Superior performance of African runners in warm humid but not in cool environmental conditions

Frank E. Marino,1 Mike I. Lambert,2 and Timothy D. Noakes2

1School of Human Movement Studies, Charles Sturt University, Bathurst NSW 2795, Australia; and 2MRC/UCT Research Unit for Exercise Science and Sports Medicine, Department of Human Biology, Faculty of Health Sciences, University of Cape Town 7725, South Africa

Submitted 5 June 2003; accepted in final form 27 August 2003


The purpose of this study was to examine the running performances and associated thermoregulatory responses of African and Caucasian runners in cool and warm conditions. On two separate occasions, 12 (n = 6 African, n = 6 Caucasian) well-trained men ran on a motorized treadmill at 70% of peak treadmill running velocity for 30 min followed by an 8-km self-paced performance run (PR) in cool (15°C) or warm (35°C) humid (60% relative humidity) conditions. Time to complete the PR in the cool condition was not different between groups (~27 min) but was significantly longer in warm conditions for Caucasian (33.0 ± 1.6 min) vs. African (29.7 ± 2.3 min, P < 0.01) runners. Rectal temperatures were not different between groups but were higher during warm compared with cool conditions. During the 8-km PR, sweat rates for Africans (25.3 ± 2.3 ml/min) were lower compared with Caucasians (32.2 ± 4.1 ml/min; P < 0.01). Relative rates of heat production were less for Africans than Caucasians in the heat. The finding that African runners ran faster only in the heat despite similar thermoregulatory responses as Caucasian runners suggests that the larger Caucasians reduce their running speed to ensure an optimal rate of heat storage without developing dangerous hyperthermia. According to this model, the superior running performance in the heat of these African runners can be partly attributed to their smaller size and hence their capacity to run faster in the heat while storing heat at the same rate as heavier Caucasian runners.

Marino, Frank E., Mike I. Lambert, and Timothy D. Noakes. Superior performance of African runners in warm humid but not in cool environmental conditions. J Appl Physiol 96: 124–130, 2004. First published August 29, 2003; 10.1152/japplphysiol.00582.2003.—The purpose of this study was to examine the running performances and associated thermoregulatory responses of African and Caucasian runners in cool and warm conditions. On two separate occasions, 12 (n = 6 African, n = 6 Caucasian) well-trained men ran on a motorized treadmill at 70% of peak treadmill running velocity for 30 min followed by an 8-km self-paced performance run (PR) in cool (15°C) or warm (35°C) humid (60% relative humidity) conditions. Time to complete the PR in the cool condition was not different between groups (~27 min) but was significantly longer in warm conditions for Caucasian (33.0 ± 1.6 min) vs. African (29.7 ± 2.3 min, P < 0.01) runners. Rectal temperatures were not different between groups but were higher during warm compared with cool conditions. During the 8-km PR, sweat rates for Africans (25.3 ± 2.3 ml/min) were lower compared with Caucasians (32.2 ± 4.1 ml/min; P < 0.01). Relative rates of heat production were less for Africans than Caucasians in the heat. The finding that African runners ran faster only in the heat despite similar thermoregulatory responses as Caucasian runners suggests that the larger Caucasians reduce their running speed to ensure an optimal rate of heat storage without developing dangerous hyperthermia. According to this model, the superior running performance in the heat of these African runners can be partly attributed to their smaller size and hence their capacity to run faster in the heat while storing heat at the same rate as heavier Caucasian runners.

There is evidence that athletes of (East) African ancestry presently dominate international distance running events (10, 22). A number of studies have searched for a physiological explanation for this apparent superiority of African athletes.

Results from early studies suggested that Africans might enjoy a superior economy of movement (18, 26, 35). Indeed, a recent study confirms that African runners had a significantly lower minimum oxygen uptake (V̇O2 min) than did Caucasian runners of matched ability but were more economical, at least over a 10-km race distance (33). In addition, African runners generally have a lower absolute V̇O2 max than do Caucasian runners of matched ability. However, these differences diminish when V̇O2 max is expressed relative to body mass (7, 32).

