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Review

Kenyan dominance in distance running[☆]

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Abstract

Critical physiological factors for performance in running are maximal oxygen consumption ($\dot{V}O_{2\max}$), fractional $\dot{V}O_{2\max}$ utilization and running economy. While Kenyan and Caucasian elite runners are able to reach very high, but similar maximal oxygen uptake levels, the $\dot{V}O_{2\max}$ of black South African elite runners seems to be slightly lower. Moreover, the studies of black and white South African runners indicate that the former are able to sustain the highest fraction of $\dot{V}O_{2\max}$ during long distance running. Results on adolescent Kenyan and Caucasian boys show that these boys are running at a similar percentage of $\dot{V}O_{2\max}$ during competition. Kenyan elite runners, however, appear to be able to run at a high % of $\dot{V}O_{2\max}$ which must then have been achieved by training. A lower energy cost of running has been demonstrated in Kenyan elite runners and in untrained adolescent Kenyan boys compared to their Caucasian counterparts. In agreement with this are the results from studies on black South African elite runners who have shown similar low energy costs during running as the Kenyan elite runners. The good running economy cannot be explained by differences in muscle fibre type as they are the same in Kenyan and Caucasian runners. The same is true when comparing untrained adolescent Kenyan boys with their Caucasian counterparts. A difference exists in BMI and body shape, and the Kenyans long, slender legs could be advantageous when running as the energy cost when running is a function of leg mass. Studies comparing the response to training of Kenyans and Caucasians have shown similar trainability with respect to $\dot{V}O_{2\max}$, running economy and oxidative enzymes. Taken all these data together it appears that running at a high fractional $\dot{V}O_{2\max}$ and having a good running economy may be the primary factors favouring the good performance of endurance athletes rather than them having a higher $\dot{V}O_{2\max}$ than other elite runners. In addition to having the proper genes to shape their bodies and thereby contributing to a good running economy, the Kenyan elite runners have trained effectively and used their potential to be in the upper range both in regard to $\dot{V}O_{2\max}$ and to a high utilization of this capacity during endurance running.

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1. Introduction

During the past two decades, the international scene of middle- and long-distance running for men has changed dramatically. Only 17 years ago, all distances from 800 m to marathon were dominated by Europeans (Matthews, 1987; Fig. 1).

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Thus, the average proportion of European achievements in the six all time top 20 lists in the distances from 800 m to marathon including steeplechase was 48.3% while the percentage of African results was 26.6% of which the Kenyans produced 13.3%. Moreover, the majority of world record holders were Europeans, and European gold medal winners at the Olympic Games and world championships were not a rarity. Today, the proportion of European achievements is reduced to 11.7%, whereas the percentage of Africans in the top has increased to 85.0%, of which 55.8% are Kenyans (IAAF, All Time Outdoor Lists, June 2003, Fig. 1). The markedly reduced occurrence of Europeans in the list is not due to them running slower now than earlier. It is simply related to the fact that runners from East-Africa in particular now run so much faster (IAAF, 2002; Matthews, 1987). Even more profound is the Kenyan dominance at the world cross-country championships, where Kenyan senior men have won the team title on the long distance every year for the past 18 years. The performances of Kenyan men in middle- and long-distance events at the Olympic Games and world championships on track underscore the Kenyan superiority.

Most of the Kenyans who are such good performers come from a group of eight small tribes

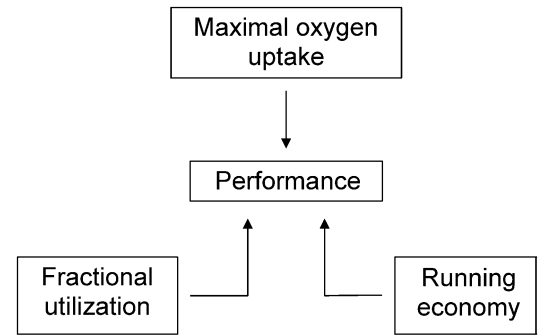


Fig. 2. Main physiological factors decisive for distance running performance.

called Kalenjin, which number only approximately three and a half million people. Among the Kalenjin tribes, the Nandis have performed the best and they constitute only approximately 2% of the Kenyan population. The question that arises is what makes Kenyan runners perform so well? Factors to consider are genetic endowment, upbringing, training and altitude (~ 2000 m.a.s.l), as outstanding performance in long distance running requires an optimal combination of high capacity for aerobic energy output, a high fractional $\dot{V}O_{2\max}$ utilization during competition and a

