Long-term fat diet adaptation effects on performance, training capacity, and fat utilization

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ABSTRACT

HELGE, J. W. Long-term fat diet adaptation effects on performance, training capacity, and fat utilization. *Med. Sci. Sports Exerc.*, Vol. 34, No. 9, pp. 1499–1504, 2002. It is well known that adaptation to a fat-rich carbohydrate-poor diet results in lower resting muscle glycogen content and a higher rate of fat oxidation during exercise when compared with a carbohydrate-rich diet. The net effect of such an adaptation could potentially be a sparing of muscle glycogen, and because muscle glycogen storage is coupled to endurance performance, it is possible that adaptation to a high-fat diet potentially could enhance endurance performance. Therefore, the first issue in this review is to critically evaluate the available evidence for a potential endurance performance enhancement after long-term fat-rich diet adaptation. Attainment of optimal performance is among other factors dependent also on the quality and quantity of the training performed. When exercise intensity is increased, there is an increased need for carbohydrates. On the other hand, consumption of a fat-rich diet decreases the storage of glycogen in both muscle and liver. Therefore, training intensity may be compromised in individuals while consuming a fat-rich diet. During submaximal exercise, fat for oxidation in muscle is recruited from plasma fatty acids, plasma triacylglycerol, and muscle triacylglycerol: the final question addressed in this review is which of these source(s) of fat contributes to the increased oxidation of fat during submaximal exercise after long-term fat diet adaptation. **Key Words:** VERY LOW-DENSITY LIPOPROTEIN TRIACYLGLYCEROL, GLYCOGEN, TRAINING

In a paper published some years ago Sherman and Lenders implicated fat loading as "the next magic bullet" in the pursuit of the optimal diet for endurance performance (37). Since then, several studies have investigated whether in fact endurance performance can be enhanced after adaptation to fat-rich diet, a research question that was initially addressed by Christensen and Hansen (5) more than 60 years ago. In this paper, focus is mainly oriented toward long-term adaptation to fat-rich diet, and discussion of short-term adaptation to fat-rich diet is available elsewhere (3,12). Fat adaptation both short and long term induces a markedly higher fat oxidation during exercise and thus a reduced carbohydrate utilization (5,30). Furthermore, when a fat-rich diet is consumed, muscle glycogen is at best maintained and in many cases lower than when compared with consuming a carbohydrate-rich diet (16,30). It is therefore not clear whether the fat-diet–induced carbohydrate sparing is sufficient to counterbalance the lower glycogen storage and thus overall lead to an increased exercise capacity. The present paper will briefly discuss the evidence available on the effect of long-term fat diet adaptation on endurance performance. Subsequently, two questions will be addressed: first, whether in the light of a reduced muscle glycogen storage it is possible to maintain training intensity while consuming a fat-rich diet, and second, which source(s) of fat that contributes to the increased oxidation of fat during submaximal exercise after long-term fat diet adaptation.

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ENDURANCE PERFORMANCE AFTER LONG-TERM ADAPTATION TO FAT-RICH DIET

When evaluating the effect of fat-rich diet on endurance performance after long-term fat diet adaptation, there is a range of factors, such as duration of the dietary period, the fat and carbohydrate content of the diets, the exercise intensity at which performance is measured, and the training status of the subjects, all of which can influence the performance outcome (12). Here focus is narrowed down to high-fat diets (>40% fat), consumed for 10 d or longer and with exercise intensity of the time to exhaustion performance test between 60 and 85% of maximal oxygen uptake ($\dot{V}O_{2max}$). In addition, two studies where time trials were used after long-term fat diet adaptation was included. The exercise intensity range of 65–85% of $\dot{V}O_{2max}$ was selected because muscle glycogen is considered to play a key role in fatigue at these intensities (17,34,35). Within the criteria given above, the majority of studies do not find any difference in endurance performance when adaptation to fat- and carbohydrate-rich diets is compared (6,11,16,19,26,30,31)(Table 1). However, a study by Lambert and colleagues (25) demonstrated that endurance performance at 60% of $\dot{V}O_{2max}$ was significantly higher after 14-d adaptation to fat-rich diet, containing 70% fat, than when compared with carbo-

TABLE 1. Endurance performance after long-term fat dietadaptation.

