Spring 5-19-2016

Metabolic Limits and Adaptation in Humans: Daily Energy Expenditure in Race Across the USA Athletes

Caitlin Thurber

Metabolic Limits and Adaptation in Humans: Daily Energy Expenditure in

"Race Across the USA" Athletes

by

Caitlin Thurber

Submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Anthropology, Hunter College
The City University of New York

2016

May 19th, 2016 — Herman Pontzer
Date — First Reader

May 19th, 2016 — Lara Dugas
Date — Second Reader

ACKNOWLEDGEMENT

I would like to thank my thesis advisor Dr. Herman Pontzer of the Anthropology Department at Hunter College for his consistent and enthusiastic help with this project. His contacts in the field of metabolic study made this research possible, and I am extremely grateful to have had the opportunity to participate in this study. Dr. Pontzer was always available to answer any questions about my research or writing, and was endlessly committed to helping me with this project. He would always be ready with a letter of recommendation or support when I needed it. I am extremely grateful for all of his encouragement and guidance.

I would also like to thank the experts who were involved in the Race Across the USA research project: Dr. Bryce Carlson, Dr. Lara Dugas, and Dr. Cara Ocobock. Without their passionate participation and input, this project would not have been possible.

I would also like to thank Dr. Lara Dugas of the Public Health Science Department at Loyola University, Stritch School of Medicine for serving as the second reader of this thesis, her knowledge and experience were vital, and I am grateful for her very valuable comments on this thesis.

I am grateful to the Race Across the USA organizers and subjects for their time and participation. None of this research would have been possible without their dedication. I would also like to thank all of the laboratory team members in the Pontzer Lab at Hunter College, especially Jenny Paltan and Lauren Christopher for their assistance with sample analysis.

I also appreciate the support I received from my employer and coworkers at Nassau Community College, especially Christine Tuaillon who served as an unofficial mentor and advisor during my academic pursuits. Her advice was invaluable while I simultaneously worked at NCC and attended Hunter College.

Finally, I must express my very profound gratitude to my parents Craig and Peggy for their unfailing support (emotional and financial) and continuous encouragement throughout my years of study. Thank you to my partner Len and the many friends who have helped me stay sane through these difficult years. Their support, care, and belief in me helped me overcome setbacks and stay focused on my graduate study. A special thank you, to Jill for always being an enthusiastic editor, and to my Mom for going above and beyond and storing urine samples in her freezer during field collection.

Caitlin Thurber

Table of Contents

Introduction

The proportion of men and women who self-report zero leisure-time physical activity has dramatically increased since 1988, from 19.1% to 51.7% in women, and from 11.4% to 43.5% in men (Ladabaum, Mannalithara, Myer, & Singh, 2014). Field experts frequently cite declining physical activity as the culprit for today's high rates of obesity (Cook, Li, & Heinrich, 2015; Ladabaum et al., 2014; Wang & Beydoun, 2007) and this explanation persists despite growing evidence to the contrary. Recent doubly labeled water (DLW) studies investigating daily energy expenditure have found that physical energy expenditure has not declined since the 1980s in developed countries (Westerterp & Speakman, 2008), and that there is no significant difference in energy expenditure between populations of low and high development/activity levels (Dugas et al., 2011; Pontzer et al., 2012). These results seem counterintuitive when confronted with widespread messaging from popular campaigns aimed at preventing obesity, like Michelle Obama's "Let's Move" (The Partnership for a Healthier America) and the recommendations of national and international health organizations to get a minimum of 30 minutes of daily activity (Physical Activity Guidlines Advisory Committee, 2008; World Health Organization, 2010). As the quest for weight loss has entered the digital age, a multitude of applications have been created that allow the user to input their food and exercise calories for the purpose of helping them keep track of calories "in" and "out" for that day. Food and exercise calories are added or subtracted from their estimated daily calorie goal, and clearly displayed on the screen of their computer or mobile device so they can monitor their daily energy balance (Duffy, 2014). However, many studies have shown that the energy imbalance provided by added physical activity are frequently lower than expected, and that the influence of length, intensity, or time range of energy expenditure can have varied effects on expenditure totals (Melanson, Keadle, Donnelly, Braun, & King, 2013; Rosenkilde et al., 2012; Ross & Janssen, 2001). A constrained model for energy expenditure was recently proposed to explain this effect, which suggests overall energy expenditure is conserved once increases in physical activity reach a certain threshold, by reducing energy in other areas of the body (Pontzer, 2015). The constrained model posits that as physical activity increases above sustainable energy levels, metabolic adjustments will occur in order to keep total daily energy expenditure (TEE) within an acceptable range. This is contrary to an additive TEE model, which is normally used to predict energy output (FAO/WHO/UNU, 2001). Using DLW and tri-axial accelerometers, Pontzer et al. observed five different African populations during normal daily activity and found that past a certain level of activity, TEE plateaued rather than continuing to increase, supporting the constrained model of energy expenditure (Pontzer et al., 2016).

While the subjects in the 2016 study represented populations with various intensity levels of daily living, ranging from "sedentary" to "vigorous", they were not participating in extreme physical activity per se, nor did they change their level of physical activity during the study. To date, very few longitudinal studies have been performed to investigate the effects of extreme physical activity on TEE. Therefore, more studies are needed to better inform the recommendations of health and government organizations, and reconcile data that indicate an energetically costly lifestyle can be sustained without expending more energy.

