

## Energy cost and kinematics of level, uphill and downhill running: fatigue-induced changes after a mountain ultramarathon

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### Abstract

This study aimed to determine whether the fatigue induced by a mountain ultramarathon (MUM) led to changes in energy cost and kinematic during level and graded running. Pre- and post-race, 14 ultratrail runners ran on a level, uphill (5%) and downhill (5%) treadmill at 10 km · h<sup>-1</sup>. Kinematic data were acquired using a photocell system. Post-race, the downhill energy cost increased by 13.1% ( $P < 0.001$ ). No change was noted in level and uphill running. Duty factor and stride frequency were increased, whereas swing time, cycle time and stride length were decreased in all conditions ( $P < 0.05$ ). Contact time was increased and the rate of force generation was decreased only in the uphill and downhill conditions ( $P < 0.05$ ). Positive correlations were observed between performance time and the pre- to post-changes in the energy cost of level ( $r = 0.52$ ,  $P = 0.04$ ) and uphill running ( $r = 0.50$ ,  $P = 0.04$ ). MUM-induced fatigue resulted in physiological and spatiotemporal changes, though the response to fatigue varied considerably between running conditions. These changes resulted in a significant increment only in the downhill energy cost. Incorporating downhill locomotion in the training programmes of ultratrailers may help to improve performance-related physiological and biomechanical parameters.

**Keywords:** energy cost, fatigue, kinematic, performance, running, ultraendurance

### Introduction

Mountain ultramarathons (MUMs) have become increasingly popular in the last decade. The energy demand during such events is likely to be at the extremes of human tolerance (Millet & Millet, 2012), inducing an extreme fatigue state that can influence both physiological and biomechanical characteristics of human locomotion (Maclaren, Gibson, Parry-Billings, & Edwards, 1989). Internal changes with fatigue may translate into external mechanical changes during an extended running exercise and affect stride characteristics at a given running speed, contributing to an increase (deterioration) in the energy cost of running ( $C_r$ ) (Hunter & Smith, 2007). Studies evaluating runners' responses to fatigue after running exercises shorter than or equal to the classic marathon distance have reported changes in physiological and biomechanical parameters (Hunter & Smith, 2007; Kyröläinen

et al., 2000; Nicol, Komi, & Marconnet, 1991), all of which negatively influence the  $C_r$ . In a fatigue state,  $C_r$  is negatively affected because fatigued muscles require greater muscle activation to generate the required force, and thus elevate the  $C_r$  (Roberts, Kram, Weyand, & Taylor, 1998). Increased muscle fatigue may be associated with decreased (deteriorated) muscle stiffness, resulting in greater attenuation of ground forces and, therefore, in an increased  $C_r$  (Avela & Komi, 1998a, 1998b; Derrick, 2004; Derrick & Mercer, 2004; Nicol, Avela, & Komi, 2006).

Data on MUM are scarce. Millet et al. (2000) found that the  $C_r$  did not change after a 65-km MUM with a cumulative elevation gain (D+) of 2500 m. Degache et al. (2013) examined the effects of fatigue induced by a 5-h hill run (mean D+ 1730 m) on running mechanics and spring-mass behaviour. They found increased step frequency and

vertical stiffness, and a decline in the downward displacement of the centre of mass and in the maximum value of vertical ground reaction force. These findings are shared by Morin, Tomazin, Edouard, and Millet (2011), who described the same changes in running biomechanics and spring-mass behaviour after a 166-km MUM (9500 m D+), but with a greater percentage change. However, both studies were conducted using level running protocols and did not analyse changes in  $C_r$  and kinematics under hill running conditions, which may be a more accurate model to study MUM performance, which is mainly characterised by large positive/negative elevation changes. Recently, Vernillo et al. (2014) examined the effects of an extreme MUM (330 km, 24,000 m D+) on  $C_r$  and kinematic of level and uphill running. They observed a decrease in uphill running  $C_r$  and an increase in both contact time and duty factor but no changes during level running.