Duration (d)	Diet Content Fat (E%)	CHO (E%)	Work Intensity (% of $\dot{V}O_{2max}$)	Performance (min)	Reference
14	59	30	50	270 ± 0	Pruett et al. (32)
14	9	87	50	262 ± 6	
14	59	30	70	164 ± 21	
14	9	87	70	193 ± 13*	
28	85	2	64	151 ± 25	Phiney et al. (30)
7	29	57	62	147 ± 13	
28	43	42	TT[1]	192 W	Simonsen et al. (38)
28	17	70	TT	207 W*	
14	67	7	60	80 ± 8*	Lambert et al. (25)
14	12	74	60	43 ± 7	
49	62	21	69	65 ± 7	Helge et al. (14)
49	20	65	69	102 ± 5*	
28	62	21	72	79 ± 8	Helge et al. (16)
28	20	65	72	79 ± 15	
28	55	36	71	46 ± 5	Pogliaghi et al. (31)
28	15	74	71	48 ± 5	
15	69	19	TT[2]	63 ± 5	Goedecke et al. (10)
15	30	53	TT	66 ± 7	
28	41	44	80[3]	53 ± 5*	Hoppeler et al. (18)
28	18	67	80	44 ± 4	
28	44	41	80[4]	47 ± 11	Horvath et al. (19)
28	33	52	80	48 ± 13	
28[5]	55[a]	30	75–80	112 ± 3	Lukaski et al. (26)
28	48[b]	37	75–80	121 ± 5*	
28	30	55	75–80	127 ± 4*	
49	62	21	69	71 ± 5	(Author's unpublished data)
49	20	65	69	100 ± 8*	

[1] Three rowing time trials over 2500 m separated by 8 min. Performance was measured as average power output.
[2] 150-min exercise at 70% $\dot{V}O_{2max}$ followed by a 40-km time trial.
[3] Running on treadmill.
[4] Subjects included male and female runners. Run on treadmill initiated with a 15-min progressive warm-up.
[5] Only three subjects included in study.
The two fat diets contained a majority of polyunsaturated FA (PUSF[a]) or saturated FA (SATF[b]). Exercise is performed as bicycle exercise if not specified.
* ($P < 0.05$) different from other diet.
CHO, carbohydrate. Data are mean ± SEM.

hydrate-rich diet. But in their study, endurance testing was preceded both by a Wingate test and exercise at 90% of $\dot{V}O_{2max}$ until exhaustion, and these data should therefore be carefully interpreted. Furthermore, a recent study found an increased endurance performance after 28 d adaptation to a 41% fat diet when compared with a carbohydrate diet (18) (Table 1). However, in this study by Hoppeler et al. (18) where a crossover design was implemented energy intake was 21% lower during the low-fat diet compared with the fat diet, but body mass and body fat content were not affected differently after the two diets. This may imply that energy intake was not optimal and maybe even deficient during the low-fat diet, and this could have attenuated performance. On the other hand, there is some evidence that fat-rich diet can be detrimental for exercise performance. Pruett (32) demonstrated that exercise endurance performance at 70% of $\dot{V}O_{2max}$ was clearly attenuated after 14 d adaptation to a fat-rich diet compared with after a carbohydrate-rich diet. Using a different exercise model, Simonsen et al. (38) demonstrated that rowing performance, measured as average power output across three rowing time trials over 2500 m separated by 8 min, was impaired after 28 d adaptation to a fat diet containing 42% of energy as fat compared with carbohydrate diet (Table 1). In a more recent study, it was demonstrated that when untrained subjects participated in a regular training program for 7 wk while consuming either a fat or a carbohydrate diet, the endurance performance was markedly attenuated after the fat diet (14). In a later study where a similar design was applied, almost identical data were obtained, showing a significant attenuation of endurance performance after 7 wk adaptation to fat diet and training ($N = 7$) when compared with adaptation to carbohydrate diet and training ($N = 6$) (Fig. 1, author's unpublished data). A recently published pilot study (only 3 subjects) by Lukaski et al. (26) demonstrated a decreased endurance performance at 70–75% of $\dot{V}O_{2max}$ after 28 d adaptation to polyunsaturated fat-rich diet compared with both saturated fat-rich diet and carbohydrate-rich diet. Further studies are needed to address whether indeed endurance performance outcome is significantly affected by the dietary fatty acid composition of high-fat diets. Thus, overall, there is evidence to suggest that endurance performance at best can only be maintained after long-term adaptation to fat-rich diets when compared with carbohydrate-rich diets, and based on this, long-term fat diet usage cannot be recommended.