An opportunity to investigate the long-term effects of extreme physical activity on metabolic adaptation arose when the Race Across the USA (RAUSA) organized a small core team of athletes to run a transcontinental race from Huntington Beach, CA to Washington DC at the rate of one marathon per day. This one-time event took a total of 20 weeks to complete, during which runners ran approximately 6 days per week. Although the energy costs of running a marathon, an ultramarathon, or other races of extraordinary lengths have been well documented, (Cooper, Nguyen, Ruby, & Schoeller, 2011; Hill & Davies, 2001; Millet et al., 2009) the RAUSA affords an exceptional opportunity to study the individual effects on energy expenditure in humans maintaining a high level of physical activity for an extended period of time.

In order to better understand the long-term effects of extreme physical activity on energy expenditure, we measured total energy expenditure, TEE (MJ/day) in six RAUSA individuals transitioning from a moderate to extreme physical activity workloads, which was maintained for approximately five months. TEE was measured in the subjects for the three different time periods; the 5 days immediately prior to the start of the race (PR), the first week of the race (WK1), and the twentieth (and final) week of the race (WK20). It was expected that TEE would increase in all subjects during WK1 after they initially increased their physical activity, but the effect on TEE after 20 weeks of maintaining a high workload was unknown. We allowed for two possible hypotheses to changes in TEE in the WK20 data: 1) No evidence of metabolic adaptation: WK20 TEE would remain elevated at a rate consistent with WK1 or WK20 TEE would increase compared to WK1 TEE, and 2) Evidence of metabolic adaption: WK20 TEE would decrease from WK1 TEE.

This paper discusses the role of physical activity on energy expenditure and the human capacity for adaptation, as well as the potential of these findings to influence commonly held ideas regarding obesity and effects of diet and exercise on weight loss. We explore the idea that individuals metabolism will adapt to increased extreme activity levels, maintained for an extended period of time in order to conserve overall energy expenditure.

Materials and Methods

Subjects

We measured total daily energy expenditure (MJ/day), in 6 adult athletes (5 males ages 34-73, 1 female age 32), participating in the RAUSA transcontinental marathon event. This race covered 4957 km during 20 weeks of running, with subjects running approximately one marathon (42 km) per day, 6 days per week from January 16th, 2015 to June 2nd, 2015. A written explanation of the experimental protocol and associated risks were provided to all subjects and their informed written consent was obtained prior to participation in the study. Permission was obtained from the organizers of the RAUSA event, and Institutional Review Boards at Hunter College and Purdue University approved the study.

Of the 6 subjects, only 3 completed the planned racecourse on the original schedule. One subject (female, age 32) dropped out of the race after 8 weeks due to running related injuries. Two subjects decided to disassociate from the race event at week 4 and continue running their own route across the country, covering a greater daily and total distance. Of these two subjects, one (male, age 36) continued to run, and the other (male, age 42) walked while carrying a backpack. Data was still collected for both of these subjects.

TEE was measured during three periods for each subject. *Pre Race (PR)* measured the five days prior to the start of the marathons. *Week 1 (WK1)* measured the first five days of marathon running. *Week 20 (WK20)* measured the twentieth and last week of running. The timing and number of days measured for the WK20 period varied slightly for the two subjects who ran separately from the RAUSA group.

Doubly Labeled Water

Doubly labeled water (DLW), consists of water (H2O) in which approximately 6% of the hydrogen molecules are ^{2}H and 10% of the oxygen molecules are ^{18}O. At the doses administered, these isotopes are detectable in the subject's urine for 2-4 weeks after ingestion, depending on their level of physical activity. The human body loses hydrogen and oxygen in the form of water, and loses oxygen additionally in the form of carbon dioxide (CO_2); therefore the ^{2}H and ^{18}O isotopes are expelled at different rates. The difference between these rates allows for measurement of CO_2 production, a product of metabolism, from which TEE can be calculated (International Atomic Energy Agency, 2009). These isotopes occur naturally and are already present in small amounts in the human body, they are stable and safe for human use (Westerterp, 2013). Subjects ingested two separate doses of DLW; the first dose was administered 6 days before the start of the race. A urine sample was collected prior to dosing (baseline), and then samples were collected once per day for the next 10 days. This schedule provided 5 days of PR TEE, and 5 days of marathon running TEE (WK1). Each subject's current body weight was closely monitored and recorded throughout the study. RAUSA subjects were weighed daily, and their individual weight was averaged for each time period and used for TEE calculations. The remaining subjects were weighed in the field as close as possible to the time of the second dose, and again whenever possible during DLW collection. Subjects were provided with single use collection cups, transfer pipettes, and 4 ml screw cap vials for collecting their samples. All samples were kept frozen or stored on ice during transport until collected by a researcher and brought to the Human Evolution & Energetics Lab at Hunter College in New York.

The second dose of DLW was administered 2 weeks before the end of the race (WK20). The same baseline and next day collection protocol was followed, however subjects were only required to collect samples every third day for the next 10-14 days. There was some variation in collection times and dose administration depending on the athlete's schedules, as described in below in "Physical Activity."

All samples were either carbon-filtered or ultra-filtered by centrifuge using Vivaspin® tubes (Viva Products, 2016) at Hunter College. Isotope concentration analysis was performed using a Picarro® Cavity Ring Down Spectrometer (Picarro, 2013) at the Pontzer Lab at Hunter College, NY, USA.

Bioelectrical Impedance

Respirometry was used to measure resting metabolic rate (RMR), using the Cosmed Fitmate Pro (Nieman et al., 2007), during 20 minute trials in Week 1 and Week 20. RMR trials were performed by Dr. Lara Dugas, and subjects were measured early in the morning after fasting overnight and at least 30 minutes resting, while in a supine position. Bioelectrical impedance was used to measure fat free mass (FFM) with a single-frequency (50kHz) analyzer (model BIA 101Q; RJL Systems, Clinton Township, MI) for the three RAUSA subjects in January, and May (Luke et al., 2013). This method was not available for RS2 and RS5, so their FFM was estimated using total body water data obtained from DLW and using a 0.73 hydration constant. The inability to account for fluctuations in body hydration due to the extreme physical activity of the athletes made bioelectrical impedance the preferred method of measuring FFM when possible.

