

Research article

High Rates of Fat Oxidation Induced by a Low-Carbohydrate, High-Fat Diet, Do Not Impair 5-km Running Performance in Competitive Recreational Athletes

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Abstract

A common belief is that high intensity exercise ($>60\%VO_{2max}$) is best sustained by high rates of carbohydrate oxidation. The belief is based, in part, on an idea developed by Krogh and Lindhard in 1920. In the 100 years since, few studies have tested its validity. We tested the null hypothesis that performance in competitive recreational athletes exercising at $>80\% VO_{2max}$, during simulated 5-km running time trials (5KTT) would be impaired during a 6-week period of adaption to a low-carbohydrate, high-fat (LCHF) diet, compared to their performances when they ate a diet higher in carbohydrate and lower in fat (HCLF). Seven male athletes (age 35.6 ± 8.4 years, height 178.7 ± 4.1 cm, weight 68.6 ± 1.6 kg) completed two maximal exercise (VO_{2max}) tests (Day 1 and 39) and four 5KTT (Day 4, 14, 28, and 42) in a fasted state during two 6-week periods when they ate either a HCLF or a LCHF diet, in a randomized counterbalanced, crossover design. Exercise performance during the VO_{2max} tests was unchanged on either diet ($p = 0.251$). Performance in the initial 5KTT was significantly slower on the LCHF diet ($p = 0.011$). There were no diet-related performance differences in the remaining three 5KTT ($p > 0.22$). Subjects exercised at $\sim 82\%VO_{2max}$. Carbohydrate oxidation provided 94% of energy on the HCLF diet, but only 65% on the LCHF diet. 5KTT performance at $\sim 82\%VO_{2max}$ was independent of the runners' habitual diet. The HCLF diet offered no advantage over a diet with a high-fat content. Since these athletes run faster than 88% of recreational distance runners in the United States (U.S.), this finding may have wide general application.

Key words: Fat oxidation, ketogenic, high carbohydrate, performance, high-fat diet, low-carbohydrate diet.

Introduction

In 1920 Krogh and Lindhard (1920) reported that “on fat diets the (exercise) fatigue became considerable and sometimes excessive. For several hours after the work on the ergometer these subjects were generally very tired when on a fat diet and much less tired or not tired at all when on carbohydrates”. Accordingly, “work is more economically performed on carbohydrate than on fat. When the work was sufficiently severe the subjects performed it with greater difficulty on fat than on carbohydrate and became much more tired”.

This historical belief that fat is an inferior metabolic fuel unable to support exercise of higher intensity, is the

singular belief that drives the prescription of high carbohydrate diets for most athletes (Hawley et al., 1998; Jeukendrup 2003; Stellingwerff and Boit, 2007; Stellingwerff et al., 2011; Burke et al., 2011; Hawley and Leckey, 2015; Costa et al., 2018; Burke and Hawley, 2018; Cermak and van Loon, 2013; Jeukendrup et al., 2000; Spriet, 2007; Williams et al., 1984; Bartlett et al., 2015; Burke, 2015) since “CHO-based fuels become the predominant energy source for trained muscle when exercise intensities are $>60\%$ of peak oxygen uptake” (Hawley and Leckey, 2015); because “endogenous fatty acid stores are substantial but do not provide muscle contractile energy (i.e. adenosine triphosphate) at rates that sustain higher exercise intensity or high force contractions” (Costa et al., 2018); because “rates of muscle fat oxidation are inadequate to support the high relative ($70 - 90\% VO_{2max}$) and absolute work rates sustained by competitive athletes during running or cycling events lasting $<2hr$ (Hawley and Leckey, 2015; Jeukendrup et al., 2000; Spriet, 2007; Williams et al., 1984)” (Leckey et al., 2015).

This doctrine is supported by key studies showing that exercise performance is impaired in athletes eating low carbohydrate high fat (LCHF) diets (Burke et al., 2017; Havemann et al., 2006), which substantially reduces rates of carbohydrate oxidation during exercise (Burke et al., 2017; Vogt et al., 2003; Cameron-Smith et al., 2003; Stellingwerff et al., 2006; Volek et al., 2016; Webster et al., 2016). For example, race walking performance during a 25-km time trial was significantly impaired after 3 weeks on a LCHF diet (Leckey et al., 2015). Rates of carbohydrate oxidation (~ 0.5 g/min) were amongst the lowest recorded in competitive athletes.

But a feature of this common belief is the relative absence of studies designed specifically to refute that hypothesis. The two studies (Burke et al., 2017; Havemann et al., 2006) most frequently cited as conclusive proof both evaluated performance during prolonged exercise, not during high intensity exercise. Neither was designed specifically to test whether carbohydrate is the essential fuel for performance at exercise intensities of $>60\%$ (Hawley and Leckey, 2015) or $75\% VO_{2max}$ (Stellingwerff and Boit, 2007; Stellingwerff et al., 2011). In addition, the period of exposure to a high fat diet in both studies (1-3 weeks) was shorter than the 4 or more weeks that is considered more optimal (Cipryan et al., 2017; Volek et al., 2016).

Furthermore, four studies (van Loon et al., 2001; Achten et al., 2003; Capostagno and Bosch, 2010; Romijn et al., 1993) cited by Leckey et al. (2015) as evidence for this carbohydrate dependence of high intensity exercise included only subjects habituated to HCLF diets. Yet it is clear that the habitual diet strongly influences the metabolic response during exercise. Thus studies of athletes who subsist on LCHF diets show that such athletes achieve higher rates of fat oxidation during exercise at intensities of 64% VO_{2max} (Volek et al., 2016), 70% VO_{2max} (Cameron-Smith et al., 2003; Stellingwerff et al., 2006), 72% VO_{2max} (Webster et al., 2016), 77% VO_{2max} (Burke et al., 2017) and even up to 89% VO_{2max} (Vogt et al., 2003) than do athletes eating higher carbohydrate diets.

Accordingly, to determine whether or not athletes can perform high intensity exercise whilst eating a LCHF diet, we studied competitive recreational athletes performing frequent 5-km laboratory time trials during adaptation to that diet. Racing at this distance is performed at higher intensities than longer races in which performance is also believed to be carbohydrate dependent (Hawley and Leckey, 2015; Spriet, 2007; Williams et al., 1984). We tested the hypothesis that the performance of competitive recreational athletes would be impaired during simulated 5km running time trials run at >80% VO_{2max} , compared to their performances when they ate a HCLF diet. This would confirm the current belief that optimum performance

during exercise at intensities of >60% (Hawley and Leckey, 2015) or >75% VO_{2max} (Stellingwerff et al., 2011) is determined by the athletes' ability to metabolize carbohydrate at high rates ("carbohydrate-dependence").

Methods

Experimental design

Participants underwent two 42-day experimental conditions (HCLF or LCHF) in a randomized (www.randomizer.org), counterbalanced, crossover design with a two week washout period between dietary interventions without feeding limitations. Participants were instructed to maintain their same training loads for the duration of the study. A maximal oxygen consumption (VO_{2max}) test was performed at baseline (Day 1) and 6 weeks (Day 39; Figure 1) following the dietary intervention. A 5-km running time trial (5KTT) was performed four times during each dietary intervention (Day 4, 14, 28, and 42; Figure 1). Subjects were instructed to refrain from caffeine and alcohol consumption for 48 hours and racing or training for 24 hours before each exercise test. Testing sessions were conducted in the morning, at least eight hours after each subject's last meal in an environment with controlled temperature and humidity (19-21°C, humidity = 35-40%). All testing took place within the Exercise Science Laboratory of the College.

