.3 l min$^{-1}$ (Xu and Montgomery 1995; Candau et al. 1998; Millet et al. 2000; Avogadro et al. 2003), with no relationship between the two parameters. Based on the estimations of cost of breathing proposed by Aaron et al. (1992), the 22.3 l min$^{-1}$ increase obtained by Candau et al. (1998) would contribute about 7 % to the global increase in $\dot{V}O_2$ demand. $\dot{V}O_2$ drift has also been supposed to be due to the effects of biochemical substances such as bradykinins and prostaglandins released by damaged muscle (Kyröläinen et al. 2000); there is, however, no experimental support for this hypothesis. Furthermore, in a study of the effect of ultra-endurance running over 90 km, comprising 3 laps on 3 consecutive days, Lazzer et al. (2012) reported that $C_r$ of the individual lap did not increase significantly with lap number; this excludes any chronic lap effect, since the muscle damage responsible for release could not be repaired within 24 h.

The contribution of altered kinematic parameters of running to increased $C_r$ has not been consistently demonstrated. The most frequently reported changes in running kinematics consist in a slight increase in SF associated with decreased SL (Candau et al. 1998; Kyröläinen et al. 2000; Avogadro et al. 2003; Place et al. 2004; Hunter and Smith 2007; Morin et al. 2011) and inconsistent changes in $t_c$ (Borrani et al. 2003; Slawinski et al. 2008; Girard et al. 2013) with little consequence for internal work. Lazzer et al. (2014) that the largest role in the increase in $C_r$ associated with the ultra-endurance running described above was played by increase in the footprint index, followed by changes in SF and changes in $k_{vert}$. According to Hunter and Smith (2007), change in SF with fatigue does not alter the difference between optimal and preferred SF. Reports of the relationship between SF and $k_{vert}$ changes are inconsistent. Dutto and Smith (2002) reported a variety of kinematic changes in a group of moderately trained runners performing a test run eliciting 80 % of their $\dot{V}O_{2max}$ to voluntary exhaustion (31–90 min); most showed a decrease, but a few an increase, in SF. Changes in $k_{vert}$ and SF correlated; Slawinski et al. (2008), however, did not find this correlation. Morin et al. (2011) reported that SF increased and both $k_{leg}$ and $k_{vert}$ decreased in the first 6 h of a 24-h run. The increase in SF was related to shortened $t_c$. These changes may thus compensate for impaired neuromuscular activation, blunting the increase in $t_c$ and thus the time for the braking force to decelerate the forward motion of the body. In this respect, altered running kinematics may not be the cause of increase but a factor limiting increase in the energy cost of running. Furthermore, Millet et al. (2012) postulated that increased SF could contribute to a limitation of the potentially harmful consequences of long-distance running by limiting the impact stress of each step and hence the development of muscle and osteoarticular damage. The contribution of biomechanical factors to limiting the $\dot{V}O_2$ drift is supported by Millet et al.'s (2000) finding that a 65 km run resulted in an 11.5 % decrease in cycling efficiency whilst $O_2$ cost of running remained unaltered.

The third putative mechanism of the progressive $\dot{V}O_2$ drift consists in altered leg muscle recruitment, which may be related to a loss of ability to generate voluntary force in the leg extensor muscles: Davies and Thompson (1986), Paavolainen et al. (1999a), Kyröläinen et al. (2000), Place et al. (2004) and Rabita et al. (2011) reported consistent reductions in maximal voluntary contraction and leg extensor muscle activation and found a correlation between these maximal activation failures and increased oxygen demand. Abe et al. (2007) compared eccentric-to-concentric ratios for the integrated EMG activity of leg extensor muscles in

fatigued and non-fatigued states. Eccentric and concentric phase durations were unaltered, and eccentric phase EMG was unchanged, but concentric phase EMG increased by about 30 %, presumably to compensate for decreased utilization of stored elastic energy. A putative mechanism in this respect could be a longer delay between stretch and shortening (Nicol et al. 1991). The involvement of force generation in the drift is supported by Westerlind et al.'s (1992) finding that 30 min bouts of downhill running (−10 % gradient), corresponding to a metabolic demand of about 40 % $\dot{V}O_{2max}$, induced increases in oxygen demand of about 15 %. The possible recruitment of less efficient type II muscle fibers to supply the fatigued type I fibers has never been directly investigated in running.