As compared with level running, the maximum possible storage and return of elastic energy is reduced in hill running because of a mismatch between the storage of elastic energy during landing and the use of that elastic energy during take-off (Gottschall & Kram, 2005). In addition, the stretch-shortening cycle is underutilised during running uphill because the ability of the muscle tendon unit to store and release elastic energy is reduced (Cavagna, Heglund, & Taylor, 1977). This results in an increased  $C_r$  proportional to the increase in slope gradient (Minetti, Ardigò, & Saibene, 1994). Conversely, during braking actions in downhill running, the leg muscles lengthen while exerting tension, performing mainly eccentric muscle actions requiring less expensive work (Gottschall & Kram, 2005). This is because eccentric muscle contractions are metabolically less expensive than concentric muscle contractions (Abbott, Bigland, & Ritchie, 1952). Research exploring the effects of an MUM on level, uphill and downhill  $C_r$  and running kinematics is still scarce.

The aim of the present study was to investigate MUM-related changes in the  $C_r$  and running kinematics during level, uphill and downhill running bouts. We hypothesised that MUM-induced fatigue leads to an increase (deterioration) in muscle stiffness which, independent of the role of elastic energy storage and return on slopes, negatively influences the level, uphill and downhill  $C_r$  and running kinematics.

## Methods

### Participants

The race organiser invited the male runners to take part in the present study through an announcement

Table I. Anthropometric characteristics of the participants before the race ( $n = 14$ ).

	Mean	s	Range
Age (years)	39.7	7.3	29.7–52.4
Body Mass PRE (kg)	73.3	7.0	59.5–82.3
Body Mass POST (kg)	70.5***	6.8	57.2–79.1
Stature (m)	1.77	0.07	1.67–1.92

Note: \*\*\*Significantly different from the PRE test session ( $P < 0.001$ ).

posted on the event website (see <http://www.trentinotrailrunning.it/collaborazioni/vigolanatrail>).

Fourteen experienced male ultratrail runners took part in the study (Table I). On average, the participants had  $11 \pm 4$  years of training in running and  $4 \pm 2$  years of ultra-endurance experience. Pre-race training consisted of 3–4 weekly sessions in which they ran for  $8.0 \pm 5.0$  h and  $58.5 \pm 28.0$  km. Before data collection, all participants gave their written informed consent after being fully informed of the study procedure and requirements and the risks involved. The experiment was conducted according to the Declaration of Helsinki and approval was obtained from the local Institutional Ethics Committee.

### Experimental overview

The MUM (Vigolana Trail®) took place at Vigolo Vattaro (Trento, Italy) in June 2014. The course is 65 km long over rough terrain at medium altitude (altitude range between 725 and 2100 m), with a total positive/negative elevation of +4000 m. The study was conducted in three phases: pre-race testing, MUM race and post-race testing. During the first phase, the participants were familiarised with the test scheme and ran for 10 min to become comfortable with treadmill running. The pre-tests were performed the week preceding the race (PRE). During the second phase, the participants ran the MUM race. During the third phase (POST), the participants were brought by car to the laboratory (~300 m away) within 5 min of finishing. The PRE and POST sessions were organised in a similar fashion. Based on previous observations (Millet et al., 2000; Vernillo et al., 2014), the running conditions were selected to maximise comfort. After apparatus calibration, gas exchange was measured at rest for 5 min with the participant standing in an upright position. Each participant completed three 5-min data collection sessions during which he ran on a level, inclined (+5%) and declined (−5%) motorised treadmill (RunRace, Technogym, Gambettola, Italy) at  $10 \text{ km} \cdot \text{h}^{-1}$  in that order. We assumed that, because of fatigue, the participants would not be

able to reach their metabolic steady state if they ran on steeper slopes and that lower treadmill speeds might have induced them to switch locomotion from running to walking. Admittedly, these constraints prevented us from studying more performance-specific slopes and/or running speeds. In order to test whether the participants had sufficient aerobic fitness to complete the protocol, while remaining at a submaximal rate of oxygen consumption, they were required to have a mean respiratory exchange ratio of  $\leq 0.9$  during the PRE testing to continue in the study (Snyder & Farley, 2011). Data on kinematic variables were acquired using a photocell system to quantify the spatiotemporal gait parameters.

