A RE-EXAMINATION OF RUNNING ENERGETICS IN AVERAGE AND ELITE DISTANCE RUNNERS

by

Matthew E. Batliner

B.A., University of Colorado at Boulder, 2010

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirement for the degree of
Master of Science
Department of Integrative Physiology
2013

This thesis entitled:
A Re-Examination of Running Energetics in Average and Elite Distance Runners
written by Matthew E. Batliner
has been approved for the Department of Integrative Physiology

____
William Byrnes, Ph.D.

____
Rodger Kram, Ph.D

____
Alena Grabowski, Ph.D

Date_____________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

IRB protocol # 12-0112

Abstract

Batliner, Matthew E. (M.S., Integrative Physiology)

A Re-Examination of Running Energetics in Average and Elite Distance Runners

Thesis directed by Associate Professor William C. Byrnes

We measured the gross rates of oxygen consumption ($\dot{V}O_2$, $mlO_2 \cdot kg^{-1} \cdot min^{-1}$) and energy expenditure ($\dot{E}$, $kcals \cdot kg^{-1} \cdot min^{-1}$), and determined the oxygen (O_2COT, $mlO_2 \cdot kg^{-1} \cdot km^{-1}$) and energetic (ECOT, $kcals \cdot kg^{-1} \cdot km^{-1}$) costs of transport in average and elite runners over a wide range of submaximal speeds. Stride frequency (SF) and length (SL) were measured at each running speed. Ten Average (10 km run time=40-60 min) and 10 Elite (10 km run time<30 min, 10 km run time<31 min at altitude) male runners performed two progressive, submaximal treadmill economy tests on a high-speed force monitoring treadmill. The tests were performed on different days and began at either 107 or 121 $meters \cdot min^{-1}$. Treadmill speed was increased 27 $meters \cdot min^{-1}$ for each subsequent stage until a rating of perceived exertion of 15 or greater (sRPE15) was reported. $\dot{V}O_2$ and $\dot{E}$ were monitored via open-circuit indirect calorimetry during these economy testing sessions. SF and SL were calculated from analysis of vertical ground reaction forces (GRF) measured for 15 seconds during the final minute of each stage. The average sRPE15 was 214 $meters \cdot min^{-1}$ for the Average runners and 308 $meters \cdot min^{-1}$ for the Elite runners. $\dot{V}O_2$ and $\dot{E}$ vs. speed relationships were best described by linear models over the range of speeds achieved by Average subjects. $\dot{V}O_2$ or $\dot{E}$ vs. speed relationships were best described by a curvilinear model over the wider range of speeds achieved by Elite runners ($p<.05$). O_2COT or ECOT was found to decrease from 107-161 $meters \cdot min^{-1}$ for Average and Elite runners. For Elite runners, a significant increase in ECOT (8.8%) and O_2COT (11.3%) was observed from 214 $meters \cdot min^{-1}$ to 308 $meters \cdot min^{-1}$ ($p<.001$). No correlation between changes in SF or SL and changes in COT was observed in Elite subjects from moderate to fast speeds. $\dot{V}O_2$ and $\dot{E}$ vs. speed relationships were linear at moderate speeds and curvilinear over wider ranges of submaximal speeds. Measurements of O_2COT and ECOT at moderate speeds underestimate the energetic demand of running at speeds approaching elite race pace. The changes in COT observed over moderate to fast running speeds were not explained by changes in SF or SL.

Table of Contents

Chapter

List of Tables

Table

List of Figures

Figure

Chapter I

Literature Review

The Energetics of Running and the Concept of Economy

For years, researchers have quantified the energetic demand of running through the measurement of the rate of oxygen consumption ($\dot{V}O_2$). It is well accepted that this measure yields an indirect estimate of the energetic demand, or aerobic cost, of running at a given speed (2,3). Though the energetic demand of running is most commonly approximated through indirect calorimetry as gross $\dot{V}O_2$, this measure does not take into account changes in substrate utilization that take place with changes in exercise intensity. In order to account for this factor, it is preferable to use gross $\dot{V}O_2$ and gross rates of carbon dioxide production ($\dot{V}CO_2$) to calculate actual rates of energy expenditure ($\dot{E}$) in kilocalories ($kcal \cdot kg^{-1} \cdot min^{-1}$) or watts ($W \cdot kg^{-1}$) (5).

$\dot{V}O_2$ and energy expenditure are often measured in absolute terms ($L \cdot O_2 min^{-1}$, $kcal \cdot min^{-1}$), but in weight bearing activities, such as running, body weight can have a profound influence on energetic demand. As a result, it is common to express the energetic demand of running relative to body mass ($mlO_2 \cdot kg^{-1} \cdot min^{-1}$, $kcal \cdot kg^{-1} \cdot min^{-1}$). Though this calculation does normalize this measure during running to an extent, it is clear that the cost of running at a given speed remains variable between individuals (2,3,15,18). This suggests other factors must influence the cost of running. The apparent individual variability of the energetic demand of running spurred the development of the concept of economy.

Daniels and Daniels (2) generally defined economy as the relationship between $\dot{V}O_2$ and the speed of running. An accurate measure of running economy allows for comparison of the energetic demand of running between individuals or groups of individuals. If an individual expends less energy to perform a given task (in the case of running, to run at a given speed) they are considered to be more economical.

Running economy may be predictive of running performance, especially within groups of well-trained runners (3,18). As a result, many researchers have become interested in accurately quantifying both changes and differences in running economy within and between individuals as a means of predicting performance. Also, researchers and athletes alike have attempted to elucidate factors that may improve running economy in order to improve subsequent performance.

Several methods have been used to compare running economy between individuals. It is common to express running economy as the gross rate of energetic demand ($\dot{V}O_2$, $mlO_2 \cdot kg^{-1} \cdot min^{-1}$; $\dot{E}$, $kcal \cdot kg^{-1} \cdot min^{-1}$) or the gross energetic demand of running a given distance (O_2COT, $mlO_2 \cdot kg^{-1} \cdot km^{-1}$; ECOT, $kcal \cdot kg^{-1} \cdot km^{-1}$) while running at specific speeds (5,6,10,14,20).

Defining and Expressing Running Economy

Running economy is often expressed as the gross rate of energetic demand, as $\dot{V}O_2$ or $\dot{E}$, while running at a fixed speed. It is important to note that this measure allows for accurate comparison of the energetic demand of running *only* at a single fixed speed. Differences in running economy may exist at different running speeds. Thus, it is difficult to predict race performances for heterogeneous groups of runners from single fixed speed measures of economy. For example, race pace for an untrained individual may be 161 m/min (~6 MPH), while a well-trained runner may have a race pace of upwards of 268-320 m/min (~10-12 MPH). Because of this large disparity in race pace, comparing the energetic demand of running at a single fixed speed between these individuals may not be representative of the energetic demand of running at both individual's race pace. Also, the slope with which $\dot{V}O_2$ increases with increasing speed can be highly variable between individuals (Figure 2) making it difficult to predict the energetic demand of running at race pace from $\dot{V}O_2$ or $\dot{E}$ measured at a single speed. As a result, measuring the gross rate of energetic demand of running at a single peed is an ineffective method for comparing running economy at race pace between individuals and, thus, does not provide a precise depiction of how differences in economy may relate to differences in performance.

It is also possible to measure gross rates of energetic demand while running across a range of submaximal speeds (3). Plots of these data reveal a unique relationship between $\dot{V}O_2$ or $\dot{E}$ and speed for each individual runner that are often described using linear regression. This results in "economy lines" with variable slopes and intercepts. An individual with a lower gross rate of the energetic demand of running over a given range of submaximal speeds is considered to be more economical (Figure 1). It is easy to make comparisons when economy lines are parallel, but, in practice, economy lines often intersect. In these cases, an individual could be less economical at slow speeds than another but more economical at faster speeds or vice versa (Figure 2). Accordingly, both the slope and the intercept of economy lines should be taken into account when analyzing individual differences in economy.

Figure 1 (adapted from Jones, 2006): A comparison of economy lines within a single individual across years of endurance training. Gross $\dot{V}O_2$ ($mlO_2 \cdot kg^{-1} \cdot min^{-1}$) increased linearly with increasing speed at both time points. This individual would be considered more economical following years of endurance training because the economy line following training (represented by triangles) is lower than the economy line measured before endurance training. Interestingly, the economy curves remained fairly parallel within this individual, suggesting endurance training had a larger influence on the intercept rather than the slope of the economy line.

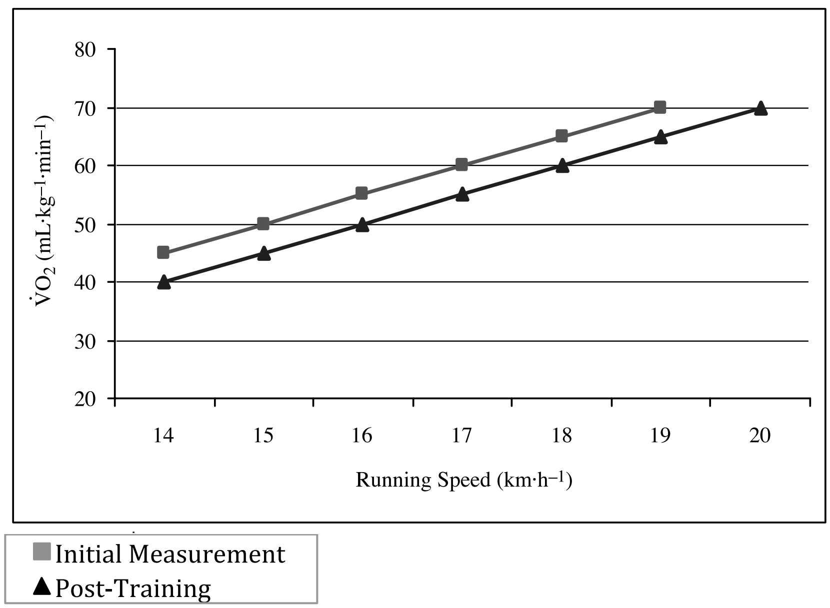
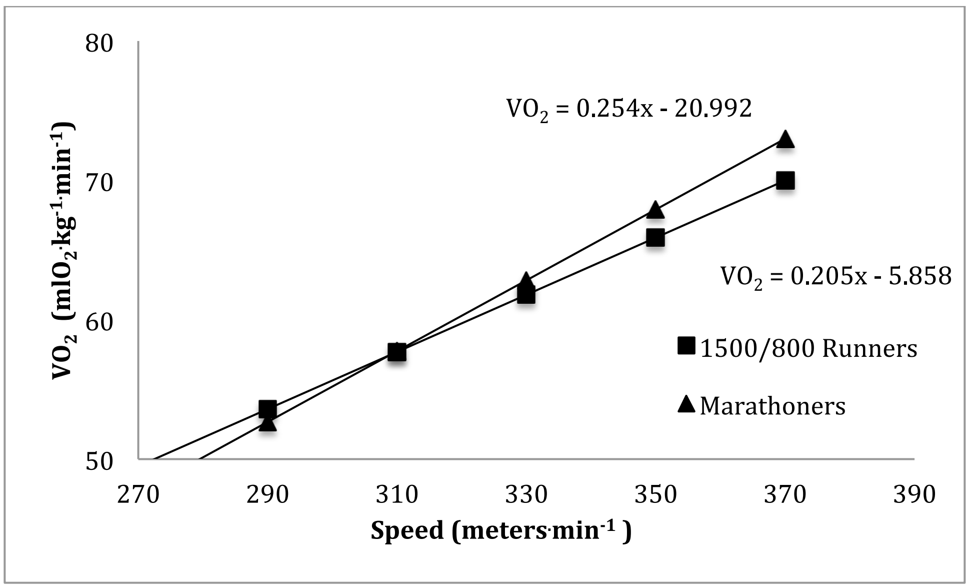


Figure 2 (adapted from Daniels and Daniels, 1992): An example of economy lines for two groups of runners that intersect. In this analysis comparing marathon vs. middle distance runners economy is largely dependent on speed. These lines suggest marathon runners (represented by circles) are more economical at slower speeds, while 800/1500 meter runners (represented by squares) were more economical at faster speeds.



It is also possible to express the energetic demand of running as the gross amount of oxygen (O_2COT, $mlO_2 \cdot kg^{-1} \cdot km^{-1}$) or energy (ECOT, $kcal \cdot kg^{-1} \cdot km^{-1}$) required to travel a given distance. Many have referred to this measure as the cost of transport (COT) (Schmidt and Nielsen, 1970; Kram and Taylor, 1990). COT has been utilized in order to compare the energetics of many forms of locomotion in humans and other animal species (10,19,20).