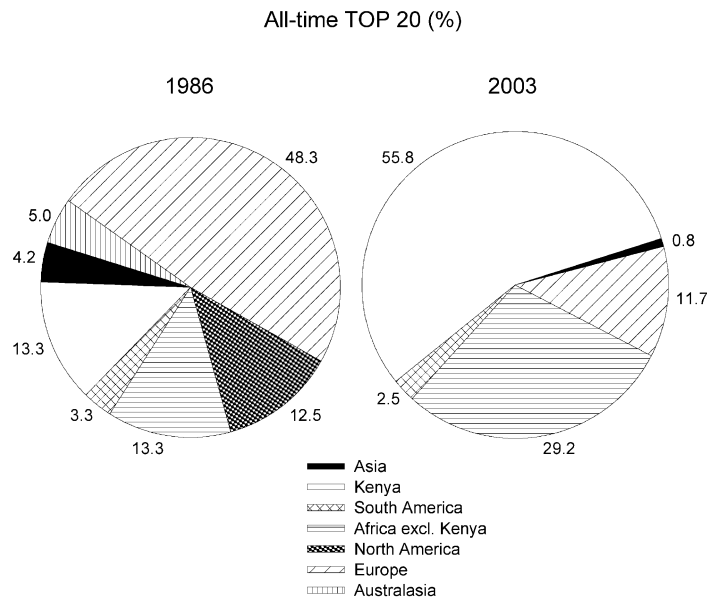


Fig. 1. Relative distribution (%) between the continents of the all-time top 20 performances in middle- and long-distance running for men in the six major distances from 800 m to marathon including steeplechase in 1986 and in June 2003. Black Americans are regarded as Africans excluding Kenyans.

good running economy (Fig. 2). Thus, high correlations have been demonstrated between $\dot{V}O_{2\max}$ and running performance in groups of runners of quite different abilities (Costill et al., 1971, 1973b; Farrell et al., 1979; Maughan and Leiper, 1983; Sjödín and Svedenhag, 1985). However, when groups of athletes with very similar running performances or athletes with a relatively narrow range of $\dot{V}O_{2\max}$ are studied, the $\dot{V}O_{2\max}$ becomes a less sensitive predictor of performance (Conley and Krahenbuhl, 1980; Sjödín and Svedenhag, 1985). A moderately close relationship exists between running economy and performance in groups of runners who are heterogeneous with respect to running ability (Sjödín and Svedenhag, 1985), whereas no correlation has been found between oxygen cost of running and performance in groups of runners with a narrow performance range (Davies and Thompson, 1979). In athletes with a relatively narrow $\dot{V}O_{2\max}$ range the running economy has been shown to be a better predictor of performance than $\dot{V}O_{2\max}$ (Conley and Krahenbuhl, 1980). Finally, several investigations have demonstrated that the $\dot{V}O_{2\max}$ fraction actually exploited throughout the race is crucial for performance in distance running (Costill et al., 1971; Davies and Thompson, 1979; Maughan and Leiper, 1983).

Although the significance of each of the above-mentioned factors may be difficult to identify in specific groups of runners (cf. Myburgh, 2003), di Prampero et al. (1986) have analysed all three factors. They could then demonstrate that a good relationship exists between performance and $\dot{V}O_{2\max}$, fractional $\dot{V}O_{2\max}$ utilization and running economy, and each factor played a significant role. Therefore, when studying performance in running one should consider all three factors. Thus, the comparison between Kenyan and non-Kenyan runners will be in respect to the runners' $\dot{V}O_{2\max}$, fractional $\dot{V}O_{2\max}$ utilization and running economy. In the following these factors as well as their trainability will be highlighted.

2. Maximal oxygen uptake

Since the early work of Hill and Lupton (1923), exercise physiologists have associated the limits of human endurance with the ability to consume oxygen at a high rate. A high maximal oxygen

uptake ($\dot{V}O_{2\max}$) is a function of training effort and natural endowment. There is no consensus of what limits $\dot{V}O_{2\max}$, but most researchers in the field agree that the capacity of cardiac output and the systemic oxygen delivery are essential, although peripheral factors (e.g. muscle capillary density) and mitochondrial capacity also play a role, especially for endurance performance. Comparing Kenyan runners with athletes of non-African descent (Saltin et al., 1995b) revealed that Kenyan elite long-distance runners have a very high $\dot{V}O_{2\max}$ ($79.9 \text{ ml kg}^{-1} \text{ min}^{-1}$), but it was not higher than the level observed in Scandinavian elite runners ($79.2 \text{ ml kg}^{-1} \text{ min}^{-1}$). In this comparison, body dimension was accounted for by dividing $\dot{V}O_{2\max}$ in l min^{-1} with body weight in kilograms. It has been questioned whether this 'scaling' is proper. When comparing various species of different sizes in the animal kingdom scaling has proven useful. Also, when comparing humans with differences in body mass the same approach has successfully been applied. There is a discussion if the exponent should be the theoretical one of 0.67 or the empirically found one of 0.70–0.75. Here the highest value (0.75) has been chosen, primarily because Svedenhag (1995), who has been studying runners, their $\dot{V}O_{2\max}$ and their running economy, preferred to use this exponent. Thus, normalizing for body weight raised to an exponent of 0.75 instead of the $\dot{V}O_{2\max}$ rate, reveals a trend for higher $\dot{V}O_{2\max}$ in the Scandinavian runners (218.7 vs. $226.1 \text{ ml kg}^{-0.75} \text{ min}^{-1}$). In the study of Kenyan elite runners, only few of the very best participated or were in top shape. The possibility exists that the very best, when top-trained, have values higher than the mean of $79.9 \text{ ml kg}^{-1} \text{ min}^{-1}$. This was true for one of the Kenyan runners (J. Machuka) who reached $84.8 \text{ ml kg}^{-1} \text{ min}^{-1}$, which is higher than the $\dot{V}O_{2\max}$ observed in any of the Scandinavian runners. This observation is in line with previous findings on the two former Kenyan world record holders, Kipchoge Keino, who had a $\dot{V}O_{2\max}$ value of 82.0 (Saltin and Åstrand, 1967) and Henry Rono who had $84.3 \text{ ml kg}^{-1} \text{ min}^{-1}$, respectively (see Saltin et al., 1995b; Henry Rono was studied by Philip Gollnick). Several studies of Caucasian elite runners have revealed $\dot{V}O_{2\max}$ values similar to these high values of Kenyan runners. Examples are the former world record holder Dave Bedford who