*Energy cost of running.* Data were filtered into 5-s blocks for analysis. Because of the time it takes for an individual to reach a steady-state condition in oxygen uptake and for the indirect calorimetry measurement (Quark CPET, Cosmed, Rome, Italy) to reflect actual energy cost, the first 4 min of each 5-min measurement were discarded in the analysis and the last 1-min sets were averaged. Oxygen uptake ( $\dot{V}O_2$ ), carbon dioxide output ( $\dot{V}CO_2$ ) and respiratory exchange ratio (RER) were measured using the gross  $\dot{V}O_2$  and  $\dot{V}CO_2$  measured during steady state in the last minute of each condition. The  $C_r$  per unit of distance was calculated starting from the difference between  $\dot{V}O_2$  at steady state minus  $\dot{V}O_2$  at rest. Then, the net energy expenditure in  $J \cdot kg^{-1} \cdot m^{-1}$  was calculated by converting the net  $\dot{V}O_2$  to the corresponding metabolic energy output using an energy equivalent of  $O_2$  ranging from 21.13 to 19.62  $kJ \cdot L^{-1}$  depending on the RER.  $C_r$  is expressed in both absolute values and percentage changes between PRE and POST. Percentage changes in level, uphill and downhill  $C_r$  ( $\Delta C_r$ ) were calculated from the POST  $C_r$  minus the PRE  $C_r$  and expressed as a percentage of the corresponding PRE  $C_r$ .

*Kinematics data acquisition and processing.* The spatiotemporal gait parameters were measured with a photocell system (Optogait, Microgate, Bolzano, Italy) described and validated elsewhere (Lienhard, Schneider, & Maffioletti, 2013). Data were acquired at a sampling frequency of 1000 Hz and automatically processed by the on-board software (version 1.9). The trial size for each condition was the minimal value, as determined from the pilot study, which would allow a reliability of 0.90 in our kinematic variables, as suggested by Mullineaux, Bartlett, and Bennett (2001). We set the minimal value for trial size at 40 steps for each condition (at least 20 cycles), for no more than 1 min of recording. Data

recording started approximately 3 min after the start of each condition.

Data for the left and the right sides were pooled since an a priori analysis showed symmetrical behaviour of the lower limbs during the different gaits. The kinematic variables calculated from the photocell system included: contact time, cycle time, stride frequency, swing time, stride length and duty factor. The inverse time of foot contact was taken as an indicator of the rate of force generation (Roberts et al., 1998). The mean of each variable in the recorded trials was used as a representative response and entered in the subsequent statistical analysis.

### Statistical analysis

Data are expressed as mean  $\pm$  standard deviation ( $s$ ). Results were tested for normal distribution using the Shapiro-Wilk  $W$  test. Analysis of covariance for repeated measures was performed to determine the possible differences between PRE and POST MUM values, with the PRE values used as a covariate. When a significant  $F$ -value was found, Bonferroni's post hoc test was applied. The magnitude of the changes was assessed using effect size (ES) statistic with 90% confidence interval (CI) and percentage change (Batterham & Hopkins, 2006; Hopkins, 2006). The ES was classified as follows:  $<0.2 = trivial$ ,  $0.2-0.6 = small$ ,  $0.6-1.2 = moderate$ ,  $1.2-2.0 = large$  and  $>2.0 = very large$  (Hopkins, 2002). Pearson's product moment correlation coefficient ( $r$ ) with 90% CI was used to examine the relationships between selected parameters. Statistical analyses were performed using IBM<sup>TM</sup> SPSS<sup>TM</sup> Statistics (version 20.0.0, IBM Corporation, Somers, NY), and the significance level was set at  $P < 0.050$ .