CAN TRAINING INTENSITY BE MAINTAINED ON A HIGH-FAT DIET?

In the literature, muscle glycogen is considered to play a key role in fatigue when exercise intensity ranges between 65 and 85% of $\dot{V}O_{2max}$ (17,34,35). Based on this fact, fat-rich diet adaptation have been used in an attempt to spare muscle glycogen and decrease carbohydrate oxidation and thus hypothetically optimize performance. Unfortunately,

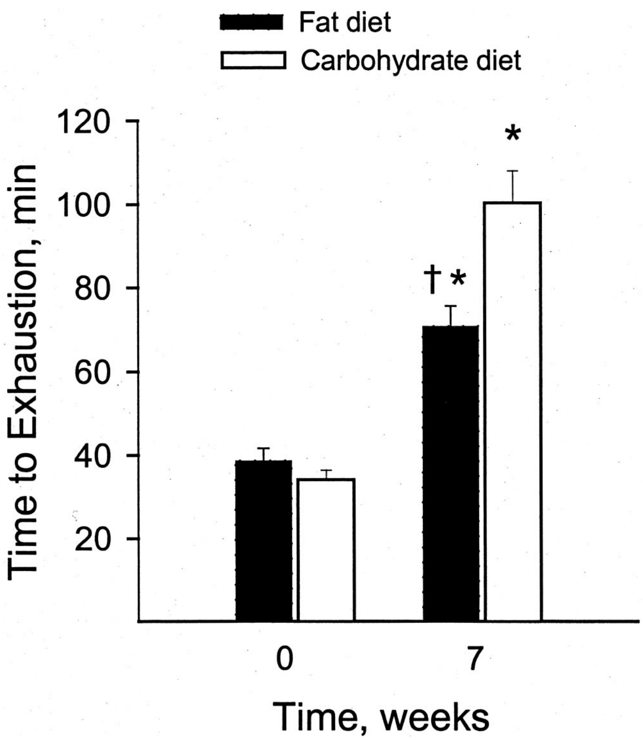

FIGURE 1—Time to exhaustion at 71% maximal oxygen uptake before and after 7-wk adaptation to training and either a fat or a carbohydrate diet. Results are mean ± SE (author's unpublished findings). * ($P < 0.05$) initial vs 7 wk; † ($P < 0.05$) fat diet vs carbohydrate-rich diet.

this carbohydrate sparing after fat diet adaptation is often accompanied by a reduced muscle (30) and liver (20) glycogen storage compared with consumption of a high-carbohydrate diet. Because a prerequisite for an optimal endurance performance is that training both in regards to quality and quantity is optimal, it is not clear whether in fact training intensity can be maintained during a long-term fat-rich diet adaptation.

Interestingly, this question was addressed already more than 70 years ago by Marsh and Murlin (27), who had one subject consume a normal, a high-fat, and a high-carbohydrate diet for 11 d. On most days, the subject undertook one or two light exercise bouts, and the following is the authors description of the subjects ability to handle the exercise during adaptation to the fat diet: "After the first two or three days the subject felt very tired and sleepy, in fact did sleep several hours between experiments, and had no desire to work or to do anything else. The work seemed harder, although actually it was the same as in the previous series. In the last few experiments the subject became dizzy on the ergometer toward the end of the work period and afterward expressed fear that he might have fallen off. But he stuck pluckily until the series was completed. The very last experiment had to be discontinued at the end of 6 2/5 min because of dizziness." (27). When the subject consumed the carbohydrate diet, all exercise tests were performed without problems. Thus, for this person, training was possible during fat diet adaptation although it did require a higher mental effort.