had a $\dot{V}O_{2\max}$ value of 85.0 ml kg⁻¹ min⁻¹ (Bergh, 1982) and Steven Prefontaine who had $\dot{V}O_{2\max}$ values of 84.4 ml kg⁻¹ min⁻¹ (Pollock, 1977). It is not mandatory to have a $\dot{V}O_{2\max}$ of 84–85 ml kg⁻¹ min⁻¹ to be successful. Kenyan elite runners as well as American elite middle- and long-distance runners may have a $\dot{V}O_{2\max}$ value just below 80 ml kg⁻¹ min⁻¹ as reported by Pollock (1977). In this respect, the studies by Coetzer et al. (1993) of black South African elite distance runners are interesting. These runners can run a half marathon in 62/39 (min:s) with a relatively low mean $\dot{V}O_{2\max}$ value of 71.5 ml kg⁻¹ min⁻¹ which is in line with the findings of 72 ml kg⁻¹ min⁻¹ in $\dot{V}O_{2\max}$ for the Munich Olympic winner Frank Shorter (Costill, personal communication). Thus, a relatively low $\dot{V}O_{2\max}$ of black South African runners seems to be a common feature at a given performance level compared to other runners in the world. Weston et al. (2000) have shown that black South African runners, with similar mean 10-km race times as white South African runners, had the lowest $\dot{V}O_{2\max}$. Likewise, black South African marathon runners with the same race time as white South African marathon runners, have a lower $\dot{V}O_{2\max}$ than the white runners when the data are normalized for differences in body mass (164 vs. 184 ml O₂ kg^{-0.75} min⁻¹) (Bosch et al., 1990).

A key question is whether untrained Africans have a high $\dot{V}O_{2\max}$ already at a young age. To answer this question untrained adolescent Nandi town boys were studied (Larsen et al., 2003b; Saltin et al., 1995b). When studied at an altitude of (~2.000 m.a.s.l), these boys had $\dot{V}O_{2\max}$ values which were in the same range as untrained Caucasian teenagers (Andersen et al., 1987) studied at sea level. It can be argued that the maximal oxygen uptake of the Kenyan boys would be higher if they were tested at sea level. However, a study by Favier et al. (1995) demonstrated that natives do not gain much in $\dot{V}O_{2\max}$ when tested at sea level. Although there may be a small difference, one also has to consider that the body mass of the Nandi boys was only ~54 kg (Larsen et al., 2003b), which is ~12 kg less than that of Caucasian boys of the same age (Andersen, 1994). If $\dot{V}O_{2\max}$ is normalized for differences in body mass with the exponent of 0.75, the Kenyan boys will actually have a lower $\dot{V}O_{2\max}$ than the Cau-

casian boys. The fact that no difference was observed with respect to $\dot{V}O_{2\max}$ between untrained Kenyan and Danish boys is in line with findings by Boulay et al. (1988), who have reviewed the literature about racial variation in work capacities and concluded that there is no valid or reliable evidence of clear racial difference in $\dot{V}O_{2\max}$.

The Kenyan world elite runners are not fostered in towns but in small villages and rural areas. When Nandi village boys were compared to Nandi town boys the former had a mean $\dot{V}O_{2\max}$ approximately 10% higher than the $\dot{V}O_{2\max}$ of the town boys (Larsen et al., 2003b). The higher $\dot{V}O_{2\max}$ of the village boys was related to more daily physical activities. Although the $\dot{V}O_{2\max}$ of the village boys is quite high, it is far from being at the level required to become an elite runner. When this is said it should also be noted that several of the Nandi village boys had a good $\dot{V}O_{2\max}$ despite limited training background. This led to the speculation that the trainability of Kenyans (the Nandis) is larger than what may be observed in Caucasians. Indeed, anecdotal evidence suggests that Kenyan runners are able to abstain from regular intense training for months, but nevertheless within months be back and, with surprisingly little training, be among the best runners in the world. A strong genetic component for $\dot{V}O_{2\max}$ to reach the very highest level (Bouchard et al., 1992, 1999; Prud'homme et al., 1984) is well documented and is then in line with better trainability. In studies to test this hypothesis of a better trainability among Nandi teenagers, no support could be obtained for this notion (Larsen et al., 2003c; Larsen and Søndergaard, In publication process). When examining the response to training of sedentary Kenyan and Danish boys with similar initial $\dot{V}O_{2\max}$, no difference could be found in trainability of Kenyans compared to Caucasians with respect to maximal oxygen uptake. Findings by Skinner et al. (2001), who compared the $\dot{V}O_{2\max}$ response to training of large groups of black and of white North Americans also showed a similar elevation of aerobic capacity in these two groups.