## Energy cost of running in female runners

Female body architecture is thought to entail less efficient running (Williams et al. 1987). Accomplished female runners have, however, a more masculine build in terms of hip width and leg length (Daniels et al. 1977). Actually, $C_r$ in men and women do not show clear-cut difference and seem uninfluenced by training status. Bransford and Howley (1977), Davies and Thompson (1979), Bhambani and Singh (1985), Bunc and Heller (1989), Helgerud et al. (1990) and Daniels and Daniels (1992) reported slightly greater cost, ranging from 2 to 10 % in sedentary and active women and elite female runners compared with males. Daniels et al. (1977) and Padilla et al. (1992) reported similar values in male and female middle-distance runners of national rank, which was confirmed by Ingham et al. (2008) and Shaw et al. (2014) in large samples of high-level runners. Ariëns et al. (1997) and Billat et al. (2003) reported lower $C_r$ in females compared to males. Jones (2006) reported in the outstanding female marathon runner, Paula Radcliffe, a value of 165 ml $O_2$ kg$^{-1}$ km$^{-1}$ consistently lower than in any male or female Caucasian elite runner.

Women are usually lighter than men. In the above-mentioned studies, weight differences were about 20 % (17.5 % in the reference group). The possible influence of M should be taken into account. Scaling with the 0.75 exponent to remove the influence of M provides inconsistent results: Helgerud (1994) reported $C_r$ relative to M to be similar in a group of female marathon runners but approximately 10–12 ml $O_2$ kg$^{-0.75}$ min$^{-1}$ lower than in males with similar performance. Billat et al. (2003) reported non-significant difference in $C_r$ between female and male Kenyan marathon runners, whether related to M or M$^{-0.75}$. As discussed above, the 0.75 exponent might not be the best way of removing the influence of body dimensions on $C_r$. In the reference group, there was no difference between the male and female cohorts in the common range
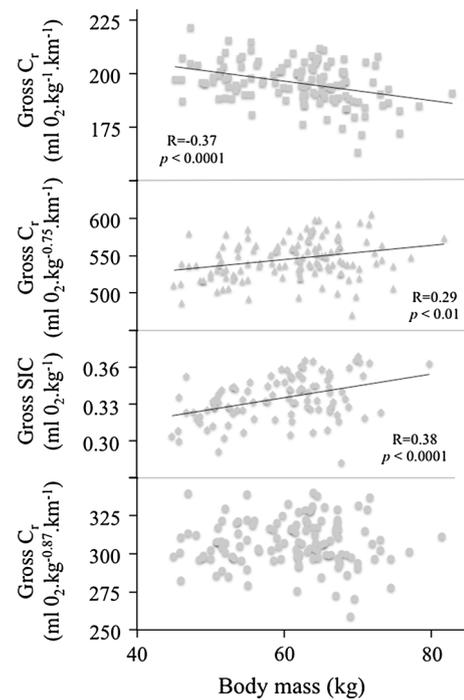


**Fig. 2** Gross $O_2$ cost of running (gross $C_r$) as a function of body mass (M; kg) in 129 competitive runners (41 women, 88 men). **a** Gross cost expressed as ml $O_2$ kg$^{-1}$ km$^{-1}$; gross $C_r = -0.471$ M + 224.47515. **b** Gross cost expressed as ml $O_2$ kg$^{-0.75}$ km$^{-1}$; gross $C_r = 0.00096$ M + 0.487. **c** Gross size-independent cost (SIC) expressed as ml $O_2$ kg$^{-1}$ S$^{-1}$; gross SIC $= 0.00092$ M + 0.282. **d** Gross cost expressed as ml $O_2$ kg$^{-0.87}$ km$^{-1}$

of 48–68 kg (Fig. 2): 197.7 ± 9.4 ml $O_2$ kg$^{-1}$ km$^{-1}$ and 197.1 ± 8.0 ml $O_2$ kg$^{-1}$ km$^{-1}$, respectively. Regression line slopes were also similar.