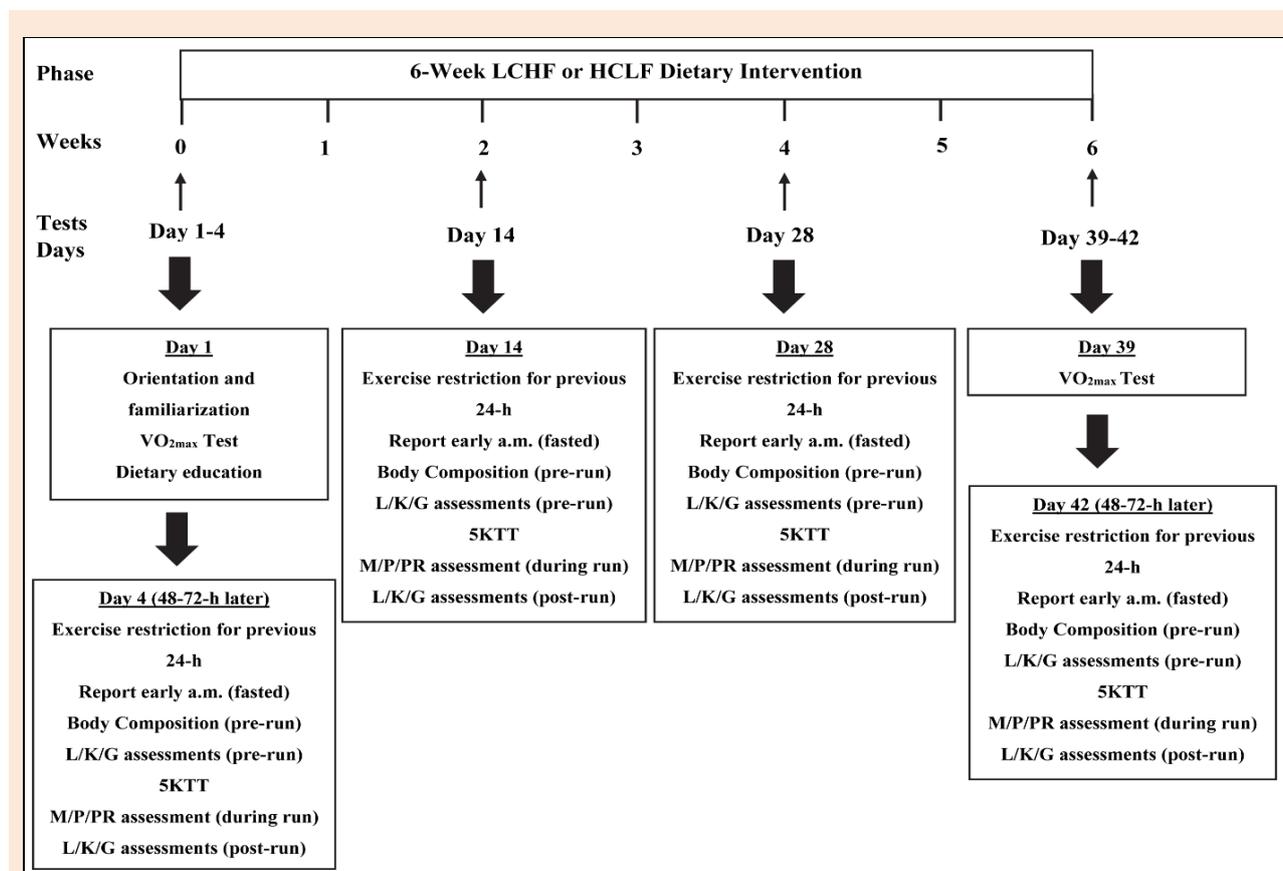


Figure 1. Timeline of experimental protocol. L/K/G = blood lactate, ketone, and glucose. M/P/PR = metabolic, physiological, and perceptual.

Participants

Seven competitive recreational distance runners participated in this study (Table 1). Included were men who: 1) have completed a 5-km distance run under 21 minutes within the last 3 months; 2) currently run a minimum of 20 miles per week; 3) are between the ages of 18 and 45 years; 4) have >2 years of running experience; 5) currently consume a carbohydrate-based diet (>50% kcals). Participants were not currently taking medications or following a LCHF or ketogenic diet. Before enrolling in the study, participants were fully informed of any associated risks and discomforts prior to giving their written informed consent to participate. The experimental protocol was approved by the Institutional Review Board of the College prior to implementation.

Table 1. Subject Characteristics (n = 7).

Variable	Mean ± SD
Age (years)	35.6 ± 8.4
Height (m)	1.79 ± 0.04
Weight (kg)	68.6 ± 1.6
BMI (kg/m ²)	21.5 ± 1.1
Body Fat (%)	5.0 ± 1.3
Fat Mass (kg)	3.5 ± 1.0
Lean Mass (kg)	65.1 ± 1.5
Number of 5-km Races	115 ± 122
Mean Running Distance Per Week (km)	63.0 ± 27.1
Running Experience (years)	15.1 ± 7.1

Familiarization procedures

Before the diet interventions began, all the experimental procedures were explained to the subjects. Participants underwent an orientation involving practice of treadmill running and familiarization to the various measurement instruments, equipment, and perceptual measures of affect (Hardy and Rejeski, 1989) and of perceived exertion (Robertson, 2004).

Exercise training monitoring

Subjects were instructed to maintain their usual training frequency during the study intervention without increasing or decreasing the training load. Baseline training volume was measured one week prior to the intervention by having subjects complete a training log (mode, duration, and intensity of each workout). Subjects were provided with a copy of their pre-trial log and instructed to maintain the same training load throughout the dietary intervention period. Training volume was assessed during the first and last week of each dietary intervention to measure compliance.

Dietary interventions

Subjects received a mandatory dietary instruction session prior to the beginning of the study. This provided detailed instructions on how to keep an accurate record of their food intake. The subjects' habitual dietary intake was assessed using a 3-day weighed dietary record, consisting of 2 week days and 1 weekend day. In addition, all subjects were required to provide a 3-day food log (2 weekdays and 1 weekend) every week during the study. Subjects were given a digital portable food scale (Ozeri ZK14-S Pronto, San Diego, CA) and instructed to weigh all food items sep-

arately if possible or to estimate the amounts. Diet information was entered into a commercial nutrient analysis software (Nutritionist Pro™, Axxya Systems, Stafford, TX). Subjects were provided with handouts summarizing the main aspects of each diet, given a list of suitable foods, and a 6-week LCHF and HCLF meal plan. The macronutrient goals were: LCHF <50g/day CHO, 75-80% fat, 15-20% protein and HCLF 60-65% CHO, 15-20% protein, 20% fat. Both diets were allowed to be consumed *ad libitum* (to full satiety). No calorie count or limits were instituted. To prevent orthostatic hypotensive symptoms, the LCHF group was advised to consume 1-2g/day of sodium (McSwiney et al., 2018). Daily measurements of blood ketones (LCHF diet) and 3-day weighed food records (LCHF and HCLF diet) ensured compliance with the dietary regimens.

The two dietary treatments that were investigated in the study are summarized below:

- 1) The HCLF diet consisted of *ad libitum* consumption of standard high-carbohydrate foods (cereals, pasta, bread, rice, and potatoes), vegetables with a high-starch content, low-fat confectionery, lean meats, and fish.
- 2) The LCHF diet consisted of *ad libitum* consumption of high-fat meats, beef (e.g., hamburger, steak), poultry (e.g., chicken, turkey), eggs, fish, cheese, peanut butternuts and seeds, low-starch vegetable products, salads with low-carbohydrate dressing, oils and water or low carbohydrate diet drinks. Foods that were avoided or consumed infrequently included fruits and fruit juices, most dairy products (with the exception of hard cheeses and heavy cream), breads, cereals, beans, rice, desserts/sweets, or any other foods containing significant amounts of carbohydrate.

