Physiological characteristics of the best Eritrean runners—exceptional running economy

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Abstract: Despite their young age, limited training history, and lack of running tradition compared with other East African endurance athletes (e.g., Kenyans and Ethiopians), male endurance runners from Eritrea have recently attained important running successes. The purposes of our study were (*i*) to document the main physical and physiological characteristics of elite black Eritrean distance runners (n = 7; age: 22 ± 3 years) and (*ii*) to compare them with those of their elite white Spanish counterparts. For this second purpose we selected a control group of elite Spanish runners (n = 9; 24 ± 2 years), owing to the traditionally high success of Spanish athletes in long-distance running compared with other white runners, especially in cross-country competitions. The subjects' main anthropometric characteristics were determined, together with their maximum oxygen uptake ($VO_{2\ max}$) and VO_2 (mL·kg^{-1}·min^{-1}), blood lactate, and ammonia concentrations while running at 17, 19, or 21 km·h^{-1}. The body mass index (18.9 ± 1.5 kg·m^{-2}) and maximal calf circumference (30.9 ± 1.5 cm) was lower in Eritreans than in Spaniards (20.5 ± 1.7 kg·m^{-2} and 33.9 ± 2.0 cm, respectively) ($p < 0.05$ and $p < 0.01$, respectively) and their lower leg (shank) length was longer (44.1 ± 3.0 cm vs. 40.6 ± 2.7 cm, respectively) ($p < 0.05$). $VO_{2\ max}$ did not differ significantly between Eritreans and Spaniards (73.8 ± 5.6 mL·kg^{-1}·min^{-1} vs. 77.8 ± 5.7 mL·kg^{-1}·min^{-1}, respectively), whereas the VO_2 cost of running was lower ($p < 0.01$) in the former (e.g., 65.9 ± 6.8 mL·kg^{-1}·min^{-1} vs. 74.8 ± 5.0 mL·kg^{-1}·min^{-1} when running at 21 km·h^{-1}). Our data suggest that the excellent running economy of Eritreans is associated, at least partly, with anthropometric variables. Comparison of their submaximal running cost with other published data suggests that superior running economy, rather than enhanced aerobic capacity, may be the common denominator in the success of black endurance runners of East African origin.

Key words: $VO_{2\ max}$, body mass index, running, performance, ammonia.

Résumé : Malgré son jeune âge, ses antécédents limités et l'absence d'une culture de l'entraînement comparativement à d'autres pays de l'Afrique de l'Est (Kenya, Éthiopie), l'Erythrée abrite des coureurs d'endurance qui se sont distingués. Les buts de cette étude sont (*i*) d'évaluer les principales caractéristiques anthropométriques et physiologiques des coureurs Érythréens, noirs, de haut niveau (n = 7; âge : 22 ± 3 ans) et (*ii*) de comparer ces données à celles de coureurs espagnols, blancs, de haut niveau. Nous avons sélectionné des Espagnols (n = 9; 24 ± 2 ans), à cause du succès bien établi de ces derniers à la course de longue distance comparativement à d'autres coureurs blancs, notamment en cross-country. On évalue les principales caractéristiques anthropométriques, le VO_{2max} en valeur absolue (L·min^{-1}) et en valeur relative à la masse corporelle (mL·kg^{-1}·min^{-1}) et la concentration de lactate et d'ammoniac au cours d'une course à des vitesses de 17, 19 et 21 km·h^{-1}. Comparativement aux Espagnols, les Érythréens ont un plus faible indice de masse corporelle (18,9 ± 1,5 kg·m^{-2} comparativement à 20,5 ± 1,7 kg·m^{-2}, p < 0,05) et une plus faible circonférence du mollet (30,9 ± 1,5 cm comparativement à 33,9 ± 2,0 cm, p < 0,01). Leur jambe (de la cheville au genou) est aussi plus longue (44,1 ± 3,0 cm comparativement à 40,6 ± 2,7 cm, p < 0,05). Le VO_{2max} des Érythréens ne diffère pas de façon significative de celui des Espagnols (73,8 ± 5,6 mL·kg^{-1}·min^{-1} et 77,8 ± 5,7 mL·kg^{-1}·min^{-1}, respectivement), mais les Érythréens ont une plus faible consommation d'oxygène à une vitesse de course de 21 km·h^{-1}(65,9 ± 6,8 mL·kg^{-1}·min^{-1} comparativement à 74,8 ± 5,0 mL·kg^{-1}·min^{-1}). D'après nos observations, la meilleure économie d'effort à la course observée chez les Érythréens est associée, du moins en partie, à des variables anthropométriques. En comparant nos observations avec celles d'autres études, une meilleure économie à la course sous-maximale apparaît davantage comme le dénominateur commun du succès des coureurs originaires de l'Afrique de l'Est plutôt qu'une meilleure capacité aérobie.

Mots clés : $VO_{2\ max}$, indice de masse corporelle, course, performance, ammoniac.

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Introduction

Black athletes of East African origin (e.g., Kenyans and Ethiopians) dominate most endurance-running events, from the 5000 m track race to the marathon. Many of the all-time best performances in these events have been achieved by Kenyans (49%) and Ethiopians (15%). In recent years, other black African endurance runners (from South Africa, Tanzania, or Zimbabwe) have also attained excellent results in international competition.

Relevant original studies (e.g., Billat et al. 2001, 2003; Bosch et al. 1990; Coetzer et al. 1993; Larsen et al. 2004; Saltin et al. 1995*a*, 1995*b*; Weston et al. 1999, 2000) are available addressing factors that might account for the superiority of black African endurance runners. A lower energy cost of running, i.e., better economy, has been demonstrated in elite Kenyan runners (Saltin et al. 1995*b*) and in runners from other parts of Africa compared with their white counterparts (Weston et al. 2000). In this regard, numerous factors can determine better running economy, such as comprehensive training background, muscle fibre type distribution and, particularly, biomechanics (Saunders et al. 2004). Although some investigations have found that better running economy is associated with a higher proportion of type I fibres (Bosco et al. 1987; Kaneko 1990; Williams and Cavanagh 1987), this cannot explain differences between Kenyans and Caucasian runners, as their muscle fibre type distribution is similar (Saltin et al. 1995*a*). Several biomechanical factors favour economy, particularly low body fat, leg mass distributed closer to the hip joint, freely chosen stride length over considerable training time, kinematics (e.g., low vertical oscillation of body centre of mass or less range of motion but greater angular velocity of plantar flexion during toe-off), kinetics (low peak reaction forces), and elastic energy, i.e., effective exploitation of mechanical energy stored in muscles during the eccentric phase of contact (with stiffer muscles eliciting the best economy) (Anderson 1996; Dalleau et al. 1998). Although much more research is needed concerning potential differences in the aforementioned biomechanical factors between East African and Caucasian endurance runners, a difference exists in body mass index (BMI) and body shape (Saltin et al. 1995*b*). Particularly, Kenyans' longer, slender legs could be advantageous (Saltin et al. 1995*b*), as work of moving the limbs comprises an important part of the metabolic cost of running (Cavagna et al. 1964; Myers and Steudel 1985).