Bosch et al. (4) compared various physiological responses of (South) African and Caucasian runners during a 42-km treadmill marathon in cool conditions and concluded that the only discernable difference was the ability of African runners to run at a higher percentage of V̇O2 max during competition. Coetzer et al. (7) have also shown greater fatigue resistance in a group of elite African runners who were able to sustain a higher %V̇O2 max during races longer than 3 km. African athletes also had lower blood lactate concentrations for a given oxygen consumption. Furthermore, African athletes fatigued less rapidly during repetitive bouts of isometric testing of the quadriceps muscles. The physiological basis for this enhanced fatigue resistance was unclear because muscle fiber types were not different between groups, although the African athletes tended to have a lower percentage of type I muscle fibers. More recently, and in support of these previous findings, Weston et al. (32) showed that African runners took 21% longer to fatigue during an incremental running test. This superior resistance to fatigue was associated with higher skeletal muscle enzyme activity and a lower proportion of type I fibers compared with Caucasian athletes. A higher skeletal muscle oxidative capacity has also been found in nonathletic persons of (West) African ancestry (29).

A fundamental problem when comparing (East and South) African and Caucasian athletes is the inherent difference in body size between the two groups given that elite East and South African athletes are generally smaller than Caucasian athletes (7, 27, 33). It has also been shown that a small body size could be an advantage in distance running, particularly in the heat (8, 19), and that lean body mass may account for differences in running performance in the heat between individuals of different sizes (34). It has been hypothesized that, as ambient temperature rises from 25 to 35°C, larger and heavier runners must run slower because the accumulation of body heat would increase body temperature to levels commonly associated with fatigue (8, 12, 19, 21). Given the evidence that African athletes seem to be more economical, have higher fatigue resistance, and are generally smaller than their Caucasian counterparts, it seems feasible to postulate that smaller East and South African runners might have an advantage over Caucasian athletes during distance running in warmer environmental conditions. We are unaware of any studies that have specifically tested this hypothesis.

Therefore, the purpose of this study was to examine whether African distance runners enjoy any advantage over Caucasian runners when running in warmer ambient conditions because, as previously postulated (8, 19), their smaller size would allow a faster running speed with a similar or lesser thermoregulatory strain.

Address for reprint requests and other correspondence: F. E. Marino, School of Human Movement Studies, Charles Sturt Univ., Bathurst NSW 2795, Australia (E-mail: fmarino@csu.edu.au).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
METHODS

Subjects. Twelve (6 African, 6 Caucasian) well-trained male endurance runners were recruited for the study. Table 1 shows the mean physical characteristics of each group. Overall, the physical characteristics of the subjects indicate that the sample for each group was comprised of representative African and Caucasian runners as those reported in previous studies (e.g., African ~57 kg; Caucasian ~67 kg) (2, 4, 7, 17, 18, 27, 33). It was assumed that subjects were not naturally heat acclimatized because the experiments were conducted during the months of September and October, at which time the daily temperature ranged from 8 to 25 °C. None of the subjects reported any international travel within the 3 mo before the experiments. All experimentation was carried out in a climate chamber. On average, the subjects maintained a training volume of 60–80 km/wk for at least 3 mo before the study. Subjects also competed in national and local running events on a regular basis. All participants were instructed to maintain a regular diet during the study period and were asked to refrain from alcohol and caffeine for at least 24 h before testing. The study was approved by the Research and Ethics Committee of the Faculty of Health Sciences of the University of Cape Town, and each subject signed a letter of consent after being informed of the risks associated with the experiment.

Descriptive measurements. Stature (cm) and body mass (kg) were determined by use of a precision stadiometer and balance (model 770, Seca, Bonn, Germany). All measurements were recorded with the subject fully instrumented and wearing light running shorts. Nine skinfold sites (biceps, triceps, subscapular, pectoral, midaxilla, mid-abdominal, suprailiac, midthigh, and medial calf) were measured in duplicate with skinfold calipers (Holtain, Crymych, UK) to the nearest millimeter. Percent body fat was estimated as previously described (14), and body surface area (A_D) was calculated from mass and height as described by DuBois and DuBois (9).