Calculations

Rates of isotope depletion (kD and kO), and dilution spaces (ND and NO) for ^{2}H and ^{18}O, were calculated using the slope intercept method and converted to mean daily CO_2 production using equation 17.15 in Speakman (Speakman, 1997), which is tailored to human subjects and assumes human-like fractionation and insensible water loss. For both *PR* and *WK1* measurements, dilution spaces were determined using the rate of isotope depletion over the 5-day pre-race period. These dilution spaces were combined with rates of depletion (kD and kO), calculated separately for the pre-race period and the first week of the Race to calculate *PR* and *WK1* TEE respectively. For WK20 TEE, dilution spaces and isotope depletion rates were measured over 10 days for the RAUSA subjects, 14 days for RS2, and 13 days for RS5.

Predicted TEE values were calculated by adding the estimated metabolic cost of running to each subject's *PR* TEE. Daily running distances were recorded by each runner throughout the Race. Using the energy cost of running, 3.92 $Jkg^{-1}m^{-1}$ as determined by the "slope" method in a meta-analysis of human walking and running cost (Rubenson et al., 2007) and multiplied by the subject's weight (m_{bw}) and distance traveled (d), such that:

$$TEE_{runcost} = 3.92\ m_{bw}d \qquad (1)$$

This value was added to the pre-race TEE (TEE_{PR}) for each subject in order to predict TEE during WK1.

$$TEE_{exp} = TEE_{PR} + TEE_{runcost} \qquad (2)$$

In order to correct TEE_{PR} for the effect of changes in body composition by WK20, the changes in m_{bw} (WK20 m_{bw} - PR m_{bw}) were multiplied by the slope of the linear regression between m_{bw}/TEE (Figure 1) and added to *PR* TEE to create a *PR* equivalent (*PREQ*) for WK20.

$$TEE_{PREQ} = PR + 0.076(\Delta m_{bw}) \qquad (3)$$

This is necessary because body size is directly correlated with TEE (Figure 1). Therefore, any weight lost or gained from Jan – May will have a corresponding effect on decreasing or increasing the baseline TEE (PR) used in our predictive calculations. Predicted WK20 TEE values were calculated using TEE_{PREQ} in place of TEE_{PR} in equation (2). Distance was recorded daily for each subject during the days when DLW samples were collected, and the mean distance for each subject was calculated for both WK1 and WK20. Predicted walking costs for RS2, who walked with a backpack during the WK20 period, were calculated using the same method as above, except that walking cost (2.06 $Jkg^{-1}m^{-1}$) was substituted for the running cost, and multiplied by the appropriate factor to account for the additional load being carried. In this case, since the load carried was less than 50% of body weight (17.5%), m_{bw} was proportionately increased by the amount of the load in order to calculate walking cost as supported by previous studies (Bastien, Willems, Schepens, & Heglund, 2005; Griffin, Roberts, & Kram, 2003; Huang & Kuo, 2014).

$$TEE_{walkcost} = 2.06\ m_{bw}(1.175)d \qquad (4)$$

Walking cost was added to TEE_{PREQ} as described in equation (2) for running cost in order to predict WK20 TEE for RS2.

Physical Activity

The three RAUSA subjects (RS1, RS3, and RS6), ran approximately 41 km per day, 6 days per week, for 20 weeks until reaching their destination in Washington D.C. The other two subjects traveled as far as Boston and their second round of TEE measurements was taken during the 2 weeks before they reached New York City. The fourth subject (RS5) ran approximately 65 km per day and reached New York 15 weeks after beginning the race. The fifth subject (RS2) was walking during the second TEE collection period with a 15 kg backpack for approximately 61 km per day and reached NY 16 weeks after beginning the race. Daily distance was carefully tracked and recorded for all subjects.

During the first week, running distances varied slightly (range 0 – 1.8 km) due to the fact the racecourse was not marked and runners were responsible for keeping track of the route. Subjects would occasionally miss a turn and need to either backtrack or detour to get back on the race route, which affected their daily distance. Runners monitored and recorded these deviations, and distance totals used to calculate individual TEE estimates were adjusted accordingly in order to improve estimation accuracy. This protocol was followed for all subjects during the final week as well.

Statistical Analyses

For WK1 and WK20, the difference between observed and expected TEE for each subject was determined, and a 95% confidence interval was calculated using MS Excel® (2010) in order to create a range for the difference between observed and expected TEE. To account for the small sample size, standard error was adjusted using appropriate t-values (Fowler, 1998). The difference between predicted and observed TEE was calculated for each subject at WK1 and WK20. Differences from expected TEE were considered significant if 0 did not fall within the 95% confidence interval for the mean of *expected – observed TEE*. Pre-race TEE data was compared to a 95% confidence interval based on previously published data of daily TEE for men and women in Western countries (Pontzer et al., 2012).