In three studies performed during the last 7 years, a number of subjects completed a supervised endurance-training program while consuming a fat-rich diet in our lab. In total, 17 subjects performed 7-wk cycle training (4 times a wk) (14,15) and seven subjects performed 4-wk cycle training (4 times a wk) (16) while consuming a fat-rich diet. All this training was supervised in the lab, and exercise intensity ranged between 60 and 85% of $\dot{V}O_{2max}$ (active breaks at 40–50% $\dot{V}O_{2max}$), and every single training session was completed. Thus, in subjects who were initially untrained to moderately trained regular endurance, training could be tolerated while a fat-rich diet containing some 62% of energy as fat was consumed. However, based on training diaries (personal comments included), it is evident that in many cases a higher mental effort was needed to sustain the scheduled exercise sessions while consuming a fat-rich diet compared with consuming a carbohydrate diet. In one study, the subjective rating of perceived exertion (Borg Scale (2)) was evaluated by the subjects every 15 min until and at exhaustion at the test before and after 7-wk adaptation to fat-rich diet ($N = 7$) and training or carbohydrate-rich diet ($N = 6$) and training (Fig. 2, author's unpublished findings). At the initial test before the initiation of training and diet, there was no difference in subjective rate of exertion, whereas after 7 wk, the exercise was perceived as more strenuous after fat-rich diet than after carbohydrate-rich diet (Fig. 2, author's unpublished findings). Interestingly, the level of exertion at exhaustion was not different between groups. Direct adverse effects of fat diet during training were sparse, although across all the training sessions reported a few cases of dizziness (3) and vomiting (1) occurred for the subjects adapting to fat-rich diet.

In elite-trained subjects, there is only limited evidence available on training capacity while consuming fat-rich diets. In a recent study by Stepto et al. (41), seven elite trained endurance athletes underwent two 4-d dietary periods consuming either a high-carbohydrate diet (70–75% carbohydrate) or a high-fat diet (>65% fat) in a crossover design with an 18-d washout period in between. During the dietary adaptation, subjects performed two controlled exercise sessions on days 1 and 4, where they exercised for 20 min at 65% of $\dot{V}O_{2max}$ and subsequently performed 8 × 5 min exercise bouts at 86% $\dot{V}O_{2max}$ interspersed with 60 s breaks. In addition to the training performed in the lab, the subjects also undertook training outside, but no difference in duration was apparent between dietary periods. The subjects were for all but one high-intensity exercise bout capable of performing the training while consuming the fat-rich diet, but interestingly the subjective rating of perceived exertion was higher on day 4 in the last few bouts after fat-rich diet when compared with the carbohydrate-rich diet. This indicates that at least for 4 d elite athletes are capable of performing training at a reasonably high intensity while consuming a fat-rich diet, although the cost is a higher subjective rate of perceived exertion.

What is then the mechanism for the higher mental effort needed to sustain exercise during fat-rich diet adaptation? Previous studies of short- (10,21) and long-term

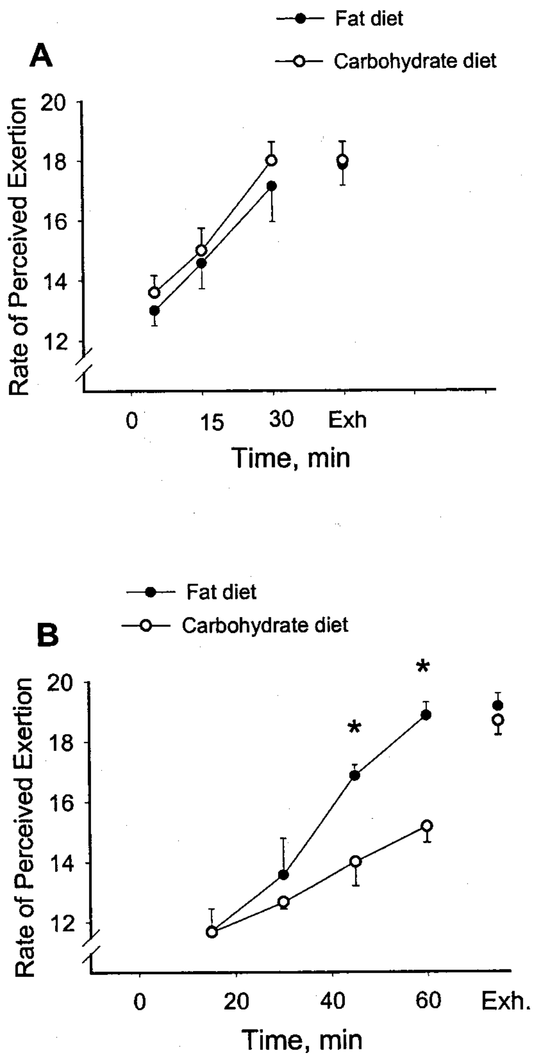

FIGURE 2—Rate of perceived exertion (Borg Scale) during submaximal exercise until exhaustion before (A) and after 7 wk (B) adaptation to training and either a fat or a carbohydrate diet. Results are mean ± SE (author's unpublished findings). Exh, exhaustion; * ($P < 0.05$) fat vs carbohydrate.