Bordering the Red Sea, Eritrea (121 320 km^2, 4.5 million inhabitants) is located in eastern Africa, between Djibouti, Sudan, and Ethiopia. After a two-and-a-half-year border war with Ethiopia that erupted in 1998 and ended in 2000, Eritrea is now an independent country, yet one of the poorest in the world. Despite their young age, their short history, and their lack of running tradition (i.e., no running during school years) compared with other East African endurance runners, male runners of Eritrean origin have recently attained important running successes, such as a bronze medal in the 2004 Olympic 10 000 m final, a silver medal in the 2004 Olympic marathon, a 2nd place finish at the 2005 World Cross-Country Championships (long race), and a 3rd place finish in the team classification of the 2004 World Cross-Country Championships (long race). No study has reported the physiological characteristics of the best distance runners from Eritrea. They do, however, provide an excellent study model owing to their success despite their relatively limited training background and also because they are altitude natives and the core part of their yearly living and training is performed at ~2600 m altitude. In this regard, questions about the causes of the remarkable success of East African endurance runners have been posed ever since their striking emergence associated with the 1968 Olympic Games held at moderate altitude in Mexico City, although an Ethiopian runner had won the 1960 and 1964 Olympic marathons. A factor of potential importance is the moderate altitude homes of successful distance runners from Ethiopia (≥2000 m) (Scott et al. 2003), Kenya (~2000 m), and now Eritrea (~2600 m). There is evidence from studies of sea-level natives travelling to moderate altitude that there are adaptations to the stress of altitude that can favour running performance, i.e., increase in red cell mass with subsequent enhancement in central oxygen transport (Levine and Stray-Gundersen 2005) and possibly improved running economy (Gore et al. 2001). On common sense grounds it might be expected that altitude natives might have similar, indeed larger, chronic adaptations to altitude that would predispose them to superior values for aerobic metabolism. Evidence to support this assumption is, however, generally lacking. Comparatively isolated studies of the aerobic cost of running have suggested that endurance runners of East African origin may have superior running economy (Saltin et al. 1995*b*). While recognizing that people of African, even restricted to East African, origin are at least as ethnically diverse as different European nationalities, the striking commonality of success in endurance running by people from this relatively small part of the planet suggests that there may be a common factor responsible. If not adaptations directly related to altitude, is it as simple as differences in running economy?

It was therefore the purpose of our study to determine the main physical and physiological characteristics of elite Eritrean distance runners, including also blood metabolites indicative of the utilization of different muscle metabolic pathways, such as anaerobic glycogenolysis (i.e., lactate) or the purine nucleotide cycle (PNC) (i.e., ammonia). The PNC is an important muscle metabolic pathway, as it plays a central role in determining muscle energy charge during intense exercise (Rico-Sanz et al. 2003). Their data were compared with those of a control group of elite Spanish white runners. The latter were chosen as controls owing to the traditional success of Spanish runners in long-distance running compared with other white runners, especially in cross-country competitions (e.g., the Spanish team has been 1 of the top 3 non-African teams in 8 of the last 11 editions of the cross-country World Championships). We hypothesized that, like other successful East African endurance runners, the Eritreans would be characterized more by better running economy than by uniquely high values of maximal cardiorespiratory capacity (VO_{2max}). Further, we hypothesized that their improved running economy would be associated, at least partly, with their anthropomorphic characteristics more than with specific muscle biochemical and (or) contractile characteristics. Regarding the latter, we determined genotypes of the gene *ACTN3*, encoding α-actinin-3, a protein that is not expressed in type I fibres as opposed to type II fibres, where it is responsible for generating forceful contractions at high velocity (MacArthur and North 2004).

Materials and methods

Subjects

Written consent was obtained from each subject according to the guidelines of the institutional ethics committee (Universidad Europea de Madrid, Spain). The study was approved by the university ethics committee and was in accordance with the Declaration of Helsinki for Human Research.

Our sample comprised the 7 best Eritrean male endurance runners (22 ± 3 y) according to their actual cross-country performance during 2004 (including a medallist in the 2004 Olympic 10 000 m race). All of them belong to the Eritrea's main ethnic group, i.e., the Tigrigna, which forms about half of the population of the country, and are descendants of parents of the same ethnic group. All of them are moderate-altitude natives, i.e., born (and have always lived) in the high central plateau of the country (altitude varying from 1800 to 3000 m). Currently, most of them they live in Asmara, the capital (altitude near 3000 m). They are all descendants of moderate-altitude natives.

All of them are specialists in cross-country races and most have just started to travel outside Eritrea (where there are few if any running tracks according to modern standards, i.e., a 400 m loop) to participate during spring–summer months in 5000 – 10 000 m track events or in some road races (Table 1). One week before being tested in our laboratory, all of the subjects had participated in either the 2004 cross-country long (~12 km) (n = 6) or junior race (~8 km) (n = 1) of the World Championships. They ranked 3rd (behind Ethiopia and Kenya) in the overall team classification of the long cross-country race.

The Eritreans' data were compared with those of a control group of elite white distance runners, made up of 9 Spaniards (24 ± 2 y), who are also cross-country specialists (mainly in races of 10–12 km distance), ranking in the top 10 in the 2004 and (or) 2005 National cross-country championships. They are all Spaniards of the same ethnic and geographic origin (i.e., from Castille (the main, central plateau of Spain; altitude ~600 m)). They have always lived and trained in Castille and have only occasionally attended altitude training camps. None of them had trained and (or) lived at moderate or high altitude in the months preceding the study and none of them had previously used a hypoxic tent to simulate altitude exposure during sleeping hours. During spring–summer months they participated mainly in 5000 – 10 000 m track races. The best performance time for all of them is below 14 min and (or) 29 min in the 5000 and 10 000 m track events, respectively (Table 1). The Spanish runners were tested in February–March 2005, i.e., while they were in their peak condition for the target competitions of the cross-country season. Before being tested in our laboratory (~600 m altitude), the Eritreans lived and trained in Europe for 1 week (at sea level) and in Madrid (~600 m altitude) for another week.

The performance of the subjects who participated in the 2004 and 2005 cross-country long race (~12 km) of the World Championships is shown in Table 2.

Table 1. Relevant track and field (or road) performance times of subjects.

Subject	Eritreans (n = 7)	Spaniards (n = 9)
1	13 min 5 s (5000m) and 27 min 22 s (10000 m)	13 min 10 s (5000 m) and 27 min 27 s (10000 m)
2	27 min 40 s (10000 m)	28 min 19 s (10000 m)
3	28 min 31 s (10000 m)	13 min 16 s (5000 m)
4	13 min 21 s (5000 m)	13 min 30 s (5000 m)
5	13 min 40 s (5000 m)	13 min 38 s (5000 m)
6	63 min 49 s (half-marathon)	13 min 31 s (5000 m)
7	64 min 51 s (half-marathon)	13 min 46 s (5000 m)
8		13 min 47 s (5000 m)
9		13 min 51 s (5000 m)

Training characteristics

We recorded the main training characteristics of each runner from his training log. The data were confirmed with each runner's coach. Subjects were asked to describe their typical training week during the last 3 months and also reported other variables related to the altitude of living and training, previous training experience, and number of sleeping hours.

Anthropometry

The subject's body mass, height, and body mass index (BMI) were recorded, together with 6 skinfold measurements (triceps, subscapular, supra-iliac, abdominal, front thigh, and median calf) using standard equipment (Holtain, Crymych, UK). All skinfold measurements were made in triplicate by the same researcher. The total leg length and those of upper (thigh) and lower (shank) leg, as well as maximal thigh and shank (i.e., calf) circumferences were measured using anatomical reference points as detailed elsewhere (Zatsiorsky et al. 1990).