2.1. Fractional utilization of $\dot{V}O_{2\max}$

The ability to sustain a high percentage of $\dot{V}O_{2\max}$ has been particularly focused upon as a predictor of endurance performance for the last

three decades (Costill et al., 1971; Davies and Thompson, 1979; Maughan and Leiper, 1983). The running velocity at which lactate begins to accumulate in the blood (V_{OBLA}) has been a helpful prognostic tool in this research where Sjödín and Jacobs (1981) have demonstrated its value to predict endurance performance. When it comes to investigations on runners of different ethnic origin only a few studies have been identified. Well-trained black as compared to white South African runners are able to run at a higher fractional $\dot{V}O_{2max}$ utilization during a 10-km race and on the marathon distances (Bosch et al., 1990; Weston et al., 2000). In addition, Coetzer et al. (1993) have demonstrated that while black and white South African elite athletes were able to run at a similar percentage of maximal oxygen uptake over distances from 1.65 to 5 km, the percentage of $\dot{V}O_{2max}$ sustained by black athletes was larger than that of white athletes in distances longer than 5 km; a difference which became larger, the longer the running distance. Part of the explanation for this difference could be that the black athletes were predominantly long-distance runners whereas the Caucasian athletes were primarily middle-distance track runners. It is of note, however, that Weston et al. (1999) also found that well-trained black as compared to white South African runners have a greater ability to sustain high-intensity distance running. It is not well studied whether Kenyan runners are able to sustain a high $\dot{V}O_{2max}$ during competition. It was shown in one runner, Kip Keino, that he utilized his whole $\dot{V}O_{2max}$ when running 5000 m and above 97–98% $\dot{V}O_{2max}$ in a 10-km race (Karlsson et al., 1968). When the average heart rate during a 5000 m competition was recorded in Nandi and Caucasian boys, the two groups utilized the same mean percentage of their maximal heart rate (Larsen et al., 2003c; Larsen and Søndergaard, In publication process). This means that if Kenyan top runners have an advantage in this respect it is likely to be the result of good training.

The majority of factors that may explain superiority in exercising at a high $\dot{V}O_{2max}$ are related to the feature of the muscles involved in the action of running. There is a moderate to strong relationship between distance running performance and the proportion of type I muscle fibres (Costill et al., 1973a; Sjödín and Jacobs, 1981), further sup-

ported by findings on well-trained cyclists (Coyle et al., 1988). In addition, Sjödín et al. (1982) have suggested that the percentage of type I muscle fibres may be an indicator of the potential ‘trainability’ of the musculature. However, extreme endurance training has been demonstrated to induce a similarly high mitochondrial oxidative capacity of type I and type II muscle fibres, in line with the fact that the contractile characteristics of a fibre and transformation of the main fibre types are not so easily affected by training, whereas the metabolic capacity is; also in the type II fibres (Jansson and Kaijser, 1977). Both Kenyan and Scandinavian elite runners have a high proportion of type I muscle fibres (Saltin et al., 1995a). Similarly, a study comparing untrained Nandi boys and Danish boys revealed no difference in the percentage of slow-twitch muscle fibres which was quite low, but with a large range (Larsen et al., 2003a). However, Kenyan junior runners have a proportion of type I muscle fibres that is high and not much different from Kenyan elite runners (~70% type I fibres) which most likely is due to selection rather than to an adaptation to the training. South African distance runners appear to differ from Kenyan runners, having less type I fibres (Coetzer et al., 1993; Weston et al., 1999). Indeed, the proportion of type I muscle fibres in the muscles of black distance runners was similar to what was found in muscles of sedentary Caucasians (Simoneau and Bouchard, 1989). Thus, Kenyan elite distance runners may have a higher proportion of type I muscle fibres than black South African distance runners, which may be one factor explaining the difference in running performance. It should be mentioned that there may be major variations in muscle fibre type composition comparing various ethnic groups in Africa. West Africans appear to have very low percentages of slow fibre types (Ama et al., 1986). In contrast, Duey et al. (1997) found no difference in the proportion of type I muscle fibres when comparing sedentary black and white North Americans; a finding that may just be the results of generations of genetic ‘mixing’ (Chakraborty et al., 1992).

2.2. Leg muscle oxidative enzymes

Muscle mitochondrial enzyme capacity is linked with the substrate metabolism during exercise. The more mitochondria, the larger the muscle lipid

consumption during exercise (Henriksson, 1977). In turn, the level of blood lactate at a given work rate is lower, the higher the activity of the oxidative enzymes (Ivy et al., 1980). Thus, a direct link exists to the oxidative potential of the muscles engaged in running and the performance level, as a running speed has to be high before blood lactate starts to become elevated (Farrell et al., 1979; Sjödin and Jacobs, 1981). Indeed, Evertsen et al. (1999) have shown positive correlations between the activity of three oxidative enzymes, citrate synthase (CS), succinate dehydrogenase (SDH) and glycerol-3 phosphate dehydrogenase (GPDH), and performance in running. Weston et al. (1999) also found a positive correlation between the CS activity and time to exhaustion when running at a given percentage of peak velocity. When comparing the CS activity of Kenyan and Scandinavian elite runners, no differences were found regardless of whether the comparisons were made between the vastus lateralis or the gastrocnemius muscle in the two groups of runners (Saltin et al., 1995a). However, in the study comparing untrained Kenyan town and village boys with untrained Danish boys revealed that CS activity of the Danish boys was ~30% higher compared to the Kenyan boys (Larsen et al., In publication process). The low CS activity of the village boys is somewhat surprising, since the $\dot{V}O_{2\max}$ of these boys and the Danish boys was similar. Kenyan and Scandinavian elite runners have similar CS activities, while 'untrained' Kenyan boys have a lower activity compared to Danish boys. Could this be explained by the Kenyans having a higher trainability with respect to CS? Probably not, seeing that the muscle enzyme activity was elevated similarly in Kenyan and Danish boys after 12 weeks of training (Larsen et al., In publication process). Weston et al. (1999) compared the CS activity in the muscles of black and white South African elite runners as well as in black and white sedentary boys. While no difference was observed between the sedentary boys, the CS activity of the black South African elite runners was ~50% higher compared to the white South African elite runners which is in contrast to the findings on Kenyans by Saltin et al. (1995a) and Larsen et al. (In publication process). This may indicate a higher trainability of the black South Africans and at the same time be an important feature that contributes to the superior performance level of these runners, con-