Results

During the five days prior to the race (PR), mean TEE for the RAUSA males was 12.57±1.85 MJ/day, which falls within an expected range of previously studied TEE values (12.25 – 13.29 MJ/day, 95% C.I.) for men in Western countries (n=53) with a mean body mass of 81.0±11.1 kg, and mean %body fat of 22.5±5.0 (Pontzer et al., 2012). Mean body mass and mean %body fat did not differ significantly in RAUSA males from the group of men in Western countries. TEE_{PR} for the only RAUSA female subject was 13.63 MJ/day, which was higher than the expected range (9.60 – 10.04 MJ/day, 95% C.I.) for women in Western countries (n=186) with a mean body mass of 74.46±12.8, and mean %body fat of 37.96±7.0 (Pontzer et al., 2012). RS4's PR total body mass of 70.80kg fell within the expected range for western women (49.31 – 99.49 kg, 95% C.I.) however, her 19.2% body fat was significantly lower than those whose energy expenditure she was being compared to (24.18 - 51.62% body fat, C.I. 95%), which could account for her higher than expected PR_{TEE}.

After five consecutive days of marathon running, mean WK1 TEE for all 6 subjects increased to 25.95± 3.69 MJ/day, which was not significantly different than expected values of 25.46± 3.17 MJ/day (Table 2). The mean distance traveled during WK1 was 43.01± 0.74 km/day.

After 20 weeks of running, mean WK20 TEE for the remaining three RAUSA runners decreased to 20.53± 3.62 MJ/day. During WK20, RAUSA runners averaged less distance per day than in WK1, at 39.95± 0.38 km/day. In RS5, TEE during the final week increased to 27.39 MJ/day, however with regard to the increased distance (64.72 km) per day that he was running, this was still 1.56 MJ below expected TEE. RS2 was also completing a greater daily distance (60.77 km/day), however his WK20 TEE was lower than his WK1 as he was walking instead of running. Additionally, his WK20 TEE was 2.40 MJ below expected. Overall TEE among all five athletes decreased to 22.39±3.94 MJ/day. The 95% confidence interval of the WK20 TEE difference from expected for all five athletes does not include 0 (-3.01, -1.36), indicating that these results are significantly lower than expected (Figure 2).

Runners' body mass decreased by 0.17kg (±1.66) from PR to WK1, and an additional 4.86kg (±4.51) decrease was observed from WK1 to WK20. Fat free mass (FFM) decreased by 4.06kg (±6.26) from WK1 to WK20, and mean %body fat decreased from 20.5% to 18.5%, a mean difference of -2.3% (±2.13). Resting metabolic rate (RMR) increased slightly from 6.88 (±1.21) MJ/day prior to the race in January to 7.29 (±1.14) MJ/day in May (n=3). Mean water throughput prior to the race was 4.79 (±1.57) L/day and increased to 8.41 (±2.09) L/day during WK1 (n=6). During WK20 mean water throughput decreased slightly from WK1 levels to 7.68 (±1.60) L/day, with the biggest decrease coming from RS2 (walking) with a difference of -3.03 L/day.

Discussion

At 22.39 – 25.95 MJ/day, RAUSA runners maintained energy expenditure levels among some of the highest ever recorded in humans. A comparison of 24 DLW studies on maximal energy expenditure in human athletes found sustained TEE as high as 48.7 MJ/day, and included data from Tour de France cyclists at 35.7 MJ/day (Cooper et al., 2011). The closest daily energy expenditure to the RAUSA athletes was 26.5 MJ/day, which was found in an ultra-endurance runner over a period of 14 days, covering 70-90 km per day with no rest days. While TEE among RAUSA subjects were not quite as high as some other extreme endurance athletes, it should be noted that the RAUSA subjects sustained these activity levels for longer than any of the other studies by at least 50 or more days.

The effects of ~5kg weight loss in the subjects by WK20 translated to a decrease of 0.37 MJ (±0.33) in the predicted WK20 TEE. Despite this correction, the 2.19 MJ (~522kCal) decrease in TEE from expected TEE in all subjects represents a significant indication that when extreme levels of physical activity are sustained over a long period of time, there is a physiological response in order to conserve energy expenditure. In addition, these metabolic changes are independent of changes in RMR (0.41 ±0.60 MJ/day), total body weight (-4.86kg ±4.31), or FFM (-1.40kg ±2.54).

During the 5 days prior to the start of the race, athletes were busy and active. Activity logs showed that many continued to run during the five days before the event began (mean = 3.96±2.43 km/day). RS4 especially, who ran an 80.47 km race on the same day as the first DLW dose administration (one day prior to PR TEE calculation), but was not factored into any of the calculations as it fell outside of the PR measurement period. This may account for the significantly elevated TEE in RS4 during the PR measurements, while none of the male subjects experienced a significantly different from expected PR TEE.

There were observed behavioral differences in the runner's activity levels while visiting them during the collection periods for the first and final weeks of the race. The initial atmosphere was defined by excitement and activity among the runners as they adjusted to their new daily routine of making and breaking camp, organizing their supplies, planning their daily meals, and running errands. Additionally, there was a lot of socializing, the need for bonding as they prepared to spend the next 5 months as a social unit resulted in taking walks or hikes together, game play, and going out at night (C. Thurber, observations, Jan 19 – 21, 2015). After almost 20 weeks of running, the scene at the campsite had quieted down considerably as the runners seemed to have fallen into an easy routine of preparing their gear and evening meals.

The atmosphere was more serene, quiet conversations prevailed rather than boisterous activity, while runners lounged at picnic benches or sat in their chairs or tents. The runners seemed used to the idea of waking up daily to run a marathon as a matter of routine, and were looking forward to the finish (C. Thurber, observations, May 29 – June 03, 2015).