Exercise tests

After a 24 h period with no hard training (≤45–60 min of easy running) and a total carbohydrate (CHO) intake of ~400 g, the subjects reported to our laboratory (~600 m altitude) on 2 consecutive days to perform the following testing sessions on a treadmill (Technogym Run Race 1400 HC, Gambettola, Italy): (i) a graded test for $VO_{2\ max}$ determination (1st day) and (ii) 3 constant-speed bouts for economy determination (2nd day). The treadmill was calibrated using a measuring wheel (Trumeter Measure Meter, Manchester, UK) (measurement error < 0.5 m per 100 m interval). A fan was placed in front of the treadmill (distance from the treadmill ~50 cm) to cool the subjects during running. Blood analyses were performed before the graded test. During all tests, gas exchange data were collected continuously using an automated breath-by-breath system (Vmax 29C, Sensormedics Corp., Yorba Linda, Calif.), which was calibrated before each exercise test according to the instructions of the manufacturers. Volume calibration was performed at differ-

Table 2. Performance times of those study subjects who participated in the 2004 and 2005 cross-country long race (~12 km) of the World Championships.

(*a*) Finishing position and time lost from winner in the 2004 World Championships	
Eritreans	Spaniards
6th (45 s)	33rd (136 s)
9th (61 s)	
22nd (113 s)	
29th (127 s)	
74th (208 s)	
(one subject did not finish the race)	

(*b*) Finishing position and time lost from winner in the 2005 World Championships	
Eritreans	Spaniards
2nd (14 s)	24th (131 s)
15th (90 s)	68th (228 s)
17th (91 s)	
20th (116 s)	

ent flow rates with a 3 L calibration syringe (SensorMedics Corp., Yorba Linda, Calif.) allowing an error ≤ 2%. Calibration of the gas analysers was performed automatically by the system using both ambient and precision reference gases (16% O_2, 4% CO_2). In previous pilot studies conducted in our laboratory, this system showed good validity when compared with the Oxycon-Pro system (i.e., intra-individual variation < 3% in the VO_2 levels of 7 professional cyclists across all workloads (eliciting VO_2 values ranging from 1 to 5 L·min^{-1})). In turn, the accuracy of the Oxycon-Pro has been shown in a previous validation study (against the'gold standard Douglas bag method) (Rietjens et al. 2001).

All testing sessions were performed under similar environmental conditions (20–24 °C, 45%–55% relative humidity) and at the same time of the day (12:00–15:00). The subjects performed the tests 3 h after consuming a breakfast containing ~100 g of CHO and no caffeinated drinks and all of them had previous experience with treadmill running, including a thorough familiarization session (duration ~30 min) with the treadmill used for the study.

Following a general warm-up, the graded test started at 11 km·h^{-1}, and running speed was increased by 0.5 km·h^{-1} every 30 s until volitional exhaustion. Treadmill inclination was kept constant at 1% (instead of 0%) in an attempt to mimic the effects of air resistance on the metabolic cost of flat outdoor running (Pugh 1970). Maximal oxygen uptake ($VO_{2\ max}$) was recorded as the highest VO_2 value obtained for any continuous 60 s period during the test. At least 2 of the following criteria were also required for the attainment of $VO_{2\ max}$: a plateau in VO_2 values (i.e., an increase in two or more consecutive 1 min mean VO_2 values of less than 1.5 mL·kg^{-1}·min^{-1} (Lucia et al. 2006)), a respiratory exchange ratio ≥ 1.15, or the attainment of a maximal HR value (HR_{max}) above 95% of the age-predicted maximum. The ventilatory threshold (VT) was determined using the criteria of an increase in both the ventilatory equivalent of oxygen ($VE \cdot VO_2^{-1}$) and end-tidal pressure of oxygen ($P_{et}O_2$) with no concomitant increase in the ventilatory equivalent of carbon dioxide ($VE \cdot VCO_2^{-1}$) (Lucia et al. 2003). Two independent experienced observers detected VT. If there was disagreement, we obtained the opinion of a third investigator.

The 3 constant-speed running tests lasted 6 min and were interspersed with 5 min recovery periods. Treadmill inclination was kept constant at 1% for the 3 tests, whereas running speed was 17, 19, and 21 km·h^{-1}, respectively. These 3 running speeds were chosen as being representative of normal training (17 km·h^{-1}), intense training (19 km·h^{-1}), and racing pace for competitions of ~10–12 km distance (21 km·h^{-1}). Oxygen uptake (VO_2), respiratory exchange ratio (RER), and heart rates (HR) (Polar S810, Polar Electro OY, Finland) were determined as the average VO_2 (mL·kg^{-1}·min^{-1}), RER, and HR (beats·min^{-1}) value, respectively, for the last 3 min period of each bout. Running economy was determined as the VO_2 cost at a given running speed, i.e., in mL·kg^{-1}·km^{-1} (Daniels and Daniels 1992). This allowed us to compare the mean values of our subjects with those previously reported in a number of relevant studies with elite endurance male runners, including black Africans (e.g., Bosch et al. 1990; Coetzer et al. 1993; Pollock 1977; Saltin et al. 1995*b*; Weston et al. 2000) (Fig. 1). For studies conducted during level treadmill running, the VO_2 cost was adjusted to 1% grade based on the model used by the ACSM (American College of Sports Medicine 2000), where VO_2 (mL·kg^{-1}·m^{-1}) at 1% for a given speed = VO_2 (mL·kg^{-1}·m^{-1}) at 0% for the same speed (m·min^{-1}) + (m·min^{-1} × 0.9 × 0.01).

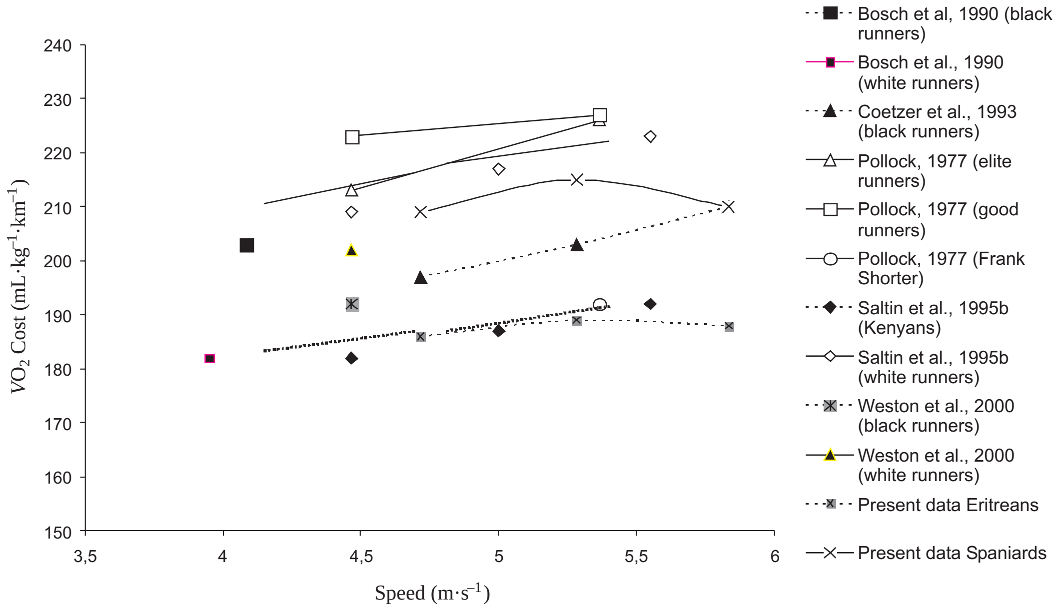
Capillary blood samples (75 µL) for the measurement of blood lactate (YSI 1500; Yellow Springs Instruments; Yellow Springs, Ohio) and ammonia were obtained from a fingertip both pre-exercise and immediately (15–20 s) after completion of each submaximal running bout. Ammonia levels in whole blood were determined with a portable instrument (Ammonia Checker, Menarini Diagnostics, Barcelona, Spain), which uses a reflectometer to optically measure the reflection intensity (45°) of reagent colour reaction in bichromatic mode. Because of the high ammonia content of sweat, sweat was carefully wiped from the fingertips using sterile gauze embedded with alcohol and dry sterile gauze, respectively, before sampling.