Maximal aerobic capacity (Day 1 and 39)

The VO_{2max} test was performed at baseline (Day 1) and 6 weeks (Day 39) following the dietary intervention (Figure 1). Participants arrived at the laboratory between 06:00 h and 09:00 h having fasted for the previous eight hours. Subjects performed an incremental test to exhaustion on a motorized treadmill (Trackmaster TMX425C treadmill, Newton, KS). Oxygen consumption (VO₂) and carbon dioxide production (VCO₂) were measured using an automated metabolic analyzer system (TrueOne 2400, Parvo-Medics, Sandy, UT) calibrated prior to each exercise test using standard calibration gases (16% O₂ and 4% CO₂), as well as a volume calibration using a 3L calibration syringe. For measurement of heart rate, subjects wore a Polar Heart Rate Monitor (Polar Electro, Kempele, Finland). To achieve their comfortable running pace, participants began running at a speed between 5-8 mph for 3 min (0% grade). After 3 min of running at 0% grade, the speed was kept constant and the grade was increased 2.5% every 2 min until volitional exhaustion. Participants' speed during the first VO_{2max} trial was recorded and was replicated during all subsequent trials to ensure consistency. Expired gas was collected and analyzed continuously, with the final 30 sec

of each stage averaged to calculate minute ventilation volume (V_E), Respiratory Rate (RR), VO_2 and VCO_2 . At the end of the test, the highest average VO_2 value recorded over a 30 second period of exercise was considered the subject's VO_{2max} .

5-km time trial and body composition (Day 4, 14, 28, and 42)

Body composition and a 5KTT was performed four times during each dietary intervention (Day 4, 14, 28, and 42; Figure 1). Participants arrived at the laboratory between 06:00 h and 09:00 h having fasted for the previous eight hours. Participants' body mass (kg) and body composition (fat and lean mass) were measured using a Tanita bioelectrical impedance analyzer (BIA) (MC-980Uplus, Tanita Corporation of America, Arlington Heights, Illinois). To determine exercise performance, participants performed a 5KTT on a motorized treadmill (TMX425C treadmill; Trackmaster, Newton, KS, USA). Before the start of the 5KTT, subjects completed a 5-minute self-paced warm-up run. Subjects were instructed to finish the 5KTT as fast as possible. The gradient was set at 0.0% grade. Participants were provided with feedback on the distance (at regular 500-m intervals) covered during each 5KTT and where not informed of the overall performance time until completion of the study. During the 5KTT, participants were allowed to adjust their pace via control buttons located on the treadmill. Participants were permitted to adjust their speed how and whenever they saw fit during the time trial. The speed indicator and timing devices was concealed from the participant's view throughout the time trial. Therefore, subjects regulated their treadmill pace according to their perceived exertion associated with the intensity of the exercise and their subjective feelings of their running capabilities (Prins et al., 2016). Heart rate (Polar Electro, Kempele, Finland), RPE (RPE-Overall; RPE-Chest; RPE-Legs) and affect (Feeling Scale) were recorded at 500-m intervals during the 5KTT. Ratings of perceived exertion and affect for the entire exercise session (session RPE and session affect) were obtained 5 minutes following the 5KTT. Metabolic gases were continuously collected during the entire time trial using a metabolic cart for assessment of RER, VO_2 , VCO_2 , V_E , RR, and substrate oxidation.

Blood sampling

Blood samples were measured prior to beginning and at the end of each 5KTT. Fingertip blood samples were collected and immediately processed for measurement of blood lactate (Lactate Plus, Nova Biomedical), ketones (β -hydroxybutyrate; Precision Xtra, Abbott Diabetes Care Inc., Alameda, CA) and glucose (Precision Xtra, Abbott Diabetes Care Inc., Alameda, CA) concentrations. Fingertip capillary samples were collected using a lancet following cleaning of the fingertip with an alcohol swab and then dried. The first droplet was wiped away with a cotton swab to remove any alcohol and the subsequent droplets were used for analysis.

Metabolic calculations

The average values for VO_2 (L/min) and VCO_2 (L/min),

were calculated over the last minute of each 2-min exercise stage in the maximal exercise test, and each minute of the 5KTT. Carbohydrate and fat oxidation rates were calculated from VO_2 and VCO_2 using the stoichiometric equations with the assumption that urinary nitrogen excretion rate is negligible ($n = 0$) (Webster et al., 2016; Frayn, 1983). Fat oxidation (g/min) = $(1.67 [VO_2]) - (1.67 [VCO_2])$ and carbohydrate oxidation (g/min) = $(4.55 [VCO_2]) - (3.21 [VO_2])$. Peak fat and carbohydrate oxidation were recorded in the stage with the highest recorded fat oxidation and carbohydrate oxidation value.

Statistical analysis

Statistical analyses were performed using SPSS version 24.0 (SPSS Inc., Chicago, IL). Statistical significance was set *a priori* at $p < 0.05$. Descriptive statistics were calculated for all variables. Normality and absence of large outliers were verified by using Shapiro-Wilks test, observing the normality plots, and residual plots. Physiological, metabolic and perceptual data collected during the 5KTT (5-km running time, mean exercise heart rate, RER, VO_2 , VCO_2 , V_E , RR, carbohydrate and fat oxidation rates, affect, RPE-Chest, RPE-Legs, RPE-Overall, session RPE and session affect) were analyzed using a 2 (condition, LCHF vs HCLF) x 4 (time) repeated measures analysis of variance. A 2 (condition, LCHF vs HCLF) x 2 (Week 1 vs Week 6) repeated measures analysis of variance was conducted to assess the effect of treatment, time, and interaction between treatment and time, on physiological and metabolic data obtained during the maximal exercise (VO_{2max}) tests. A 2 (condition, LCHF vs HCLF) x 2 (pre 5KTT vs post 5KTT) x 4 (time) repeated measures analysis of variance was conducted to assess the effect of treatment, time, and interaction between treatment and time, on blood lactate, blood ketones, and blood glucose. Paired samples *t*-tests were used to analyze differences between macronutrient composition and training load between the two dietary interventions. The assumption of sphericity was confirmed using Mauchly's test. Greenhouse-Geisser epsilon corrections were used when the sphericity assumption was violated. Partial-eta squared (η^2p) was used to report effect size with 0.01 considered small, 0.06 medium, and 0.14 large effects.

Results

Dietary and exercise adherence

Energy intake was the same for each diet (Table 2). Subjects ingested less than 50g/d of carbohydrate when on the LCHF diet compared to 402g/day on the HCLF diet (6% vs 56%, respectively of total daily calories; $p = 0.001$). Protein and fat intake were significantly higher on the LCHF diet compared to the HCLF diet ($p = 0.001$; Table 2). There were no significant differences for total weekly training time or weekly running distance during each 6-week dietary intervention (all p 's > 0.44 ; online supplementary Table S3). When on the LCHF diet, subjects' capillary blood β HB concentrations did not significantly change ($p = 0.284$) and averaged 0.5 ± 0.05 mmol/L during the 6-week LCHF dietary intervention (online supplementary Figure S1).

Table 2. Summary of dietary intake during the 42-day dietary adaptation periods. Values are mean \pm SD (n=7).

Diet	LCHF	HCLF	P Value
Energy (Kcal/day)	2947 \pm 284	2837 \pm 251	0.686
Carbohydrate (g)	43 \pm 6.0	402 \pm 32	0.001
Protein (g)	184 \pm 28	106 \pm 9	0.001
Fat (g)	226 \pm 21	89 \pm 14	0.001
Carbohydrate (%)	6.0 \pm 1.3	56.4 \pm 2.6	0.001
Protein (%)	25.1 \pm 1.5	15.3 \pm 1.1	0.001
Fat (%)	68.6 \pm 2.1	27.8 \pm 2.3	0.001

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat. Determined from 3 day 24-hour weighed dietary food records including 1 weekend day.

