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DIETARY LIPID FORM AND FUNCTION

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Lipids are a diverse group of chemical compounds that share the common characteristic of being insoluble in water but soluble in organic solvents. The term lipid encompasses triglycerides, the most abundant lipid in the body, and their constituent fatty acids as well as cholesterol, phospholipids, and sterols. This review will focus upon fats and oils, which are the most significant dietary lipids. Lipids that are solid at room temperature are known as fats, and those that are liquid at room temperature are known as oils, although they are also generically referred to as fats.

The fatty acid molecule, which is common to most lipids, consists of a chain of carbon atoms (C3-C24). At one end of the molecule, designated the alpha end, is a carboxyl group (COOH), and at the other end, the omega end, there is a methyl group. When all of the bonds between the carbon atoms are single bonds, the fatty acid is said to be saturated (e.g., stearic acid). In contrast, when one or more of the carbon to carbon (C-C) bonds is a double bond, it is said to be unsaturated. While a fatty acid molecule with a single double bond is known as a monounsaturated fatty acid (e.g., oleic acid), one with two or more double bonds is said to be a polyunsaturated fatty acid (PUFA) (e.g., linoleic acid).

Fats and oils are not made up from a single type or category of fatty acid but are complex mixtures of many different fatty acids. Fatty acids combine with glycerol to form triglycerides (three fatty acids plus one glycerol), which are the main component of both fats and oils. Fats are usually high in triglycerides containing predominantly saturated fatty acids and are less affected by heat, so they tend to be solid at room temperature. In contrast, oils are usually high in triglycerides, containing predominantly monounsaturated or polyunsaturated fatty acids. Oils are susceptible to the effects of heat and, as a result, are usually liquid at room temperature.

Saturated fatty acids have a very ordered, straight-chain structure, which allows them to pack together very tightly; unsaturated fatty acids tend to be less orderly and only loosely packed. This arrangement makes the latter more susceptible to the effects of heat, so they tend to become liquid or melt at lower temperatures. The other factor that affects the characteristics of fat, which contains predominantly saturated fatty acids, is C-C chain length. Long-chain saturated fatty acids tend to produce fats that are solid at room temperature, yet those containing a predominance of medium- (C6–C10) or short-chain (up to C6) fatty acids prove to be the exceptions, remaining liquid at room temperature.

Table 1. Comparison of dietary fats and oils in terms of saturated fatty acid and the most common unsaturated fatty acids (Wardlaw, 1999).

Fats and Oil	*Saturated fatty acid %*	*Linoleic acid %*	*Alpha-linolenic acid %*	*Mono-unsaturated fatty acids %*
Olive Oil	14	8	1	77
Canola (Rapeseed) Oil	6	22	10	62
Corn Oil	13	61	—	25
Sunflower Oil	11	69	—	20
Soybean Oil	15	54	7	24
Safflower Oil	10	77	trace	13
Coconut Oil	92	2	—	6
Tallow	41	11	1	47

Omega-3 and Omega-6 Series

The position of the first C-C double bond within an unsaturated fatty acid affects its metabolism by the body, and this feature is used to further classify unsaturated fatty acids. Omega-3 fatty acids are those that have their first C-C double bond between the third and fourth carbon atom from the methyl group or omega end. Similarly, omega-6 fatty acids are those that have their first C-C double bond between the sixth and seventh carbon atom from the omega end, and omega-9 fatty acids are those with their first C-C double bond between the ninth and tenth carbon atoms from the omega end.

In feed ingredients, alpha-linolenic acid, which is found in high concentrations in linseed oil and cod liver oil, is the major omega-3 fatty acid; linoleic acid, which is found in high concentrations in corn and soya oil, is the primary omega-6 fatty acid; and oleic acid, which is found in high concentrations in olive and many other vegetable oils, is the major omega-9 fatty acid.

As with humans (Wardlaw, 1999), horses are unlikely to be able to synthesize fatty acids, which have their first C-C double bond before the ninth carbon atom from the omega end. In other words, the omega-3 and omega-6 fatty acids must be provided by the diet and are termed essential fatty acids (EFA). Fatty acids from the omega-3 and omega-6 series perform numerous important functions within the body: parts of vital body structures, components of phospholipids, roles in immune function, roles in vision, and integration into cell membranes.

Additionally, both alpha-linolenic and linoleic acids are metabolized further by cells and used in the synthesis of hormone-like substances called eicosanoids.