Familiarization and incremental running tests. During a familiarization session, peak oxygen uptake (V_O2peak) and peak treadmill running velocity (PTV) were determined in moderate environmental conditions in which the ambient temperature, relative humidity, and wind velocity were set at 21.0 ± 0.6 °C, 50.0 ± 0.9%, and 5.0 ± 0.6 km/h, respectively. The individual V_O2peak and PTV were determined on a motorized treadmill (Powerjog EG30, Sports Engineering, Birming- ham, UK) set at a 1% gradient. Subjects started running at 12 km/h with speed increments of 1 km/h every minute until they could no longer keep pace. The last increment in speed that could be maintained for at least 1 min was defined as the PTV. During the incremental tests, the subjects wore a nose clip and breathed through a mouthpiece connected to an automated gas analyzer (Oxycon Alpha, Jaeger). Before each test, the gas analyzer was calibrated with gases of known concentration and the ventilometer was calibrated with a 3-liter syringe (Hans Rudolph, Vacumed, Ventura, CA). Oxygen consumption, CO2 production, minute ventilation, and respiratory exchange ratio were calculated for each breath. V_O2peak (mL·kg⁻¹·min⁻¹) was the average of the highest values attained over the final minute of exercise. After the measurements of V_O2peak and PTV, the subjects rested for ~5–7 min and then performed a familiarization run on the treadmill to minimize a “learning effect” for the subsequent experimental trials. They began the familiarization trial by running at 70% of PTV for 1–2 min and then as far as possible in 10 min by adjusting their running speed with a touch pad on the side arm of the treadmill.

Experimental trials. Each trial was conducted at the same time of day so that the effect of circadian variation could be minimized. During each trial, relative humidity and wind velocity were kept constant at 60.3 ± 0.8% and 15.1 ± 0.6 km/h, respectively, while the ambient temperature was set at either 15 or 35 °C.

Before the experimental trials, the subjects voided and inserted a rectal thermistor (Mon-a-therm, Mallinckrodt, OH) secured by a bead 10 cm beyond the anal sphincter. Four skin thermistors were then secured as previously described (25), and subjects were fitted with a heart rate monitor (Sport Tester, Polar Electro, Kempele, Finland).

The subject then entered the climate chamber and started a submaximal run for 30 min at 70% PTV (range 14.7–16.1 km/h). Thereafter, there was a 5-min interval during which the subject removed socks and shoes and was toweled dry, reweighed, and permitted to drink up to 300 mL of distilled water. The subject was then prepared for an 8-km performance run that was to be completed as fast as possible by adjusting the running speed. The running speed was noted at the end of each minute and at the end of exercise. A mean running speed was calculated at the end of each 5-min interval and when subjects completed the 8 km. An overall mean running speed was calculated for the time taken to complete the run. The changes in body mass were adjusted for fluid ingested and were used to calculate total body water rates (without correction for metabolic fuel utilization during the trial).

Throughout the submaximal and 8-km trials, rectal and skin temperatures at four sites (chest, arm, thigh, leg) were monitored continuously with a teletehermometer (YSI model 4002, Yellow Springs, OH) and recorded at 5-min intervals. Mean skin temperature was calculated as previously described (25).

Heart rate and subjective measurements. Heart rate was monitored continuously and recorded at 5-min intervals with a Polar heart rate monitor (Sport Tester, Polar Electro). Rating of perceived exertion (RPE) was measured at 5-min intervals as previously described (3).

Heat production, storage, and dissipation. Although varying slightly with running economy, heat production in runners has been shown to amount to ~4 kJ·kg body mass⁻¹·km⁻¹ (20). Therefore, rate of heat production (H) in watts (W) is equal to the product of the runner’s body mass (in kg), the running speed (v, in m/s), and ~4 J produced per kilogram of body mass. The rate of heat storage (S) was estimated with the equation \( S = (3.48 \times 10^5) \times (\text{body mass} \times T_a \times \text{Tb}^{-1}) \), where \( 3.48 \times 10^5 \) is the specific heat of body tissue (in J·kg⁻¹·°C⁻¹), \( T_a \) is the change (\( \Delta T \)) in mean body temperature \( (T_b) \) calculated from \( T_b = 0.87 T_r + 0.13 T_a \), where \( T_r \) is rectal temperature and \( T_a \) is mean skin temperature, over the exercise period in seconds, and \( A_D \) is body surface area in square meters. Heat loss via potential evaporation \( (E_p) \) was calculated from the predicted sweat rates determined from changes in body mass and the 40.55 kJ·mol latent heat of evaporation of water and its 18 g·mol molecular weight. The evaporation of 1 liter of sweat per hour dissipates ~675 J/s or W, assuming that all the sweat is evaporated (8). Potential rates of heat loss via convection (C) and radiation \( (R) \) were estimated with the following equations (20)