sidering their low $\dot{V}O_{2\max}$. Finally, it is of note that, when comparing untrained black Africans of West and Central African origin with untrained Caucasians, Ama et al. (1986) found no difference in the activity of oxidative enzymes, despite the fact that these Africans had a low percentage of type I fibres in their muscle.

2.3. HAD

In the early studies of Kenyan runners it was observed that they possessed a higher activity of the β -oxidative enzyme HAD (3-hydroxyacyl-CoA-dehydrogenase activity) in their muscles (Saltin et al., 1995a). When comparing untrained Kenyan town, village and Danish boys, no differences in HAD activity could be observed (Larsen et al., 2003a). Moreover, after 12 weeks of endurance training, the activity of this enzyme became only slightly increased or not at all. Ama et al. (1986) observed a similar HAD activity in sedentary black West Africans and Caucasians. The very high HAD activity in the leg muscles of Kenyan elite runners could be the result of years with both intense and long-lasting training. Some support for this suggestion is found in data by Weston et al. (1999), which demonstrate that black South African athletes have a higher HAD activity as compared to white South African athletes.

2.4. Capillaries

Capillarisation is one of the factors determining the oxidative profile of the musculature and it is closely related to $\dot{V}O_{2\max}$. The capillary density has also been shown to correlate positively with the running velocity at which blood lactate begins to accumulate (Sjödin and Jacobs, 1981). A moderate correlation ($r=0.63$) is only found between muscle capillarity and the mean marathon running velocity during competition (Sjödin and Jacobs, 1981). When comparing the capillarisation of Kenyan and Danish elite runners, Saltin et al. (1995a) observed only a tendency for a higher capillarisation of the Kenyan elite runners. Larsen et al. (In publication process) also demonstrated that untrained Kenyan boys from a rural area and Danish boys with the same $\dot{V}O_{2\max}$ had similar capillarisation. As could be anticipated Kenyan town boys had ~10% fewer capillaries per mm^2 compared to the aforementioned two groups of boys seeing

that they had a lower $\dot{V}O_{2\max}$. Thus, it appears that both Kenyans and Caucasians adhere to the general finding of a close coupling between muscle capillaries and $\dot{V}O_{2\max}$. Less evidence is available in regard to whether the % $\dot{V}O_{2\max}$ that a runner can sustain is a function of the number of capillaries in the muscles engaged in the running.

2.5. Plasma lactate and ammonia responses

As discussed above, the blood lactate response to submaximal running is a good predictor of endurance running performance and primarily reflects the local metabolic response in the 'running muscles'. Kenyan elite runners have lower blood lactate levels, both at altitude and at sea level, when running at a given exercise intensity compared to other elite runners. The difference is most pronounced at high exercise intensities. When comparing well-trained black and white South African distance runners, Weston et al. (1999) have demonstrated that the level of blood lactate was significantly lower in the black African athletes compared to the Caucasians, when running at 88% of peak velocity. Furthermore, the study revealed that the black South African runners accumulated lactate at a slower rate with increasing exercise intensity.

With the accumulation of lactate in the blood the ammonia concentration usually also increases. This is also true for Kenyan elite runners but only at very high exercise intensities and then to a lower extent than other elite runners (Saltin et al., 1995b). In addition, the peak ammonia concentration following a maximal test was only half to one third in the Kenyan runners as compared to other elite runners. In line with the findings on elite runners, a trend for lower blood ammonia concentrations was found in Kenyan town and village boys compared to Danish boys at submaximal running velocities (Larsen et al., 2003b; Larsen and Søndergaard, In publication process). These studies also revealed that the peak ammonia concentration was ~50% higher in the Danish as compared to the Kenyan boys. Following a period of endurance running, the blood ammonia level was reduced in Kenyan town and village boys whereas no change was noted in the Danish boys. In contrast to these findings, Weston et al. (2000) found that the ammonia level in the blood was significantly higher at race pace in well-trained

black as compared to white South African 10 km runners. These blood ammonia data warrant further exploration, as they may explain some metabolic regulations in the muscles of Nandi runners, in turn affecting critical fatiguing factors, either peripherally in the muscle or at a more central level.