These differences in non-exercise physical activity (non-ex PA) levels may account for the discrepancy between expected and observed energy expenditure. It may be that runners (knowingly or unconsciously) made adjustments to their daily activity levels in order compensate for the added energy needs of running a marathon every day. Levine et al. (Levine et al., 2005) found that a discrepancy of around 2.5 hours/day between groups that either spent more time sitting vs. standing/ambulating could translate to a difference of 352 kcal/day (in mildly obese subjects). However, since non-exercise activity levels were not measured in the RAUSA subjects, it is unknown how greatly they factored into the decreased TEE observed in the data. While it may be plausible that RAUSA subjects spent two or more hours being less active per day, their leaner body types (requiring less ambulatory cost) would require a much larger time loss to account for the 522 kcal/day difference. Therefore, it is unlikely that a decrease in non-ex PA alone would account for the decreases in energy expenditure observed during week 20.

Studies have also shown that increasing physical activity will lead to a decrease in energy/functionality in other body systems; common examples of this are low mineral bone density and amenorrhea among female athletes (Marcus et al., 1985; Torstveit & Sundgot-Borgen, 2005). Rosenkilde et al. (Rosenkilde et al., 2012) observes a threshold for loss of body weight and fat mass in groups of moderate and high levels of energy expenditure. The constrained model for energy expenditure proposed by Pontzer et al. (Pontzer et al., 2016) suggests that the threshold for physical activity maintains TEE around ~2,600 kcal/day, much lower than the amounts sustained by RAUSA athletes (~5,400 kcal/day). This indicates that while metabolic adaptation may have some effect on decreasing TEE in cases of extreme energy expenditure, there is a limit to the amount of energy that can be constrained with added physical activity. More research in the mechanisms that control allocation of energy would be needed in order to better understand what the explanation is for the decrease in energy expenditure observed here.

Due to the complexities of this experiment and of the human body, none of the theories proposed here provide a perfect explanation of the gap between expected and observed TEE in week 20. Individual variation, sex, and age can also affect TEE, therefore, it is most likely that a combination of these factors as well as non-ex PA compensation, and metabolic adaptation, are responsible for the observed decrease in energy expenditure among RAUSA athletes.

Limitations

The small sample size of n=5 was a limiting factor in this study. In addition, the unique circumstances that led to the opportunity for this study make it a difficult one to repeat. The scope of the analysis was limited by the loss of the only female subject participating in the event; therefore no female data exists to determine whether sexes differ in their ability to adapt to extreme physical activity.

Future Directions

Although there was a wide range of ages among the subjects, the sample size was too small to determine any significant correlation between age and degree of metabolic adaptation. Future studies with a larger sample size would be needed in order verify if any changes to metabolic adaptation occur with age. Additionally, future research would be needed to determine if there is any difference in the size of adaptation between males and females. The effects of energy intake were not analyzed here, however dietary data was recorded during this study, and forthcoming studies will be of great interest in order to determine if the effect of this variable on energy expenditure and metabolic adaptation.

Conclusion

The decreases in energy expenditure observed in the RAUSA data supports evidence of metabolic adaptation in extremely active humans to high levels of physical activity over an extended period of time. Despite the small number of subjects, there is still a wide range of ages, as well as variation with respect to body mass between the subjects. This data is part of a growing body of research, which all indicate a similar trend; that increases in physical activity do not have an infinitely additive effect on energy expenditure. Therefore, when concerning issues of obesity and weight loss, the accuracy of exercise calorie counts should be reconsidered, as evidence indicates that the metabolic equation is more complex than simply subtracting caloric energy expenditure from caloric intake.

Tables & Figures

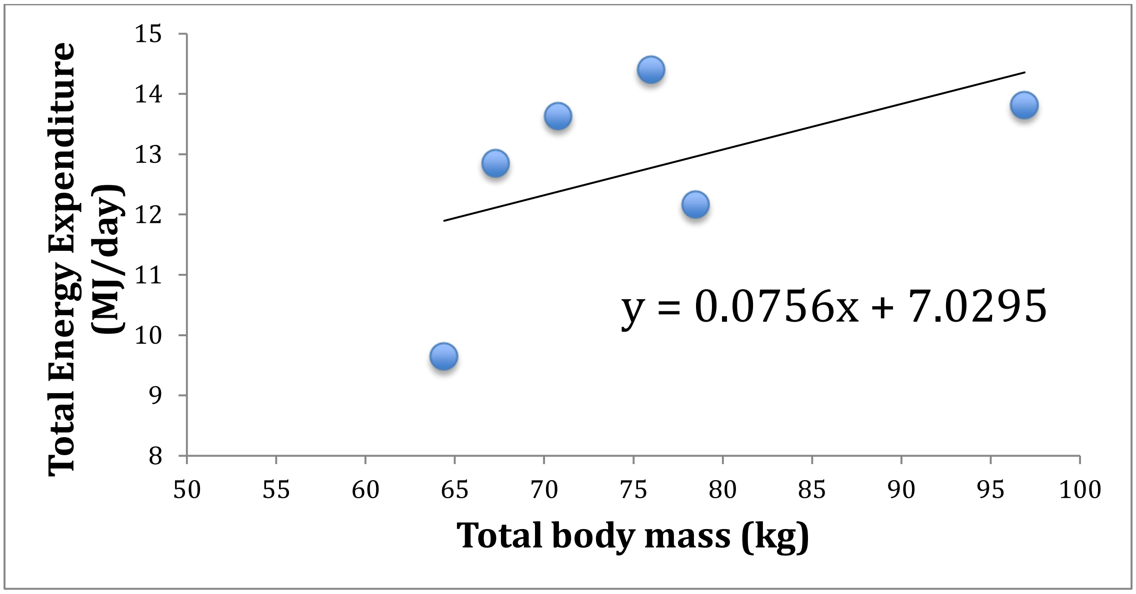

Figure 1: Linear regression of TEE vs. Body mass. Slope is used to correct TEE_{PR} for week 20