It is frequently asserted that gross COT remains constant across all sub-maximal running speeds in humans (4,6,7,14). In other words, the energy consumed in running a mile fast or slow is the same (10). If this assertion is correct, the measurement of COT at any sub-maximal running speed is representative of the energetic demand of running at any submaximal speed. Thus, COT measures obtained at any submaximal running speed may yield measures of running economy for comparison between heterogeneous groups of runners with vastly different competitive race paces.

Influence of Training and Performance Level on Running Economy

Each of the previously described methods of expressing the energetic demand of running has been employed by investigators to determine factors that influence running economy. Some factors that have consistently been observed to be associated with running economy are endurance-training status and performance ability (3,9,18). Morgan et al. (18) compared running economy, expressed as O_2COT, of good, sub-elite, and elite runners, classified based on 10 km performances, to non-runners. It was found that all of the trained runners exhibited better economy than non-runners, suggesting that endurance-training status may influence running economy. Further, within groups of trained runners, individuals with better performance ability were found to be more economical, with runners classified as elite exhibiting better economy than sub-elite and good runners (Figure 3). Also, within each group of trained runners, a large variation in economy was found, demonstrating that economy may be a valid predictor of performance even within the trained running groups. These data provide evidence that running economy is influenced by training status and may be a good predictor of performance both within and between groups of trained runners.

There is also evidence that years of training can improve running economy (Figure 4). Jones (9) examined the running economy of the world record holding female marathon runner over an eleven-year training period. It was found that running economy improved significantly in this individual over this period. These data suggests that vigorous training over the course of years can result in significant improvements in running economy, not only between groups of individuals, but within a single individual over time.

Figure 3 (adapted from Morgan, 1995): The oxygen cost of running a given distance (O2COT) for subjects classified as elite, sub-elite, good, and untrained based on race performance. Elite runners exhibit a significantly lower energetic demand of running than sub-elite and good runners

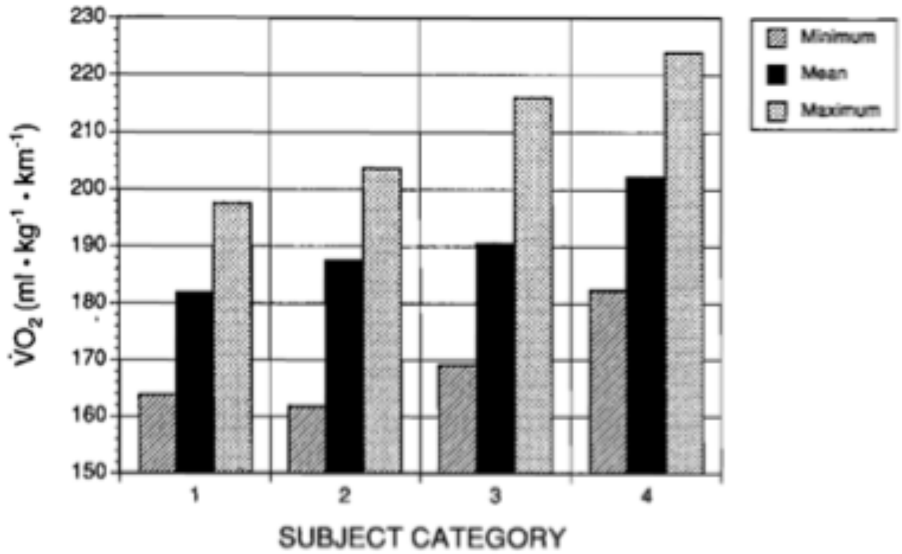
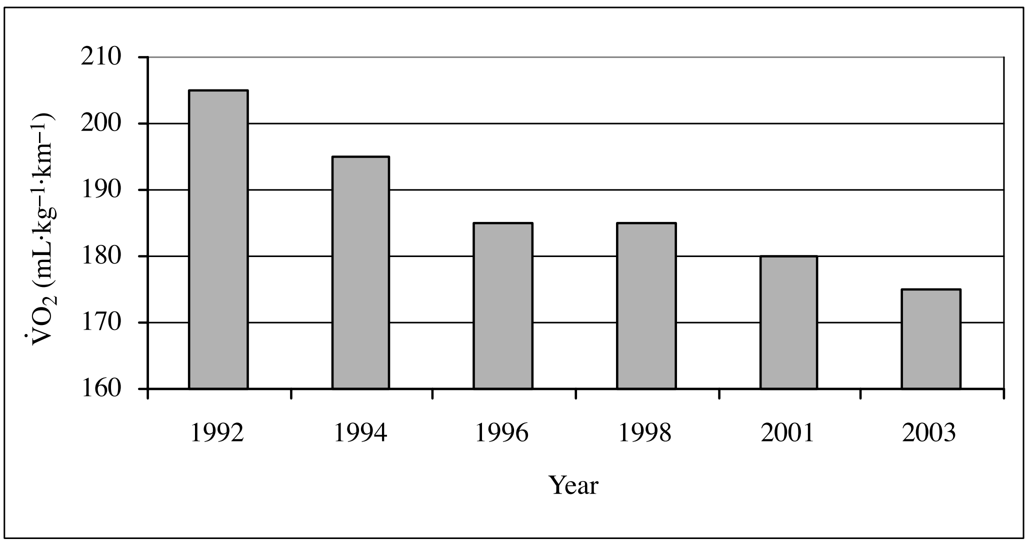


Figure 4 (adapted from Jones, 2006): O_2COT of a world record holding female marathon runner over an eleven-year training period (1992-2003). O_2COT significantly decreased over the period, indicating an improvement in economy as a result of prolonged vigorous training.



Controversy With Measures of Running Economy

Though the relationships between training, performance level, and running economy are well documented, the best method to express and compare running economy between individuals and groups of runners remains unclear. Recently, the assumption that COT is independent of running speed has come into question (21,22). Many investigations have reported COT to be independent of submaximal running speed (1,6,14,15,16), but recent findings suggest this assumption may not always be valid (21,22).

Several confounding factors may have influenced data leading to the assumption of an invariant COT with respect to submaximal running speed. It is possible that the running ability of subjects in previous investigations may have influenced findings. Subjects were often untrained or average runners (14,16). Our analysis of data compiled from several studies suggests that there may be differences in COT over a wide range of speeds, especially in elite distance runners (3,22). Using the linear regression of data collected by Daniels and Daniels (3) on elite marathon runners, we extrapolated $\dot{V}O_2$ values to slower submaximal speeds approaching race pace of an average runner (Figure 5). We then calculated O_2COT from gross $\dot{V}O_2$ for Daniels and Daniels' elite marathon runners over a wide range of submaximal running speeds. O_2COT was calculated by dividing the mean $\dot{V}O_2$ by running speed at each speed measured (Figure 6). These data suggest that gross COT is, in fact, influenced by speed in these runners, with O_2COT increasing substantially at faster running speeds.

It is important to note that the $\dot{V}O_2$ at slow speeds was not measured in these elite runners, but was predicted from extrapolation of linear regression of the $\dot{V}O_2$-speed relationship. However, the data derived from this prediction suggests that gross COT increases as speed increases in these individuals over the entire range of speeds. In reality, the predicted values are probably unrealistic at slower speeds, because the predicted COT values are significantly lower than any ever previously measured.

Data collected from previous pilot investigations in our laboratory, suggest runners of Average performance levels (males with 10 km times in the range of 40-60 minutes) exhibit a relatively constant COT across speed. Because average running populations are capable of running at only a small range of moderate submaximal running speeds, it was not possible to measure the energetic demand of running at fast submaximal speeds that approach Elite race pace in these runners. It is possible that the invariant COT reported in many previous investigations may be a consequence of measuring the energetic demand of running in untrained or average running populations over only moderate submaximal speeds. Also, the ability to sustain faster running speeds may influence the trends in COT across speed (Figure 6).

Preliminary data from our laboratory suggests that changes in stride frequency (SF) could explain differences in trends in COT at slow and fast submaximal running speeds. We found that trends in SF across speed tend to follow those of the COT, with stride frequency remaining fairly constant across moderate speeds and increasing at faster speeds (Figure 9).

Figure 5: The predicted gross O_2COT derived from Daniels and Daniels (1992) elite male marathon runners (solid line) and the actual measured gross O_2COT for average male runners with 10 km times in the range of 40-50 minutes (dashed line, Hunt) over a range of slower running speeds (150-250 meters·min^{-1}). O_2COT remains fairly constant across the range of speeds in the slower individuals, whereas predicted O_2COT appears to increase with increasing speed in the elite marathon runners.

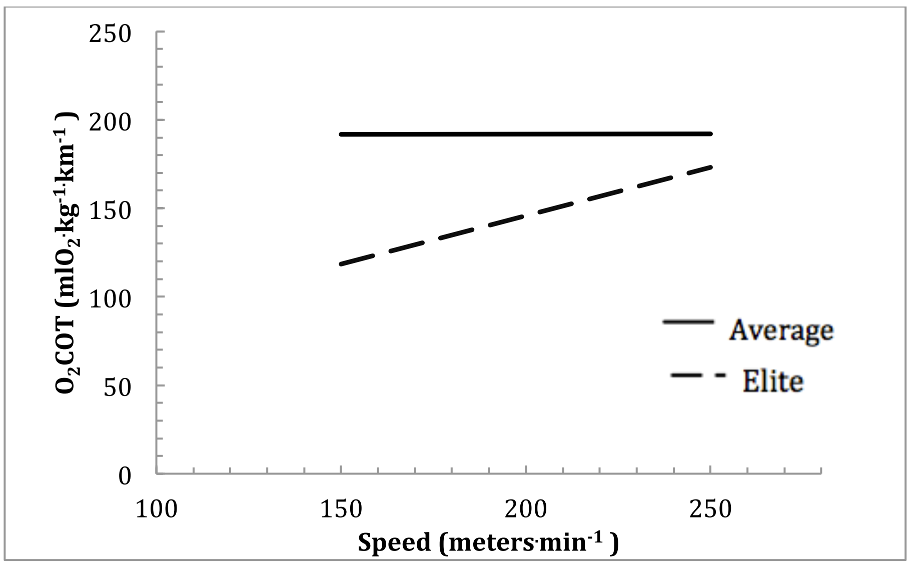


Figure 6: Derived gross O_2COT values from actual measured $\dot{V}O_2$ by Daniels and Daniels (1992) elite marathon runners. O_2COT increases significantly with increasing speed. $\dot{V}O_2$ was measured at fast speeds only. As a result, we lack data for gross COT at slow speeds in these elite runners.

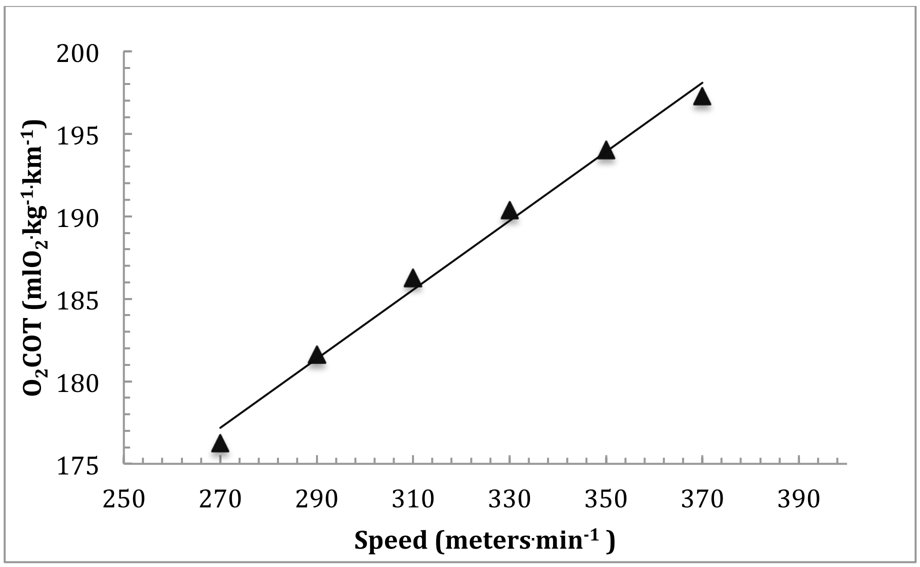


Figure 7: The actual measured values of O_2COT for a single well-trained female from slow (120 meters·min^{-1}) to fast speeds (281 meters·min^{-1}). O_2COT does not remain constant across speed in this individual, and seems to level off or increase at slow speeds.