### Results

The time of the winner of this MUM race was 6 h 40 min 07 s and the average time of the study participants was 9 h 45 min 41 s (range, 6 h 58 min 34 s to 14 h 12 min 32 s). Body mass decreased by 3.8% between the PRE and POST MUM ( $P < 0.001$ , ES =  $0.38 \pm 0.11$ , *small*). In general,  $\dot{V}O_2$  increased rapidly in all participants without a discernible delay at the onset of exercises and approached a plateau during the three running conditions. A steady-state  $\dot{V}O_2$  was attained within 4 min in each condition without any additional increase (slow component).

As shown in Figure 1A,  $\dot{V}O_2$  significantly increased from PRE to POST for both level (+7.8%,  $P = 0.002$ , ES =  $0.86 \pm 0.36$ ) and downhill (+12.9%,  $P < 0.001$ , ES =  $1.17 \pm 0.34$ ) running but did not change significantly for uphill running

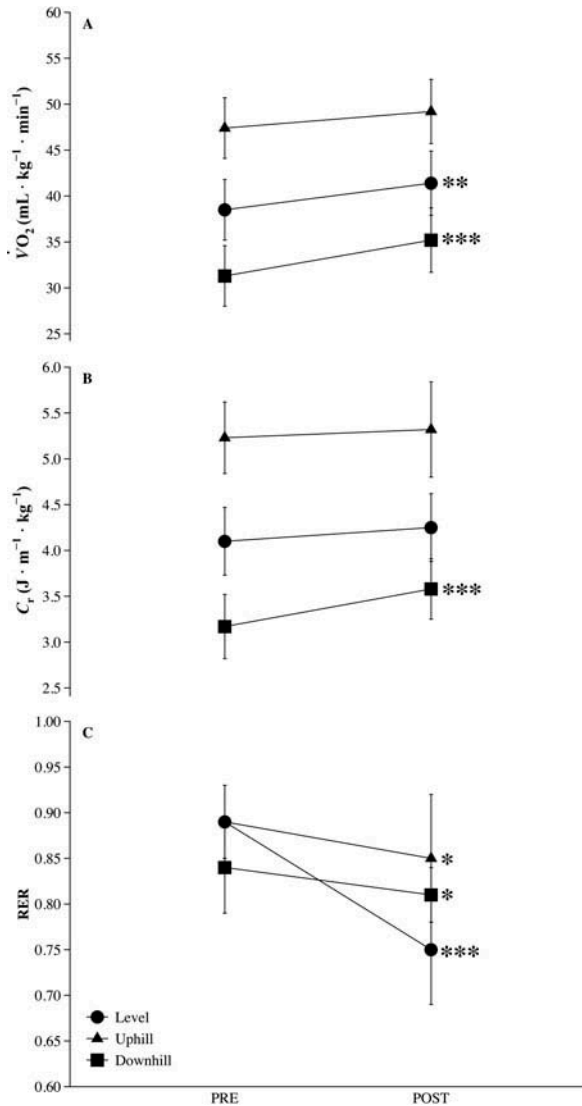


Figure 1. Differences in oxygen uptake ( $\dot{V}O_2$ , Panel A), energy cost of running ( $C_r$ , Panel B), and respiratory exchange ratio (RER, Panel C) before (PRE) and after (POST) the MUM ( $n = 14$ ). \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . Standard deviations were omitted for clarity.

Level: running  $10 \text{ km} \cdot \text{h}^{-1}$ . Uphill: running  $10 \text{ km} \cdot \text{h}^{-1}$  at +5%. Downhill: running  $10 \text{ km} \cdot \text{h}^{-1}$  at -5%.