Maximal exercise (VO_{2max}) testing

The graded exercise test time to exhaustion (TTE) was not different between dietary interventions ($p = 0.251$, $\eta^2p = 0.212$) and did not change during the trial ($p = 1.00$; Table 3). VO_{2max} increased in the LCHF and HCLF conditions during each 6-week intervention period ($p = 0.027$) but was not significantly different between diets ($p = 0.435$, $\eta^2p = 0.104$). Mean ($p = 0.001$, $\eta^2p = .838$) and maximum ($p = 0.009$, $\eta^2p = 0.711$) carbohydrate oxidation rates were significantly higher on the HCLF diet, and mean ($p = 0.001$, $\eta^2p = 0.893$) and maximum ($p = 0.001$, $\eta^2p = 0.887$) fat oxidation rates were significantly higher on the LCHF diet. Peak rates of fat oxidation (1.26 ± 0.20 g/min) on the LCHF diet were 63% higher than those measured on the HCLF diet (0.66 ± 0.23 g/min; Table 3; online supplementary Figure S2). In contrast, peak carbohydrate oxidation rates were 32% lower on the LCHF diet compared to the HCLF diet (Table 3). Peak ($p = 0.004$, $\eta^2p = 0.772$) and mean ($p = 0.001$, $\eta^2p = 0.909$) RER were significantly lower (10% and 15%, respectively) after 6 weeks on the LCHF diet compared to the HCLF diet; Table 3).

5-km time trial performance

There were no differences in 5KTT performance between LCHF (1214 ± 135 sec) and HCLF (1198.0 ± 130) across the four time trials ($M_{diff} = 16$ sec; 95% CI, -19 to 51; $p = 0.301$, $\eta^2p = 0.176$; Day 4, 14, 28, and 42; Table 4; Figure 2). In comparison to the mean time for the HCLF diet, the LCHF diet resulted in an average significant decrease in performance for the first 5KTT ($M_{diff} = 49$ sec; 95% CI, 15 to 82; $p = 0.011$, $\eta^2p = 0.683$; Day 4; Table 4; Figure 2). No significant differences in performance were noted between the LCHF and HCLF condition for any of the other time trials ($M_{diff} = 32$ sec; 95% CI, -26 to 91; $p = 0.224$, $\eta^2p = 0.235$, Day 14; $M_{diff} = -5$ sec; 95% CI, -51 to 41; $p = 0.806$, $\eta^2p = 0.011$, Day 28; $M_{diff} = -12$ sec; 95% CI, -108 to 85; $p = 0.777$, $\eta^2p = 0.014$, Day 42; Table 4; Figure 2). Five subjects ran faster on the HCLF diet while two subjects ran faster on the LCHF diet. No learning effect between the eight different time trials was observed ($p = 0.738$). In addition, intraclass correlation coefficients were computed for all conditions of all participants of the 5KTT and was reported to be ICC $r = 0.980$ with a 95% confidence interval of 0.932–0.995.

Physiological, metabolic, and perceptual responses during the 5-km time trials

Mean VO_2 (L/min, $p = 0.041$, $\eta^2p = 0.530$; and ml/kg/min, $p = 0.012$, $\eta^2p = 0.680$) and rate of fat oxidation ($p = 0.001$, $\eta^2p = 0.988$) were significantly higher (3%, 3%, and 138%, respectively) on the LCHF diet, respectively; Table 4; online supplementary Figure S3). Mean carbohydrate oxidation rate was significantly higher (41%) on the HCLF diet ($p = 0.001$, $\eta^2p = 0.984$; Table 4; online supplementary Figure S3) whereas mean RER ($p = 0.001$, $\eta^2p = 0.958$), VCO_2 ($p = 0.001$, $\eta^2p = 0.907$) and Respiratory Rate ($p = 0.029$, $\eta^2p = 0.576$) were significantly lower (11%, 6%, 5%, respectively) on the LCHF diet (Table 4).

Table 3. Measurements during maximal exercise (VO_{2max}) testing (n = 7). Values are Mean \pm SD.

Variables	LCHF		HCLF		P Value		
	Pre Day 1	Post Day 39	Pre Day 1	Post Day 39	Condition	Time	Interaction
Maximal Data							
Time to Exhaustion (sec)	844.3 \pm 87.3	818.6 \pm 114.5	775.7 \pm 107.4	801.4 \pm 74.9	0.251	1.000	0.206
VO_{2max} (ml/kg/min)	61.6 \pm 3.1	62.9 \pm 6.9	60.6 \pm 8.4	62.5 \pm 6.0	0.435	0.027	0.854
VO_{2max} (L/min)	4.2 \pm 0.2	4.3 \pm 0.6	4.2 \pm 0.6	4.3 \pm 0.4	0.476	0.088	0.773
VCO_{2max} (L/min)	4.6 \pm 0.3	4.4 \pm 0.7	4.7 \pm 0.7	4.9 \pm 0.5	0.022	0.812	0.316
HR_{max} (b/min)	180.9 \pm 11.4	181.1 \pm 10.0	178.6 \pm 15.0	179.2 \pm 10.5	0.195	0.757	0.881
V_{Emax} (L/min)	115.3 \pm 26.1	121.3 \pm 23.5	119.0 \pm 17.1	125.2 \pm 20.9	0.514	0.086	0.987
RR_{max} (bpm)	47 \pm 10	47 \pm 8	48 \pm 8	47 \pm 9	0.774	0.920	0.613
Peak RER	1.09 \pm 0.09	1.03 \pm 0.08	1.13 \pm 0.07	1.14 \pm 0.05	0.004	0.176	0.072
Peak Carbohydrate Oxidation (g/min)	7.2 \pm 1.5	6.2 \pm 1.6	8.0 \pm 1.5	8.5 \pm 1.2	0.009	0.522	0.148
Peak Fat Oxidation (g/min)	1.01 \pm 0.21	1.26 \pm 0.20	0.67 \pm 0.14	0.66 \pm 0.23	0.001	0.093	0.072
Average Data							
Mean VO_2 (ml/kg/min)	44.8 \pm 2.5	45.2 \pm 4.0	43.7 \pm 4.4	44.3 \pm 3.1	0.134	0.588	0.906
Mean VO_2 (L/min)	3.1 \pm 0.2	3.1 \pm 0.3	3.0 \pm 0.3	3.0 \pm 0.2	0.283	0.738	0.523
Mean VCO_2 (L/min)	2.8 \pm 0.3	2.6 \pm 0.3	2.9 \pm 0.4	3.0 \pm 0.2	0.015	0.465	0.149
Mean V_E (L/min)	70.7 \pm 19.0	71.9 \pm 15.9	72.9 \pm 13.0	77.4 \pm 14.5	0.216	0.053	0.588
Mean RR (bpm)	34 \pm 7	34 \pm 6	36 \pm 8	36 \pm 8	0.064	0.850	0.845
Mean RER	0.9 \pm 0.06	0.83 \pm 0.05	0.95 \pm 0.04	0.96 \pm 0.03	0.001	0.042	0.050
Mean Carbohydrate Oxidation (g/min)	3.0 \pm 0.9	2.1 \pm 0.8	3.6 \pm 0.8	3.7 \pm 0.4	0.001	0.106	0.075
Mean Fat Oxidation (g/min)	0.43 \pm 0.34	0.74 \pm 0.25	0.16 \pm 0.22	0.13 \pm 0.18	0.001	0.032	0.047

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat; VO_2 = oxygen consumption; VCO_2 = carbon dioxide production; HR = heart rate; RER = Respiratory exchange ratio; V_E = ventilation; RR = Respiratory Rate

Table 4. Physiological, metabolic, respiratory, and performance data collected during the 5 km time trials (N = 7). Values are Mean \pm SD.