Similar $C_r$ are associated with consistent differences in running parameters between men and women. Women are not the same as men geometrically. Elite female runners have shorter legs relative to stature and lighter leg extremities than their male counterparts (Williams et al. 1987). Mechanical running variables are also different: compared with elite male runners, at any given running speed elite female runners showed greater angular hip flexion, angular velocity in hip flexion and extension and stride length relative to stature and less vertical oscillation relative to leg length (Williams et al. 1987). These differences at given running speeds might be due to women's shorter height. Chapman et al. (2012) demonstrated that stride frequency normalized to height was consistently higher in women and associated with shorter $t_c$ at a given running speed. These kinematic differences are not accounted for by any difference in muscle neural activation: Mero and Komi (1986) reported leg muscle EMG activity and leg stiffness to be similar in male and female runners at similar sub-maximal speeds. Fletcher et al. (2013) found less Achilles

tendon stiffness in male than in female trained runners, $C_r$ being inversely related to stiffness in the whole group. It is noteworthy that Barnes et al. (2014) reported 27 % less Achilles tendon moment arm length associated with non-significantly lower $C_r$. There is a discrepancy between this absence of difference in cost of running and the strong relationship between the two variables, suggesting that both greater ability to reuse stored elastic energy and shorter Achilles tendon moment arm merely compensate for disadvantages in women's $C_r$ that remain to be elucidated.

## Differences between ethnic groups

Kenyan dominance in long- and middle-distance running, reviewed by Larsen (2003), is well established. Lucia et al. (2006) discussed the growing participation of other East African populations in this pattern of dominance, and specifically of Eritreans, who belong to the same ethnic groups as a large proportion of Ethiopians. This dominance cannot be explained on energetic grounds: black African runners show neither greater $\dot{V}O_{2max}$ nor higher fractional $\dot{V}O_{2max}$ utilization than Caucasian elite runners (Tam et al. 2012). This shifts the focus to $C_r$ and the extent to which this lower cost may account for this ethnic dominance. Saltin et al. (1995) were the first to demonstrate a lower $C_r$ in top Kenyan runners compared with very good Swedish runners. Lucia et al. (2006) made a similar comparison between elite Eritrean and Spanish runners: the Eritreans' $C_r$ was 15 % lower than the Spaniards'. Lucia et al. (2008) measured the lowest gross $O_2$ cost of running value ever reported in the Eritrean cross-country runner Tadesse Zerisenay (three World Championship medals in 2009): 150 ml $O_2$ kg$^{-1}$ km$^{-1}$; actually, the 9.2 m s$^{-1}$ $v_a$max calculated from this $C_r$ and the 83 ml kg$^{-1}$ min$^{-1}$ $\dot{V}O_{2max}$ value reported in the study seem unrealistic. Apparently inconsistent results were obtained in black South Africans: Weston et al. (2000) reported 7 % lower $C_r$ in black than white marathon runners of similar rank; in contrast, Coetzer et al. (1993) and Bosch et al. (1990) found similar values in black and white South African populations.

Actually, the difference between African and Caucasian runners is not that clear-cut: low is not specific to elite black African runners: Tam et al. (2012) reported similar low-average $O_2$ cost of running values in groups of elite Kenyan and European marathon runners; the individual net values measured in two of the best marathon runners, the Kenyan Elijah Keitany (2 h 06.41 min) and the Swiss Viktor Röthlin (2 h 07.23 min), were both low: 165 and 164 ml $O_2$ kg$^{-1}$ km$^{-1}$, respectively (not significantly different from the value measured in the 1972 gold medal winner Frank Shorter, of about 160 ml $O_2$ kg$^{-1}$ km$^{-1}$, as reported by Saltin et al. (1995)). These comparisons do not take into
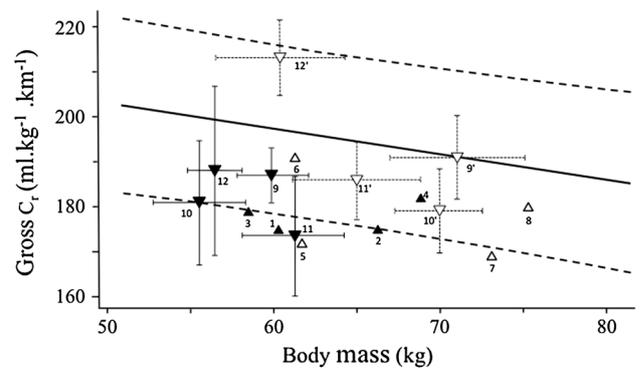


