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## Introduction

Muscles become fatigued during exercise primarily due to glycogen depletion. Consequently much study has been focused on dietary methods to maintain glycogen levels in the hopes of preventing fatigue and increasing exercise endurance. Research in this area has primarily focused on the effects that high carbohydrate diets have on prolonging glycogen supply (2). On the other hand relatively few studies have examined the effect a high fat diet can have on endurance. The effects of ketogenic diets are not as clear as those of high carbohydrate diets, although some benefits may be seen.

#### Animal Studies

Research in animal models has demonstrated that high fat diets can have a beneficial effect on endurance. In one of the earlier studies to show this effect, Miller et al. (11) put rats on either a high fat or a high carbohydrate diet (% energy from carbohydrates, fat, and protein was 1/78/21 and 69/11/20 respectively). After up to five weeks of adaptation to these diets, they tested the rats on a treadmill. The researchers found that those who had been on the high fat diet had a significantly longer time to exhaustion than those who had been on the high fat diet. Simi et al. (17) found similar results for rats on either a 0/80/20 or a 65/11/24 diet. Rats on the high fat diet were able to run significantly longer than rats on the high carbohydrate diet, and they also had significantly higher VO2max readings.

The exercise endurance of dogs has also been found to increase under high fat diets. In a somewhat anecdotal paper Kronfeld (7) reported that switching racing-sled dogs from a high carbohydrate diet (% energy from carbohydrates, fat, and protein 39/32/29) to a high fat diet consisting of mainly seal meat (0/66/34) caused the dogs to transform from slow and easily tiring into animals of significantly improved stamina. Kronfeld et al. (8) followed this up by testing the effects of three different levels of fat and carbohydrates on some basic physiological characteristics of racing-sled dogs. They found that a diet consisting of 0% calories from carbohydrate, 41% from fat, and 59% protein raised plasma free fatty acid concentrations significantly more than diets consisting of 27/28/45 and 46/19/35 carbohydrate/fat/protein calories.

#### Human Trials

While results in animals seem to point towards a beneficial effect for high fat diets, results from human studies have been inconsistent. In the short term high fat intake does not seem to be effective in increasing exercise performance over a high carbohydrate diet. A study done on trained cyclists found that those who consumed a high fat meal four hours prior to exercise had slightly smaller endurance capacities compared to those who ate a high carbohydrate meal instead (14). Consumption of a high fat meal (68% of energy from fat) after a bout of exercise also did not produce a higher exercise capacity in exercise done twelve hours later (compared to an isocaloric high carbohydrate meal with 83% total energy from carbohydrate) (18).

After a longer period of adjustment to a high fat diet, there seems to be an improvement in exercise capacity. Muoio et al. (12) gave trained runners either a normal, high fat, or high carbohydrate diet for seven days. The percentages of energy from carbohydrate, fat, and protein for the respective diets were 61/24/14, 50/38/12, and 73/15/12. After the one-week period of adjustment to the diet, running time to exhaustion was measured. The runners on the high fat diet had a significantly longer time to exhaustion than those on the carbohydrate and normal diets. VO2max was also significantly higher for runners who had been on the high fat diet.

In another study demonstrating an improved exercise endurance from a high fat diet, Lambert et al. (9) gave a group of trained cyclists either a diet consisting of 7% carbohydrate, 70% fat, and 23% protein calories or a high carbohydrate diet (74% carbohydrate, 12% fat, 14% protein) for two weeks. Following this they measured their exercise capacities, and then switched them to the other diet for two weeks. They found that the time to exhaustion during moderate intensity exercise (65% of VO2max) was significantly longer for cyclists while they were on the high fat diet.

In contrast to these results, other researchers have found that high fat diets do not improve exercise endurance over high carbohydrate diets. Helge et al. (5) subjected cyclists to seven weeks of training on either a high fat or high carbohydrate diet (carbohydrate/fat/protein %: 21/62/17 or 65/20/15). The mean time to exhaustion for the high fat group was significantly lower than for the high carbohydrate group, although both groups did better than they had before beginning the training program. During the eighth week both groups were placed on a high carbohydrate diet. The high fat group's endurance increased significantly, but still did not match that of the high carbohydrate group.

Helge's group followed their 1996 paper with a similar experiment in which they measured exercise endurance after four weeks (6). After this period of time, the endurance of the high fat group did not differ significantly from that of the high carbohydrate group. However, after continuing the diets two weeks longer, they discovered that the high carbohydrate training group continued to better their time to endurance while the high fat group remained about the same as at four weeks.

#### Physiological Basis For Endurance Changes

The chief hypothesis behind enhanced endurance following high fat diets is that higher levels of free fatty acids and fat oxidation allow glycogen to be used more sparingly. As a result, muscles do not deplete their glycogen stores and are able to exercise longer. This hypothesis has been tested and observed in numerous animal and human models, especially recently with the advent of sophisticated methods to biopsy and test muscle tissues.