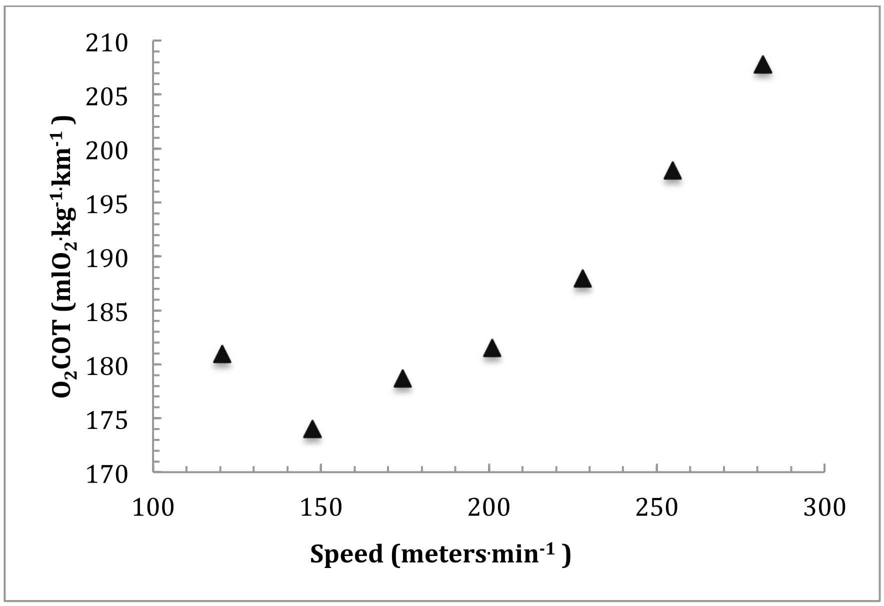


Figure 8: O_2COT at actual measured speeds for Daniels and Daniels (1992) elite marathoners (Elite) and an average female runner (Average). As is typical, energetic demand was measured over a fast range of speeds in the Elite runners and a slower range of speeds in the Average runner, as Average runners are not capable of sustaining faster speeds aerobically.

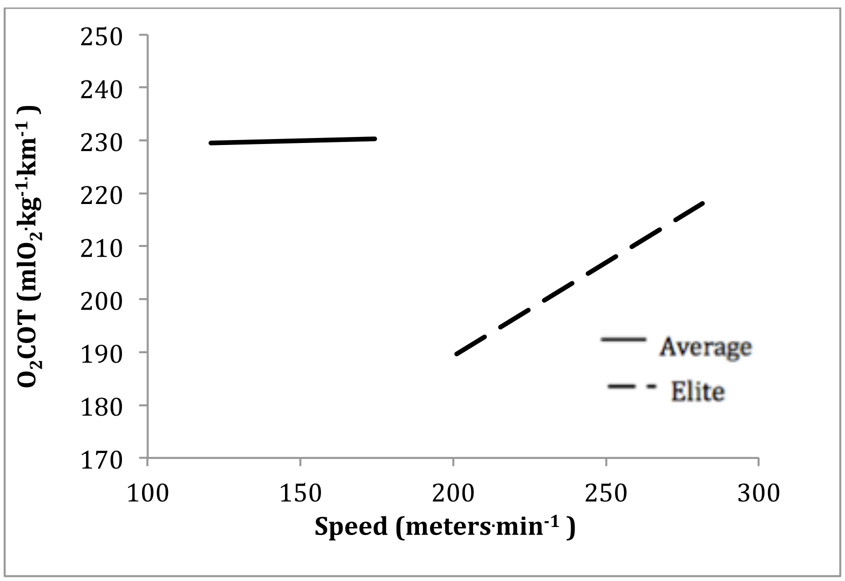
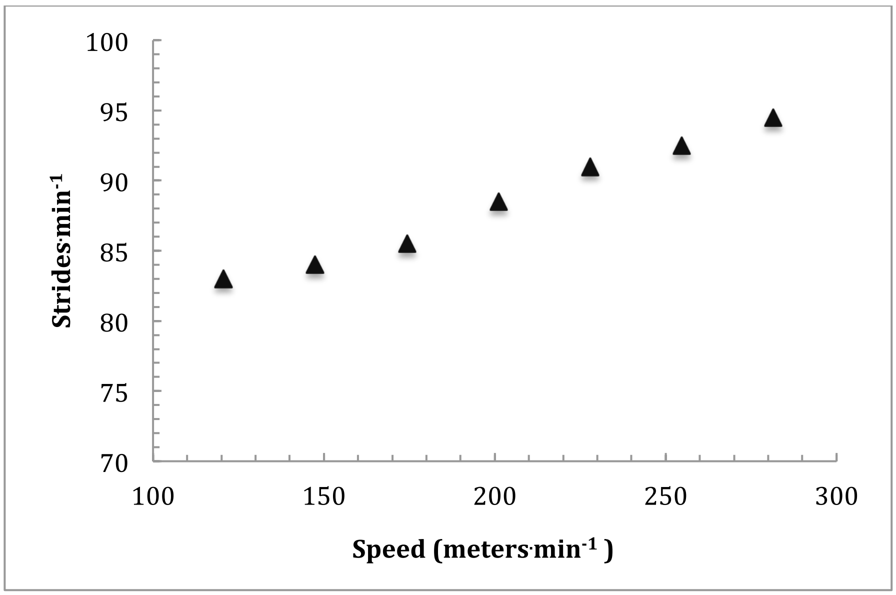


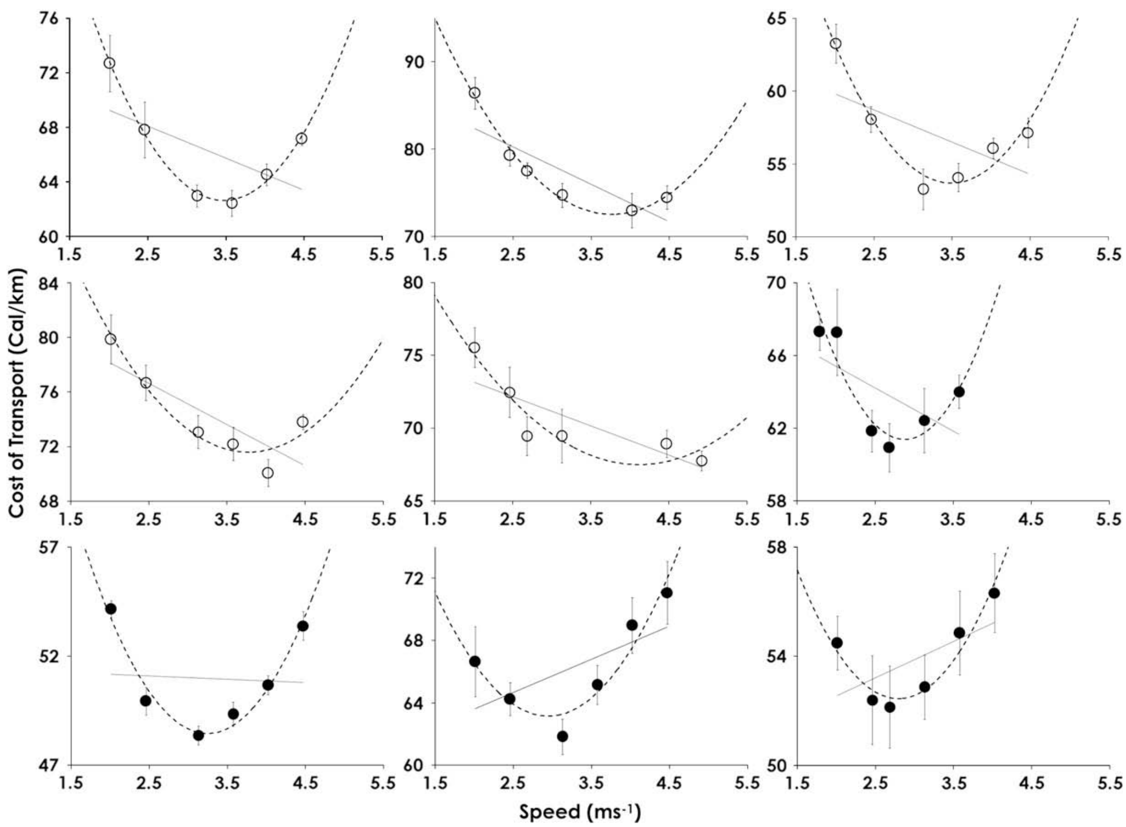
Figure 9: SF (strides·min^{-1}) across a wide range of speeds in an elite female runner. SF appears to remain relatively constant at slower speeds and increases at faster speeds. This trend mirrors that of the COT across slow to fast speeds in Elite runners, suggesting that changes in SF may correlate to changes in COT at faster speeds in Elite runners.



Recently, Steudel-Numbers and Wall-Scheffler (21) examined the gross ECOT of male and female runners at six speeds ranging from very slow (~4 MPH) to very fast (~10.1-10.9 MPH). Over this wide range of submaximal running speeds, ECOT was found to increase at both slow and fast running speeds resulting in U-shaped COT-speed relationships (Figure 10).

Steudel-Numbers and Wall-Scheffler did not attempt to determine whether any differences in COT exist on the basis of performance level or training status. As a consequence, it is not possible to discern whether their results were influenced by these factors. Also, Steudel-Numbers and Wall-Scheffler did not provide any mechanism explaining changes in COT at various speeds. It is logical to conclude that there must be a physiological or biomechanical explanation for the changes in COT across speed observed by Steudel-Numbers and Wall-Scheffler, but these factors remain unclear. However, these data demonstrate that fixed speed measurements of COT may not provide accurate depictions of the energetic demand of running at all submaximal running speeds. As a result, the best method for comparing the energetic demand of running between individuals and groups of runners across speed remains unclear.

Figure 10 (adapted from Steudel-Numbers and Wall-Scheffler, 2008): ECOT of subjects running from low to high speeds (males=open circles, females=closed circles). A U-shaped ECOT-speed relationship speed is observed.



Chapter II

Introduction

The energetic demand of running at a given submaximal speed, often referred to as running economy, is a key determinant of distance running performance (18). There is wide inter-individual variability in the energetic demand of running at a given submaximal speed, even when normalized per kg of body mass within groups of runners of similar performance capacity (6,18). However, controversy exists over the best way to define and/or express the energetic demand of running.

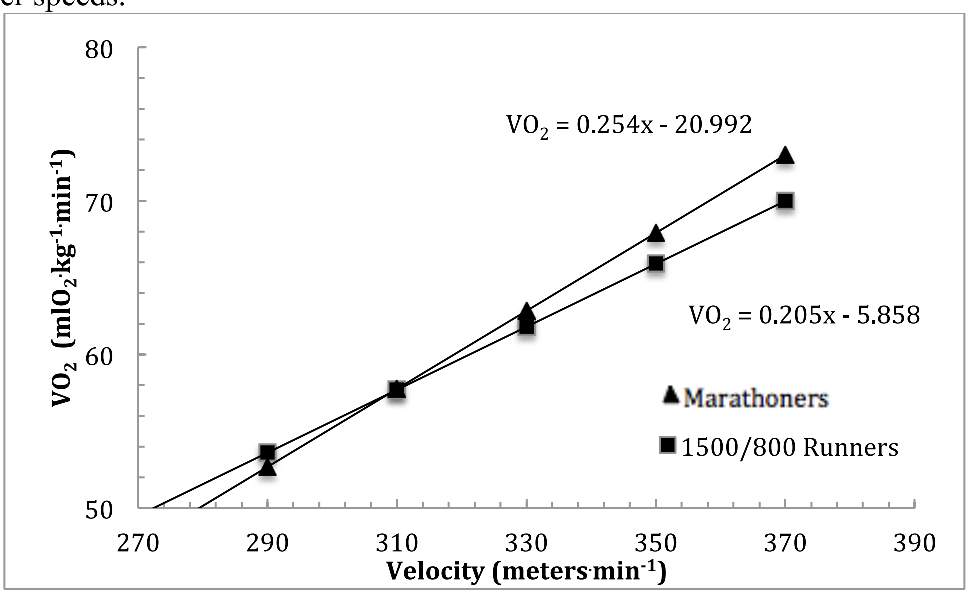
The energetic demand of running is most commonly approximated through expired gas analysis as the gross rate of oxygen consumption ($\dot{V}O_2$, $mlO_2 \cdot kg^{-1} \cdot min^{-1}$) while running at specific speeds. Because substrate utilization changes with exercise intensity, it is more appropriate to express the energetic demand of running by using submaximal $\dot{V}O_2$ and rates of carbon dioxide production ($\dot{V}CO_2$) to calculate actual rates of energy expenditure ($\dot{E}$), expressed in kilocalories ($kcal \cdot kg^{-1} \cdot min^{-1}$) or watts ($W \cdot kg^{-1}$) (5).