	LCHF Running Trials					HCLF Running Trials					P Value		
	Day 4	Day 14	Day 28	Day 42	Mean	Day 4	Day 14	Day 28	Day 42	Mean	COND	Time	Interaction
Mean $\dot{V}O_2$ (L/min)	3.5 \pm 0.5	3.6 \pm 0.6	3.7 \pm 0.5	3.7 \pm 0.8	3.6 \pm 0.6	3.6 \pm 0.5	3.6 \pm 0.5	3.6 \pm 0.5	3.4 \pm 0.7	3.5 \pm 0.5	0.041	0.842	0.207
Mean $\dot{V}CO_2$ (L/min)	3.1 \pm 0.5	3.2 \pm 0.6	3.2 \pm 0.5	3.3 \pm 0.8	3.2 \pm 0.6	3.5 \pm 0.5	3.5 \pm 0.6	3.5 \pm 0.6	3.3 \pm 0.8	3.4 \pm 0.6	0.001	0.840	0.340
RER	0.89 \pm 0.04	0.87 \pm 0.05	0.87 \pm 0.05	0.86 \pm 0.05	0.87 \pm 0.04	0.97 \pm 0.04	0.97 \pm 0.04	0.98 \pm 0.03	0.96 \pm 0.05	0.97 \pm 0.03	0.001	0.280	0.578
Mean $\dot{V}O_2$ (ml/kg/min)	51.3 \pm 7.2	52.6 \pm 8.0	54.1 \pm 6.7	55.2 \pm 11.1	53.3 \pm 7.8	52.0 \pm 7.4	52.7 \pm 7.1	51.9 \pm 7.0	49.7 \pm 10.5	51.6 \pm 7.2	0.012	0.857	0.168
Mean $\dot{V}O_2$ (% $\dot{V}O_{2max}$)	82.2 \pm 6.6	84.2 \pm 8.0	86.9 \pm 8.3	88.2 \pm 12.9	85.4 \pm 7.8	84.4 \pm 7.6	85.6 \pm 4.7	84.3 \pm 5.7	80.8 \pm 13.7	83.8 \pm 6.0	0.340	0.836	0.187
V_E (L/min)	86.9 \pm 24.3	87.8 \pm 26.6	93.0 \pm 22.1	99.0 \pm 29.3	91.7 \pm 24.2	93.5 \pm 13.5	93.3 \pm 9.7	93.3 \pm 11.1	95.0 \pm 26.1	93.8 \pm 13.1	0.743	0.424	0.472
RR (bpm)	42.7 \pm 6.6	42.4 \pm 6.7	43.0 \pm 6.2	43.4 \pm 7.2	42.9 \pm 6.6	44.7 \pm 7.9	44.9 \pm 8.6	44.3 \pm 7.6	44.9 \pm 7.7	44.7 \pm 7.7	0.029	0.923	0.720
Mean Carbohydrate Oxidation (g/min)	3.0 \pm 0.9	2.9 \pm 1.1	3.0 \pm 0.9	2.9 \pm 1.3	2.9 \pm 1.0	4.4 \pm 0.9	4.4 \pm 1.1	4.6 \pm 1.0	4.1 \pm 1.4	4.4 \pm 0.9	0.001	0.618	0.753
Mean Fat Oxidation (g/min)	0.63 \pm 0.15	0.71 \pm 0.23	0.71 \pm 0.15	0.78 \pm 0.26	0.71 \pm 0.18	0.14 \pm 0.18	0.14 \pm 0.24	0.08 \pm 0.18	0.17 \pm 0.20	0.13 \pm 0.16	0.001	0.156	0.586
Heart Rate (b \cdot min $^{-1}$)	172 \pm 13	175 \pm 10	172 \pm 13	172 \pm 15	173 \pm 12	171 \pm 12	171 \pm 13	168 \pm 14	167 \pm 16	169 \pm 13	0.051	0.349	0.696
Time (sec)	1231 \pm 137	1217 \pm 153	1198 \pm 116	1211 \pm 152	1214 \pm 135	1182 \pm 119	1185 \pm 138	1203 \pm 143	1223 \pm 175	1198 \pm 130	0.301	0.920	0.282

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat; COND= Condition; HR = heart rate; RER = Respiratory exchange ratio; $\dot{V}O_2$ = oxygen consumption; $\dot{V}CO_2$ = carbon dioxide production; V_E = ventilation; RR = Respiratory Rate.

No significant differences between diets were observed for mean percentage of maximal oxygen consumption (% $\dot{V}O_{2max}$; $p = 0.340$), mean V_E ($p = 0.743$), mean heart rate ($p = 0.051$; Table 4), mean RPE (Chest, legs, overall; $p = 0.933$, $p = 0.680$, $p = 0.486$, respectively), mean session RPE ($p = 0.325$), and mean session affect ($p = 0.419$; online supplementary Table S1). None of aforementioned variables changed significantly during the course of the four time trials over the 6 weeks of the experiment (all p 's > 0.34).

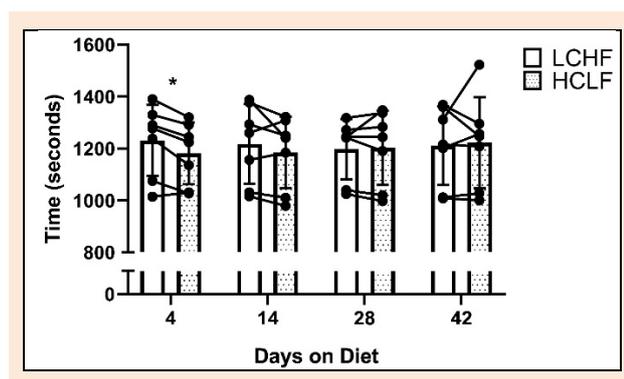


Figure 2. Mean and individual 5-km time trial running times for LCHF and HCLF. Values are Mean \pm SE. (N=7). * Significant difference between LCHF and HCLF conditions ($p < 0.05$).

Blood metabolite data

Blood lactate and glucose concentrations rose from baseline to the end of exercise ($p < 0.001$) but there were no significant differences between conditions at any time point ($p > 0.05$; online supplementary Table S2). Blood

β HB was significantly higher both before and after exercise on the LCHF diet compared to the HCLF diet ($p = 0.004$; online supplementary Table S3).

Body composition data

There were no changes in body mass ($p = 0.549$), body fat ($p = 0.176$), fat mass, ($p = 0.160$) and lean mass ($p = 0.549$) on either diet and across time trials ($p > 0.05$; online supplementary Table S4).

Discussion

There were five relevant findings in this study. First, we document that subjects reduced their carbohydrate and increased their fat intakes appropriately when following the LCHF diet for 42 days. Second, subjects maintained their performances during maximal ($\dot{V}O_{2max}$) exercise testing. Third, running performance was impaired during the initial 5KTT which was performed within the first ~4 days of exposure to the LCHF diet. However, running performance on the LCHF diet improved thereafter. Accordingly, the fourth relevant finding was that 5KTT performance was the same on both diets for the remainder of the 6 weeks trial. Finally, athletes ran at ~82% $\dot{V}O_{2max}$ during the 5KTTs. This exceeds the apparent threshold intensity of 60-75% $\dot{V}O_{2max}$, at which it is believed that fat oxidation is no longer able to support high intensity exercise (Hawley and Leckey, 2015; Stellingwerff and Boit, 2007; Stellingwerff et al., 2011; Costa et al., 2018).

The first relevant finding was that subjects reduced their carbohydrate and increased their fat intakes appropriately when following the LCHF intervention diet (Table 2).

Proof that the subjects correctly followed the LCHF diet were their elevated blood ketone concentrations (online supplementary Figure S1). Evidence that the subjects had adapted metabolically, at least in part to the higher fat diet, was the significantly higher rates of fat oxidation during maximal exercise (Table 3) and during the 5KTTs (Table 4).

Our next important finding was the absolute $\text{VO}_{2\text{max}}$ value and exercise time to exhaustion during the $\text{VO}_{2\text{max}}$ test, was the same independent of diet (Table 3). Peak workload – also measured as exercise time to exhaustion – rather than measured $\text{VO}_{2\text{max}}$ value is the better measure of athletic ability (Noakes et al., 1990). A high fat diet increases the oxygen cost of running at any speed (Table 3) as previously reported (Burke et al., 2017). As a result, because of a higher VO_2 at any running speed whilst eating the LCHF diet, athletes might achieve the same $\text{VO}_{2\text{max}}$ but at a lower peak work rate or a reduced exercise time to exhaustion when eating the HCLF diet. Thus, equivalent $\text{VO}_{2\text{max}}$ values on both diets could falsely hide an impaired exercise performance on the LCHF diet, resulting from the increased oxygen cost of running (Noakes and Tucker, 2004).