Blood analysis and genotype determination

Resting blood samples were obtained from an antecubital vein with vacutainers containing EDTA and SST gel, respectively, to determine red cell count, haematocrit, and haemoglobin levels with a Sismex XE-2100 haematology analyzer (Sysmex, Kobe, Japan) and to extract genomic DNA according to standard phenol–chloroform procedures, followed by alcohol precipitation.

We determined genotypes of the *ACTN3*gene encoding for α-actinin-3, a protein that, together with α-actinin-2, constitutes the predominant component of the sarcomeric Z line, where it forms a lattice structure that anchors actinin-containing thin filaments and stabilizes the muscle contractile apparatus (MacArthur and North 2004). As opposed to α-actinin-2, the expression of α-actinin-3 is largely restricted to type II fibres (MacArthur and North 2004). In these fibres, α-actinin-3 is responsible for generating forceful contractions at high velocity (MacArthur and North 2004). A significant proportion of endurance athletes are known to be totally deficient in this protein, as they are

Fig. 1. Comparison of the profile of the running VO_2 cost (in our subjects (Eritreans and Spaniards)) and in those of previous research on elite runners. For studies conducted during level treadmill running, the VO_2 cost (mL $O_2 \cdot kg^{-1} \cdot km^{-1}$) was adjusted to 1% grade based on the model used by the ACSM (American College of Sports Medicine 2000), where VO_2 ($mL \cdot kg^{-1} \cdot m^{-1}$) at 1% for a given speed = VO_2 ($mL \cdot kg^{-1} \cdot m^{-1}$) at 0% for the same speed ($m \cdot min^{-1}$) + ($m \cdot min^{-1} \times 0.9 \times 0.01$).



homozygous for a premature stop codon polymorphism ($R_{577} \rightarrow X$) in the *ACTN3* gene (Yang et al. 2003). The polymerase chain reaction (PCR) was performed to amplify the sequence containing the mutation. *ACTN3* genotypes were established by enzymatic digestion of amplicons with *Dde*I as determined elsewhere (Mills et al. 2001). The $R_{577} \rightarrow X$ change creates a restriction site resulting in fragments of 108, 97, and 86 bp. Digestion of the *R577* allele resulted in fragments of 205 and 86 bp, which were analyzed by capillary electrophoresis with an ABI Prism 310 genetic analyzer (Applied Biosystems, Foster City, Calif.).

Statistical analysis

Owing to the relatively small sample size (n = 9 and n = 7 in each group, respectively), the non-parametric Mann–Whitney U test was used to compare training, physical (anthropometric), blood, and physiological variables measured in both groups. Owing to the small sample size of both groups in terms of population genetics, comparisons of *ACTN3* genotype distributions were not performed. In addition, we determined the correlation between running economy and anthropometric characteristics (e.g., maximal shank (calf) circumference) in all subjects using the Pearson technique. The level of significance was set at $p < 0.05$.

Results

Training characteristics

The training characteristics of both groups are described in Table 3. Training experience and training volume were significantly lower in the Eritreans ($p < 0.01$ and $p < 0.05$, respectively). Except in the case of one Eritrean runner, who used to run and walk to school during childhood, no other subject had any training background during school years.

Anthropometric variables

The BMI, maximal calf circumference, and sum of 6 skinfolds were lower in Eritreans than in the Spaniards ($p < 0.05$), whereas shank length was greater ($p < 0.05$) (Table 4).

Blood analysis and genotype

No significant difference was found in haematology variables between groups (Table 5). *ACTN3* genotype data are shown in Table 6. Two Eritrean runners (~29% of total) were completely deficient in α-actinin-3, whereas as 4 Spanish runners (~44%) showed complete deficiency of this protein.

Physiological variables

There were no significant differences in $VO_{2\ max}$ ($mL \cdot kg^{-1} \cdot min^{-1}$) between groups, although $VO_{2\ max}$ uncorrected for body mass ($L \cdot min^{-1}$) was significantly higher in the Spaniards (Table 7). The mean value of VO_2 ($mL \cdot kg^{-1} \cdot min^{-1}$) and $\%VO_{2\ max}$ was significantly lower in Eritreans at all running speeds (17, 19, and 21 $km \cdot h^{-1}$). Lactate and ammonia levels were also higher in the Eritreans at all running speeds. Values of RER were significantly higher in Eritrean runners at 17 and 19 $km \cdot h^{-1}$. The VT occurred at lower speeds in Eritreans ($p < 0.01$).

Compared with the Spanish runners, the VO_2 cost of running ($mL \cdot kg^{-1} \cdot km^{-1}$) was significantly ($p < 0.05$) lower in the Eritreans, 187.7 ± 19.1 $mL \cdot kg^{-1} \cdot km^{-1}$ vs. 213.0 ± 8.5 $mL \cdot kg^{-1} \cdot km^{-1}$. Figure 1 shows the profile of the VO_2 cost of running ($mL \cdot kg^{-1} \cdot km^{-1}$) in our subjects compared with that reported in previous studies with well-trained and elite male runners (Bosch et al. 1990; Coetzer et al. 1993; Pollock 1977; Saltin et al. 1995*b*; Weston et al. 2000). The mean values of our Eritrean runners are among the lowest reported in the literature (and virtually identical to the 2 for-

Table 3. Mean (± SD) training characteristics of the subjects.

	Eritreans (n = 7)	Spaniards (n = 9)
Usual living and training altitude (m)	2590±313	589±198**
Previous experience of regular training (y)	2.7±1.6	12.3±2.7**
Typical training volume during the previous 3 months (km·week^{-1})	105±12	129±10*
Maximum training volume during the previous 3 months (km·week^{-1})	120±10	166±16*
Amount of rest (d·week^{-1})	0.5±0.5	0.5±0.4
No. of training sessions per week	7.8±1.6	9.2±2.4
Weight training (yes or no)	No (n = 7)	Yes (n = 9)
Skill and (or) technique training (yes or no)	Yes (n = 4)	Yes (n = 9)
	No (n = 3)	
Stretching (yes or no)	Yes (n = 10)	Yes (n = 9)
Massage (yes or no)	Yes (n = 6)	Yes (n = 7)
	No (n = 1)	
Sleeping habits (h·d^{-1})	11±2	8.5±1.2*

Note: *, p < 0.05; **, p < 0.01.

mer Kenyan champions (Saltin et al. 1995*b*), and the lowest that have been reported at competitive speeds (21 km·h^{-1} or 350 m·min^{-1}). The profile of the VO_2 cost of running in the Spaniards was typical of other reported values in white runners.

Finally, maximal calf circumference was significantly associated with the VO_2 cost (mL·kg^{-1}·min^{-1}) of running at 21 km·h^{-1} (R = 0.554, p < 0.05) (Fig. 2), but not at lower speeds. We found no other correlation between the VO_2 cost of running at 19, 20, or 21 km·h^{-1}, on one hand, and anthropometric characteristics (body mass, BMI, etc), on the other.

Discussion

This is the first study to document the physiological characteristics of Eritrean distance runners, who were evaluated when they were in their peak condition, 1 week after ranking 3rd in the team competition in the 2004 cross-country World Championships. This group of athletes is of interest to exercise physiologists because they are altitude natives (~2600 m), training and living during long periods at higher altitudes than most athletes in the world and because they have attained a high competition level despite their young age and their lack of training background during childhood and school years (as opposed to Kenyans or Ethiopians). Finally, the very poor, predominantly rural economy of Eritrea (even more so than Kenya or Ethiopia) makes competitive distance running one of the very few possible athletic outlets for young Eritreans to escape from poverty and seek a better quality of life.