#### High Levels of Dietary Fat Slow Glycogen Depletion

Reynolds et al. (15) demonstrated that increasing fat in one's diet decreases glycogen usage. They gave dogs either a high fat diet (carbohydrate/fat/protein: 15/60/25) or a high carbohydrate diet (60/15/25) and trained them for 20 weeks on a treadmill. During the training period they ran the dogs through a series of aerobic and anaerobic exercise tests and performed muscle biopsies before and after the tests. The researchers found that dogs on the high carbohydrate diets had more total muscle glycogen (TMG) prior to exercise and that their TMG declined further following exercise than the high fat fed dogs. From these results they concluded that the high carbohydrate fed dogs were using glycogen more rapidly than the high fat fed dogs.

A study done on rats demonstrated the same effect of fat on glycogen usage (13). Rats were fed a high fat (78.7% of total energy) or high carbohydrate diet (68.7% of total energy) for five weeks. After this period they were subjected to moderate intensity treadmill exercise, and at different time points during the exercise, muscle samples were taken. Rats on the high fat diet had significantly lower rates of glycogen usage than the high carbohydrate diet at 0-10 minutes into the exercise (985  $\pm$  295 nmol/g/min vs. 1593  $\pm$  144 nmol/g/min). At 11-20 minutes this gap was even more distinct (356  $\pm$  61 nmol/g/min vs. 1055  $\pm$  272 nmol/g/min).

The reason that high fat diets can spare glycogen usage while maintaining or increasing exercise performance is because they increase the supply and oxidation of fat in muscles. Free fatty acid levels have been measured in numerous studies, and there seems to be a clear correlation between increasing dietary fat and increased levels of free fatty acids (3,6,8). Studies have also found that fat oxidation is concomitantly increased. The respiratory exchange ratio (RER) is lower in exercising humans and animals on high fat diets, indicating that more of their energy was coming from lipids (4,5,10). Interestingly, unsaturated fats in the diet seem to lower RER more than saturated fats (16).

#### Biochemical Mechanisms of Increased Fat Oxidation

Increases in enzyme activity may be responsible for increased oxidation. Two such enzymes catalyze crucial steps in fat oxidation: b -hydroxy-acyl-CoA-dehydrogenase (b -HAD) and citrate synthase (6,10,11). In fatty acid metabolism, fatty acids are first linked to coenzyme A, forming acyl CoA. Through a series of reactions, one of which involves b -HAD, acyl CoA is converted into acetyl CoA (20). Acetyl

CoA then reacts with oxaloacetate in a reaction catalyzed by citrate synthase thereby entering the citric acid cycle (19).

Increasing the activity of citrate synthase and b -HAD should therefore allow more energy to be derived from fatty acid energy sources (5,10,11). Although the increased activity of citrate synthase may be attributed to increased carbohydrate metabolism as well as higher rates of fat oxidation, b -HAD is exclusively used in fatty acid metabolism. The increased activities of b -HAD therefore indicate that more fatty acid oxidation is occurring in high fat adapted individuals.

## Regulation of Muscle Adaptation

Relatively few studies have been done on the regulation of carbohydrate/fat oxidation in muscle. Regulation may be achieved simply via altered substrate availability rather than by a change in the amount or activity of enzymes that catalyze steps in fat oxidation or glycogenolysis. However there does seem to be some regulation of glycogen phosphorylase, the enzyme that catalyzes the first step of glycogenolysis. Dyck et al. (1) fed cyclists a high fat emulsion that raised their plasma free fatty acid levels. Subsequently, muscle biopsies taken during exercise showed that glycogen phosphorylase activity was decreased. This corresponded to lower levels of AMP, which is an allosteric activator of this enzyme. Thus it seems that high levels of free fatty acids may act to decrease the activity of glycogen phosphorylase thereby shifting energy utilization towards fat oxidation.

An interesting corollary to these changes in muscle physiology is that there may be an increase in mitochondrial density in muscle of animals on high fat diets. Taylor et al. (21) reported that a high fat diet increased the number of mitochondria in the muscles of exercising dogs. No further research appears to confirm these results.

# Conclusion

Consuming a high fat diet has been shown to cause changes in muscle physiology, but its effect on exercise endurance remains controversial. Part of the inconsistency between the animal and human results may be explained by differences in the percentage of calories from carbohydrate. The high fat diets given to animals contained little carbohydrate, usually 0-1% of total calories. The human diets on the other hand typically contained a moderate amount (10-20%) of their energy from carbohydrates. When Helge et al. (4) gave rats a diet with moderate carbohydrate (20/65/15) and compared endurance to rats on a high carbohydrate diet (20/10/70), they found that there was no difference between the two groups. Since the diets that seemed to improve exercise efficiency were those with the least carbohydrate and most animal studies are done this way, perhaps the answer to resolving the controversy over the effectiveness of ketogenic diets lies in performing more animal studies with moderate carbohydrate diets and studying how free fatty acid levels and muscle energy utilization changes.

If the secret to obtaining endurance advantages lies in a diet that contains very little carbohydrate and massive amounts of fat (>60% total energy), such a diet would probably not present a very useful ergogenic aid. Not only would one probably develop higher morbidity from weight gain and increased adiposity, such a diet would be difficult to design and unpalatable to most athletes. Although ketogenic diets may be useful in treatment of childhood epilepsy (22), the muscle physiological changes caused by this diet do not seem to be clear enough to recommend it to anyone seeking an endurance advantage.

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