3. Running economy

Running economy is expressed as the steady-state submaximal oxygen uptake at a given running velocity. The lower the $\dot{V}O_2$ at a given submaximal running speed, the better the running economy. Dill et al. (1930) were probably the first to suggest differences in the amount of oxygen that different athletes actually require when running at the same speed. Indeed, at a given running speed, the submaximal oxygen requirement ($\text{ml kg}^{-1} \text{min}^{-1}$) has been shown to vary considerably between subjects (Svedenhag and Sjödin, 1984).

The oxygen cost of running at a given running velocity normalized for difference in body mass is lower in Kenyan elite runners than in other elite runners (Saltin et al., 1995b). This is consistent with findings on black South African runners. Thus, when comparing well-trained black and white South African runners with similar mean 10 km race times, the former had the lowest oxygen cost when running, regardless of whether this was expressed per kg or using the exponent 0.67–0.75 kg of body mass. There is no consensus, however, as Bosch et al. (1990) found the same oxygen uptake ($\text{ml kg}^{-1} \text{km}^{-1}$) in black and white South African marathon runners with varying performance levels. Using 'scaling' there was a difference, with the black South African marathon runners having the lowest value (519 vs. 555 $\text{ml kg}^{-0.75} \text{km}^{-1}$).

Low oxygen cost of running seems to be a common feature of Kenyans at least for the tribes belonging to the Kalenjin. Thus, a study of untrained adolescent Kenyan boys from the Nandi tribe indicates that the running economy of these boys is better than in untrained Danish boys of a similar age (Larsen et al., 2000; Larsen and Søndergaard, In publication process). In addition, the study of Nandi boys revealed a similar running economy of town and village boys, although the village boys had a higher $\dot{V}O_{2\max}$ and a higher physical activity level than the town boys (Larsen

et al., 2003b). Furthermore, two studies investigating the response to training on the oxygen cost of running of Kenyan and Danish boys (Larsen et al., 2003c; Larsen and Søndergaard, In publication process) have shown a similar and quite small trainability of running economy of the two groups of boys.

Some investigators have found that a higher proportion of slow-twitch fibres is associated with better running economy (Bosco et al., 1987; Kaneko, 1990; Williams and Cavanagh, 1987). This indicates that different contractile and metabolic profiles within muscles may be a contributing factor also in regard to a good running economy. The question is whether this can explain the whole difference in oxygen costs. The answer is probably no! Body shape and mass of the legs may play a more important role. Kenyan elite distance runners have a low BMI and a more slender body shape compared to Caucasian elite distance runners (Saltin et al., 1995b). Furthermore, a study of untrained adolescent Kenyan boys (Larsen et al., 2003b) indicated that they also have a low body mass and a very low BMI compared to the majority of boys of similar age from other continents. Moreover, Kenyan boys' circumference of the lower leg seems to be smaller compared to Caucasian boys (Larsen et al., 2003b). Classical studies of human locomotion (Cavagna et al., 1964; Fenn, 1930) indicate that the work of moving the limbs comprises a substantial part of the metabolic cost of running, just as load-carrying experiments (e.g. Myers and Steudel, 1985) have shown that adding a few grams of mass on the feet/ankle evokes an increase in the metabolic rate. Therefore, it can be hypothesized that the superior running economy of the Kenyan runners is primarily due to the fact that they have slender limbs with low masses allowing them to run with a minimal energy used for swinging the limbs.

4. Conclusions

Maximal oxygen uptake, fractional utilization of $\dot{V}O_{2\max}$ during running and running economy are crucial factors for running success. Investigations of these key factors indicate that the Kenyan superiority in distance running is to a large extent due to a unique combination of these factors. Especially the running economy of the Kenyans has been shown to be proficient, where body shape appears to be critical. However, seeing that, e.g.

many Ethiopians, black South Africans and Indians seem to have almost the same body shape as the Kenyan Kalenjins (Larsen et al., 2003b), it may be speculated why runners from these countries have far from reached the same level in distance running as the Kenyans. Indeed, black South African elite runners have actually been shown to have a running economy similar to the Kenyans. What they 'lack' is probably either a high $\dot{V}O_{2\max}$ or the ability to use a sufficiently high percentage of their $\dot{V}O_{2\max}$ when running.

After realizing the talent for running of the Kalenjins, western managers and coaches have brought in financial resources and knowledge about running to Kenya, and they have thereby in a 'western' manner contributed to the development of the Kenyan potential and the Kenyan success in distance running. Whether this could happen in other parts of the world is an intriguing question. Are there other places in the world, where people possess a genetic endowment and the physiological properties crucial for athletic performance similar to what is seen in Kalenjins in regard to running and where the socio-economic, political and cultural environment will support a similar development? Yes, probably, but then for other athletic performance than distance running, as the Kalenjin tribe may be unique.