(+3.9%,  $P = 0.169$ , ES =  $0.40 \pm 0.49$ ). There were no significant changes in level (+3.9%,  $P = 0.080$ , ES =  $0.38 \pm 0.38$ ) or uphill (+2.1%,  $P = 0.534$ , ES =  $0.18 \pm 0.54$ )  $C_r$  between the PRE and POST MUM.  $C_r$  was 13.1% higher at POST as compared with the PRE only in the downhill condition ( $P < 0.001$ , ES =  $1.15 \pm 0.35$ ) (Figure 1B). RER significantly decreased from PRE to POST for level (-15.6%,  $P < 0.001$ , ES =  $2.72 \pm 0.66$ ), uphill (-5.1%,  $P = 0.024$ , ES =  $0.80 \pm 0.58$ ) and downhill (-3.0%,  $P = 0.008$ , ES =  $0.64 \pm 0.70$ ) running (Figure 1C).

There was a significant change between PRE and POST in all the kinematic data recorded in the level running condition (Table II). In the uphill and downhill running conditions, there were significant changes in the kinematic data, except for contact time and the rate of force generation (Tables III and IV, respectively). In all three conditions, there was a significant decrease in the cycle time and an increase in the duty factor.

Finally, positive correlations were observed between performance time and  $\Delta C_r$  on level and uphill running ( $r = 0.52 \pm 0.36$ ,  $P = 0.044$  and  $r = 0.50 \pm 0.36$ ,  $P = 0.042$ , respectively) (Figure 2).

## Discussion

The main findings of this study were that (i) MUM-induced fatigue affected only downhill  $C_r$  and (ii) there were positive correlations between performance time and  $\Delta C_r$  in level and uphill running.

RER at a given intensity is known to decrease with time (Costill, 1970). The present study corroborates previous studies on ultrarunning events where RER decreased by 15.6%, 11% and 7.3% between pre and post 24-h treadmill exercise (Gimenez, Kerherve, Messonnier, Feasson, & Millet, 2013), a simulated 60-km ultramarathon (Schena et al., 2014) and a 65-km MUM (2500 m D+) (Millet et al., 2000), respectively. However, it differs from

Table II. Differences in kinematic variables measured during level running at  $10 \text{ km} \cdot \text{h}^{-1}$  before (PRE) and after (POST) the MUM ( $n = 14$ ).

Variable	PRE			POST			% change	ES	$\pm 90\%$ CI
	Mean	$s$	Range	Mean	$s$	Range			
Contact time (s)	0.291	0.022	0.265–0.333	0.303**	0.021	0.277–0.346	+4.2	0.52	0.27
Duty factor (%)	39.8	2.9	33.7–44.7	43.0***	2.1	39.6–47.3	+19.1	1.19	0.40
Rate of force generation ( $\text{s}^{-1}$ )	3.46	0.25	3.00–3.76	3.32**	0.22	2.89–3.61	-3.9	0.56	0.28
Swing time (s)	0.440	0.030	0.378–0.499	0.401***	0.029	0.362–0.499	-8.6	1.25	0.44
Cycle time (s)	0.731	0.028	0.684–0.777	0.704**	0.040	0.657–0.778	-3.7	0.73	0.34
Stride frequency (Hz)	1.37	0.05	1.29–1.46	1.42**	0.08	1.28–1.52	+3.9	0.76	0.35
Stride length (m)	2.05	0.08	1.91–2.18	1.97**	0.11	1.84–2.18	-3.5	0.73	0.34

Notes: ES, effect size; CI, confidence interval.

\*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

Table III. Differences in kinematic variables measured during uphill running at  $10 \text{ km} \cdot \text{h}^{-1}$  (+5%) before (PRE) and after (POST) the MUM ( $n = 14$ ).