Investigators have employed multiple strategies to compare the energetic demand of running between individuals and groups of individuals. A simple and common method is to compare submaximal $\dot{V}O_2$ or $\dot{E}$ when running at a single fixed speed. This may be an effective method for comparing the energetic demand of running if the relative intensity of running at a single fixed speed is similar for a group of runners. However, to predict race performance, measures of running economy should be representative of the energetic demand of running at speeds approaching race pace (6). No single speed can be chosen that is representative of the energetic demand of running at race pace in runners of different performance abilities. As a result, measuring the rate of energetic demand at a single fixed speed of running is an inappropriate method for comparing the running economy of heterogeneous groups of runners.

It is also common to compare the gross rate of the energetic demand of running, as $\dot{V}O_2$ or $\dot{E}$, across multiple submaximal speeds. Plotting the gross rate of energetic demand of running at several submaximal running speeds results in unique $\dot{V}O_2$ or $\dot{E}$-speed relationships for each runner. Linear regression of these relationships results in "economy lines" with unique slopes and intercepts (2,3). When economy lines are parallel they are easily interpreted, with more economical runners exhibiting a lower gross rate of energetic demand over the range of speeds observed. But, in practice, there can be large variability in individual slopes and intercepts of economy lines (3). Due to this variability, it is not uncommon for individual or group economy lines to intersect.

For example, Daniels and Daniels (3) plotted average $\dot{V}O_2$ at five fast submaximal speeds for groups of elite middle distance (800/1500 meter) and marathon runners (Figure 11). Linear regression of these data resulted in intersecting economy lines with middle distance runners, on average, exhibiting lower submaximal $\dot{V}O_2$ than marathon runners at faster speeds that approach middle distance race pace, but higher $\dot{V}O_2$ at slower speeds that approach marathon race pace. Due to the variation in the slopes and intercepts of the economy lines for these groups, any comparison of economy is dependent on the speed of running. In other words, it is inappropriate to determine which group is more economical without specifying the speed at which the comparison is made.

Figure 11 (adapted from Daniels and Daniels, 1992): A plot of the linear relationship between $\dot{V}O_2$ and speed (economy lines) for elite marathon and middle distance (1500/800) runners at 5 submaximal speeds››. Because the economy lines intersect, the interpretation of economy is dependent on speed. In this situation, middle distance runners are more economical at faster speeds, and marathon runners are more economical at slower speeds.



Another method of expressing running economy is to calculate the energetic demand of running a given distance, or the "cost of transport" (COT) (19,20). COT is calculated in several ways. One method is to divide the gross metabolic rate by the velocity of running yielding the amount of energy (ECOT, $kcals \cdot kg^{-1} \cdot km^{-1}$, or $J \cdot kg^{-1} \cdot km^{-1}$ or oxygen consumption (O_2COT, $mlO_2 \cdot kg^{-1} \cdot km^{-1}$) needed to transport a kg of body mass a certain distance forward (gross COT) (4,5,6,19,20,21). Several previous investigations have reported COT, expressed in this manner, to be independent of submaximal running speed (4,5,6,14), suggesting that, in humans, the energetic cost of running a given distance fast or slow is the same (10). If this is true, gross COT calculated at any submaximal running speed would allow for fair comparison of the economy between individuals or groups of runners differing in competitive race pace.

A related method of determining COT is to calculate the slope of economy lines as COT (slope COT) (16). However, considering only the slope of economy lines ignores the effects of the linear intercept, which influences the relationship between gross COT and speed even in runners with identical slopes and perfectly linear economy lines (Figure 2). Slope COT assumes that the intercept of economy lines is only moderately variable between individuals or groups of runners. This assumption is clearly not valid, as there is wide variability in intercepts of economy lines with reported intercepts ranging from 2.8 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$ (6) to -20.99 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$ (3).

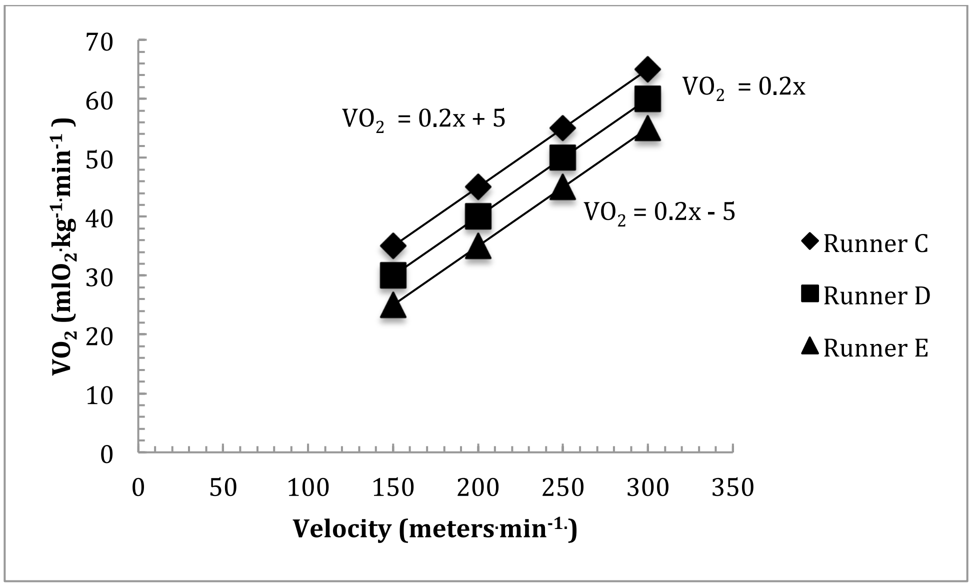
The variability in the intercept of economy lines exerts a profound influence on the relationship between gross COT and running speed. In fact, perfectly linear economy lines result in an invariant gross COT with respect to running speed only if the intercept of the relationship is zero. If the intercept of a perfectly linear economy line is greater than zero, gross COT decreases with increasing speed and if the intercept is less than zero, gross COT increases with increasing speed (Figure 12).

Because both the slope and intercept of economy lines for individual runners vary, another source of confusion can emerge. As shown in Figure 13, if runner F has a higher gross $\dot{V}O_2$ at all speeds tested but has a smaller slope of their economy line, are they less or more economical than runner G? Comparison of economy using slope COT, would suggest runner F is more economical, but clearly this not the case at the measured speeds. The same problems can emerge when comparing the energetic demand of running between groups of runners (3).

Finally, controversy exists as to whether the relationship between the submaximal rate of energetic demand and speed is linear as is usually reported. Steudel-Numbers and Wall-Scheffler (21) report an $\dot{E}$-speed relationship over a wide range of submaximal running speeds in well-trained runners that is better modeled as curvilinear. This curvilinear relationship suggests that economy lines may be better described as “economy curves” over a wider range of submaximal running speeds. A curvilinear relationship between $\dot{V}O_2$ or $\dot{E}$ and speed results in a greater gross COT at fast and slow running speeds (Figure 14).

Figure 12: Three hypothetical runners with perfectly linear $\dot{V}O_2$-speed relationships (economy lines) differing only in the linear intercept. Runner C exhibits a positive intercept resulting in a gross COT that decreases with increasing speed. The economy line of Runner D has an intercept of zero resulting in an invariant gross COT across all speeds. Runner E exhibits a negative intercept resulting in gross COT increasing with increasing speed.

A.)



B.)

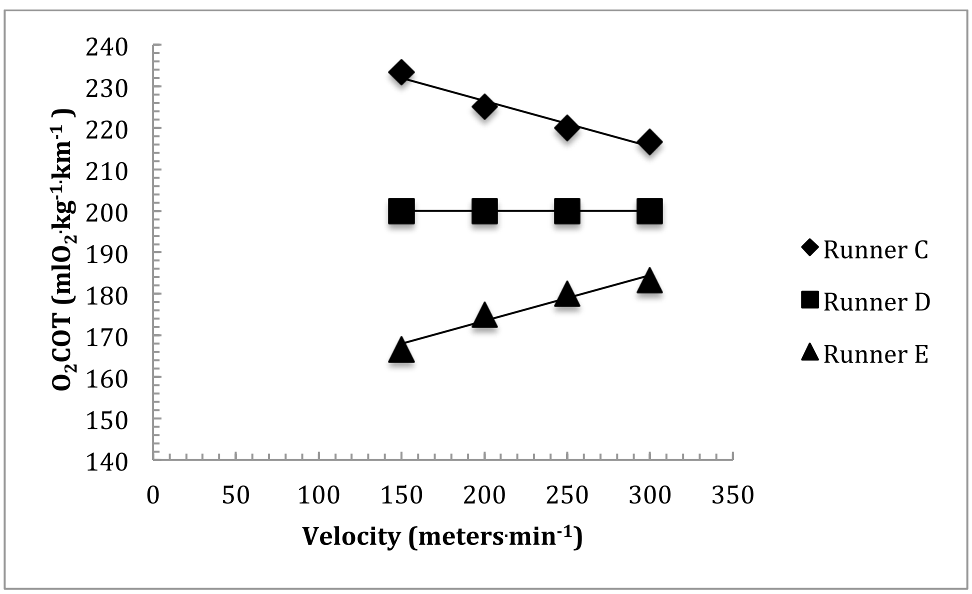


Figure 13: Hypothetical Runner F exhibits a smaller slope, but greater gross $\dot{V}O_2$ than hypothetical Runner G at the measured speeds. Slope COT would suggest Runner F is more economical, while gross $\dot{V}O_2$ suggest Runner G is more economical.