Omega-6 fatty acids are converted primarily to arachadonic acid, and omega-3 fatty acids are converted to eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). Further biochemical modification results in the production of eicosanoids, including substances called prostaglandins, prostacyclin, thromboxanes, and leukotrienes. Unlike regular hormones such as insulin or the thyroid hormones, these “local hormones” are used where they are produced and are not transported to their site of action in the blood.

The omega-3 and omega-6 fatty acids follow different biochemical pathways to produce distinct types of prostaglandins and thromboxanes, each of which has very different effects in the body. The eicosanoids are potent regulators of vital body functions such as blood pressure, blood clotting, and immune and inflammatory responses. In general terms, the eicosanoids produced from omega-6 fatty acids tend to increase inflammatory processes and blood clotting. Eicosanoids produced from omega-3 fatty acids tend to decrease blood clotting and inflammatory response, although this is a gross simplification as the mechanisms involved are very complex. The physical and functional properties of cell membranes are affected by the relative fatty-acid composition of membrane-bound phospholipids, which can be altered according to the fatty-acid composition of dietary triglycerides. The different biochemical pathways involved in eicosanoid production utilize and therefore compete for the same enzymes, so the degree of inflammation, for example, is influenced by the relative proportions of omega-6 and omega-3 fatty acids present in cell membranes (Baur, 1994).

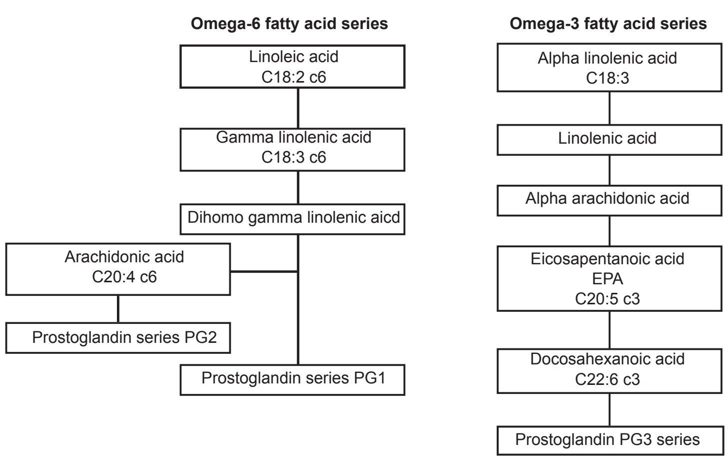

Figure 1. Biochemical pathways involved in eicosanoid production.

The reputed beneficial effects of the omega-3 fatty acids are largely due to the conversion of EPA and DHA to the prostaglandin PG3 series. However, the conversion of the parent precursor alpha-linolenic acid to both EPA and DHA is relatively innefficient due to low activities of the enzyme delta-6 desaturase (Baur, 1994). In domestic animals, dietary supplementation with omega-3 fatty acids may be a useful adjunct to treatment of renal disease, rheumatoid arthritis, cutaneous inflammatory disorders, autoimmune disease, and possibly cancer (Baur, 1994). While there are few studies on dietary omega-3 fatty acids in horses, Henry et al. (1991) reported that dietary intervention with rations rich in alpha-linolenic acid in the form of linseed oil were potentially useful in preventing some of the deleterious effects of endotoxemia in horses. Recently, a double-blind crossover trial using Icelandic ponies predisposed to recurrent seasonal pruritis (sweet itch) revealed that supplementation with linseed (flax), a rich source of alpha-linolenic acid, improved the average skin-test response to *Culicoides*, the biting fly implicated in the condition (Pearson-O'Neill et al., 2002).

A minimum requirement for linolenic acid of 0.1% has been recommended for horses (Vitec, 1987), where the requirement for linoleic acid is considered to be close to 1-4% of the total dry matter intake (Vitec, 1987). Although there are no published guidelines for horses regarding the optimum ratio of C6 to C3 fatty acids in the diet, the consensus in other animals seems to be a ratio of about 10:1 (Vitec, 1987). An EFA deficiency in other species is characterized by a dry lusterless coat, scaly skin, and predisposition to skin infections. However, a true EFA deficiency with similar symptoms has not been documented in horses, despite diets with a very low total fat and linoleic acid content being fed (0.05% and .03%, respectively) (Sallmann et al., 1991). The only finding linked to this low intake of fat was a reduction in the plasma and tissue levels of vitamin E, which may reflect reduced absorption from the diet.

The number and position of the double bonds in omega-3 fatty acids makes them particularly susceptible to oxidation, leading to the formation of hydroperoxides, which are at best unpalatable but will also contribute to cell membrane destruction in vivo. These oils should be protected from rancidity by suitable antioxidant products, and additional vitamin E is needed to protect them once they have been ingested.