\[
C = (T_h - T_r) \times 0.85 A_D \times 8.3
\]

\[
R = (T_h - T_a) A_D \times 5.2
\]

where \( T_h - T_r \) is the difference between mean skin temperature and the ambient air (in °C), \( v \) is the square root of the velocity of air flow over the skin in (m/s), \( A_D \) is the body surface area (in m²), and 8.3 and 5.2 are heat transfer coefficients (in W·m⁻²·°C⁻¹), and \( T_h - T_a \) is the difference between mean skin temperature and mean radiant

Table 1. Characteristics of African and Caucasian runners

<table>
<thead>
<tr>
<th></th>
<th>African</th>
<th>Caucasian</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height, cm</td>
<td>167.4±4.4</td>
<td>183.4±6.5*</td>
</tr>
<tr>
<td>Mass, kg</td>
<td>59.3±4.4</td>
<td>76.6±9.3*</td>
</tr>
<tr>
<td>A_D, m²</td>
<td>1.66±0.1</td>
<td>1.98±0.2*</td>
</tr>
<tr>
<td>%BF</td>
<td>5.1±0.2</td>
<td>5.3±0.3</td>
</tr>
<tr>
<td>Skinfold, mm</td>
<td>49.1±2.0</td>
<td>55.5±3.2</td>
</tr>
<tr>
<td>V_O2peak, mL·kg⁻¹·min⁻¹</td>
<td>62.6±3.5</td>
<td>64.3±3.0</td>
</tr>
<tr>
<td>PTV, km/h⁻¹</td>
<td>21.2±0.8</td>
<td>20.8±1.2</td>
</tr>
</tbody>
</table>

Values are means ± SD. A_D, body surface area; %BF, percent body fat; V_O2peak, peak oxygen uptake; PTV, peak treadmill velocity. *P < 0.01 compared with African.
temperature of the walls of the climate chamber. The required evaporation ($E_a$) was estimated from the residual component from $H \pm S \pm C \pm R$.

Statistics. Separate ANOVAs for repeated measures on time and trials were applied to determine treatment effects during exercise. If a main effect was detected post hoc, comparisons were made with either Tukey’s honestly significant difference test for pairwise comparisons or simple main effects for significant interactions. Significance was accepted at $P < 0.05$. All data are presented as means $\pm$ SD.

RESULTS

Performance run. The African runners completed the performance run in cool (15°C) conditions in 27.4 ± 1.0 min, which was not different from the 27.4 ± 0.4 min for Caucasian runners. African runners ran marginally slower (29.7 ± 2.3 min) in the heat (35°C), but this was not significant. In contrast, compared with their time in the cool condition, Caucasian runners ran slower in the heat (33.0 ± 1.6 min vs. 27.4 ± 0.4; $P < 0.05$).

Figure 1 shows the mean running speed at 5-min intervals for both groups during the submaximal and performance runs in each ambient condition. During the performance run in cool conditions, mean running speed for Caucasian runners was 17.5 ± 0.6 (range 17.0–17.7) km/h and was similar to the mean running speed of 17.4 ± 0.8 (range 16.8–18.4) km/h for the African runners. Conversely, during the performance run in the heat, Caucasian runners were only able to maintain a mean running speed of 14.5 ± 0.7 (range 13.8–16.6) km/h compared with the mean running speed of 16.0 ± 1.2 km/h ($P < 0.01$) (range 15.2–16.7 km/h) for the African runners. Thus running speed in the heat was significantly slower at all time points for Caucasian runners compared with their performance in the cool condition (Fig. 1). In contrast, the speed of the African runners was significantly reduced only at the last two time points compared with their performance in the cool conditions (Fig. 1).