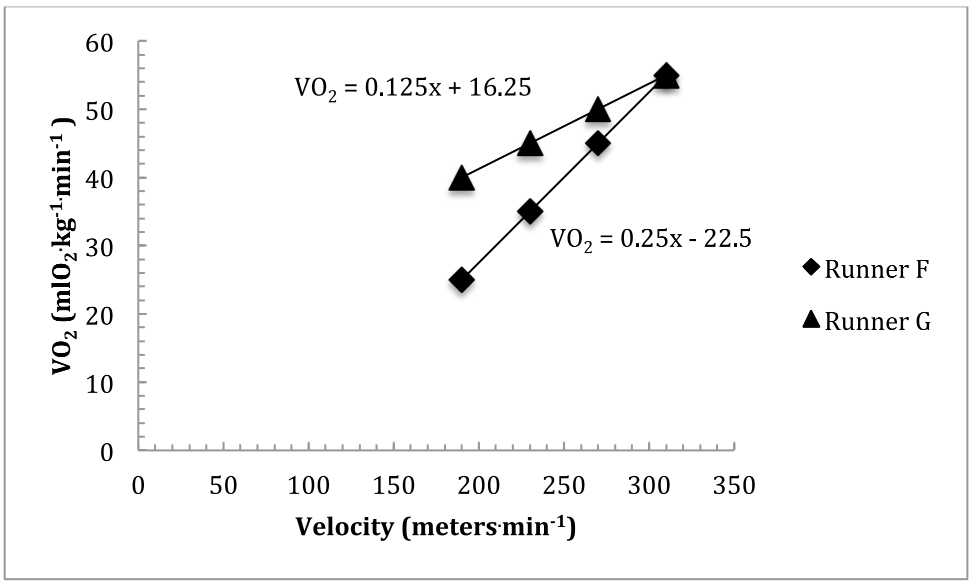
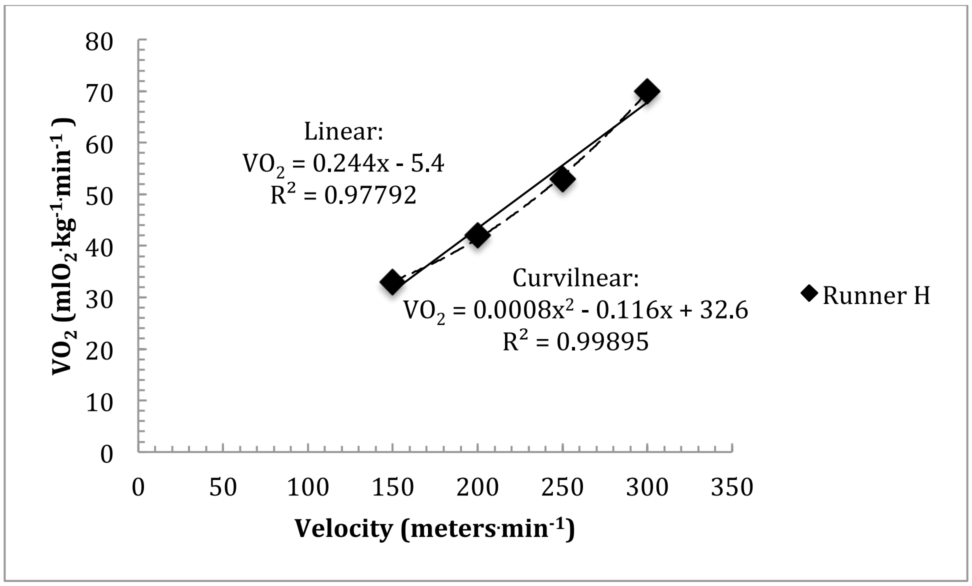
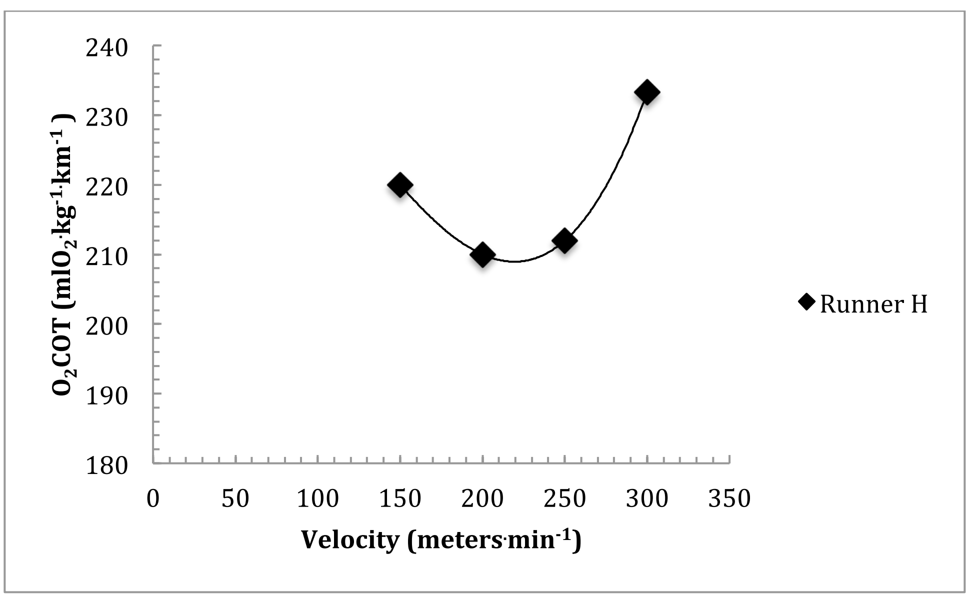


Figure 14: A hypothetical example of a curvilinear $\dot{V}O_2$-speed relationship. When the relationship between the rate of energetic demand and speed is curvilinear (A), COT will increase at fast and slow velocities (B).

A.)



B.)



These findings are not in agreement with the invariant gross COT-speed relationship that is commonly reported (1,4,5,6,14,16). Many studies reporting an invariant gross COT measured the energetic demand of running across only moderate submaximal running speeds in average runners (4,14). Investigations that have measured the energetic demand of running either at very fast speeds (3,6,12,22) or across a wide range of submaximal speeds (21) are not in agreement. Some have found an increasing gross COT at faster running speeds (3,12,22), others report an invariant gross COT at all measured running speeds (6,7), and one reported an increasing gross COT at both fast and slow speeds (21). These data challenge the idea that gross COT is independent of speed across *all* submaximal-running speeds.

No clear explanation has been offered as to why running speed might affect gross COT. Some studies using over ground running protocols suggest that increases in gross COT with increasing running speed may be due to an increase in aerodynamic resistance at faster running speeds (6,22). However, that idea does not provide an explanation for the investigations in which increases in gross COT with speed were observed during treadmill running protocols (3,22). It has been suggested that changes in the gross COT-speed relationship may be explained by changes in running mechanics, as biomechanical parameters have been previously shown to correlate with the energetic demand of running (10,19,23).

The present study examined the relationship between the energetic demand of running over a wide range of submaximal running speeds in both average and elite distance runners. We also aimed to determine the association between changes in stride length (SL) and frequency (SF) on the energetic demand of running at different speeds.

We hypothesized that the relationship between the gross rate of energetic demand and speed would best be described as curvilinear across a wide range of submaximal running speeds. As a result of curvilinear relationships between the gross rate of energetic demand and speed, we hypothesized that gross COT would be greater at slow and fast running speeds. Further, we hypothesized that changes in gross COT with increasing running speed could be correlated with changes in stride frequency (SF) and stride length (SL).

Chapter III
Methods

Subjects:

Twenty healthy male runners (10 Average and 10 Elite) aged 18-35 years volunteered to participate in this study. Subjects were classified into "Average" or "Elite" groups based on past year 10 km run performance time. The Average group included runners who ran at least three times per week and were capable of running 10 km in the range of 40-60 minutes. Because the aim of this study was to observe how the energetic demand of running varies across a wide range of velocities, Average subjects were required to be capable of sustaining a reliance an aerobic metabolism while running at a minimum velocity of ~215 $meters \cdot min^{-1}$ (8 MPH) in order to provide an adequate number of data points for analysis. The Elite group was limited to currently training runners capable of running 10 km in less than 30 minutes at sea level, or less than 31 minutes at the local altitude of Boulder, Colorado (~1600 m). Descriptive data for our subjects can be found in Table 1.   All subjects were informed of the risks involved with participation in the study and gave written informed consent before participating as per the University of Colorado at Boulder Institutional Review Board (IRB).

Study Time Course:

Subjects were asked to report to the laboratory two hours post-prandial in order to control for the effects of diet on energy expenditure during metabolic testing. Metabolic and biomechanical parameters were collected during two treadmill-running sessions occurring 48 hours apart over a range of 6-10 submaximal running speeds. The protocol was performed in two sessions to minimize session duration and minimize any fatigue effects.

Force Treadmills:

Submaximal running tests were performed on either a custom-made (11) or Treadmetrix (Park City, UT) high-speed motorized force-measuring treadmill (FTM). These treadmills measure ground reaction forces (GRF) exerted on the treadmill belt in the vertical and anterior posterior directions. GRF were sampled at 1000 Hz. A custom software program was used to detect the instants of touch-down and toe-off from the filtered vertical GRF data using a 40 N threshold. These data were used to determine stride frequency (SF) and stride length (SL) over a 15 second period. After collecting data for 3 average and 3 elite subjects, a mechanical problem with the custom-made force treadmill forced a switch to the Treadmetrix high-speed force treadmill for the remainder of the study. After repairs were made to the custom-made force treadmill, we determined that the force measurements obtained with the two devices were equivalent.

Experimental Procedures

During the experimental trials, rate of oxygen consumption ($\dot{V}O_2$,$mlO_2 \cdot kg^{-1} \cdot min^{-1}$), rate of carbon dioxide production ($\dot{V}CO_2$, $mlCO_2 \cdot kg^{-1} \cdot min^{-1}$), rate of energy expenditure ($\dot{E}$, $kcal \cdot kg^{-1} \cdot min^{-1}$), expired pulmonary ventilation rate (VE, $L \cdot min^{-1}$), tidal volume (V_t, L), respiratory rate (RR, $breaths \cdot min^{-1}$), and respiratory exchange ratio (RER) were measured using a computerized indirect calorimetry system by Parvomedics (Sandy, UT). The indirect calorimetry system was calibrated before each testing session. Gas fractions were calibrated with room air and a primary standard gas mixture within the physiological range (16.01% O_2 and 4.01% CO_2). The volume was calibrated using a 3L syringe at five distinct flow rates within the expected range of the study protocol. Calibration was considered to be complete when recorded volumes were within 1% of the calibration volumes, and gas fractions were within 0.3% of calibration values (e.g. 20.93 ± 0.06%). Respiratory measurements were averaged every 15 seconds. To ensure that only steady-state values were used, data during the last two minutes of each four-minute stage were recorded (minutes 2:00 – 4:00).

Submaximal economy test #1 began at a velocity ~107 meters/min (4 MPH) and submaximal economy test #2 began at ~120 meters·min^{-1} (4.5 MPH). Running velocities were verified using a high-accuracy contact tachometer (Shimpo, Itasca, IL) during the initial 30 seconds of each running stage. Subjects ran for 4-minutes at the initial velocity. Treadmill velocity was then increased ~27 meters·min^{-1} (1 MPH) in each subsequent stage. During the final minute of each 4-minute stage, subjects were asked to provide a rating of perceived exertion (RPE) on the Borg (6-20) scale (Eston et al, 1987) and GRF were recorded for a 15 second period. After the completion of each 4-minte stage, subjects were asked to straddle the treadmill and a finger-prick blood sample was obtained to determine blood lactate (La) concentration. La sample collection was designed to be complete within 1 minute of the completion of each 4-minute stage. Blood La samples were stored and analyzed in duplicate with an YSI 2300 STAT Plus Lactate Analyzer.

This protocol continued until subjects reached a running velocity that elicited an RPE of 15. Previous data have suggested that an RPE value of 16 represents an exercise intensity that corresponds closely to La threshold (13). To assure that subjects were below La threshold we ended submaximal economy testing when subjects reached a more conservative RPE of 15.

$\dot{V}O_2$max testing was performed after the completion of submaximal economy test #1. Subjects were allowed a minimum of 5 minutes of recovery after completion of submaximal economy test #1. $\dot{V}O_2$ was measured using open-circuit indirect calorimetry as described above. Subjects ran at the velocity that elicited an RPE of 15 during submaximal economy test #1 on a level grade for the initial two minutes of testing. Subsequently, grade was increased by 1% each minute until exhaustion. Subjects were instructed to run until they felt they could no longer match the speed of the treadmill. At that point, they were instructed to straddle the treadmill belt. $\dot{V}O_2$max was determined to be the highest 15-second mean $\dot{V}O_2$ value obtained during the protocol. Our criteria for reaching $\dot{V}O_2$ max required at least two of the following: a plateau in oxygen consumption, an RPE of 20, or a respiratory exchange ratio (RER) over 1.15.

Analysis:

Descriptive statistical analyses were performed to determine means and standard deviations (SD) of metabolic and biomechanical parameters for both Average and Elite groups at each submaximal speed. Individual linear and 2nd order curvilinear regressions were fit to mean $\dot{V}O_2$ and $\dot{E}$ values producing economy lines and curves. R^2 values were calculated to assess the strength of fit for both regression methods. Comparisons between economy line and economy curve model fits were performed using a paired samples *t*-test.

A linear-mixed model was used to determine main effects of speed and group classification on mean $\dot{V}O_2$, $\dot{E}$, O_2COT , and ECOT. This model was also used to compare each of these variables across speed to values obtained at the fastest submaximal speed achieved in each group, because this speed is assumed to be the speed that most closely represents race pace for each group. A stepwise multiple linear regression was performed to determine the association between changes in biomechanical parameters, O_2COT, and ECOT. All figures are presented as mean values ±SD.

Subject Demographics

Average and Elite groups did not differ significantly in age. By design, the average group exhibited significantly slower mean 10 km personal bests and lower mean $\dot{V}O_2$max values when compared to the elite group ($p<.001$). Individual and mean age, 10 km personal best, $\dot{V}O_2$max, and sRPE15 values can be found in Table 1.

Table 1: Individual age, 10 km personal best achieved in the previous year, VO_2max, sRPE15 values. Means presented ±SD.