EFA nutrition in the horse is of great interest due to its clinical relevance, and the lack of research in this area offers great scope for future investigatations. However, the relationship between eicosanoids and their essential fatty acid precursors is complex and requires thorough investigation before dietary recommendations can realistically be made.

Fat or Oil Supplementation

Fats and oils are regularly added to the diets of horses and have proven to be both palatable and highly digestible. They are usually added to the diet to increase energy density, which offers an advantage when appetite limits the provision of adequate energy to maintain condition or when a reduced intake of hydrolyzable carbohydrate (CHO-H) is advocated from a clinical standpoint. Diets characterized by high fiber content, oil supplementation, and reduced levels of CHO-H have been recommended for horses with a predisposition to equine rhabdomyolysis syndrome (ERS) and have also been advocated as being safer for laminitic horses (Harris and Naylor, 2001). The recent implication of high-glycemic diets in developmental orthopedic disease has initiated interest in fat supplementation as a means of restricting CHO-H intake to reduce the glycemic nature of feeds, thus making them suitable for young stock (Ralston, 1995; Pagan et al., 2001). Additionally, it is common practice for horse owners or trainers to supplement the diet with oil in order to gain from its reputed benefits on exercise performance, both for endurance and sprint exercise.

Low levels of oil have been added to commercial formulations for many years, acting as a dust suppressant and easing the passage of ingredients through manufacturing plants, which reduces the buildup of debris on plant machinery. Likewise, horse owners have fed oil for many years, prior to the current fashion for fat supplementation, in the form of cod liver oil or boiled linseed with the premise of improving coat condition and promoting weight gain. The maximum level at which fat or oil can be added to the diet is largely dependent on the physical restraints of feed manufacture, such as if it is fed as part of a cube or mix. Top-dressing allows much larger quantities of oil to be added to the diet as does the use of straight feedstuffs such as cooked linseed or rice bran; however, feed refusal may become an issue at very high levels of inclusion.

Palatability

Both vegetable oil and animal fats have proven to be palatable in horses. Bowman et al. (1979) compared the palatability of 10 different types of fat and oil using a cafeteria-style palatability test. In each palatability trial, corn oil was used as a control feed and was tested against three blends of either vegetable and animal fat, vegetable oils only, or animal fats only. In each case, the oil or fat source was added to a concentrate feed at a level of 15% (by weight). Corn oil was found to be the most palatable when compared to either of the other three sources offered. In an extension of this trial, the relative palatability of each fat or oil was calculated by comparison against the acceptability of corn oil using multiple measurements taken over 7-10 days. During each trial, corn oil was found to be the most acceptable followed in relative terms by a vegetable and animal fat blend with a linoleic acid content of 30.8% (Holland et al., 1998). Please refer to Figure 2. This trial looked at palatability over a relatively short period of time (10 days), but other digestibility and exercise-oriented studies over the years have fed oil- or fat-supplemented diets for periods of between three weeks and 16 months with few reported palatability issues. Harris et al. (1999) reported good feed intake during a 16-month trial where horses were fed a basal diet (7% of digestible energy [DE] as oil) supplemented with either a highly unsaturated (soya) or saturated (coconut) vegetable oil providing a final level of 27% of the total DE intake as oil.

Furthermore, there were no references made to any significant palatability problems during this trial. Care should be taken when extrapolating palatability data for specific oil sources from country to country as different processing techniques can affect palatability.

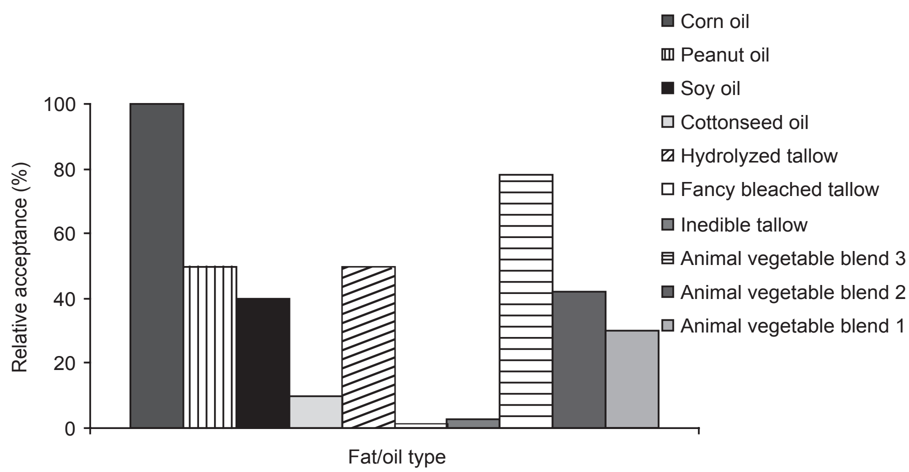

Figure 2. Relative acceptance of fats used in palatability experiments compared to corn oil (Holland et al., 1998).