Thermoregulatory responses, heat production, storage, and dissipation. During the submaximal and performance runs, mean skin temperatures were not different between African and Caucasian runners (Fig. 2). However, during cool conditions, the mean skin temperature ranged from 24.5 to 25.7°C compared with a range of 33.9–34.9°C during the warm condition. Mean skin temperatures at 5-min intervals were significantly different between ambient conditions for both groups (Fig. 2). Rectal temperature increased over time during the submaximal run from preexercise to approximately 37.8°C in cool conditions and ~38.4°C in warm conditions for both groups. However, the sole difference between groups became apparent in warm conditions during the remaining 10 min of the performance run, when Caucasian athletes reached higher rectal temperatures than when they ran in cool conditions (Fig. 2) despite the fact that they were running significantly slower. Rectal temperatures at the end of the performance run were 38.7 ± 0.4°C in cool and 39.2 ± 0.2°C ($P < 0.05$) in warm conditions for African runners and 38.6 ± 0.5°C in cool and 39.5 ± 0.5°C ($P < 0.05$) in warm conditions for Caucasian runners. The rate of increase in rectal temperature during the submaximal run was similar in cool and warm conditions but was 2.2°C/h for African runners and 3.2°C/h ($P < 0.05$) for Caucasian runners. This rate of increase was reduced for both groups during the performance run in warm conditions and was similar for African (1.6°C/h) and Caucasian (1.8°C/h) runners.

The total body sweat rates for the combined submaximal and performance runs in cool conditions were 13.1 ± 2.2 ml/min for African runners and 19.5 ± 5.0 ml/min for Caucasian runners, but these were not significantly different. Compared
with the cool conditions, the sweat rate increased during warm conditions to 22.1 ± 3.0 ml/min for Africans and 28.9 ± 4.1 ml/min ($P < 0.03$) for Caucasian runners. Figure 3 shows the separate total body sweat rates for submaximal and performance runs in both cool and warm conditions. The sweat rate for African runners was similar during submaximal (13.3 ± 2.8 ml/min) and performance (12.8 ± 2.5 ml/min) runs in cool conditions. In warm conditions, the sweat rate tended to increase in the African runners from the submaximal to performance runs (18.9 ± 6.0 ml/min vs. 25.3 ± 2.3 ml/min), but this was not significant. Caucasian runners tended to sweat more than Africans in the cool condition (20.1 ± 3.3 vs. 18.9 ± 6.0 ml/min), although this was not significant during either submaximal or the performance runs. During warm conditions, the heart rate for the African runners was 149 ± 6 beats/min compared with 176 ± 7 beats/min ($P < 0.01$) for Caucasian runners. The heart rate was significantly lower for African runners at each 5-min interval during the submaximal run in cool conditions from 10 to 30 min (Fig. 4). During the submaximal run in the cool condition, the average heart rate for the African runners was 149 ± 10 beats/min compared with 160 ± 7 beats/min ($P < 0.01$) for Caucasian runners. The heart rate was significantly higher during the submaximal run for Caucasian runners at each 5-min interval from 10 to 30 min in the warm condition. The mean heart rate for the Caucasian runners was 179 ± 5 beats/min compared with 160 ± 8 beats/min ($P < 0.01$) for Africans during the submaximal run in warm conditions (Fig. 4).

During the performance run in cool conditions, the mean heart rate was 171 ± 4 beats/min for the African runners compared with 176 ± 6 beats/min for Caucasians, which was not significantly different. The African runners commenced the

![Figure 3. Total body sweat rate during the submaximal run (SS) at 70% peak treadmill velocity and during the 8-km performance run (P). Cool conditions (T ≤ 22.1°C): • Africans (A); ● Caucasians (C). Warm conditions (T ≥ 35°C): ○ Africans; □ Caucasians. *$P < 0.01$ compared with cool conditions; †$P < 0.05$ compared with Africans.](https://jap.physiology.org/doi/abs/10.1152/jappl.00529.2003)

Table 2. Heat exchange values for African and Caucasian runners in each submaximal and 8-km performance runs in cool (15 °C) and warm (35 °C) humid conditions