Variable	PRE			POST			% change	ES	$\pm 90\%$ CI
	Mean	$s$	Range	Mean	$s$	Range			
Contact time (s)	0.295	0.020	0.271–0.331	0.300	0.023	0.269–0.344	+3.4	0.21	0.20
Duty factor (%)	41.0	2.0	39.2–46.2	43.2***	2.0	39.2–46.2	+5.6	0.97	0.33
Rate of force generation ( $\text{s}^{-1}$ )	3.40	0.23	3.02–3.69	3.35	0.25	2.91–3.72	-1.5	0.20	0.21
Swing time (s)	0.424	0.026	0.368–0.474	0.393***	0.030	0.352–0.446	-7.3	1.06	0.42
Cycle time (s)	0.719	0.032	0.674–0.772	0.693**	0.044	0.638–0.775	-3.7	0.64	0.33
Stride frequency (Hz)	1.39	0.06	1.29–1.48	1.45**	0.9	1.29–1.57	+4.0	0.67	0.34
Stride length (m)	2.01	0.09	1.89–2.17	1.93**	0.12	1.78–2.17	-3.7	0.66	0.33

Notes: ES, effect size; CI, confidence interval.

\*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

 Table IV. Differences in kinematic variables measured during downhill running at  $10 \text{ km} \cdot \text{h}^{-1}$  (-5%) before (PRE) and after (POST) the MUM ( $n = 14$ ).

Variable	PRE			POST			% change	ES	$\pm 90\%$ CI
	Mean	$s$	Range	Mean	$s$	Range			
Contact time (s)	0.296	0.025	0.273–0.348	0.300	0.024	0.268–0.346	+1.6	0.17	0.20
Duty factor (%)	39.0	2.8	35.7–43.7	41.2***	2.5	38.6–45.7	+7.0	0.92	0.35
Rate of force generation ( $\text{s}^{-1}$ )	3.40	0.26	2.87–3.66	3.35	0.25	2.89–3.73	-1.4	0.19	0.23
Swing time (s)	0.462	0.030	0.387–0.504	0.420***	0.030	0.370–0.471	-8.8	1.30	0.47
Cycle time (s)	0.757	0.033	0.688–0.823	0.720***	0.039	0.659–0.878	-4.8	0.96	0.38
Stride frequency (Hz)	1.32	0.06	1.21–1.45	1.39***	0.07	1.27–1.52	+5.3	0.96	0.38
Stride length (m)	2.12	0.09	1.9–2.3	2.02***	0.11	1.85–2.20	-4.9	0.96	0.38

Notes: ES, effect size; CI, confidence interval.

\*\*\* $P < 0.001$ .