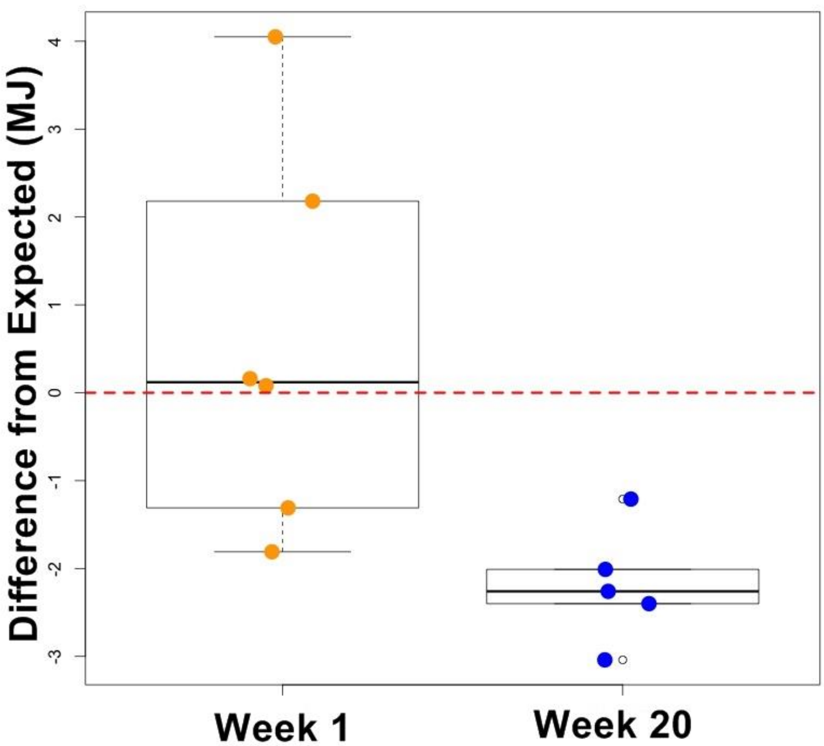

Figure 2: Differences in observed/estimated TEE among all athletes during Week 1 (n=6) and Week 20 (n=5). Dotted line represents observed TEE = expected TEE. Created in R® (R Core Team, 2014)

Table 1: Demographic information for RAUSA subjects; sex, age, height, weight, resting metabolic rate, fat free mass, percent fat

Subject	Sex	Age	Height (m)	PR mass (kg)	WK1 mass (kg)	WK20 mass (kg)	WK20 mass change	WK1 FFM (kg)	WK20 FFM (kg)	WK20 FFM change	WK1 %Fat	WK20 %Fat	WK20 %Fat change	Jan RMR (MJ)	May RMR (MJ)	RMR Change
RS1	M	73	1.75	64.40	63.7	61.72	-2.68	49.20	49.70	0.50	23.60	19.50	-4.10	5.48	6.11	0.63
RS6	M	34	1.80	78.50	78.3	73.90	-4.60	63.20	60.70	-2.50	19.50	17.80	-1.70	7.65	7.38	-0.27
RS3	M	53	1.78	76.00	73.7	71.90	-4.10	63.90	61.90	-2.00	15.90	13.90	-2.00	7.50	8.38	0.88
RS2	M	41	1.80	96.90	97.5	84.80	-12.10	68.04	63.33	-4.71	29.80	25.30	-4.50	-	-	-
RS5	M	36	1.80	67.30	69.9	66.50	-0.80	54.25	55.97	1.72	15.00	15.80	0.80	-	-	-
RS4	F	32	1.73	70.80	69.8	-	-	56.67	-	-	19.20	-	-	-	-	-
Mean	-	-	-	75.65	75.48	71.76	-4.86	58.93	54.21	-1.40	20.58	23.44	-2.30	6.88	7.29	0.41
Median	-	-	-	73.40	71.80	71.90	-4.10	57.36	55.97	-2.00	21.40	22.40	-2.00	7.50	7.38	0.63
SD	-	-	-	11.66	11.82	8.71	4.31	7.03	5.55	2.54	5.48	4.36	2.13	6.88	7.29	0.60

Table 2: TEE and Distance measurements for January through May in RAUSA subjects

Subject	TEE PR (MJ)	Expected MJ cost of WK1	TEE WK1 Exp	TEE WK1 (MJ)	TEE WK1 difference from Exp	WK20 PR EQ (MJ)	Expected MJ cost of WK20	TEE WK20 Expected	TEE WK20 (MJ)	TEE WK20 difference from Exp	Jan distance (m/day)	May distance (m/day)	Distance difference Jan/May
RS1	9.64	10.73	20.37	22.38	2.01	9.44	9.61	19.05	17.04	-2.01	42985	39716	-3269
RS6	12.16	13.08	25.24	23.59	-1.65	11.81	11.52	23.33	20.28	-3.04	42615	39750	-2865
RS3	14.40	12.35	26.75	30.98	4.23	14.09	11.38	25.47	24.26	-1.21	42750	40388	-2362
RS2	13.81	16.29	30.10	29.87	-0.23	12.90	12.47	25.37	22.97	-2.40	42621	60765	18144
RS5	12.84	11.68	24.52	22.95	-1.58	12.78	16.87	29.66	27.39	-2.26	42615	64718	22103
RS4	13.63	12.17	25.80	25.93	0.13	-	-	-	-	-	44488	-	-
Mean	12.75	12.72	25.46	25.95	0.49	12.48	12.37	24.57	22.39	-2.19	43012	49067	6350
Median	13.24	12.26	25.52	24.76	-0.05	12.86	11.52	25.37	22.97	-2.26	42686	40388	-2362
SD	1.71	1.92	3.17	3.69	2.27	1.74	2.72	3.85	3.94	0.66	737	12563	12655