Our finding that $VO_{2\ max}$ (normalized to body mass (mL·kg^{-1}·min^{-1})) was not different between Eritrean and Spanish controls is in line with previous research with other East African endurance runners. Saltin and co-workers (Saltin et al. 1995*b*) found that senior Kenyan elite long-distance runners have similar $VO_{2\ max}$ values (~80 mL·kg^{-1}·min^{-1}) at sea level compared with Scandinavian elite runners (~79 mL·kg^{-1}·min^{-1}). Coetzer et al. (1993) reported relatively low $VO_{2\ max}$ values in elite black South African endurance runners (71.5 mL·kg^{-1}·min^{-1}). Thus, the $VO_{2\ max}$ values of top-level Eritrean runners (~74 mL·kg^{-1}·min^{-1}) fit into the range between those of elite Kenyan and South African endurance runners. On the other hand, when $VO_{2\ max}$ was not normalized to body mass, this variable had lower mean values in Eritreans. Our findings are in agreement with those of previous studies on black South African endurance runners (Coetzer et al. 1993; Weston et al. 2000) showing that, if any difference exists, the absolute maximal aerobic capacity tends to be lower in East African endurance runners. These athletes are, however, favoured by their low mass and BMI, particularly as far as running economy is concerned. Our data suggest that the dominance in endurance running by athletes of East African origin is to a large extent attributable to better running economy. Although the experience of living and training at high altitude may confer some advantageous adaptations of aerobic power (Levine and Stray-Gundersen 1997), it appears that the consistent difference observed in elite endurance runners of East African origin is more likely due, at least partly, to anthropometrically attributable economy of movement than to polycythemia-attributable increases in $VO_{2\ max}$.

Our findings are in overall agreement with those of Saltin and co-workers (Saltin et al. 1995*b*), who found that the oxygen cost at a given running speed normalized for difference in body mass raised to an exponent of 0.75 is lower in East African elite endurance runners (Kenyans) than in their white counterparts. Low cost of running is indeed a common feature of Kenyans for the tribes belonging to the Kalenjin, e.g., the Nandi (Larsen 2003). A study of untrained adolescent Kenyan boys from the Nandi tribe indicated that the running economy of these boys is better than in untrained, age-matched Danish controls (Larsen 2003). Although there is no consensus (Bosch et al. 1990; Coetzer et al. 1993), this is also consistent with findings in black South African endurance runners (Weston et al. 2000). Although the possible contributions of several biomechanical factors (vertical oscillation of body centre of mass or range of motion, angular velocity of plantar flexion during toe-off, peak reaction forces, etc. (Anderson 1996; Dalleau et al. 1998)) influencing the energetic cost of running remain to be evaluated in black East African endurance runners, it seems that the superior economy of Kenyan runners is largely attributable to their low BMI and to their slender limbs with low masses that allow them to run with minimal energy used for swinging the limbs (Saltin et al. 1995*b*). Furthermore, the body di-

Table 4. Mean (± SD) anthropometric characteristics of Eritrean and Spanish runners.

	Eritreans (n = 7)	Spaniards (n = 9)
Height (cm)	174±8	172±6
Mass (kg)	57.2±3.3	60.5±7.8
BMI ($kg \cdot m^{-2}$)	18.9±1.5	20.5±1.7*
Sum of 6 skinfolds (mm)	28.5±2.4	33.2±3.7*
Total leg length (cm)	92.3±6.5	92.6±3.6
Upper leg (thigh) length (cm)	48.2±4.0	51.9±3.6
Lower leg (shank) length (cm)	44.1±3.0	40.6±2.7*
Maximal thigh circumference (cm)	48.1±2.3	50.3±3.1
Maximal shank (or calf) circumference (cm)	30.9±1.5	33.9±2.0**

Note: Skinfold sites were triceps, subscapular, supra-iliac, abdominal, front thigh and medial calf. *, $p < 0.05$; **, $p < 0.01$.

Table 5. Haematological variables (mean (± SD)).

	Eritreans (n = 7)	Spaniards (n = 9)
Red cell count ($10^6 \cdot \mu L^{-1}$)	5.04±0.17	4.95±0.16
Haematocrit (%)	45.1±1.2	45.2±1.1
[Haemoglobin] ($g \cdot dL^{-1}$)	15.4±0.3	15.1±0.4

mensions of adolescent Nandi town and village boys correspond well with findings in Kenyan adult elite runners, i.e., they are very slender with relatively long legs (Larsen et al. 2004). Our subjects, who belong to the Tigrigna ethnic group (which is also one of the predominant ethnic groups in Ethiopia (Scott et al. 2003)) also exhibited low BMI (~19, similar to that of top-level Kenyan runners) (Saltin et al. 1995*b*) and long, slender shanks (lower calf circumference) compared with their white counterparts. As an example, the potential influence of leg mass in the energetic cost of running is illustrated in Fig. 2, which shows the significant association between VO_2 when running at apparoximately a 10 km race pace (21 $km \cdot h^{-1}$) and the maximal calf circumference of all subjects (both Eritreans and Spaniards). (However, it must be also noted that such an association did not exist within the Eritrean group, which, except for one subject, was highly homogeneous in the values of maximal calf circumference.) Finally, and keeping in mind the difficulty of establishing comparisons between different studies, using different equipment for VO_2 measurement, the mean running economy of Eritreans as a group was among the best ever reported in the literature, especially at high speeds (21 $km \cdot h^{-1}$ or 5.8 $m \cdot s^{-1}$) (Fig. 1). Further, the mean running VO_2 cost of one Eritrean for the 3 speeds (17, 19, and 21 $km \cdot h^{-1}$) was of 153 $mL \cdot km^{-1} \cdot kg^{-1}$, which is one of the lowest individual values ever reported, e.g., clearly below the value of ~180 $mL \cdot km^{-1} \cdot kg^{-1}$ in the former running champion Steve Scott (Conley et al. 1984) and considerably lower than that of Kenyan champions (Saltin et al. 1995*b*).

Previous research has found that improved running economy is associated with a higher proportion of type I fibres (Bosco et al. 1987; Kaneko 1990; Williams and Cavanagh 1987). To assess this possible association in our subjects, we determined genotypes of the *ACTN3* gene , which encodes α-actinin-3, a protein that is not expressed in type I fibres, but is expressed in type II fibres (MacArthur and North 2004). Our findings do not support an association between improved running economy and specific contractile and (or) metabolic properties in Eritrean runners, as (*i*) the proportion of subjects totally deficient in α-actinin-3 was lower in the Eritreans (though this statement must be considered with great caution owing to the very small population size) and (*ii*) both ammonia (which is mainly released from type II fibres during intense exercise (Dudley et al. 1983)) and lactate concentrations, together with RER values, were higher in the Eritreans. Elite Kenyan (Saltin et al. 1995*b*) and elite black South African endurance runners (Weston et al. 1999) have lower lactate levels than their white counterparts during submaximal running. In contrast with these findings, Weston et al. (1999) found significantly higher ammonia levels at race pace in well-trained black South African endurance runners than in white South Africans. Our findings are thus in agreement with the later study and emphasize that the improved economy of Eritrean runners is more likely associated with their favourable anthropometric characteristics (or maybe with potential biomechanical factors that remain to be elucidated) than with specific fibre characteristics. Our Eritrean subjects potentially showed more reliance on type II fibres than their Spanish controls when running at high submaximal speeds, as their ammonia, lactate, and RER values were higher. Concerning the lower lactate levels of Eritreans, some caution is needed given the difficulty of stating that lower lactate levels are solely dueto reduced lactate release from type II fibres to blood and (or) increased clearance. Nevertheless, an important marker of adaptation to endurance training, the VT (Meyer et al. 2005), occurred at lower running speeds in Eritreans, probably as a result of their relatively low training volume. Indeed, we found a positive, significant correlation between the mean training volume ($km \cdot week^{-1}$) of all the subjects and the running speed eliciting their VT (R = 0.77; $p <$ 0.05). It must be emphasised, on the other hand, that the Eritreans had a lower VO_2 cost of running despite their short training history, relatively lower training volume, and low running speed at VT compared with Spaniards. Thus, we could hypothesize that excessively high training volumes are not a prerequisite for achieving a good running economy and (or) that in the near future, favourable training adaptations associated to a more solid training background (including maybe further improvement in running economy) could still be expected in Eritrean endurance runners.