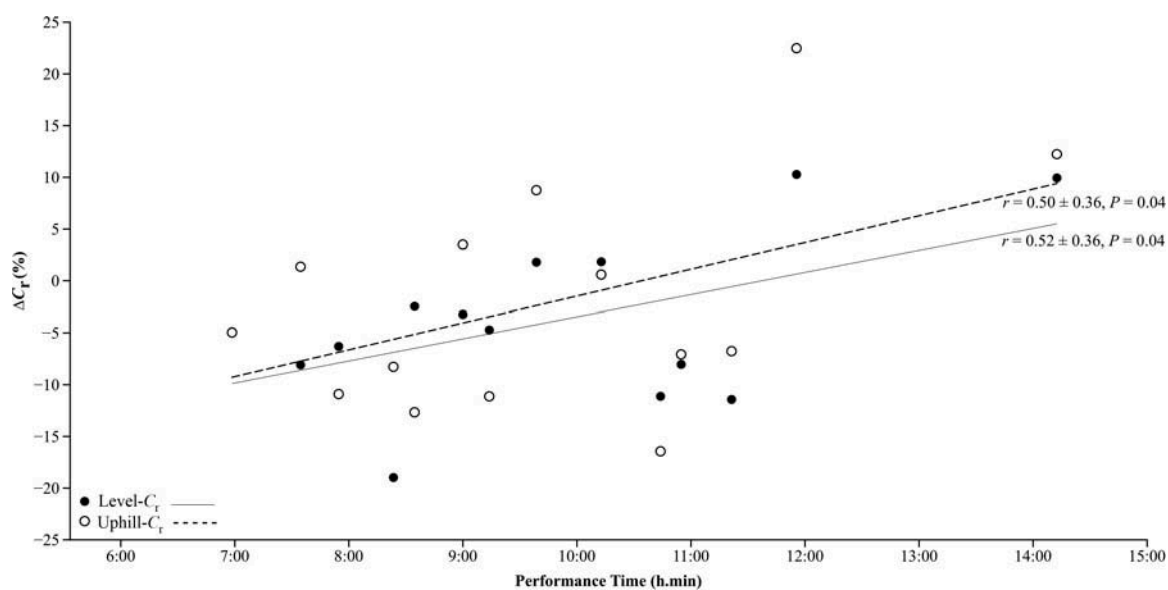


Figure 2. Relationships between the performance time of the MUM and differences in the energy cost of level and uphill running ( $\Delta C_r$ ) between PRE and POST-MUM measured at  $10 \text{ km} \cdot \text{h}^{-1}$ , 0%, and +5%, respectively ( $n = 14$ ). The 90% confidence intervals were omitted for clarity.



that previously observed by Vernillo et al. (2014) where RER did not change after an extreme MUM, likely because of the multistage nature of the competition in which the runners were allowed adequate energy intake throughout the race, thus maintaining the efficiency of ATP aerobic resynthesis.

The change in RER represents a shift in substrate utilisation from carbohydrates to fats. This is in line with previous findings (Gimenez et al., 2013; Millet et al., 2000; Schena et al., 2014) and it is likely to be the consequence of the progressive depletion of glycogen stores during an MUM. The significant decrease in RER has an obvious impact on the calculation of  $C_r$  whose decrease is inevitably overestimated when the changes in the caloric equivalent of oxygen are not properly considered and only the volume of oxygen per unit of distance ( $\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) is calculated (Peronnet & Massicotte, 1991). In the present study, the decrease in RER minimised the increase in  $C_r$  in comparison with the increase in  $\dot{V}O_2$  only during the level and uphill running conditions (Figure 1), where non-significant differences from PRE to POST were observed (+3.9% and +2.1%, respectively). In contrast, the downhill  $C_r$  significantly increased by 13.1%, suggesting that other factors such as changes in running biomechanics patterns could also affect  $C_r$ .

Across all conditions, cycle time decreased by 4% with a concomitant increase in stride frequency and duty factor (Tables II and IV). Contact time and the rate of force generation are closely correlated with changes in  $C_r$  (Kram & Taylor, 1990) because  $C_r$  is largely determined by the rate at which force must be generated by the muscles that support the body during the stance phase (Roberts et al., 1998). In the present study, an increase in the duty factor was determined by a decrease in the cycle time in all three conditions and by significant changes in both the contact time and the rate of force generation only during level running (Table II). This finding contrasts with previous studies that found no change or a decrease in either contact time or the rate of force generation during level running after MUMs (Degache et al., 2013; Morin et al., 2011; Vernillo et al., 2014). A possible explanation for this discrepancy may lie in the different speeds used between studies, as well as the different characteristics of the MUMs (in terms of total distance and D+) that led to different fatigue-induced alterations in running biomechanics. Taken together, these results suggest that the participants reorganised their running biomechanics towards a longer duty factor, indicating that longer time was spent in propulsion and that the rate at which the reaction forces must be generated decreased from PRE to POST.

Changing stride frequency at a given running speed is also known to strongly affect  $C_r$  (Cavanagh & Williams, 1982). In the present study, this assumption seems to hold true only in the downhill running condition where the stride frequency increased by 5.3% (Table IV), corresponding to an increase in the downhill  $C_r$  of 13.1%. Because of the large eccentric work mainly performed during the downhill section of the race of the present MUM (-3371 m), it seems reasonable to assume that the participants experienced strength loss (Fourchet et al., 2012; Millet et al., 2002; Saugy et al., 2013). They were also noted to have increased levels of inflammatory and muscle damage markers, as well as structural and functional alterations, which ultimately reduced maximal force-generating capacity (Millet et al., 2011; Saugy et al., 2013). This phenomenon reduced the capacity for muscle stretch and some delay between the first (eccentric) and the second (concentric) action in the stretch-shortening cycle (Nicol et al., 2006), leading to changes in stride biomechanics (Noakes, 2000).