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>African 15 °C Submax</td>
<td>967±67</td>
<td>21±1</td>
<td>−755±93</td>
<td>−538±113</td>
<td>−232±40†</td>
</tr>
<tr>
<td>8-km PR</td>
<td>1,126±97</td>
<td>29±1</td>
<td>−620±159</td>
<td>−475±92</td>
<td>−355±135</td>
</tr>
<tr>
<td>Caucasian 15 °C Submax</td>
<td>1,271±170‡</td>
<td>71±4‡</td>
<td>−759±184</td>
<td>−769±93‡</td>
<td>−583±157</td>
</tr>
<tr>
<td>8-km PR</td>
<td>1,458±178‡</td>
<td>81±4‡</td>
<td>−742±180</td>
<td>−777±94‡</td>
<td>−797±103</td>
</tr>
<tr>
<td>African 35 °C Submax</td>
<td>967±67</td>
<td>123±4*‡‡</td>
<td>26±12*</td>
<td>−765±143†</td>
<td>−1,116±63*</td>
</tr>
<tr>
<td>8-km PR</td>
<td>1,062±143</td>
<td>73±2*</td>
<td>45±19*</td>
<td>−1,014±92*</td>
<td>−1,180±149*</td>
</tr>
<tr>
<td>Caucasian 35 °C Submax</td>
<td>1,271±170‡</td>
<td>106±5*‡‡</td>
<td>19±12‡</td>
<td>−1,012±133‡‡</td>
<td>−1,397±175‡‡</td>
</tr>
<tr>
<td>8-km PR</td>
<td>1,244±169‡</td>
<td>44±2‡</td>
<td>78±33*</td>
<td>−1,435±182*</td>
<td>−1,367±106‡‡</td>
</tr>
</tbody>
</table>

Values are means ± SD. $H$, heat production; $S$, rate of heat storage; $C + R$, heat loss via convection ($C$) and radiation ($R$); $E_P$, potential evaporation; $E_R$, required evaporation. Submax, 30-min submaximal treadmill run; 8-km PR, 8-km performance run. *Different between ambient conditions ($P < 0.05$); †different between submaximal and performance runs ($P < 0.05$); ‡different between groups ($P < 0.05$).
performance run in cool conditions with a lower heart rate (35–40 min) than Caucasians, but this difference was not evident for the remainder of the run (Fig. 4). The mean heart rate during the performance run in warm conditions was 185 ± 7 beats/min for Caucasians and 182 ± 6 beats/min for Africans. However, there were no differences in heart rates at any time between Africans and Caucasians during the performance run in warm conditions (Fig. 4). Heart rates at the end of the performance run in the cool condition were 191 ± 6 and 186 ± 7 beats/min for Caucasians and Africans, respectively, and in warm conditions terminal heart rates were 189 ± 6 and 186 ± 9 beats/min for Caucasians and Africans, respectively.

RPE during the submaximal run in the cool condition tended to be lower for African (9 ± 1 units) compared with Caucasian runners (11 ± 1 units), but this difference was not significant (Fig. 4). In warm conditions during the submaximal run, Caucasian runners also tended to report higher RPE responses (12 ± 2 units), but again these were not significant. There were no discernable differences in RPE during the performance runs in any condition other than the generally lower RPE of the African runners (12 ± 3 units) in the cool condition (Fig. 4). RPE during the performance runs in warm conditions were ~15 units for both groups.

DISCUSSION

Previous studies have shown that anthropometric characteristics such as mass, surface area-to-mass ratio, adiposity, and muscularity are key factors in determining individual heat strain levels during exercise (1, 13). In particular, runners with a low body mass have a distinct thermal advantage when running in conditions in which heat-dissipation mechanisms are at their limit (8, 19, 34). Specifically, as the ambient temperature rises from 25 to 35°C with a relative humidity >60%, larger heavier runners are unable to maintain a similar running pace compared with their smaller counterparts because this entails faster rates of heat accumulation and hence the more rapid onset of a limiting hyperthermia (8, 19). Although the difference in size between the African and Caucasian runners in the present study was significant, the physical characteristics of the African runners are not dissimilar to those reported in previous studies comparing physiological responses and performances of elite African and Caucasian athletes (2, 4, 7, 17, 18, 33). The present findings in addition to the observation that African athletes are generally smaller than their Caucasian counterparts suggest that the body size of the Africans provides an advantage during distance running, particularly in the heat. Conversely, for the Caucasian runners, their larger size presents a disadvantage during distance running in the heat, whereby it seems that these athletes adopt an anticipatory reduction in running speed and hence the rate of heat production, such that a limiting hyperthermia is not reached before the successful completion of the exercise bout.