**Fig. 3** Gross $O_2$ cost of running (gross $C_r$) of African and Caucasian runners reported in the literature. The values are superimposed on the regression line as a function of body mass and 95 % confidence intervals of prediction of the male runners reference group. *1* Julius Korir (Saltin et al. 1995); *2* Joseph Ngugi (Saltin et al. 1995); *3* Martin Lel (Tam et al. 2012); *4* Elijah Keitany (Tam et al. 2012); *5* Frank Shorter (Saltin et al. 1995); *6* Viktor Röthlin (Tam et al. 2012); *7* Derek Clayton (Saltin et al. 1995); *8* Jim Ryun (Daniels 1974). *9 & 9′*, respectively, African and Caucasian runners (Bosch et al. 1990). *10 & 10′*, respectively, African and Caucasian runners (Coetzer et al. 1993). *11 & 11′*, respectively, African and Caucasian runners (Weston et al. 2000). *12 & 12′*, respectively, African and Caucasian runners (Lucia et al. 2006)

account the usually lower M of African runners, which blunts the differences in $C_r$. Plotting the M-gross $C_r$ coordinates on the general relationship in the reference group of Caucasian runners (Fig. 3) makes it clear that all the African cohorts, although not clustering separately from Caucasian cohorts, were positioned well below the regression line, closer to the 95 % lower confidence limit than most of their Caucasian counterparts. In measurements made in the same conditions (Bosch et al. 1990; Coetzer et al. 1993; Weston et al. 2000; Lucia et al. 2006), Africans were compared with heavier similarly ranked Caucasian runners whose $C_r$ were low compared to the reference group. This explains the apparently inconsistent results for the South African runners.

The above-cited studies generally focused on outstanding athletes. Studies of East African recreational or good non-championship runners are lacking. The question arises as to whether the low $C_r$ frequently found in East African runners is attributable to a genetic endowment common to African populations or to selection bias? Larsen et al.'s (2004) study of prepubertal Nandi boys, whose $C_r$ was lower than in untrained Caucasian boys, suggests that this low cost is inherent. This was further confirmed by Larsen et al. (2005), who showed similar and quite small trainability of cost of running in Danish and Kenyan boys. The inherent low $C_r$ common to Africans thus increases the probability of satisfying all the physiological requirements of elite middle- and long-distance running. If so,

while those elite Caucasian runners who combine very low $C_r$ with high $\dot{V}O_{2max}$ are exceptions whose performances are celebrated for decades, elite East African runners are the best of a population benefitting from a shared inherent advantage. The present high turnover of East African champions supports this hypothesis.

Is cost of running the only physiological characteristic underlying East African dominance? The distribution of metabolic factors determining running performance has not been systematically investigated in African populations. It is noteworthy that individuals with low $C_r$ are less subject to heat accumulation (Arsac et al. 2013). This, along with lower body mass index, may be a factor of the greater ability to sustain high-intensity distance running demonstrated by black South African runners (Coetzer et al. 1993, Weston et al. 1999). In this respect, the very low $C_r$ measured by Ferretti et al. (1991) in Pygmies weighing $57.2 \pm 4.8$ kg (net cost $= 156 \pm 14$ ml kg$^{-1}$ km$^{-1}$ which is in the range of elite African runners of similar body mass) may be an example of adaptation–selection: Pygmies are used to running over long distances for hunting in hot humid environments.