Subject	Group	Age (years)	10 km Time (min)	VO2max ($mlO_2 \cdot kg \cdot min^{-1}$)	sRPE15 ($meters \cdot min^{-1}$)
1	Average	23	45.5	55.1	282
2	Average	23	48.0	48.7	255
3	Average	24	44.5	57.9	255
4	Average	30	46.3	61.9	255
5	Average	25	49.0	52.7	228
6	Average	30	52.0	44.7	215
7	Average	27	46.0	54.0	228
8	Average	25	44.0	55.9	241
9	Average	28	41.0	56.6	241
10	Average	27	44.4	59.8	255
Mean	**-------**	**26.2±2.6**	**46.1±3.0****	**54.7±5.1****	**245.5±19.1****
11	Elite	21	30.7*	72.1	308
12	Elite	24	29.0	78.8	308
13	Elite	28	30.5*	59.9	308
14	Elite	24	29.1	83.8	335
15	Elite	25	29.0	76.8	322
16	Elite	26	30.8*	71.3	308
17	Elite	28	29.85	66.0	322
18	Elite	23	29.25	70.2	322
19	Elite	32	30.8*	67.6	308
20	Elite	28	29.9	68.2	308
Mean	**-------**	**25.9±3.2**	**29.89±.8****	**71.47±6.9****	**314.9±9.7****

*=Time achieved at altitude, **Significant group difference ($p<.05$)

Chapter IV

Results

Submaximal Economy Test Results:

During submaximal economy testing, all Average subjects completed stages up to a speed of 215 meters$\cdot$min^{-1}, while Elite subjects completed stages up to a speed of 308 meters$\cdot$min^{-1} before reaching sRPE15. All metabolic data were analyzed over the ranges of speeds completed by all subjects in each group (Average: 107-215 meters$\cdot$min^{-1}; Elite: 107-308 meters$\cdot$min^{-1}). Individual sRPE15 values are presented in Table 2.

The Average group was significantly less economical than the Elite group over comparable speeds (107-215 meters$\cdot$min^{-1}) when expressed as $\dot{V}O_2$ ($p<.01$), $\dot{E}$ ($p<.001$), O_2COT ($p<.01$), and ECOT ($p<.001$). For the Average group, no differences were observed between economy line and economy curve fits of the mean $\dot{V}O_2$ and $\dot{E}$ vs. speed relationships ($p>.05$). Economy curves were found to better fit mean $\dot{V}O_2$ and $\dot{E}$ vs. speed relationships than economy lines for the Elite group ($p<.05$). Plots of mean $\dot{V}O_2$ and $\dot{E}$ vs. speed for can be found in Figures 5 and 6. Mean slopes, intercepts, and R^2 values for economy lines and curves were calculated for each group and are presented in Figures 15 and 16.

Figure 15: Plot of mean values of the rate of oxygen consumption $\dot{V}O_2$ vs. running speed for Average and Elite subjects. Mean slopes, intercepts, and R^2 values for economy lines and curves were calculated and fit to this data.

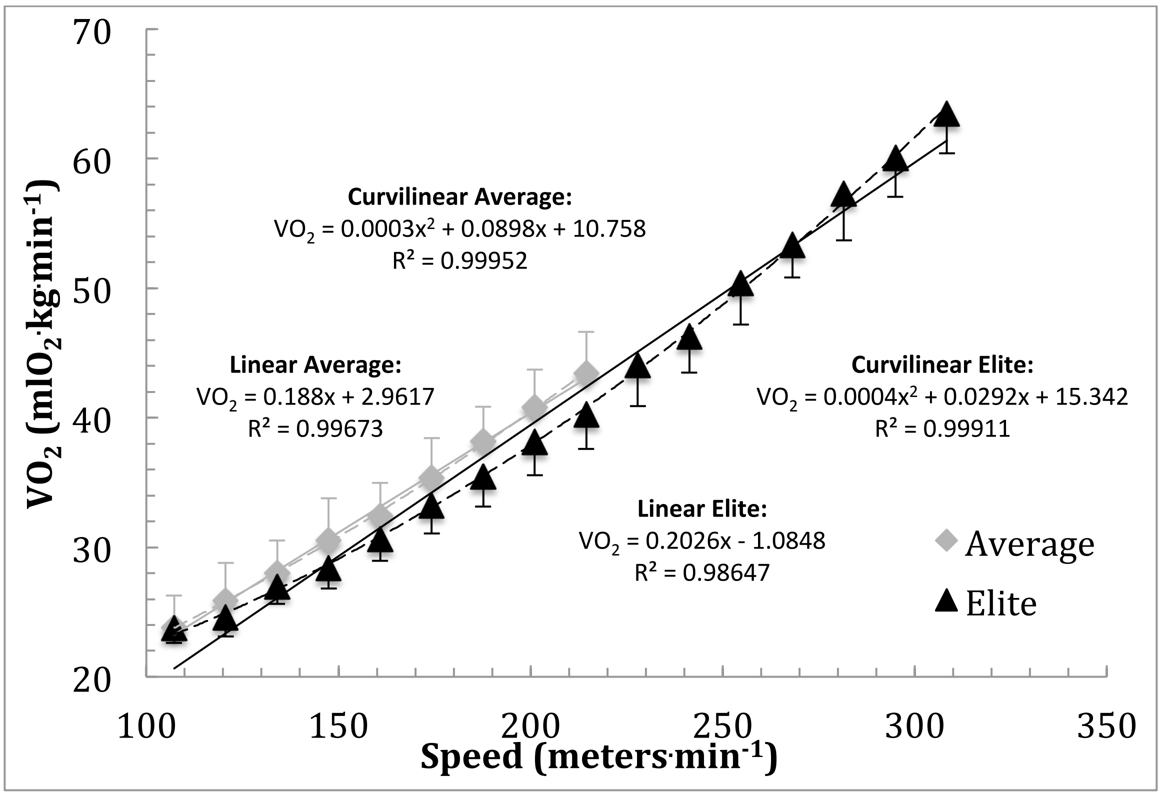
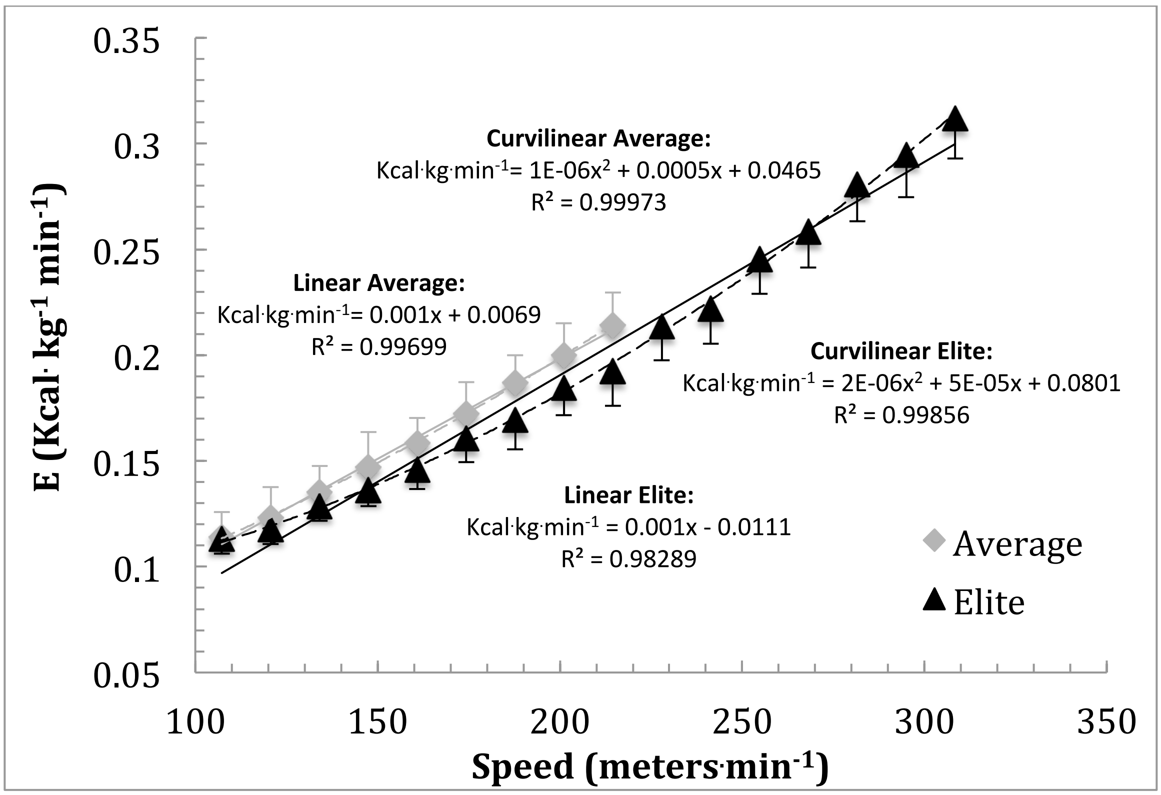


Figure 16: Plot of mean values of the rate of energy expenditure (Ė) vs. running speed for Average and Elite groups. Mean slopes, intercepts, and R^2 values for economy lines and curves were calculated and fit to this data



In the Average group, a 10.2% and 7.9% decrease in O_2COT and ECOT was observed over the slow running speed range of 107-161 meters·min^{-1}. No main effect of speed on O_2COT or ECOT was observed over the moderate speed range of 161-215 meters·min^{-1} for Average subjects. A significant main-effect of speed on both O_2COT ($p<.001$) and ECOT ($p<.001$) was observed in Elite subject with a maximum 8.8% and 11.3% increase in O_2COT and ECOT, respectively, occurring between 215 and 308 meters·min^{-1} (the fastest submaximal speed achieved by the Elite group). O_2COT and ECOT at speeds of 147-241 meters·min^{-1} were 6-9% lower than O_2COT and 7-11% lower than ECOT values at 308 meters·min^{-1} in Elite subjects ($p<.05$). Similar to the Average group, significant decreases in O_2COT and ECOT were observed over the slow running speed range of 107-161 meters·min^{-1} and no effect was of speed was observed for either measure over the moderate running speed range of 161-215 meters·min^{-1} in the Elite group. O_2COT and ECOT vs. speed plots can be found in Figures 17 and 18. Mean changes in COT values for Elite subjects at each measured speed from 308 meters·min^{-1} can be found in Table 2.

Figure 17: A plot of mean O_2COT values ($mlO_2 \cdot kg^{-1} \cdot km^{-1}$) at each measured speed for Average and Elite groups.

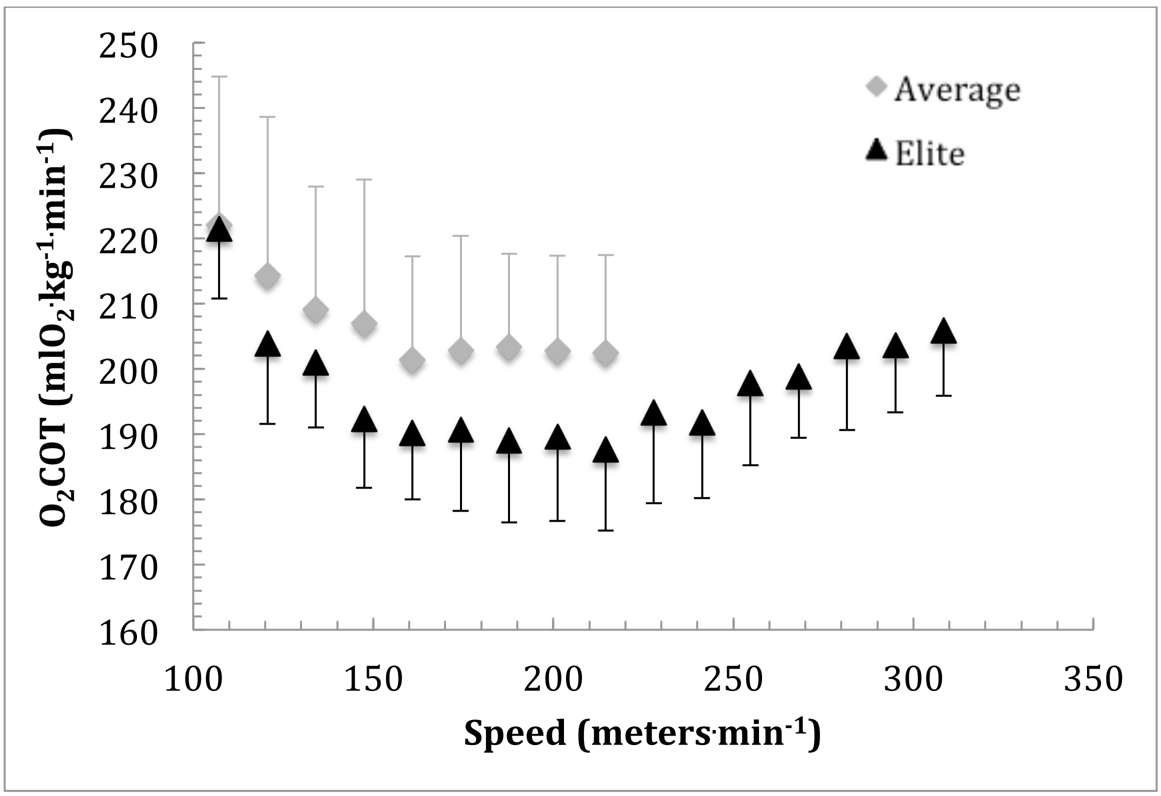


Figure 18: A plot of mean ECOT values at each measured speed (kcal·kg^{-1}·km^{-1}) for Average and Elite groups.