adaptation (14) to fat-rich diet reveal a significantly higher catecholamine response as well as heart rate during submaximal exercise compared with when a carbohydrate-rich diet was consumed, thus indicating that both short- and long-term fat diet adaptation induces an increased activity in the sympathetic nervous system during exercise. Furthermore, there is evidence that 14 d of low-fat diet adaptation in healthy female subjects lead to an increased parasympathetic response when compared with a diet with a higher fat content (28). Based on the evidence above, it seems likely that a changed autonomic nervous system activity—increased sympathetic and possibly decreased parasympathetic response—due to the fat diet consumption is contributing to the increased perception of exertion experienced during exercise. However, the exact explanation for the coupling between the fat-diet–induced increase in sympathetic response and the increased perception of exertion during submaximal exercise remains to be demonstrated. Obviously, the higher mental strain and in addition the higher heart rate during exercise while consuming a fat-rich diet will imply that exercise intensity needs to be controlled by objective measures such as oxygen uptake or power output to secure that intensity is indeed as requested.

FAT OXIDATION AFTER FAT DIET ADAPTATION: WHICH FAT SOURCES CONTRIBUTE TO THE INCREASED OXIDATION OF FAT DURING SUBMAXIMAL EXERCISE?

It is well known that adaptation to a fat-rich diet will lead to measurable changes in the capacity to store (in muscle), recruit, transport, and oxidize fat (9,13,23,30). In consequence of these adaptations both short- (5,24) and long-term (14,30) fat diet adaptation leads to an increased fat oxidation during exercise. However, only few studies have actually addressed which fat source(s) that contribute to this increased fat oxidation?

During exercise, fat is recruited for oxidation both from the plasma in the form of free FA (and albumin bound FA) and as very low-density lipoprotein triacylglycerol (VLDL-TG) and from muscle as triacylglycerol either from intra- or extracellular stores (42). In a recent study, Schrauwen and colleagues (36) applied a stable isotope tracer technique to investigate the substrate utilization after 7-d adaptation to either fat-rich (60% fat, 25% carbohydrate) or carbohydrate-rich diet (30% fat, 55% carbohydrate). In their study, the plasma FA oxidation was similar between diets, and therefore it was concluded that the higher fat oxidation (190%) observed during exercise at 50% of W_{max} after the fat diet was derived from muscle and/or plasma triacylglycerol (36). In a recently published study (15), we investigated the effect of long-term adaptation to training and either fat rich or carbohydrate-rich diet on substrate utilization during submaximal exercise. After 7-wk adaptation to diet and training, we combined the application of the stable isotope tracer technique with the arteriovenous balance technique (flow determined by thermodilution) during 60 min of submaximal bicycle exercise at 70% of $\dot{V}O_{2max}$. In addition, we obtained muscle biopsies from m vastus lateralis before and after exercise. By using this approach, it was evident that across the leg the fat-diet–induced increase in fat oxidation was derived from an increased utilization of VLDL-TG (calculated from the Fick principle) and from a stable isotope determined increased utilization of plasma fatty acids (Fig. 3 (15)). We were not able to measure a significant biochemical breakdown of muscle triacylglycerol across the exercise bout and, as such, concluded that muscle triacylglycerol was not a prime contributor to the increased fat oxidation. In contrast to Schrauwen and colleagues (36), we observed increased plasma FA utilization, but this may simply be due to the difference in duration of the dietary period; theirs was 7 d and we used 7 wk and furthermore added training as an intervention. It has previously been demonstrated that FA originating from VLDL-TG con-