Two factors were identified as potentially responsible for the low $C_r$ shown by many African runners. The lesser leg thickness of East African runners, reported by Saltin et al. (1995), Lucia et al. (2006) and Kong and de Heer (2008), is one probable factor, relating to a low moment of inertia of the leg about the hip. Myers and Steudel (1985) found that loading shanks and ankles by 1.8 kg per leg resulted in, respectively, 12.1 and 24.3 % increases in cost. The difference in leg perimeter between Caucasians and Africans could account for a consistently lower mass difference. Lucia et al. (2006) measured a significant 9 % difference in calf circumference between elite Eritrean runners and their Spanish counterparts. This was confirmed by Kong and De Heer (2008). On the other hand, Lucia et al. (2006) found shanks 10 % longer than in Spaniards; the extent to which smaller calf circumference was counterbalanced by the longer shank was not addressed. A negative relationship between circumference and cost of running was found in the whole group of Eritrean and Spanish runners, but was weak and significant only at 21 km h$^{-1}$. Although it certainly contributes, a few hundred grams' difference may not be the only factor responsible for the consistently lower $C_r$ of black Africans. Scholz et al. (2008) found leg volume to be related to calcaneal tuberosity length and the moment arm of the Achilles tendon, which in turn are strongly related to cost of running. The slender legs of Africans could thus be an indicator of shorter calcaneal tuberosity length, explaining their lower $C_r$. The second putative factor could be a specific stretch–shortening cycle pattern resulting in more efficient storage and reuse of elastic energy. Sano et al. (2013) compared triceps surae length

change and EMG activity during repetitive maximal hopping in international level Kenyan runners, versus physically active Caucasian controls: they found greater stiffness and greater shortening-to-stretching ratio in the Kenyans' medial gastrocnemius, accounting for more efficient storage and reuse of elastic energy, accompanied by shorter contact times. Kong and de Heer (2008) reported about 10 % shorter contact time in elite Kenyan runners than Caucasian counterparts. As discussed above, shorter contact time would reduce $C_r$ by reducing the time for braking forces to decelerate the forward motion of the body. The smaller triceps surae length changes observed during hopping led Sano et al. (2013) to conclude that muscle fascicles were operating at optimal working range. All these factors are related to better efficiency in hopping. The extent to which similar mechanisms operate during running remains to be investigated.

Metabolic specificities have been proposed as a further putative factor. Kenyan and Eritrean runners are native to high altitudes and most of their training is performed at around 2,000 m for Kenyans and 2,600 m for Eritreans (Lucia et al. 2006). This could account for their lower $C_r$, in line with the observation by Hochachka et al. (1991) that Andean natives are more efficient in cycling than lowlanders, although this concerned a different population living at a higher altitude (around 4,000 m), and there are no consistent data to support the hypothesis as refers to east-Africans. South African runners show low cost of running but are sea-level dwellers (Bosch et al. 1990; Weston et al. 2000). The cycling efficiency of East Africans has yet to be assessed. Nielsen et al. (2013) reported the resting metabolism of male and female African Americans to be, respectively, 9 and 7 % lower than Caucasian counterparts, corresponding to a 0.3 ml O$_2$ min$^{-1}$ kg$^{-1}$ difference, which may be considered negligible relative to the $\dot{V}O_2$ achieved during running.

## Conclusion

Williams and Cavanagh's (1987) statement that no single variable or small subset of variables can explain differences in RE between individuals remains valid, but some factors may now be clearly assessed. Recent advances in knowledge concern the modulation of elastic energy by the combined effects of changes in body stiffness, joint moment arms and stride frequency. The small effects of increased running speed or duration on cost of running leaves open the question of the consistency of these changes. In this respect, more attention should be paid to measurement validity. The use of automatic systems beyond their limits of calibration exacerbates the doubt. The contrast between the large differences (about 20 %) in

$C_r$ between individuals and the small changes (7 % at the most) found in response to training must be underlined; they plead in favor of a major role of inherent factors. This interpretation is, however, challenged by the large improvement in $C_r$ reported by the single long-term study of an outstanding female championship runner. Among the factors accounting for differences in $C_r$ between individuals, calcaneal tuberosity length seems to be of major importance, accounting for a very high percentage of running cost variance; this, however, was only recently described (Scholz et al. 2008), and its major contribution to the cost variance needs confirmation. The role of this factor in the specificities of female and African runners deserves further investigation.

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