Table 6. Genotype determinations of the gene (*ACTN3*) encoding α-actinin-3.

Genotype	Eritreans (n = 7)	Spaniards (n = 9)
RR	2 (28.6%)	2 (22.2%)
RX	3 (42.8%)	3 (33.3%)
XX	2 (28.6%)	4 (44.4%)

Note: XX, subjects homozygous for the $R_{577} \rightarrow X$ polymorphism and thus with complete deficiency of α-actinin-3; RX, subjects with partial deficiency of α-actinin-3; and RR, subjects showing no $R_{577} \rightarrow X$ polymorphism.

Lower ammonia levels, similar to those exhibited by Ken-

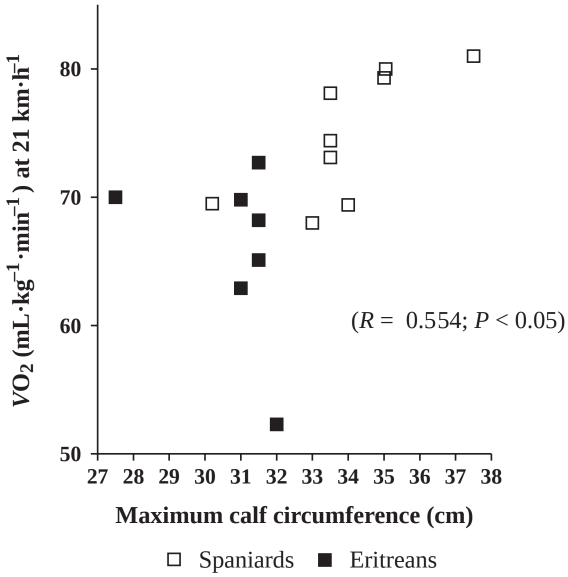
Table 7. Mean (± SD) physiological variables of Eritrean and Spanish runners.

(*a*) Graded tests		
	Eritreans (n = 7)	Spaniards (n = 9)
Peak treadmill speed ($km \cdot h^{-1}$)	23.3±0.5	23.1±0.7
$VO_{2\ max}$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	73.8±5.6	77.8±6.1*
$VO_{2\ max}$ ($L \cdot min^{-1}$)	4.2±0.3	4.7±0.4*
HR_{max} ($beats \cdot min^{-1}$)	189±1	188±6
VT (%$VO_{2\ max}$)	62.4±8.0	67.5±10.2
VT ($km \cdot h^{-1}$)	15.0±0.9	16.6±0.7**
(*b*) Constant tests at 17 $km \cdot h^{-1}$		
	Eritreans (n = 7)	Spaniards (n = 9)
% peak treadmill speed	73.0±1.5	73.6±2.2
VO_2 ($mL \cdot kg^{-1} \cdot min^{-1}$)	52.5±6.4	59.7±3.1*
%VO_{2max}	71.1±6.0	76.7±3.8*
HR ($beats \cdot min^{-1}$)	156±5	159±11
%HR_{max}	82.5±2.6	84.0±3.4
RER	0.87±0.04	0.82±0.03*
[BLa] ($mmol \cdot l^{-1}$)	2.7±0.4	1.6±0.9*
[NH_3] ($\mu mol \cdot L^{-1}$)	155.3±48.3	72.1±15.1**
(*c*) Constant tests at 19 $km \cdot h^{-1}$		
	Eritreans (n = 7)	Spaniards (n = 9)
% peak treadmill speed	81.5±1.7	82.3±2.4
VO_2 ($mL \cdot kg^{-1} \cdot min^{-1}$)	60.0±4.9	68.6±3.2**
%$VO_{2\ max}$	81.3±6.5	88.2±4.8**
HR ($beats \cdot min^{-1}$)	169±5	172±9
%HR_{max}	89.4±3.0	91.5±1.9
RER	0.91±0.02	0.87±0.02**
[BLa]($mmol \cdot L^{-1}$)	3.8±0.7	2.8±1.0*
[NH_3] ($\mu mol \cdot L^{-1}$)	195.0±101.5	98.3±33.9*
(*d*) Constant tests at 21 $km \cdot h^{-1}$		
	Eritreans (n = 7)	Spaniards (n = 9)
% peak treadmill speed	90.1±1.9	90.9±2.7
VO_2 ($mL \cdot kg^{-1} \cdot min^{-1}$)	65.9±6.8	74.8±5.0*
%$VO_{2\ max}$	89.3±9.0	96.1±7.7*
HR ($beats \cdot min^{-1}$)	183±5	183±8
%HR_{max}	96.8±2.3	96.8±1.0
RER	0.98±0.05	0.94±0.03
[BLa] ($mmol \cdot L^{-1}$)	6.3±1.8	5.6±0.9
[NH_3] ($\mu mol \cdot L^{-1}$)	213.7±91.3	131.1±22.2*

Note: $VO_{2\ max}$, maximal oxygen uptake; HR_{max}, maximal heart rate; RER, respiratory exchange ratio; VT, ventilatory threshold; BLa, blood lactate; *, $p < 0.05$ for Eritreans vs. Spaniards; **, $p < 0.01$ for Eritreans vs. Spaniards.

yans, might confer some performance benefit as, during prolonged, strenuous exercise, elevated levels of blood ammonia result in increased cerebral uptake and accumulation of this metabolite with subsequent occurrence of central fatigue, e.g., through altered neurotransmitter metabolism and impaired voluntary activation of motor neurons (Nybo et al. 2005). However, one of our Eritrean subjects, who is currently the second best cross-country runner in the World, also exhibited higher ammonia levels than those experienced by Spanish runners. Despite the potential role of ammonia on central fatigue during exhaustive exercise, a high activity of the adenosine monophosphate deaminase (AMPD) enzyme in working muscles could also confer some performance benefit despite producing higher ammonia levels. The AMPD reaction (AMP → IMP (inosine monophosphate) + NH_3 (ammonia)) is the initial reaction of the purine nucleotide cycle, which plays a central role in recharging the energy levels of active fibres during intense exercise (Rico-Sanz et al. 2003). At the very high speeds and near-maximal intensities at which endurance events (5000 or 10 000 m races) are currently performed by top-level runners, which is potentially associated with a decrease in the total nucleotide pool, AMPD might be an important regulator of muscle metabolism, despite the resulting hyperammonemia (Rubio et al. 2005). It is most likely that such high competitive performance requires the ability to recruit type II fibres. In overall agreement with our findings, Weston et al. (1999) found black South-African endurance runners to have a

Fig. 2. Relationship between economy at a running speed of 21 km·h^{-1} and maximal shank (calf) circumference in all subjects. R, Pearson's product–moment correlation coefficient.



lower percentage of type I fibres than their white counterparts. It was suggested that this is the appropriate fibre type profile for the modern 5000 – 10 000 m runner owing to the increasing speed and glycolytic demands of these events.