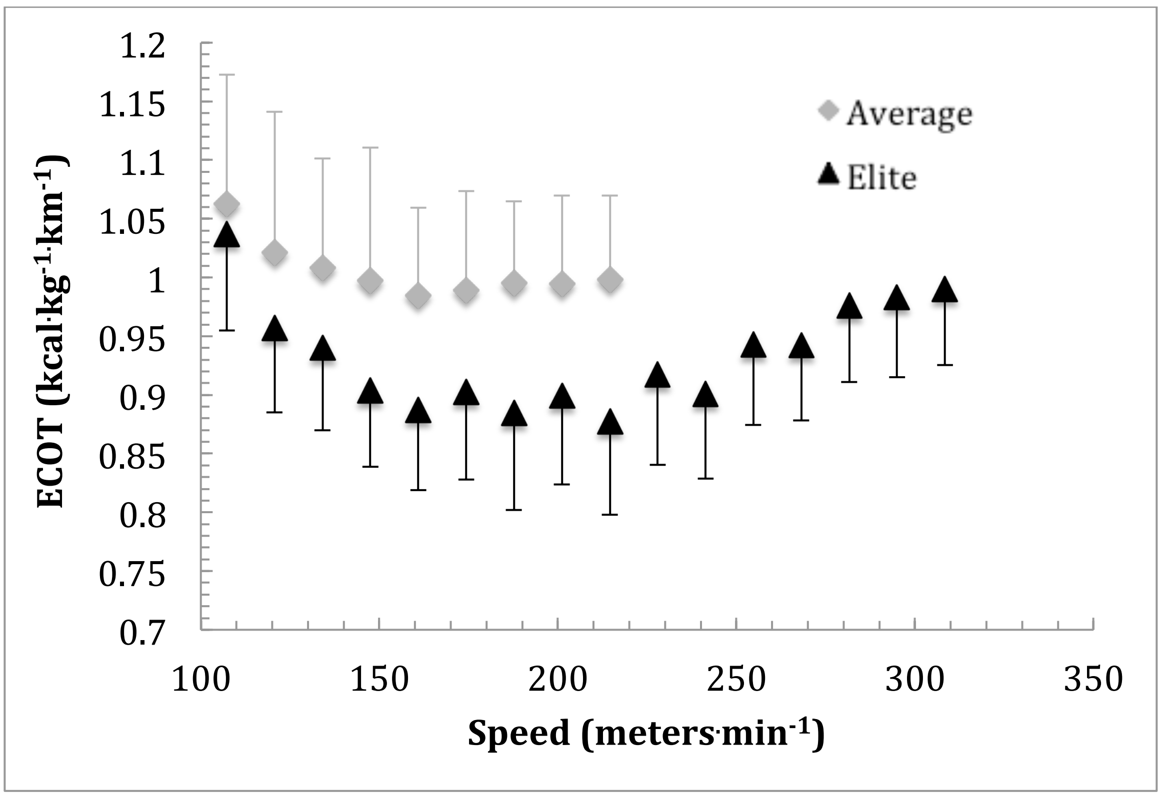


Table 2: Mean differences in O_2COT and ECOT values for Elite subjects from O2COT and ECOT at 308 meters·min^{-1} presented as absolute (COT-COT(308)) and percent differences.

Speed (meters·min^{-1})	**O_2COT-O_2COT(308)**	**% Difference**	**ECOT-ECOT(308)**	**% Difference**
107	15.60*	7.58*	0.047	4.75
121	-1.94	-0.94	-0.03	-3.33
134	-4.87	-2.36	-0.05	-5.05
147	-13.45*	-6.53*	-.086*	-8.68*
161	-15.69*	-7.62*	-.103*	-10.40*
174	-15.15*	-7.36*	-.087*	-8.79*
188	-16.88*	-8.20*	-.106*	-10.70*
201	-16.22*	-7.88*	-.091*	-9.19*
215	-18.20*	-8.84*	-.112*	-11.31*
228	-12.52*	-6.08*	-.073*	-7.37*
241	-14.04*	-6.82*	-.089*	-8.99*
255	-8.01	-3.89	-0.05	-4.75
269	-6.98	-3.39	-0.05	-4.85
282	-2.39	-1.14	-0.01	-1.41
295	-2.19	-1.07	-0.01	-0.71

*=Significant difference ($p<.05$)

SF and SL:

Fourteen of twenty subjects did not exhibit adequate aerial phases during slow running speeds of 107 and 121 meters·min^{-1} to accurately measure SF and SL. These speeds were omitted from analysis and SF/SL were analyzed over the range of 134 meters·min^{-1} to the sRPE15 for each group (Average: 215 meters·min^{-1}, Elite: 308 meters·min^{-1}).

In both groups both SF and SL increased significantly with increasing speed ($p<.001$), with SL increasing at a greater rate in both groups. 6 and 11% increases in SF were observed, while 51 and 106% increases in SL were observed for Average and Elite groups respectively. No significant differences in SF and SL were observed between Average and Elite groups over comparable speeds (134-215 meters·min^{-1}).

It was not possible to correlate changes in SF and SL to changes in energetic demand in the Average group, as no changes in mean gross COT were observed for the group. Changes in SF and SL were not found to correlate with changes in O_2COT or ECOT ($p>.05$) from 215 meters·min^{-1}, the point at which an increase in gross COT was observed, to the sRPE15 of 308 meters·min^{-1} for the Elite group. Plots of SF and SL vs. running speed can be found in Figures 19 and 20.

Figure 19: Mean SF (±SD) from 134 meters·min^{-1} to sRPE15 for Average and Elite groups.

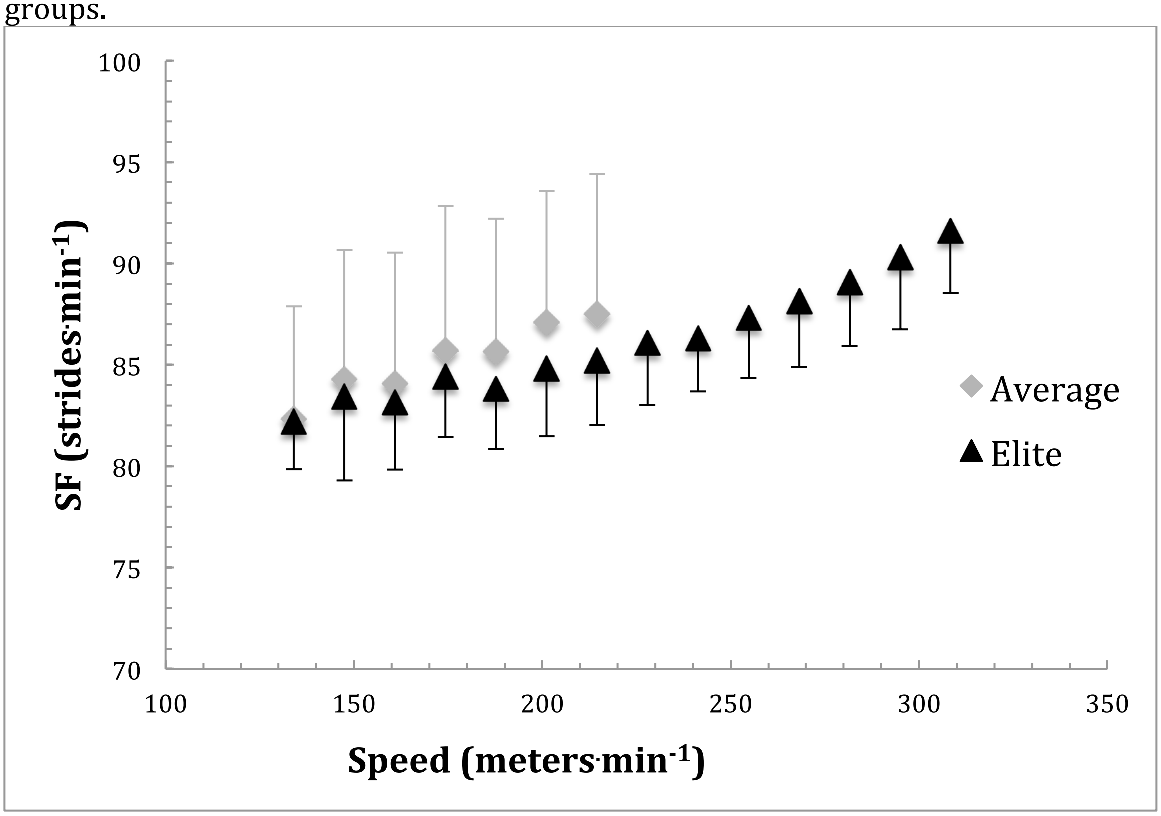
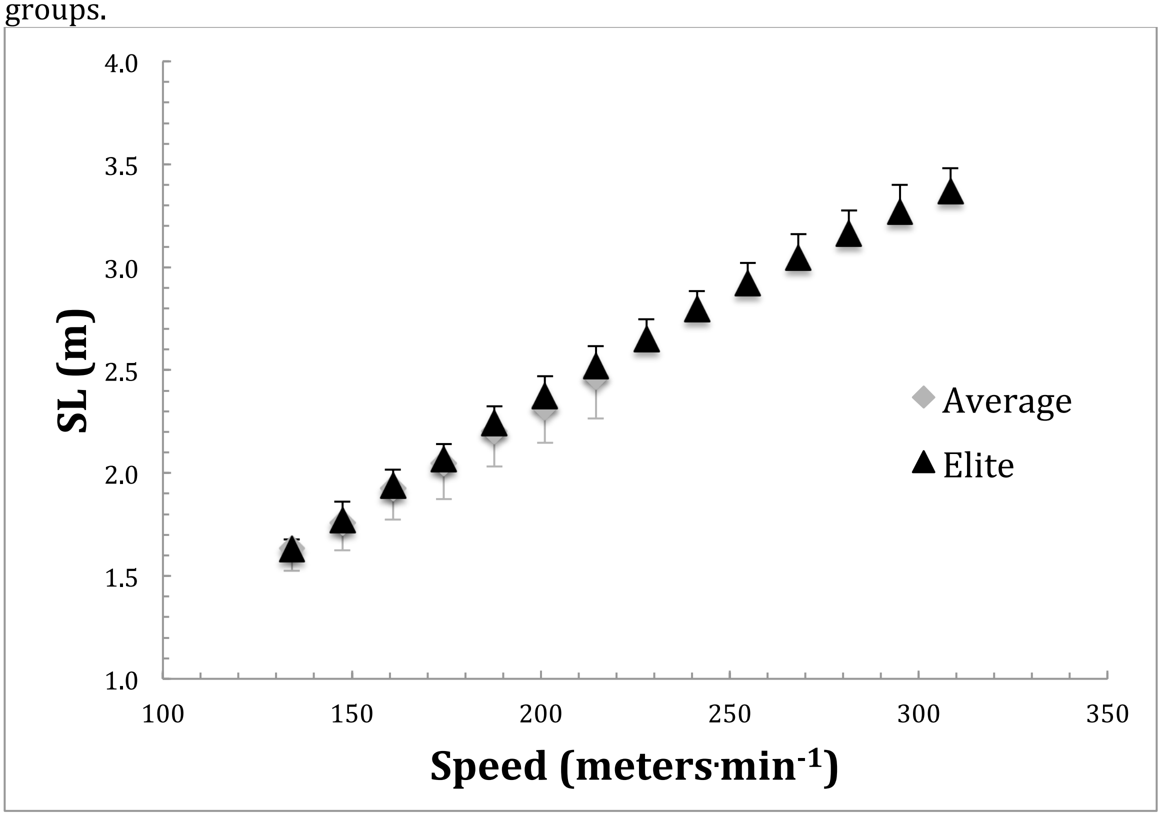


Figure 20: Mean SL (±SD) from 134 meters·min^{-1} to sRPE15 for Average and Elite groups.



Chapter V

Discussion

This investigation had two primary hypotheses. First, we hypothesized that the relationship between the gross rate of energetic demand and speed would be best described as curvilinear across a wide range of submaximal running speeds resulting in increases in gross COT at slow and fast running speeds. Second, we hypothesized that changes in gross COT with increasing running speed would be correlated with changes in stride frequency (SF) and stride length (SL). Our data do not support our initial hypothesis for the Average group, but they do for Elite group, which was capable of running at a much wider range of submaximal running speeds than the Average group.