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References

- Ama, P.F.M., Simoneau, J.A., Boulay, M.R., Serresse, O., Thériault, G., Bouchard, C., 1986. Skeletal muscle characteristics in sedentary Black and Caucasian males. *J. Appl. Physiol.* 61, 1758–1761.
- Andersen, L.B., 1994. Blood pressure, physical fitness and physical activity in 17-year-old Danish adolescents. *J. Int. Med.* 236, 323–330.
- Andersen, L.B., Henckel, P., Saltin, B., 1987. Maximal oxygen uptake in Danish adolescents 16–19 years of age. *Eur. J. Appl. Physiol.* 56, 74–82.
- Bergh, U., 1982. *Physiology of Cross-Country Ski-Racing*. Human Kinetics,ampaign, Illinois.
- Bosch, A.N., Goslin, B.R., Noakes, T.D., Dennis, S.C., 1990. Physiological differences between black and white runners during a treadmill marathon. *Eur. J. Appl. Physiol.* 61, 68–72.
- Bosco, C., Montanari, G., Ribacchi, R., Giovinali, 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.* 56, 138–143.
- Bouchard, C., An, P., Rice, T., Skinner, J.S., Wilmore, J.H., Gagnon, J., et al., 1999. Familial aggregation of $\dot{V}O_{2\max}$ response to exercise training: results from the HERITAGE Family Study. *J. Appl. Physiol.* 87, 1003–1008.
- Bouchard, C., Dionne, F.T., Simoneau, J.A., Boulay, M.R., 1992. Genetics of aerobic and anaerobic performances. *Exerc. Sport Sci. Rev.* 20, 27–58.
- Boulay, M.R., Ama, P.F., Bouchard, C., 1988. Racial variation in work capacities and powers. *Can. J. Sport Sci.* 13, 127–135.
- Cavagna, G.A., Saibene, F.P., Margaria, R., 1964. Mechanical work in running. *J. Appl. Physiol.* 19, 249–256.
- Chakraborty, R., Kamboh, M.I., Nwankwo, M., Ferrell, R.E., 1992. Caucasian genes in American blacks: new data. *Am. J. Hum. Genet.* 50, 145–155.
- Coetzer, P., Noakes, T.D., Sanders, B., Lambert, M.I., Bosch, A.N., Wiggins, T., et al., 1993. Superior fatigue resistance of elite black South African distance runners. *J. Appl. Physiol.* 75, 1822–1827.
- Conley, D.L., Krahenbuhl, G.S., 1980. Running economy and distance running performance of highly trained athletes. *Med. Sci. Sports Exerc.* 12, 357–360.
- Costill, D.L., Branam, G., Eddy, D., Sparks, K., 1971. Determinants of marathon running success. *Int. Z. Angew. Physiol.* 29, 249–254.
- Costill, D.L., Gollnick, P.D., Jansson, E.D., Saltin, B., Stein, E.M., 1973a. Glycogen depletion pattern in human muscle fibres during distance running. *Acta Physiol. Scand.* 89, 374–383.
- Costill, D.L., Thomason, H., Roberts, E., 1973b. Fractional utilization of the aerobic capacity during distance running. *Med. Sci. Sports Exerc.* 5, 248–252.
- Coyle, E.F., Coggan, A.R., Hopper, M.K., Walters, T.J., 1988. Determinants of endurance in well-trained cyclists. *J. Appl. Physiol.* 64, 2622–2630.
- Davies, C.T.M., Thompson, M.W., 1979. Aerobic performance of female marathon and male ultramarathon athletes. *Eur. J. Appl. Physiol.* 41, 233–245.
- di Prampero, P.E., Atchou, G., Brückner, J.-C., Moia, C., 1986. The energetics of endurance running. *Eur. J. Appl. Physiol. Occup. Physiol.* 55, 259–266.
- Dill, D.B., Talbert, J.H., Edwards, H.T., 1930. Studies in muscular activity. VI: response of several individuals to a fixed task. *J. Physiol.* 69, 267–305.
- Duey, W.J., Bassett Jr., D.R., Torok, D.J., Howley, E.T., Bond, V., Mancuso, P., Trudell, R., 1997. Skeletal muscle fibre type and capillary density in college-aged blacks and whites. *Ann. Hum. Biol.* 24, 323–331.
- Evertsen, F., Medbø, J.I., Jebens, E., Gjøvaag, T.F., 1999. Effect of training on the activity of five muscle enzymes studied on elite cross-country skiers. *Acta Physiol. Scand.* 167, 247–257.
- Farrell, P.A., Wilmore, J.H., Coyle, E.F., Billing, J.E., Costill, D.L., 1979. Plasma lactate accumulation and distance running performance. *Med. Sci. Sports.* 11, 338–344.
- Favier, R., Spielfogel, H., Desplanches, D., Ferretti, G., Kayser, B., Hoppeler, H., 1995. Maximal exercise performance in chronic hypoxia and acute normoxia in high-altitude natives. *J. Appl. Physiol.* 78, 1868–1874.
- Fenn, W.O., 1930. Frictional and kinetic factors in the work of sprint running. *Am. J. Physiol.* 92, 583–611.
- Henriksson, J., 1977. Training induced adaptation of skeletal muscle and metabolism during submaximal exercise. *J. Physiol. (Lond.)* 270, 661–675.
- Hill, A.V., Lupton, H., 1923. Muscular exercise, lactic acid, and the supply and utilization of oxygen. *Quart. J. Med.* 16, 135–171.
- Ivy, J.L., Withers, R.T., van Handel, P.J., Elger, D.H., Costill, D.L., 1980. Muscle respiratory capacity and fiber type as determinants of the lactate threshold. *J. Appl. Physiol.: Respirat. Environ. Exerc. Physiol.* 48, 523–527.
- Jansson, E., Kaijser, L., 1977. Muscle adaptation to extreme endurance training in man. *Acta Physiol. Scand.* 100, 315–324.
- Kaneko, M., 1990. Mechanics and energetics in running with special reference to efficiency. *J. Biomechanics* 23, 57–63.
- Karlsson, J., Hermansen, L., Agnevik, G., Saltin, B. 1968. *Running (in Swedish)*. Framtiden, Stockholm, Sweden.
- Larsen, H.B., Søndergaard, H., Nolan, T., Asp, S., Christensen, D.L., Saltin, B., 2000. Trainability of Kenyan village boys compared to Kenyan town boys. *J. Physiol. (Lond.)* 528P, 42P–43P.
- Larsen, H.B., Andersen, J.L., Nolan, T., Søndergaard, H. 2003a. Muscle morphology and enzyme activity in adolescent Kenyan Nandi town and village boys. In publishing process.
- Larsen, H.B., Christensen, D.L., Nolan, T., Søndergaard, H. 2003b. Body proportions, aerobic exercise capacity and physical activity level of adolescent Nandi boys in western Kenya. In publishing process.
- Larsen, H.B., Nolan, T., Borch, C., Søndergaard, H., 2003c. Training response of adolescent Kenyan town and village boys to endurance running. *Scand. J. Med. Sci. Sports.* In press.
- Larsen, H.B., Søndergaard, H. Training response of adolescent Caucasian boys to endurance running. In publication process.