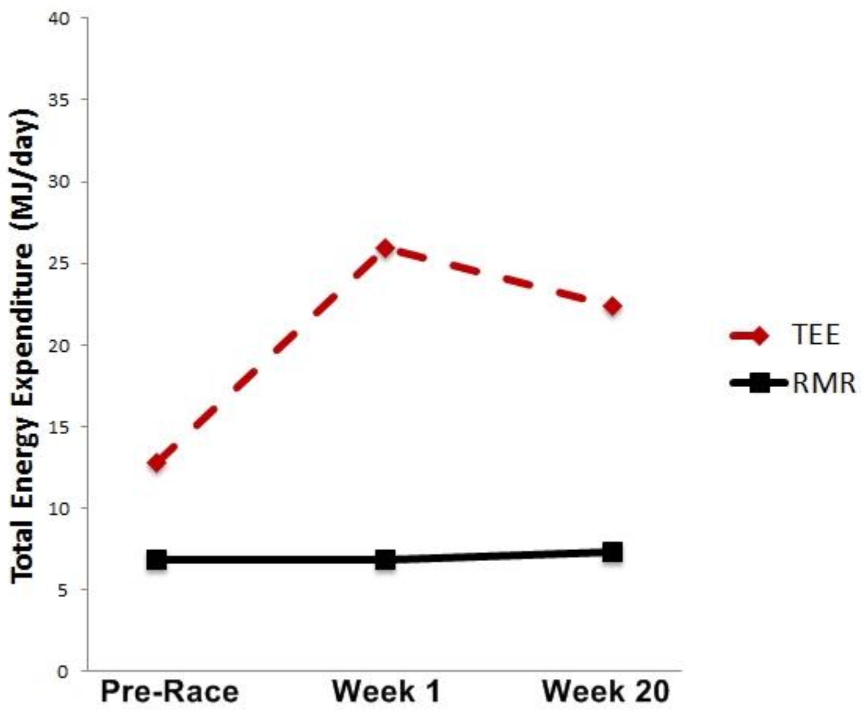

Figure 3: Average changes in RMR and TEE from January (n=6) to May (n=5) in all athletes.

Table 3: Water throughput for PR, WK1 and WK20 in all subjects.

Subject	H_2O PR (L/day)	H_2O WK1 (L/day)	H_2O WK20 (L/day)	WK1 H_2O change	WK20 H_2O change
RS1	2.84	5.52	6.53	2.68	1.01
RS6	4.00	7.55	8.09	3.55	0.54
RS3	6.34	10.74	10.14	4.40	-0.60
RS2	3.92	9.96	6.06	6.04	-3.90
RS5	4.67	6.79	7.56	2.12	0.77
RS4	6.96	9.90	-	2.94	-
Mean	4.79	8.41	7.68	3.62	-0.44
Median	4.34	8.73	7.56	3.25	0.54
SD	1.57	2.09	1.60	1.42	2.03

Works Cited

Bastien, G. J., Willems, P. A., Schepens, B., & Heglund, N. C. (2005). Effect of load and speed on the energetic cost of human walking. *Eur J Appl Physiol, 94*(1-2), 76-83. doi:10.1007/s00421-004-1286-z

Cook, B. G., Li, D., & Heinrich, K. M. (2015). Obesity, Physical Activity, and Sedentary Behavior of Youth With Learning Disabilities and ADHD. *J Learn Disabil, 48*(6), 563-576. doi:10.1177/0022219413518582

Cooper, J. A., Nguyen, D. D., Ruby, B. C., & Schoeller, D. A. (2011). Maximal sustained levels of energy expenditure in humans during exercise. *Med Sci Sports Exerc, 43*(12), 2359-2367. doi:10.1249/MSS.0b013e31822430ed

Duffy, J. (2014, May 08). MyFitnessPal (for iPhone). *PCMag.com*.

Dugas, L. R., Harders, R., Merrill, S., Ebersole, K., Shoham, D. A., Rush, E. C., . . . Luke, A. (2011). Energy expenditure in adults living in developing compared with industrialized countries: a meta-analysis of doubly labeled water studies. *Am J Clin Nutr, 93*(2), 427-441. doi:10.3945/ajcn.110.007278

FAO/WHO/UNU. (2001). *Human energy requirements*. Rome: United Nations.

Fowler, J. C., Lou; Jarvis, Phil. (1998). *Practical Statistics for Field Biology, 2nd Edition*. West Sussex: John Wiley and Sons.

Griffin, T. M., Roberts, T. J., & Kram, R. (2003). Metabolic cost of generating muscular force in human walking: insights from load-carrying and speed experiments. *J Appl Physiol (1985), 95*(1), 172-183. doi:10.1152/japplphysiol.00944.2002

Hill, R., & Davies, P. (2001). Energy expenditure during 2 wk of an ultra-endurance run around Australia. *Medicine and Science in Sports and Exercise*, 148-151. doi:10.1097/00005768-200101000-00022

Huang, T. W., & Kuo, A. D. (2014). Mechanics and energetics of load carriage during human walking. *J Exp Biol, 217*(Pt 4), 605-613. doi:10.1242/jeb.091587

International Atomic Energy Agency. (2009). *IAEA Human Health Series No. 3. Assessment of Body Composition and Total Energy Expenditure in Humans Using Stable Isotope Techniques*. Vienna: IAEA.