In the present study, African and Caucasian subjects had similar percent body fat, but Caucasian runners were ~17 kg heavier than the African runners. Thus, when running at the same pace, African runners produced less heat than did the Caucasian runners and had lower rates of heat storage and lower potential evaporation in cool conditions, in which the environment does not limit rates of heat loss (8). The rate of increase in rectal temperature during the submaximal run was similar for Caucasians and Africans, with the end submaximal rectal temperature reaching identical levels for each group for almost identical running speeds (14.8 vs. 14.6 km/h). This confirms that under cool conditions the larger Caucasians are able to thermoregulate as effectively as smaller African runners and can finish the submaximal run with identical rectal temperatures as these smaller African runners. However, this was not achieved without some cost, because Caucasian runners had higher, but not significant, sweat rates (Fig. 3) and significantly higher heart rates (Fig. 4) even under these cool conditions in which their pacing strategy was imposed and not self-selected.

Similarly, during the performance run in the cool conditions, African and Caucasian runners self-selected the same pacing strategy so that their overall performance was similar (Fig. 1). However, there was a trend for African runners to progressively increase their speeds throughout the performance trial with some evidence for an "end-spurt" from 45 min to the end of the trial (Fig. 1). In contrast, in the heat, the Caucasian runners ran significantly slower from the initiation of the trial, compared with their performance in the cool condition. Furthermore, in both African and Caucasian runners, running speeds fell progressively after 40 min and were significantly
lower in Caucasian than in African runners in the final two time points in the trial (Fig. 1).

Presently it is thought that exercise in the heat is limited by an elevated and limiting critical body temperature such that subjects will continue to exercise until a limiting core body temperature is reached at which point exercise terminates (21, 24). It is also thought that a critical limiting temperature acts directly on the central nervous system by reducing the drive or motivation for further exercise (5, 21, 23). However, this interpretation comes from studies in which the work rate is fixed and externally imposed so that the athlete is unable to alter their rate of heat production in response to the prevailing environmental conditions. In contrast, the findings of the present study indicate that performance in the heat is not limited solely by the attainment of a critical terminal rectal temperature per se but rather is regulated by the rate of increase in rectal temperature and hence the rate of heat storage based on the anticipated duration of the exercise bout. This ensures that the critical (limiting) core body temperature is not reached before the anticipated completion of the specific exercise bout. Interestingly, the rate of increase in rectal temperature during the performance trial was similar between African and Caucasian runners, with identical terminal rectal temperatures for both groups in cool (38.7 vs. 38.6°C) and warm (39.2 vs. 39.5°C) conditions even though the Caucasian runners took ~3.22 min longer to complete the performance run.

It has been previously suggested that athletes must arrange the energy consumption per unit time with respect to the finishing point (31). In the present example, both groups of athletes would need to draw on previous experience and arrange the required energy consumption relative to the anticipated rate of heat production and storage. The evidence for this anticipatory regulation of exercise performance in the present study is the following: First, the rate of increase in core temperature was similar for African and Caucasian runners in both warm and cool conditions. Second, running speed was significantly slower in Caucasian runners when they ran in the heat than in the cool, suggesting that they ran slower specifically to ensure that their rate of heat accumulation was similar to that in cool conditions, thereby ensuring that a limiting hyperpyrexia did not occur before the anticipated termination of the exercise bout. Third, Caucasian runners ran slower immediately from the onset of the performance trial in the heat (Fig. 1) when their rectal temperatures were 38.2°C (Fig. 2) and identical to values measured in African runners who were running substantially faster at that time. This indicates the action of an anticipatory process that reduced the running speed of Caucasian runners in the heat long before they developed a significant hyperpyrexia. Hence, the slower running speed of the Caucasian runners in the heat could not be explained by the attainment and maintenance of higher rectal temperatures for the duration of the performance trial. Fourth, both groups progressively reduced their running speeds during the latter half of the time trial in the heat but maintained (Caucasian) or increased (African) their speed when running in cool conditions. Despite, or more likely because of, these changes in running speed and hence in metabolic rate, the rate of heating was similar in all conditions.