This finding that the LCHF diet did not impair either the measured $\text{VO}_{2\text{max}}$ or the exercise time to exhaustion during the $\text{VO}_{2\text{max}}$ test clearly conflicts with the traditional doctrine (Krogh and Lindhard, 1920; Hawley et al., 1998; Jeukendrup 2003; Stellingwerff and Boit, 2007; Stellingwerff et al., 2011; Burke et al., 2011; Hawley and Leckey, 2015; Costa et al., 2018; Burke and Hawley, 2018; Cermak and van Loon, 2013; Jeukendrup et al., 2000; Spriet, 2007; Williams et al., 1984; Bartlett et al., 2015; Burke, 2015; Leckey et al., 2015). Yet many have reported this finding (Vogt et al., 2003; Horvath et al., 2000; Paoli et al., 2012; Cipryan et al., 2017; Heatherly et al., 2018; Miele et al., 2018). A logical counter-argument is that even when eating a LCHF diet, subjects still have substantial muscle glycogen stores (Volek et al., 2016; Webster et al., 2016; Hoppeler et al., 1999; Van Proeyen et al., 2010). This muscle glycogen would be more than adequate to fuel single bouts of high intensity exercise. As a result, persons eating an LCHF diet would still be able to perform some high intensity exercise, even if only of the short duration required to measure the $\text{VO}_{2\text{max}}$.

But others (Hetlelid et al., 2015) have argued that the fastest athletes show higher rates of fat, but not carbohydrate oxidation during exercise at $94\%\text{VO}_{2\text{max}}$. In that study, the superior running ability of the fastest sprinters “was explained by their nearly threefold higher rates of fat oxidation at high intensity” (without any evidence for superior rates of carbohydrate use). Another study showed that fat oxidation provided 20% of the energy requirements for the fifth and seventh repetitions in interval repetitions at $86\%\text{VO}_{2\text{max}}$ (Stepsto et al., 2001). These studies show that a substantial contribution of fat oxidation to energy use even at very high exercise intensities, may have been overlooked in the past.

The third key finding was that performance in the initial 5KTT, after subjects had been eating the LCHF diet for ~4 days, was significantly impaired (Figure 1). This has been reported frequently (Krogh and Lindhard, 1920; Kark

et al., 1945; Bergstrom et al., 1967).

The fourth key finding was that performances in the second and all subsequent 5KTTs were the same on both diets (Figure 2). During this period athletes maintained the same training load (online supplementary Table S3). Others found that adaptation to a LCHF diet did not impair 5-km exercise performance (Heatherly et al., 2018). In fact, 6 of the 8 athletes in that study improved their performance after 3 weeks on the LCHF diet. Our failure to show an impaired exercise performance in those eating the LCHF diet disproves the belief that chronic dietary-induced changes in skeletal muscle metabolism must impair exercise performance in all persons eating this diet (Stellingwerff et al., 2006). Instead we argue that performance during exercise is a centrally-regulated outcome (Noakes et al., 2005; Amann et al., 2006; Venhorst et al., 2018) in which the key performance determinant is the extent to which the athlete chooses to continue recruiting a large skeletal muscle mass in the face of changing physiological, emotional and motivational inputs (Venhorst et al., 2018). A diet change could act on many different components of the human biology, either singly or in combination.

The fifth important finding was that athletes achieved an exercise intensity $>82\%$ of $\text{VO}_{2\text{max}}$ during these time trials (Table 4) and were able to extract a substantial percentage of their energy from fat oxidation at that exercise intensity. This is important because this exercise intensity is well above the supposed “carbohydrate dependent” prescriptive exercise intensity of $60\text{--}75\%\text{VO}_{2\text{max}}$ (Stellingwerff and Boit, 2007; Stellingwerff et al., 2011; Hawley and Leckey, 2015; Costa et al., 2018).

Calculations based on data in Table 4 also reveal that during the 5KTTs, subjects derived 94% of their total energy expenditure from carbohydrate oxidation when eating the HCLF diet; this reduced to 65% on the LCHF. Thus, even when exercising at $\sim 82\%\text{VO}_{2\text{max}}$, fat-adapted athletes oxidized fat at rates 5.25 times faster than when they ate the HCLF diet (6.3 vs 1.2Kcal/min). Yet their rates of carbohydrate oxidation (11.6 vs 17.5Kcal/min) were still 66% of that achieved during the HCLF diet. Other studies show that fat oxidation in athletes adapted to the LCHF diet provided 52% of total energy during 20 minutes of exercise at $70\%\text{VO}_{2\text{max}}$ (Cameron-Smith et al., 2003); 69% during 2 hours of exercise at $72\%\text{VO}_{2\text{max}}$ (Webster et al., 2016); approximately 80% during a 100-km cycling time trial (McSwiney et al., 2018), and 87% during 3 hours’ exercise at $64\%\text{VO}_{2\text{max}}$ (Volek et al., 2016).

It is argued that athletes eating a LCHF diet develop impaired “metabolic flexibility” (Burke, 2015). This experiment shows the opposite. On the HCLF diet subjects showed an almost complete dependence on carbohydrate oxidation during exercise at $>80\%\text{VO}_{2\text{max}}$. In contrast when eating the LCHF diet, athletes retained the capacity to oxidize both fat and carbohydrate at high rates during exercise at that intensity whilst maintaining their performance capacity. Superior metabolic flexibility would likely be beneficial during ultradistance events as maximal fat oxidation rate measured during a graded exercise test is a significant predictor of performance time during the Ironman Triathlon (Frandsen et al., 2017).

The study of Burke et al (2017) shows how quickly

major changes in metabolism can develop in athletes adopting a LCHF diet. After just 3 weeks exposure to a LCHF diet, elite race walkers increased the amount of energy derived from fat during the final kilometer of a 25km time trial when exercising at 77% $\text{VO}_{2\text{max}}$, from 33% on a HCLF diet to 86% on a LCHF diet (their Figure 5). As a result, the LCHF diet caused the percentage contribution of carbohydrate to total energy expenditure to fall from 66% on the HCLF diet to 14% on the LCHF diet.

Finally, when properly trained these athletes, able to run 5-km in ~20 minutes, should be able to run a 26-mile marathon in 3hr18min (Noakes, 1991) making them faster than 88% of the estimated 500,000 U.S marathon finishers (Marathon Statistics, 2019). This might suggest that the overwhelming majority of competitive recreational US marathon runners may not need to eat a HCLF diet in order to optimize their performance.

Limitations

Multiple limitations should be considered with interpretation of the present study. The present study included a small number of subjects participating in the experiment and bioelectrical impedance was used for body composition analysis. In addition, intramuscular glycogen levels were not directly measured, which could have enhanced our understanding of the results. Additionally, a 2-week washout period may have been insufficient to eliminate carry-over effects of the previous dietary intervention. However, random allocation slightly reduced the influence of the short washout period. Lastly, diets were consumed *ad libitum* and subjects were instructed not to change their training load for the duration of the study. Therefore, we were reliant on subjects to accurately comply with each dietary intervention and to monitor their training appropriately.

Conclusion

In summary, our study shows that compared to when they ate a HCLF diet, running performance during 5KTTs run at ~80% $\text{VO}_{2\text{max}}$ and during which 35% of energy was derived from fat oxidation was not impaired when athletes ate a LCHF diet for between 13 to 42 days. In contrast when eating the HCLF diet, 94% of energy was derived from carbohydrate oxidation without any improvement in performance.

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Key points

- We found that athletes running 5km time trials at >80%VO_{2max} performed equally well when eating diets high in either carbohydrate or fat for 14 days or more.
- But performance during the initial maximal exercise test performed within 4 days of adopting the low carbohydrate diet was impaired.
- Athletes involved in higher intensity exercise (>60% VO_{2max}) are usually advised to eat high carbohydrate diets (7-12g carbohydrate/kg body weight/day). Our study shows that the vast majority of recreational athletes (best marathon times slower than 3hrs 20min) may not need to eat high carbohydrate diets to optimize performance in both racing and training.