- Larsen, H.B., Søndergaard, H., Asp, S., Calbet, J.A.L., Saltin, B., Skeletal muscle adaptation to endurance running in adolescent Kenyan town and village boys and in Danish boys. In publication process.
- Matthews, P., 1987. World and Continental Records. In: Athletics'87. International Track and Field Annual. London and International Publishers Ltd, London and Simon and Schuster Ltd, London, pp. 249–266.
- Maughan, R.J., Leiper, J.B., 1983. Aerobic capacity and fractional utilisation of aerobic capacity in elite and non-elite male and female marathon runners. *Eur. J. Appl. Physiol. Occup. Physiol.* 52, 80–87.
- Myburgh, K.H., 2003. What makes an endurance athlete world class? Not simply a physiological conundrum. *Comp. Biochem. Physiol. A*.
- Myers, M.J., Steudel, K., 1985. Effect of limb mass and its distribution on the energetic cost of running. *J. Exp. Biol.* 116, 363–373.
- Pollock, M.L., 1977. Submaximal and maximal working capacity of elite distance runners. Part I: cardiorespiratory aspects. *Ann. NY Acad. Sci.* 301, 310–327.
- Prud'homme, D., Bouchard, C., Leblanc, C., Landry, F., Fontaine, E., 1984. Sensitivity of maximal aerobic power to training is genotype-dependent. *Med. Sci. Sports Exerc.* 16, 489–493.
- Saltin, B., Kim, C.K., Terrados, N., Larsen, H., Svedenhag, S., Rolf, C.J., 1995a. Morphology, enzyme activities and buffer capacity in leg muscles of Kenyan and Scandinavian runners. *Scand. J. Med. Sci. Sports.* 5, 222–230.
- Saltin, B., Larsen, H., Terrados, N., Bangsbo, J., Bak, T., Kim, C.K., et al., 1995b. 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.
- Saltin, B., Åstrand, P.-O., 1967. Maximal oxygen uptake in athletes. *J. Appl. Physiol.* 23, 353–358.
- Simoneau, J.-A., Bouchard, C., 1989. Human variation in skeletal muscle fiber-type proportion and enzyme activities. *Am. J. Physiol.* 257, E567–E572.
- Sjödin, B., Jacobs, B., 1981. Onset of blood lactate accumulation and marathon running performance. *Int. J. Sports Med.* 2, 23–26.
- Sjödin, B., Jacobs, I., Svedenhag, J., 1982. Changes in onset of blood lactate accumulation (OBLA) and muscle enzymes after training at OBLA. *Eur. J. Appl. Physiol.* 49, 45–57.
- Sjödin, B., Svedenhag, J., 1985. Applied physiology of marathon running. *Sports Med.* 2, 83–99.
- Skinner, J.S., Jaskólski, A., Jaskólska, A., Krasnoff, J., Gagnon, J., Leon, A.S., et al., 2001. Age, sex, race, initial fitness, and response to training: the HERITAGE Family Study. *J. Appl. Physiol.* 90, 1770–1776.
- Svedenhag, J., 1995. Maximal and submaximal oxygen uptake during running: how should body mass be accounted for? *Scand. J. Med. Sci. Sports.* 5, 175–180.
- Svedenhag, J., Sjödin, B., 1984. Maximal and submaximal oxygen uptakes and blood lactate levels in elite male middle- and long-distance runners. *Int. J. Sports Med.* 5, 255–261.
- Weston, A.R., Karamizrak, O., Smith, A., Noakes, T.D., Myburgh, K.H., 1999. African runners exhibit greater fatigue resistance, lower lactate accumulation, and higher oxidative enzyme activity. *J. Appl. Physiol.* 86, 915–923.
- Weston, A.R., Mbambo, Z., Myburgh, K.H., 2000. Running economy of African and Caucasian distance runners. *Med. Sci. Sports Exerc.* 32, 1130–1134.
- Williams, K.R., Cavanagh, P.R., 1987. Relationship between distance running mechanics, running economy, and performance. *J. Appl. Physiol.* 63, 1236–1245.