One further aspect of interest in Eritrean runners is that they are altitude natives and most of their yearly living and training is performed at ~2600 m altitude, i.e., above the typical training altitude for Kenyans (around 2000 m) (Larsen 2003; Saltin et al. 1995*b*). Altitude exposure could improve sea-level performance, although the possible benefits of living and training at altitude for an improved sea-level performance are yet to be clearly established. One potential beneficial adaptation could be improved economy. Although a number of studies have shown that the $V\mathrm{O}_2$ cost of submaximal endurance exercise remains unchanged after intermittent (Levine and Stray-Gundersen 1997; Piehl Aulin et al. 1998) or chronic exposure to hypoxia (Grassi et al. 1996) Wolfel et al. (1991) and Weston et al. (2000) have reported greater economy in black South-African endurance runners who were sea-level dwellers than in their white South-African counterparts, other authors have found increases in cycling or running economy after intermittent (Gore et al. 2001; Katayama et al. 2003; Saunders et al. 2004) or chronic hypoxic exposure (Green et al. 2000). Keeping in mind that more research is necessary to elucidate the mechanisms responsible for the potential improvement in running economy with altitude living and (or) training, a possible contributory mechanism is a shift toward increased dependence on glucose metabolism and away from reliance on fat metabolism, since glucose is a more efficient fuel in terms of generating ATP on a per mole of O_2 basis (Brooks et al. 1991). The higher RER values of Eritreans (especially at 17 and 19 km·h^{-1}), indicating a higher reliance on carbohydrate metabolism, would be in agreement with the aforementioned hypothesis. On the other hand, although chronic altitude exposure has the potential to increase blood oxygen transport capacity, which would confer a clear performance advantage in endurance events, the Eritreans' haemoglobin levels (15.4 g·dL^{-1}) were not significantly different from those of Spaniards (15.1 g·dL^{-1}), with both levels comparable with those reported at sea level in elite Kenyans (14.9 g·dL^{-1}) and Scandinavians (14.6 g·dL^{-1}) (Saltin et al. 1995*b*). The reason for the lack of difference between Eritreans (altitude natives) and Spaniards might lie, at least partly, in the fact that Eritreans spent ~2 weeks in Europe (≤600 m altitude) before testing, which could have resulted in haemodilution. In any case, our findings, together with those reported by Saltin et al. (1995*b*) suggest that, if present, the potential benefits of moderate altitude training (~2000 m for Kenyans and ~2600 m for Eritreans) are not necessarily related to improvements in $V\mathrm{O}_{2\,\max}$.

In summary, top-level Eritrean runners are characterized by a high running economy compared with Spanish controls. Their improved running economy is most likely associated, at least partly, with anthropometric characteristics, rather than with any specific metabolic property of the working muscle. We hypothesize that, to a certain extent, these runners could be among the few to challenge Ethiopians' and Kenyans' dominance in endurance running events in the forseeable future.

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References

American College of Sports Medicine. 2000. ACSM's Guidelines for Exercise Testing and Prescription, 6th edition. Lippincott, Williams & Wilkins, Philadelphia, Pa. pp. 303.

Anderson, T. 1996. Biomechanics and running economy. Sports Med. **22**: 76–89. PMID:8857704.

Billat, V.L., Demarle, A., Slawinski, J., Paiva, M., and Koralsztein, P. 2001. Physical and training characteristics of top-class marathon runners. Med. Sci. Sports Exerc. **33**: 2089–2097. PMID:11740304.

Billat, V., Lepretre, P.M., Heugas, A.M., Laurence, M.H., Salim, D., and Koralsztein, J.P.A. 2003. Training and bioenergetic characteristics in elite male and female Kenyan runners. Med. Sci. Sports Exerc. **35**: 297–304. doi:10.1249/01.MSS.0000053556.59992.A9. PMID:12569219.

Bosch, A.N., Goslin, B.R., Noakes, T.D., and Dennis, S.C. 1990. Physiological differences between black and white runners during a treadmill marathon. Eur. J. Appl. Physiol. Occup. Physiol. **61**: 68–72. PMID:2289500.

Bosco, C., Montanari, G., Ribacchi, R., Giovenali, P., Latteri, F., Iachelli, G., et al. 1987. Relationship between the efficiency of muscular work during jumping and the energetics of running. Eur. J. Appl. Physiol. Occup. Physiol. **56**: 138–143. PMID:3569218.

Brooks, G.A., Butterfield, G.E., Wolfe, R.R., Groves, B.M., Mazzeo, R.S., Sutton, J.R., Wolfel, E.E., and Reeves, J.T. 1991. Increased dependence on blood glucose after acclimatization to 4,300 m. J. Appl. Physiol. **70**: 919–927. PMID:2022585.

Cavagna, G.A., Saibene, F.P., and Margaria, R. 1964. Mechanical work in running. J. Appl. Physiol. **19**: 249–256. PMID:14155290.

Coetzer, P., Noakes, T.D., Sanders, B., Lambert, M.I., Bosch, A.N., Wiggins, T., and Dennis, S.C. 1993. Superior fatigue resistance of elite black South African distance runners. J. Appl. Physiol. **75**: 1822–1827. PMID:8282637.

Conley, D.L., Krahenbuhl, G.S., Burkett, L.N., and Millar, A.N. 1984. Following Steve Scott: Physiological changes accompanying training. Phys. Sportsmed. **12**: 103–106.

Dalleau, G., Belli, A., Bourdin, M., and Lacour, J.R. 1998. The spring-mass model and the energy cost of treadmill running. Eur. J. Appl. Physiol. Occup. Physiol. **77**: 257–263. doi:10.1007/s004210050330. PMID:9535587.

Daniels, J., and Daniels, N. 1992. Running economy of elite male and elite female runners. Med. Sci. Sports Exerc. **24**: 483–489. PMID:1560747.

Dudley, G.A., Staron, R.S., Murray, T.F., Hagerman, F.C., and Luginbuhl, A. 1983. Muscle fiber composition and blood ammonia levels after intense exercise in humans. J. Appl. Physiol. **54**: 582–586. PMID:6833053.

Gore, C.J., Hahn, A.G., Aughey, R.J., Martin, D.T., Ashenden, M.J., Clark, S.A., et al. 2001. Live high:train low increases muscle buffer capacity and submaximal cycling efficiency. Acta Physiol. Scand. **173**: 275–286. doi:10.1046/j.1365-201X.2001.00906.x. PMID:11736690.

Grassi, B., Marzorati, M., Kayser, B., Bordini, M., Colombini, A., Conti, M., Marconi, C., and Cerretelli, P. 1996. Peak blood lactate and blood lactate vs. workload during acclimatization to 5,050 m and in deacclimatization. J. Appl. Physiol. **80**: 685–692. PMID:8929616.

Green, H.J., Roy, B., Grant, S., Hughson, R., Burnett, M., Otto, C., et al. 2000. Increases in submaximal cycling efficiency mediated by altitude acclimatization. J. Appl. Physiol. **89**: 1189–1197. PMID:10956368.

Kaneko, M. 1990. Mechanics and energetics in running with special reference to efficiency. J. Biomech. **23**: Suppl. 1, 57–63. doi:10.1016/0021-9290(90)90041-Z. PMID:2081745.

Katayama, K., Matsuo, H., Ishida, K., Mori, S., and Miyamura, M. 2003. Intermittent hypoxia improves endurance performance and submaximal exercise efficiency. High Alt. Med. Biol. **4**: 291–304. doi:10.1089/152702903769192250. PMID:14561235.