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Supplementary Tables and Figures

Table S1. 5-km time trial perceptual data (n = 7). Values are Mean ± SD.

	LCHF Running Trials					HCLF Running Trials					P Value		
	Day 4	Day 14	Day 28	Day 42	Mean	Day 4	Day 14	Day 28	Day 42	Mean	Condition	Time	Interaction
Affect	-0.9 ± 1.73	-0.7 ± 1.74	-0.9 ± 1.49	-0.9 ± 1.51	-0.9 ± 0.11	-0.5 ± 1.52	-0.9 ± 1.41	-0.8 ± 1.64	-0.9 ± 1.48	-0.8 ± 0.20	0.661	0.946	0.494
RPE-C	6.0 ± 1.52	5.7 ± 1.27	6.0 ± 1.04	6.0 ± 1.05	5.9 ± 0.14	5.7 ± 1.12	6.2 ± 1.62	5.8 ± 1.36	6.0 ± 1.25	5.9 ± 0.23	0.933	0.904	0.122
RPE-L	6.0 ± 1.20	6.1 ± 0.81	5.9 ± 0.83	6.2 ± 0.80	6.0 ± 0.13	5.8 ± 1.04	5.9 ± 1.21	5.7 ± 1.36	6.2 ± 0.78	5.9 ± 0.23	0.680	0.355	0.947
RPE-O	6.1 ± 1.21	6.3 ± 0.97	6.2 ± 0.83	6.4 ± 0.76	6.2 ± 0.11	6.0 ± 0.99	6.2 ± 1.11	5.9 ± 1.30	6.3 ± 1.06	6.1 ± 0.18	0.486	0.606	0.654
Session RPE	7.9 ± 1.46	7.9 ± 0.84	7.1 ± 1.07	6.9 ± 1.21	7.4 ± 0.53	7.1 ± 0.90	7.0 ± 1.41	7.0 ± 1.41	7.3 ± 1.38	7.1 ± 0.14	0.325	0.484	0.112
Session Affect	-2.1 ± 1.95	-2.0 ± 1.41	-1.7 ± 1.38	-1.4 ± 1.81	-1.8 ± 0.32	-1.3 ± 1.60	-1.3 ± 2.29	-1.6 ± 1.90	-2.0 ± 1.53	-1.5 ± 0.34	0.419	0.996	0.282

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat; RPE-O = RPE for overall body; RPE-C = RPE for chest; RPE-L = RPE for legs; RPE = rating of perceived exertion (OMNI rating of exertion)

Table S2. Blood metabolite data (n = 7). Values are Mean ± SD.

		LCHF Running Trials				HCLF Running Trials				P Value		
		Day 4	Day 14	Day 28	Day 42	Day 4	Day 14	Day 28	Day 42	Condition	Time	Interaction
Blood Glucose (mg/dl)	Pre	80.6 ± 3.2	85.7 ± 4.2	84.0 ± 6.5	82.6 ± 9.1	89.3 ± 10.4	91.1 ± 12.3	86.0 ± 9.5	87.1 ± 8.6	0.063	0.603	0.126
	Post	114.4 ± 17.0	134.7 ± 21.5	129.3 ± 18.1	134.4 ± 25.8	144.9 ± 29.2	131.0 ± 22.8	132.4 ± 24.9	141.3 ± 22.4			
Blood Lactate (mmol/L)	Pre	1.60 ± 1.09	1.37 ± 1.25	1.01 ± 0.80	1.10 ± 0.53	1.01 ± 0.58	1.09 ± 0.39	0.79 ± 0.16	1.27 ± 0.53	0.417	0.529	0.838
	Post	5.29 ± 2.16	7.20 ± 4.17	7.04 ± 3.15	5.30 ± 1.99	5.31 ± 1.82	6.09 ± 3.31	6.16 ± 3.16	5.36 ± 2.36			
Blood Ketone (mmol/L)	Pre	0.66 ± 0.28	0.40 ± 0.17	0.47 ± 0.26	0.64 ± 0.57	0.11 ± 0.04	0.13 ± 0.05	0.16 ± 0.05	0.17 ± 0.05	0.004	0.617	0.082
	Post	0.37 ± 0.16	0.31 ± 0.11	0.36 ± 0.09	0.36 ± 0.21	0.13 ± 0.05	0.16 ± 0.05	0.16 ± 0.05	0.14 ± 0.05			

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat; Pre = immediately before time trial; Post = immediately after time trial.

Table S3. Training load (n = 7). Values are Mean ± SD.

	LCHF			HCLF		
	Week 1	Week 6	P Value	Week 1	Week 6	P Value
Training Load (min/week)	317 ± 156	326 ± 119	0.636	302 ± 112	328 ± 145	0.446
Training Load (km/week)	51.6 ± 26.0	50.1 ± 20.8	0.718	48.7 ± 19.1	51.9 ± 23.7	0.622

LCHF, very low carbohydrate high fat; HCLF, high carbohydrate low fat

Table S4. Body composition data (n = 7). Values are Mean ± SD.

	LCHF Running Trials					HCLF Running Trials					P Value		
	Day 4	Day 14	Day 28	Day 42	Mean	Day 4	Day 14	Day 28	Day 42	Mean	Condition	Time	Interaction
Weight (kg)	69.2 ± 4.9	70.2 ± 4.8	70.2 ± 4.8	69.7 ± 5.1	69.8 ± 0.5	68.4 ± 1.6	68.2 ± 2.0	68.6 ± 1.6	68.5 ± 1.2	68.4 ± 0.2	0.549	0.446	0.313
Body Fat (%)	6.1 ± 1.4	5.9 ± 1.4	5.7 ± 1.5	5.4 ± 0.8	5.8 ± 0.3	5.5 ± 1.2	6.7 ± 1.8	7.2 ± 2.5	6.3 ± 2.0	6.4 ± 0.8	0.176	0.396	0.173
Fat Mass (kg)	3.8 ± 1.2	4.0 ± 1.0	3.9 ± 1.1	3.6 ± 0.6	3.8 ± 0.2	3.8 ± 0.9	4.5 ± 1.5	5.0 ± 1.8	4.3 ± 1.4	4.4 ± 0.5	0.160	0.310	0.361
Lean Mass (kg)	63.4 ± 1.6	63.9 ± 1.6	64.0 ± 1.9	63.8 ± 1.5	63.8 ± 0.3	64.6 ± 1.3	63.6 ± 1.7	63.6 ± 1.3	64.2 ± 1.5	64.0 ± 0.5	0.549	0.909	0.109