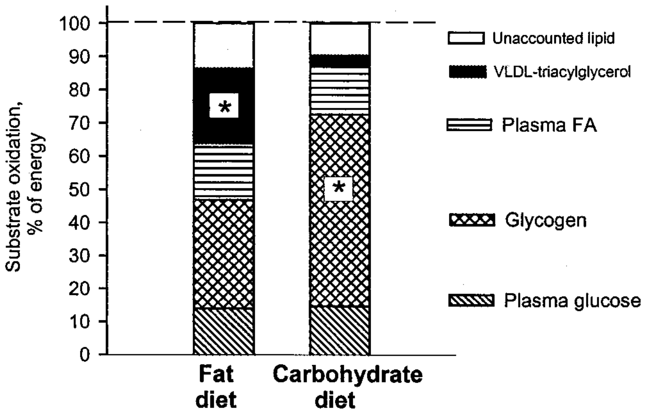

FIGURE 3—Contribution of blood and muscle derived substrates to total fuel oxidation in the leg during exercise in the fasted state after 7 wk of training and adaptation to either a fat or a carbohydrate diet. The substrate contribution from muscle glycogen was determined as net breakdown multiplied by the estimated active muscle mass of the leg (4 kg) (modified from (15)). Values are means. * ($P < 0.05$) fat diet vs carbohydrate diet.

tributed to fat oxidation in a trained leg during exercise (22), a finding that is coherent with a fat diet induced increase in muscle lipoprotein lipase activity (23). Thus overall, this suggests that during exercise, fat recruited from both plasma and plasma VLDL-TG, but not muscle triacylglycerol, is responsible for the increased fat oxidation after long-term fat diet adaptation. It is intriguing that muscle triacylglycerol utilization is not increased after a fat diet considering that a high dietary fat content will lead to an increased muscle triacylglycerol storage (16,23) and *vice versa* a low dietary fat content a decreased muscle triacylglycerol storage (7,40). However, the substrate balance in our recent paper (15) demonstrates that a minor fraction of lipid is unaccounted for, and it is not possible to exclude that this fraction or parts of it could potentially be muscle triacylglycerol. It is important to realize that the issue of muscle triacylglycerol utilization during exercise is controversial. Under normal dietary conditions, several studies originating from independent laboratories using different methodologies could not demonstrate muscle triacylglycerol utilization during exercise (1,22,33,39,40), whereas others found a significant breakdown amounting to approximately 20–35% (4,8,29,36). As such, final conclusions on the role of muscle triacylglycerol during exercise after fat diet adaptation must be left for future studies and the advent of a very precise analysis method.

CONCLUSION

Overall, there is evidence to suggest that endurance performance at best can only be maintained after long-term adaptation to fat-rich diets when compared with carbohydrate-rich diets, and therefore long-term fat diet usage cannot be recommended as a tool to improve endurance performance. There is good evidence that a reasonably high training intensity was possible over prolonged periods of fat diet consumption in untrained to moderately trained subjects, and that high intensity interval training could be tolerated by elite athletes during short-term fat-rich diet adaptation. However, in both untrained, moderately trained, and elite athletes, a higher mental effort was required to perform the exercise training, possibly due to a fat-diet–induced higher sympathetic nervous activation. This necessarily implies that if fat diet adaptation is applied under "free living conditions," it will be very important to secure that training intensity is not decreased due to the higher "stress" level. Unfortunately, there is still a clear lack of mechanistic understanding both in relation to performance and in relation to metabolic adaptation after prolonged fat diet adaptation, and further studies are necessary before more final conclusions are possible.

In perspective. Already more than 80 years ago, Krogh and Lindhard (24) studied the effects of dietary manipulations on substrate utilization during exercise. In that study, six subjects (including Krogh and Lindhard) participated in a crossover design in which a 3-d very-high-fat or very-high-carbohydrate diet was consumed. Exercise was performed on the Krogh bicycle ergometer and the following is the author's observations on the effect of diet on fatigue. "1. The fatigue at different quotients. The subjects J.L, G.L, A.K., and O.H. observed distinct differences in the facility (or difficulty) with which the prescribed amount of work was performed, coincident with changes in diet and noted that on fat diets the fatigue became considerable and sometimes excessive. For several hours after the work on the ergometer these subjects were generally very tired.... The subjects R.E. and A.M.N. failed to observe any appreciable difference between work on the two diets." (24). A similar divergent individual performance response after prolonged adaptation to a very high fat diet can be found in a paper by Phinney and Colleagues (30), and although we now 80 years after can explain a large part of the biochemical adaptations behind the adaptations observed by Krogh and Lindhard (24), there is to the best of my knowledge still not solid evidence to explain these individual differences. Thus, future studies should address whether indeed there is such an individual response to high fat diets and subsequently provide the physiological explanation behind a such difference.

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