Larsen, H.B. 2003. Kenyan dominance in distance running. Comp. Biochem. Physiol. A Mol. Integr. Physiol. **136**: 161–170. PMID:14527638.

Larsen, H.B., Christensen, D.L., Nolan, T., and Sondergaard, H. 2004. Body dimensions, exercise capacity and physical activity level of adolescent Nandi boys in western Kenya. Ann. Hum. Biol. **31**: 159–173. PMID:15204359.

Levine, B.D., and Stray-Gundersen, J. 1997. "Living high-training low": effect of moderate-altitude acclimatization with low-altitude training on performance. J. Appl. Physiol. **83**: 102–112. PMID:9216951.

Levine, B.D., and Stray-Gundersen, J. 2005. Point: positive effects of intermittent hypoxia (live high:train low) on exercise performance are mediated primarily by augmented red cell volume. J. Appl. Physiol. **99**: 2053–2055. doi:10.1152/japplphysiol.00877.2005. PMID:16227463.

Lucia, A., Hoyos, J., Santalla, A., Earnest, C., and Chicharro, J.L. 2003. Tour de France versus Vuelta a España: which is harder? Med. Sci. Sports Exerc. **35**: 872–878. PMID:12750600.

Lucia, A., Rabadan, M., Hoyos, J., Hernandez-Capilla, M., Perez, M., San Juan, A.F., Earnest, C.P., and Chicharro, J.L. 2006. Frequency of the VO_{2max} plateau phenomenon in world-class cyclists. Int. J. Sports Med. In press.

MacArthur, D.G., and North, K.N. 2004. A gene for speed? The evolution and function of alpha-actinin-3. Bioessays, **26**: 786–795. doi:10.1002/bies.20061. PMID:15221860.

Meyer, T., Lucia, A., Earnest, C.P., and Kindermann, W. 2005. A conceptual framework for performance diagnosis and training prescription from submaximal gas exchange parameters–theory and application. Int. J. Sports Med. **26**: Suppl. 1, S38–S48. doi:10.1055/s-2004-830514. PMID:15702455.

Mills, M., Yang, N., Weinberger, R., Vander Woude, D.L., Beggs, A.H., Easteal, S., and North, K. 2001. Differential expression of the actin-binding proteins, alpha-actinin-2 and –3, in different species: implications for the evolution of functional redundancy. Hum. Mol. Gen. **10**: 1335–1346. PMID:11440986.

Myers, M.J., and Steudel, K. 1985. Effect of limb mass and its distribution on the energetic cost of running. J. Exp. Biol. **116**: 363–373. PMID:4056656.

Nybo, L., Dalsgaard, M.K., Steensberg, A., Moller, K., and Secher, M.H. 2005. Cerebral ammonia uptake and accumulation during prolonged exercise in humans. J. Physiol. **563**: 285–290. PMID:15611036.

Piehl Aulin, K., Svedenhag, J., Wide, L., Berglund, B., and Saltin, B. 1998. Short-term intermittent normobaric hypoxia- haematological, physiological and mental effects. Scand. J. Med. Sci. Sports, **8**: 132–137. PMID:9659672.

Pollock, M.L. 1977. Submaximal and maximal working capacity of elite distance runners. Part I: Cardiorespiratory aspects. Ann. N. Y. Acad. Sci. **301**: 310–322. PMID:270924.

Pugh, L.G. 1970. Oxygen intake in track and treadmill running with observations on the effect of air resistance. J. Physiol. **207**: 823–835. PMID:5532903.

Rico-Sanz, J., Rankinen, T., Joanisse, D.R., Leon, A.S., Skinner, J.S., Wilmore, J.H., Rao, D.C., and Bouchard, C. 2003. Associations between cardiorespiratory responses to exercise and the C34T AMPD1 gene polymorphism in the HERITAGE Family study. Physiol. Genomics, **14**: 161–166. PMID:12783984.

Rietjens, G.J., Kuipers, H., Kester, A.D., and Keizer, H.A. 2001. Validation of a computerized metabolic measurement system (Oxycon-Pro) during low and high intensity exercise. Int. J. Sports Med. **22**: 291–294. doi:10.1055/s-2001-14342. PMID:11414673.

Rubio, J.C., Martin, M.A., Rabadan, M., Gomez-Gallego, F., San Juan, A.F., Alonso, J.M., et al. 2005. Frequency of the C34T mutation of the AMPD1 gene in World-class endurance athletes -does this mutation impair performance? J. Appl. Physiol. **98**: 2108–2112. doi:10.1152/japplphysiol.01371.2004. PMID:15677729.

Saltin, B., Kim, C.K., Terrados, N., Larsen, H., Svedenhag, J., and Rolf, C.J. 1995*a*. Morphology, enzyme activities and buffer capacity in leg muscles of Kenyan and Scandinavian runners. Scand. J. Med. Sci. Sports, **5**: 222–230. PMID:7552767.

Saltin, B., Larsen, H., Terrados, N., Bangsbo, J., Bak, T., Kim, C.K., Svedenhag, J., and Rolf, C.J. 1995*b*. Aerobic exercise capacity at sea level and at altitude in Kenyan boys, junior and senior runners compared with Scandinavian runners. Scand. J. Med. Sci. Sports, **5**: 209–221. PMID:7552766.

Saunders, P.U., Telford, R.D., Pyne, D.B., Cunningham, R.B., Gore, C.J., Hahn, A.G., and Hawley, J.A. 2004. Improved running economy in elite runners after 20 days of simulated moderate-altitude exposure. J. Appl. Physiol. **96**: 931–937. PMID:14607850.

Scott, R.A., Georgiades, E., Wilson, R.H., Goodwin, W.H., Wolde, B., and Pitsiladis, Y.P. 2003. Demographic characteristics of elite Ethiopian endurance runners. Med. Sci. Sports Exerc. **35**: 1727–1732. doi:10.1249/01.MSS.0000089335.85254.89. PMID:14523311.

Weston, A.R., Karamizrak, O., Smith, A., Noakes, T.D., and Myburgh, K.H. 1999. African runners exhibit greater fatigue resistance, lower lactate accumulation, and higher oxidative enzyme activity. J. Appl. Physiol. **86**: 915–923. PMID:10066705.

Weston, A.R., Mbambo, Z., and Myburgh, K.H. 2000. Running economy of African and Caucasian distance runners. Med. Sci. Sports Exerc. **32**: 1130–1134. PMID:10862541.

Williams, K.R., and Cavanagh, P.R. 1987. Relationship between distance running mechanics, running economy, and performance. J. Appl. Physiol. **63**: 1236–1245. PMID:3654469.

Wolfel, E.E., Groves, B.M., Brooks, G.A., Butterfield, G.E., Mazzeo, R.S., Moore, L.S., et al. 1991. Oxygen transport during steady-state submaximal exercise in chronic hypoxia. J. Appl. Physiol. **70**: 1129–1136. PMID:2032978.

Yang, N., Macarthur, D.G., Gulbin, J.P., Hahn, A.G., Beggs, A.H., Easteal, S.H., and North, K. 2003. ACTN3 genotype is associated with human elite athletic performance. Am. J. Hum. Genet. **73**: 627–631. doi:10.1086/377590. PMID:12879365.

Zatsiorsky, V., Seluyanov, V., and Cugunova, L. 1990. In vivo body segment inertial parameters determination using a gamma-scanner method. *In* Biomechanics of human motion: applications in rehabilitation, sports and ergonomics. *Edited by* B. Berme and A. Capozzo. Betec Corporation, Worthington, Ohio. pp. 186–202.