Indeed, we are not the first to suggest that humans pace themselves during exercise in the heat specifically to prevent an excessive rate of heat production for the anticipated duration of the exercise bout (15). Tattersen et al. (30) found that the core temperature response of elite cyclists performing a 30-min time trial in moderate and warm humid conditions was similar, with terminal core temperature values for each condition reaching 39.0 and 39.2°C, respectively. Despite the similar core temperature response, mean power output was 6.5% lower in the warm humid conditions, essentially similar to the present findings. These authors concluded that, during self-paced exercise, cyclists select a power output that allows them to maintain a body temperature below a critical limit during exercise.

Thus the fact that the African runners were able to run at ~1.5 km/h faster than the Caucasian runners during the performance run with identical terminal rectal temperatures and a lower rate of heat storage suggests that these African runners were more efficient in either heat production or heat dissipation when forced to run in limiting environmental conditions. The possibility that heat dissipation might have been more efficient for Africans than Caucasians can be discounted on the basis of the high humidity in the present trial (20). However, heat production was higher for Caucasians in both cool and warm conditions even though African runners ran at higher speeds. This can be explained by the higher body mass of the Caucasians, although this was partly offset by their lower running speed. Another possibility is that African runners were more economical at higher gait speeds. Generally, efficiency of skeletal muscle is improved from 45% at 8 km/h to 80% at 32 km/h (6). However, Weston et al. (33) have shown that at 16 km/h African athletes were at least 5% more efficient than Caucasian runners, with this difference increasing to 8% when corrected for differences in body mass. It is noteworthy that in the present study the mean running speed in the heat for African runners was 16 km/h.

Another possibility explaining the different performances of African and Caucasian runners was the heart rate response. It was evident that Caucasian runners had a significantly higher cardiovascular strain during the submaximal run in the heat compared with the African runners (Fig. 4). This difference disappeared in both cool and warm conditions during the 8-km performance run. The fact that the Caucasians ran slower during the performance run in the heat but at similar heart rates as those measured in cool conditions and comparable to that measured in the African runners suggests that the cardiovascular strain was similar in all conditions. However, it has been shown that heat stress reduces V O2 max by 8% despite heart rate and core temperature reaching similar peak values as in the control condition (11). These authors also showed that, in trained humans, severe heat stress reduces V O2 max by accelerating the decline in cardiac output and mean arterial pressure, leading to decrements in exercising muscle blood flow, oxygen delivery, and uptake. If this is the case, then African runners must be able to maintain a higher cardiac output or alternatively a higher oxygen extraction from the working muscles for any given running speed because the V O2 max values for both groups were similar. This supports previous findings that suggest that African runners are able to maintain a higher %V O2 max during a treadmill marathon (4) and at 10- and 21.1-km distances (7). It is also noteworthy that all runners finished the performance run with identical heart rates irrespective of ambient conditions. Although it remains unclear why these athletes would finish the self-paced run with identical heart rates,
it is possible that terminal heart rate is yet another means by which the body self-regulates pacing during prolonged exercise.

In summary, this study shows that African and Caucasian runners of equivalent running ability in cool conditions and with similar maximal physiological characteristics, but with marked differences in body size and mass but not in body fat content, perform quite differently during an 8-km time trial in the heat. In particular, African runners were able to run ~1.5 km/h faster than Caucasian runners. Because this difference in running speed was apparent from the onset of the time trial, when rectal temperatures were the same in African and Caucasian runners and were only modestly elevated (~38°C), the slower running speed of the Caucasian runners was not caused by their reaching a higher limiting core temperature earlier in exercise than did the African runners. Rather, these findings implicate an anticipatory exercise response, the goal of which is to ensure an increase in core body temperature that does not produce a critical limiting temperature before the anticipated termination of the exercise bout. This anticipatory response would control the exercise work rate by regulating the number of motor units that are recruited or derecruited during prolonged exercise in the heat (16, 28).

In conclusion, the superior running performance of African runners in the heat in this study would likely be explained by physiological adaptations, in particular their smaller body mass and perhaps a greater capacity for heat loss in hot environmental conditions, both of which allow African runners to self-regulate pacing during exercise and attenuate the physiological stress signals to the central nervous system so that physiological limits are not prematurely reached.

GRANTS

F. E. Marino was supported by a Charles Sturt University Special Studies Program Grant. T. D. Noakes and M. J. Lambert were supported by The Harry Crossley and Nellie Atkinson Staff Research Funds of the University of Cape Town, the Medical Research Council of South Africa, and Discovery Health Propriety.

REFERENCES