LCHF, low carbohydrate high fat; HCLF, high carbohydrate low fat

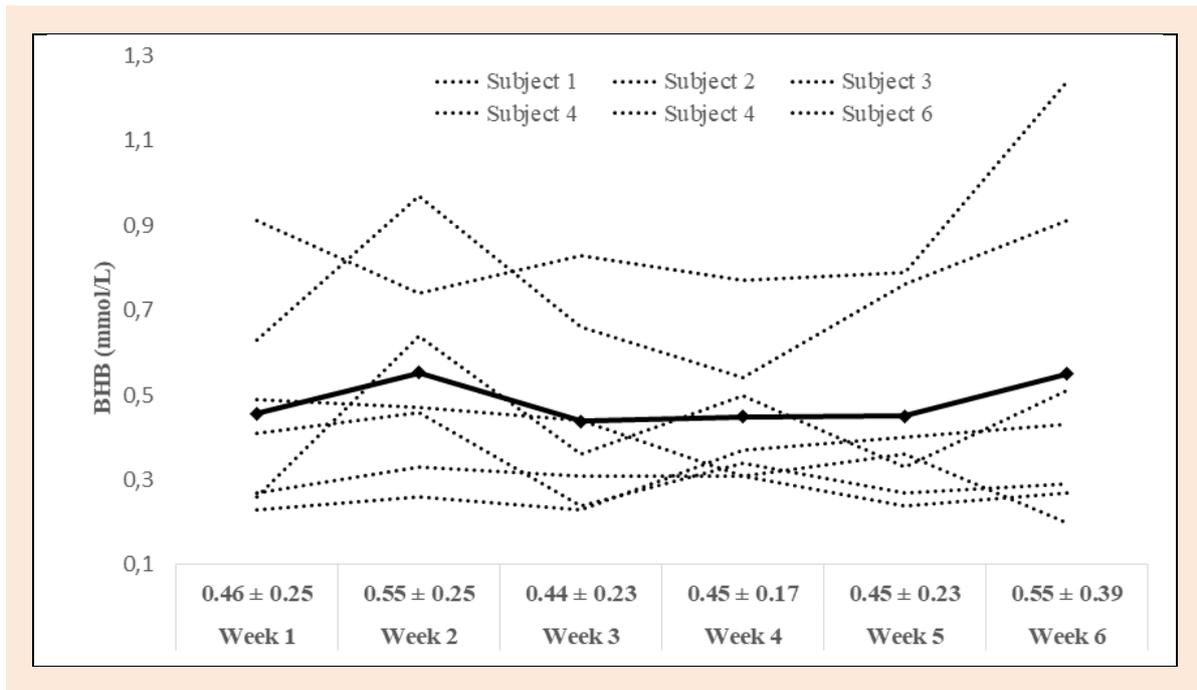


Figure S1. Individual weekly blood beta-hydroxybutyrate (BHB) levels. Solid black line indicates mean.

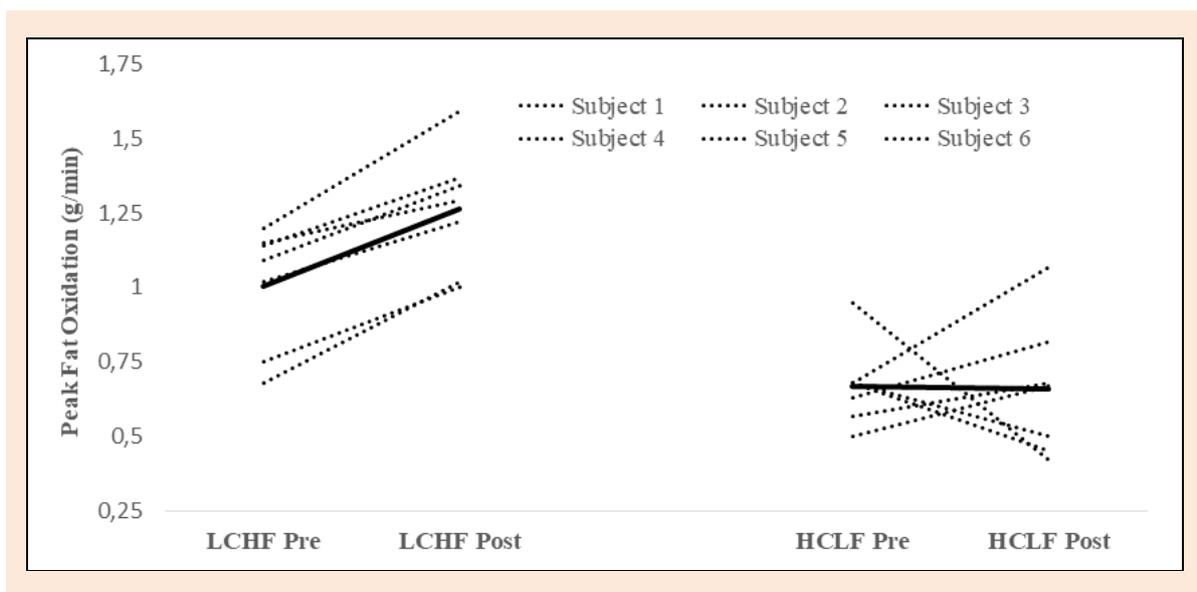


Figure S2. Individual peak fat oxidation rates measured during the maximal exercise test (VO_{2max}). Mean responses between groups were significantly different ($p = 0.001$). Solid lines indicate mean. LCHF, very low carbohydrate high fat; HCLF, high carbohydrate low fat. Pre = Day 1; Post = Day 39.

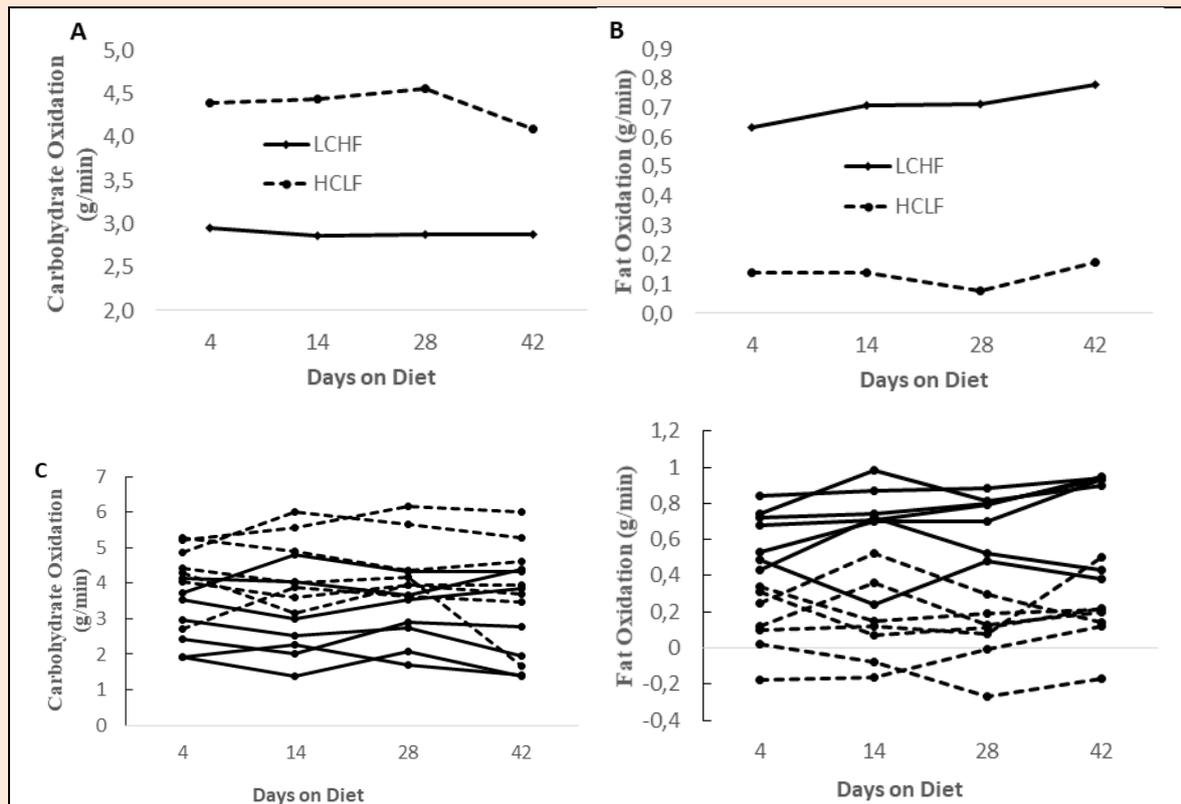


Figure S3. Substrate utilization during the four 5-km time trials. Rate of carbohydrate oxidation (A) and fat oxidation (B). Individual values are shown for rates of carbohydrate oxidation (C) and rates of fat oxidation (D). Data presented as mean \pm SD; $n = 7$. *Significant differences between conditions. Dashed lines represent high carbohydrate low fat treatment and solid lines represent low carbohydrate high fat treatment. LCHF, very low carbohydrate high fat; HCLF, high carbohydrate low fat.