Ladabaum, U., Mannalithara, A., Myer, P. A., & Singh, G. (2014). Obesity, abdominal obesity, physical activity, and caloric intake in US adults: 1988 to 2010. *Am J Med, 127*(8), 717-727 e712. doi:10.1016/j.amjmed.2014.02.026

Levine, J. A., Lanningham-Foster, L. M., McCrady, S. K., Krizan, A. C., Olson, L. R., Kane, P. H., . . . Clark, M. M. (2005). Interindividual variation in posture allocation: possible role in human obesity. *Science, 307*(5709), 584-586. doi:10.1126/science.1106561

Luke, A., Bovet, P., Forrester, T. E., Lambert, E. V., Plange-Rhule, J., Dugas, L. R., . . . Schoeller, D. A. (2013). Prediction of fat-free mass using bioelectrical impedance analysis in young adults from five populations of African origin. *Eur J Clin Nutr, 67*(9), 956-960. doi:10.1038/ejcn.2013.123

Marcus, R., Cann, C., Madvig, P., Minkoff, J., Goddard, M., Bayer, M., . . . Genant, H. (1985). Menstrual Function and Bone Mass in Elite Women Distance Runners: Endocrine and Metabolic Features. *Annals of Internal Medicine, 102*(2), 158-163. doi:10.7326/0003-4819-102-2-158

Melanson, E. L., Keadle, S. K., Donnelly, J. E., Braun, B., & King, N. A. (2013). Resistance to exercise-induced weight loss: compensatory behavioral adaptations. *Med Sci Sports Exerc, 45*(8), 1600-1609. doi:10.1249/MSS.0b013e31828ba942

Millet, G. Y., Morin, J. B., Degache, F., Edouard, P., Feasson, L., Verney, J., & Oullion, R. (2009). Running from Paris to Beijing: biomechanical and physiological consequences. *Eur J Appl Physiol, 107*(6), 731-738. doi:10.1007/s00421-009-1194-3

Nieman, D., Lasasso, H., Austin, M., Pearce, S., McInnis, T., & Unick, J. (2007). Validation of Cosmed's Fitmate in measuring exercise metabolism. *Res Sports Med, 15*(1), 67-75.

Physical Activity Guidlines Advisory Committee. (2008). *Physical Activity Guidlines Advisory Committee Report*. Washington, DC.

Picarro. (2013). PICARRO L2140-i δ18O/δ17O/δD/17O-excess High-Precision Isotopic Water Analyzer. Santa Clara, CA.

Pontzer, H. (2015). Constrained Total Energy Expenditure and the Evolutionary Biology of Energy Balance. *Exerc Sport Sci Rev, 43*(3), 110-116. doi:10.1249/JES.0000000000000048

Pontzer, H., Durazo-Arvizu, R., Dugas, L. R., Plange-Rhule, J., Bovet, P., Forrester, T. E., Luke, A. (2016). Constrained Total Energy Expenditure and Metabolic Adaptation to Physical Activity in Adult Humans. *Curr Biol, 26*(3), 410-417. doi:10.1016/j.cub.2015.12.046

Pontzer, H., Raichlen, D. A., Wood, B. M., Mabulla, A. Z., Racette, S. B., & Marlowe, F. W. (2012). Hunter-gatherer energetics and human obesity. *PLoS ONE, 7*(7), e40503. doi:10.1371/journal.pone.0040503

R Core Team. (2014). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing Retrieved from http://www.R-project.org/

Rosenkilde, M., Auerbach, P., Reichkendler, M. H., Ploug, T., Stallknecht, B. M., & Sjodin, A. (2012). Body fat loss and compensatory mechanisms in response to different doses of aerobic exercise--a randomized controlled trial in overweight sedentary males. *Am J Physiol Regul Integr Comp Physiol, 303*(6), R571-579. doi:10.1152/ajpregu.00141.2012

Ross, R., & Janssen, I. A. N. (2001). Physical activity, total and regional obesity: dose-response considerations. *Medicine and Science in Sports and Exercise, 33*(Supplement), S521-S527. doi:10.1097/00005768-200106001-00023

Rubenson, J., Heliams, D. B., Maloney, S. K., Withers, P. C., Lloyd, D. G., & Fournier, P. A. (2007). Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses. *J Exp Biol, 210*(Pt 20), 3513-3524. doi:10.1242/jeb.000992

Speakman, J. R. (1997). *Doubly labelled water: theory and practice*. London: Chapman and Hall.

The Partnership for a Healthier America. (2016). Let's Move. Retrieved from http://www.letsmove.gov/

Torstveit, M. K., & Sundgot-Borgen, J. (2005). The Female Athlete Triad Exists in Both Elite Athletes and Controls. *Medicine & Science in Sports & Exercise, 37*(9), 1449-1459. doi:10.1249/01.mss.0000177678.73041.38

Viva Products. (2016). Vivaspin® 4 and Vivaspin® 6 Data Sheet. Gloucestershire

Wang, Y., & Beydoun, M. A. (2007). The obesity epidemic in the United States--gender, age, socioeconomic, racial/ethnic, and geographic characteristics: a systematic review and meta-regression analysis. *Epidemiol Rev, 29*, 6-28. doi:10.1093/epirev/mxm007

Westerterp, K. (2013). Physical activity and physical activity induced energy expenditure in humans: measurement, determinants, and effects. *Frontiers in Physiology, 4*, 90. doi:10.3389/fphys.2013.00090

Westerterp, K., & Speakman, J. (2008). Physical activity energy expenditure has not declined since the 1980s and matches energy expenditures of wild mammals. *Int J Obes (Lond), 32*(8), 1256-1263. doi:10.1038/ijo.2008.74

World Health Organization. (2010). *Global Recommendations on Physical Activity for Health*. (978 92 4 159 997 9). Geneva: WHO Press.