According to the spring-mass model, there is a clear relationship between stride frequency and muscle stiffness (Farley & Gonzalez, 1996). Given that  $C_r$  is inversely related to muscle stiffness (Dalleau, Belli, Bourdin, & Lacour, 1998; Heise & Martin, 1998), changes in stiffness associated with fatigue could have induced the participants to generate ground forces at lower rates. However, contact time and the rate of force generation did not significantly change between PRE and POST. This suggests that, in order to maintain the same rate of ground force generation despite decreased (deteriorated) muscle stiffness, the participants used a less economic running style because the fatigued muscles required greater muscle activation to generate the same force during the downhill running condition, and this could have elevated the specific  $C_r$  (Derrick, 2004; Derrick & Mercer, 2004).

Finally, the positive correlations between the performance time and level ( $r = 0.52 \pm 0.36$ ,  $P = 0.04$ ) and uphill  $\Delta C_r$  ( $r = 0.50 \pm 0.36$ ,  $P = 0.04$ ) (Figure 2) running indicate that the slower participants running the race were also those whose level and uphill  $C_r$  deteriorated most after the MUM. Although a significant correlation does not denote cause and effect, it provides additional data suggesting that the importance of having low values of level and uphill  $C_r$ , and particularly to be a “nonaugmented” during performance, is highly significant in ultra-long-distance runs. This may corroborate the debate on the importance of  $C_r$  in ultraendurance performance (Millet, 2012; Millet, Hoffman, & Morin, 2012), supporting the concept that  $C_r$  may play an important role in determining ultra-long-distance performance.

This study has some limitations. The gait characteristics observed on a treadmill may differ from those during overground running. However, treadmill-based analysis of running biomechanics can be generalised to overground running biomechanics up to a speed of  $18 \text{ km} \cdot \text{h}^{-1}$  (Riley et al., 2008; Williams, 1985). Moreover, use of the treadmill ensures steady-state conditions (Hanley & Mohan, 2014; Riley et al., 2008) that cannot be obtained with overground running. Another study limitation concerns the hill running conditions applied in the present study. During uphill running at shallow grades, the elastic energy storage is similar to that of level running. However, the muscles must perform additional positive work to travel uphill, though some energy recovery occurs with each step, whereas during downhill running, some positive mechanical energy generation is still needed even at shallow grades, though more dissipation occurs than generation (Snyder, Kram, & Gottschall, 2012). That said, we cannot be completely sure that the use of a steeper slope would have given different results. Furthermore, the incline chosen in the present study may not accurately reflect the ecological conditions of MUMs (where steeper slopes can be found). We set the running conditions to minimise participant discomfort after the race (Millet et al., 2000; Vernillo et al., 2014), presuming that the participants would probably not be able to reach their metabolic steady state while running on a steeper slope and that lower speeds might have induced them to switch locomotion from running to walking. Further, the order was fixed so that the investigators could change the treadmill slope, which was time consuming. This order also limited the effect of muscle damage from the downhill trials (Snyder & Farley, 2011).

## Conclusions

In summary, we noted changes in both physiological and biomechanical characteristics after an MUM, though the responses to fatigue varied considerably among the participants. The significant increase in downhill  $C_r$  was likely due to the downhill running condition itself, which was mostly affected by post-race muscular fatigue and negatively influenced muscle stiffness and the downhill  $C_r$ . These data show the importance of incorporating downhill locomotion in the training programmes of ultratrail runners to improve the various physiological and biomechanical parameters relevant to ultraendurance performance.

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