The majority of previous studies examining the relationship between the energetic demand of running and submaximal running speed have done so over a narrow range of moderate submaximal running speeds in average to good runners (1,4,5,14) or over a narrow range of faster submaximal running speeds in sub-elite or elite runners (3,6,22). As a result, the energetic demand-speed relationship over the entire range of running speeds, from very slow to fast speeds that approach elite race pace, was not well understood. In the present study, we quantified the energetic demand of running in both Average and Elite runners (groups capable of sustaining different ranges of submaximal running speeds) over a wider range of submaximal running speeds than has been previously reported.

It is generally accepted that a strong, positive linear relationship exists between the gross rate of energetic demand (as $\dot{V}O_2$ or $\dot{E}$) and submaximal running speed (4,14). We observed this to be true over the submaximal running speed ranges sustained by our

Average and Elite runners. However, $\dot{V}O_2$ and $\dot{E}$-speed relationships over a wider range of submaximal running speeds achieved by our Elite runners were *better* defined as curvilinear. These data are in agreement with previous findings by Steudel-Numbers and Wall-Scheffler (21) of a curvilinear relationship between $\dot{E}$ and speed over a similar range of submaximal running speeds.

The curvilinear relationship observed here suggests that the slope and intercept of the relationship between $\dot{V}O_2$ or $\dot{E}$ and submaximal running speed are variable over the range of speeds sustained by our Elite runners. Over a range of moderate submaximal running speeds (161-215 $meters \cdot min^{-1}$) linear regression of the $\dot{V}O_2$-speed relationship for Elite runners results in an intercept 1.6 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$; a value approaching those reported previously over a similar range of submaximal running speeds (6). However, when a linear regression was performed over the four fastest submaximal running speeds achieved by our Elite group (268-308 $meters \cdot min^{-1}$), the intercept of the $\dot{V}O_2$-speed relationship drops substantially to -12.9 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$. This value is similar to those reported for Daniels and Daniels' (3) elite middle distance (-5.9 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$) and marathon runners (-20.9 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$) over a similar range of fast submaximal running speeds (290-370 $meters \cdot min^{-1}$). This finding suggests that the range of speeds over which the rate of energetic demand is observed may be critically important, especially when used to calculate parameters from linear extrapolation of this relationship.

Linear extrapolation of the relationship between the rate of energetic demand and running speed is a common method used to calculate several physiological parameters thought to be predictive of performance, including the velocity at $\dot{V}O_2max$ ($v\dot{V}O_2max$) and anaerobic reserve capacity (7,9). Our data suggest that these measures can be extremely variable depending on the range of speeds over which linear extrapolation is performed. For example, $v\dot{V}O_2max$ in our Elite subjects calculated over the moderate speed range of 161-215 meters·min^{-1} is ~50 meters·min^{-1} faster than $v\dot{V}O_2max$ when calculated over the faster range of 268-308 meters·min^{-1} (387 vs. 340 meters·min^{-1}). This difference amounts to nearly four minutes over 10 km; a massive difference for an elite distance runner.

As expected, variability in the slopes and intercepts of $\dot{V}O_2$ and $\dot{E}$-speed relationships were found to also influence the relationship between gross COT and submaximal running speed. Rates of energetic demand were converted to gross COT, as O_2COT and ECOT, at each measured submaximal speed. Elite gross O_2COT and ECOT were found to increase up to 8.8% and 11.3% respectively from moderate to fast submaximal speeds, suggesting that moderate speed measures of gross COT significantly underestimate the energetic demand of running at speed approaching Elite race pace. Interestingly, significant decreases in mean O_2COT and ECOT of 10.2% and 7.9% were observed in the Average group from slow to moderate running speeds. This change suggests that, though no significant difference between linear and curvilinear models were observed for the rate of energetic demand-speed relationship in the Average group, a meaningful change in the slope and intercept of the relationship occurred at slow speeds that resulted in a significant decrease in gross COT from slow to moderate running speeds.

This finding is not in agreement with multiple previous reports of an invariant COT with respect to submaximal running speed (4,6,7,14), but supports the findings of Steudel-Numbers and Wall-Scheffler (21) who observed an increase in ECOT at fast and slow running speeds in sub-elite to elite distance runners over a wide range of submaximal running speeds. Tam et al. (22) report an increasing O_2COT with increasing speed at fast running speeds in elite Kenyan distance runners. Because Tam et al. utilized an over-ground running protocol, they suggest that this finding is the result of an increasing contribution of aerodynamic resistance to the energetic demand of running at fast speeds. However, we observe Elite gross COT to increase at both slow and fast running speeds during treadmill running in which aerodynamic resistance is negligible. Further, gross $\dot{V}O_2$ reported by Daniels and Daniels (3) in elite marathon runners during fast treadmill running also results in an increasing gross O_2COT with increasing running speed. These data suggest that an increase in gross COT at fast running speeds is likely to due to factors other than increases in aerodynamic resistance alone.

COT is a commonly used measure for the comparison of the energetic demand of multiple forms of locomotion both between heterogeneous groups of human runners (18) and even species (10,17,19,20). It has long been presumed that COT is independent of submaximal running speed in humans (1,4,6,7,14) making it a seemingly effective measure for comparing the energetic demand of running, even between runners with substantial differences in competitive race pace. Our findings demonstrate that gross COT may, in fact, be dependent on submaximal running speed, with moderate speed measures significantly underestimating the energetic demand of fast running. These data emphasize the importance of choosing representative range of running speeds in order to make accurate measures and comparisons of running economy between individuals and groups of runners, especially if those measures are meant to be predictive of running performance. Because most runners compete at paces above the La threshold, it may be difficult to accurately measure energetic demand at competitive race pace. Accordingly, we suggest that future investigations measure the energetic demand of Elite runners at fast speeds that correspond closely to the runner's La threshold in order to best estimate the energetic demand of competitive running.

Finally, we hypothesized that changes in gross COT would be correlated to changes in SF and SL over a wider range of speeds, as previous data has suggested that running mechanics may exert an influence on the energetic demand of running (10,19,23). However, no differences in SF or SL were observed between Average and Elite groups. Further, changes in SF and SL were not found to correlate with changes in gross COT from moderate to fast speeds for the Elite group. It is possible that other mechanical and physiological factors, including foot ground contact times, vertical ground reaction forces, and changes muscle fiber recruitment, may be more explanatory of changes in gross COT across speed.

SF and SL were found to increase with increasing running speed. Increases in SL with increasing running speed are well documented (8). Our data provide further evidence that increases in SL are primarily responsible for increases in running speed, with SL increasing 51 and 106% over the submaximal speed range of Average and Elite runners respectively. SF was also observed to increase with increasing speed in both groups, but the increases in SF were mild (6 and 11% for Average and Elite groups) in comparison to the increases SL over the range of speeds measured.

Clearly, the notable aspects of this study were the Elite subject population and the range of speeds over which the energetic demand of running was observed. The major conclusion from this investigation is that the energetic demand of running at a narrow range of moderate submaximal running speeds is not representative of the energetic demand of running at a wider range of speeds; a range requiring a subject population capable of sustaining faster submaximal running speeds. It should be noted that it is likely that the differences in energetic demand-speed relationships observed here between Average and Elite groups are a result of the differences in the range of speeds measured and not an inherent physiological or biomechanical difference between the groups. In other words, we would expect to observe similar energetic demand-speed relationships if the Average group was somehow capable of sustaining a similar wide range of submaximal running speeds sustained by the Elite group. Though it is likely that changes in the energetic demand of running with increasing running speed are due to changes in running mechanics, changes in SF and SL were not found to explain changes in energetic demand over the wide range of speeds sustained by Elite runners.

There were several limitations of this protocol. The subject population included only male subjects and as a result it is not possible determine influence of sex on the energetic demand-submaximal running speed relationship. Also, this investigation focused only on the energetic demand of submaximal running. Most runners compete at a speed above La threshold, and as a result we were not able to accurately quantify the relationship between the energetic demand of running at competitive race paces. Finally, all this investigation was performed at a moderate altitude of ~1600 meters. We are unable to determine whether this factor exerted any influence on the relationships observed.

Future studies should examine whether the relationships reported here hold true in other subject populations, including female athletes as well as runners of different event specialties (e.g. marathon or middle distance runners). It would also be beneficial to observe the energetic demand-speed relationships, as both aerobic and anaerobic demand, from moderate speeds to speeds that fall above La threshold, and thus more closely approximate race pace, in Average and Elite runners.

References:

1. **Carrier, D.R., 1984.** The energetic paradox of human running and hominid evolution. Curr. Anthropol. 25, 483–495.

2. **Daniels, J., 1985.** A physiologist's view of running economy. Med. Sci. Sports Exerc. 17, 332-338.

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

4. **Di Prampero, G., Atchou, J.C., Moia C., 1986.** The energetics of endurance running. Eur J Appl Physiol. 55:259-266

5. **Fletcher, J., Esau, S., MacIntosh, B., 2009**. Economy of Running: beyond the measurement of oxygen uptake. J Appl Physiol 107:1918-1922.

6. **Helgerud, J., Storind, O., Hoff, J., 2009.** Are there differences in economy at different velocities for well-trained distance runners? Eur J Appl Physiol 108:1099–1105.

7. **Helgerud, J., 1994.** Maximal oxygen uptake, anaerobic threshold and running economy in women and men with similar performance level in marathons. Eur J Appl Physiol 68:155–161

8. **Hoyt, D., Wickler, S., Coggar, E., 1999.** Time of contact and step length: The effect of limb length, running speed, load carrying, and incline. J. Exp. Biol. 203, 221-227.

9. **Jones, A., 2006.** The physiology of the world record holder for the women's marathon. International Journal of Sports Science & Coaching. Vol. 1, No. 2, 101-116.

10. **Kram, R., Taylor, CR., 1990.** Economy of running: a new perspective. Nature. 346, 265 – 267.

11. **Kram R., Griffin TM., Donelan JM, Chan YH., 1998.** Force treadmill for measuring vertical and horizontal ground reaction forces. J Appl. Physiol., 85(2), 764-769.

12. **Lacour, R., Padilla-Magunacelaya, S., Barthelemy, J., Dormois, D., 1990.** The energetics of middle-distance running. Eur J Appl Physiol 60:38–43

13. **Lim, A., Peterman, J., Turner, B., Livingston, L., Byrnes, W., 2011.** Comparison of male and female road cyclists under identical stage race conditions. Med. Sci. Sports Exerc. 43, 846-852.

14. **Margaria, R., Cerretelli, P., Aghemo, P., Sassi, G., 1963.** Energy cost of running. J. Appl. Physiol. 18, 367–370.

15. **McCardel, W., Katch, F., Katch, V., 2007.** Exercise Physiology: Energy, Nutrition, and Human Performance, sixth ed. Lippincott, Williams and Wilkens, New York.

16. **Menier, D., Pugh, L., 1968.** The relation of oxygen intake and velocity of walking and running competition walkers. J Physiol. (Lond.) 197, 717-721

17. **Miller, R., Umberger, B., Hamill, J., Caldwell, G., 2012.** Evaluation of the minimum energy hypothesis and other potential optimal criteria for human running. Proc Biol Sci. 279, 1498-14505.

18. **Morgan, D et al., 1995.** Variation in the aerobic demand among trained and untrained subjects. Med. Sci. Sports Exerc. Vol. 27, No. 3, 404-409.

19. **Roberts, T., Kram, R., Weyand, P., Taylor, CR., 1998.** Energetics of bipedal running. I. Metabolic cost of generating force. J Exp Biol 201, 2745-2751.

20. **Schmidt-Nielsen, K., 1972.** Locomotion: Energy cost of swimming, flying, and running. Science. 177, 222-228.

21. **Steudel-Numbers, K., Wall-Scheffler, C., 2009.** Optimal running speed and the evolution of hominin hunting strategies. Journal of Human Evolution. 56, 355–360.

22. **Tam, E., Rossi, H., Moia, C., Beradelli, C., Rosa, G., Capelli, C., Ferretti, G., 2012.** Energetics of running in top-level marathon runners from Kenya. Eur J Appl Physiol.

23. **Tartaruga, M., Brisswater, J., Peyre-Taratuga, L., Avila, A., Alberton, C., Coertjens, M., Cadore, E., Tiggemann, C., Silva, E., Kruel, L., 2012**. The relationship between running economy and biomechanical variables in distance runners. Research Quarterly for Exercise and Sport. 83, 367-375.