Digestibility

Both DE and metabolizable energy (ME) have consistently been reported to increase as a result of the addition of fat or oil to the diet (Hollands and Cuddeford, 1992; McCann et al., 1987; Rich et al., 1981). However, the form in which the fat is available (i.e., free in the form of oil or animal fat, or encapsulated in cereal grains or oilseeds) may affect its digestibility (McCann et al., 1987). Fat is digested predominantly in the small intestine, whereas cell wall material is fermented in the hindgut. The encapsulation of oil in cereal grains or oilseeds may affect its digestibility, as some fiber may have to be digested to free the integral oil. Kronfeld et al. (2001) suggested that the lower apparent digestibility of this endogenous oil as opposed to supplemental oil may indeed be related to differences in the nature of ether extract; alternatively, the authors proposed a rate-limiting effect of lipase activity related to the oil content of the diet or even the presence of a lipase inhibitor in an ingredient of the endogenous oil source. In ruminants, the addition of vegetable oils to the diet has been shown to have a negative impact on fiber digestibility. Free vegetable oil coats the fiber fraction, disrupting ruminal fermentation. Integral oil does not appear to have the same effect, probably because the oil is released more slowly (Coppock and Wilks, 1991). In contrast, no apparent adverse effect on neutral detergent fiber (NDF) or acid detergent fiber (ADF) was reported in horses fed a high-fiber diet supplemented with oil (4-17% of DM)

(Hollands and Cuddeford, 1992). Likewise, Kronfeld et al. (2001) reported that fat and oil had no associative effect on fiber digestibility when hay- and grain-based diets were supplemented with various sources and levels of oil. Recent work by Jansen et al. (2001), however, has suggested that total tract fiber digestibility is in fact affected by oil supplementation.

In contrast to the work of Hollands and Cuddeford (1992), Kronfeld et al. (2001) reported a substantial negative associative effect of fat or oil supplementation on crude protein digestibility in a high proportion of digestibility trials recently reviewed.

Apparent absorption of calcium and magnesium are reportedly unchanged by the addition of fat or oil to the diet (Rich et al., 1981; McCann et al., 1987). This is in contrast to work in other species where fat-supplemented diets have been associated with reduced calcium absorption, possibly due to the formation of calcium soaps in the small intestine as discussed by Hollands and Cuddeford (1992). These authors also reported an increase in the apparent digestibility of phosphorus in response to oil supplementation, which they suggest may be due to enhanced absorption of phosphorus in the small intestine.

Glycemic Response

The energy density of feeds can be increased through the addition of oil, making the inclusion of high levels of cereal grains unnecessary. Diets that are high in fiber and low in nonstructural carbohydrates (sugar and starch) are now more common. The energy density in these feeds is increased through the addition of supplemental oil. Glycemic response and insulin release is significantly lower in response to diets that are high in fiber and oil in comparison to more traditional grain-based feeds (Williams et al., 2001) and also for grain-based feeds that are top-dressed with oil (Pagan et al., 1999). The reduction in glycemic response to feeding is partly due to the lower starch and sugar content of these former feeds but is also likely to be influenced by the presence of oil in the latter. The presence of fats and oils in the small intestine stimulates the secretion of a hormone called cholecystokinin. This hormone decreases gastric motility and delays gastric emptying, thus affecting transit time and the rate of prececal starch digestibility. Additionally, the increased energy density achieved through the addition of oil often means that meal size can be reduced, which again will affect transit time and hence glycemic response.

Behavior

Fat or oil supplemented diets have been reputed to modify behavior in excitable horses. Holland et al. (1996) provided the first quantitative evidence of this by reporting that spontaneous activity and reactivity, evaluated as response to pressure, loud noise, and sudden visual stimuli, was reduced in horses fed a diet supplemented with soy lecithin and corn oil. Lecithins are a group of phospholipids that contain two fatty acids, a phophate group, and a choline molecule. They function as emulsifiers of fat by breaking it down into small droplets or micelles. They form a bridge between the fat and water, allowing mixture with water. Lecithins are produced by the liver and are released into the small intestine, where they emulsify dietary fats and oils and enlarge the surface area over which digestive enzymes can act. The reputed effect of soy lecithin and corn oil on behavior is relevant not only for leisure horses but also for those with a predisposition towards ERS. Stress and nervousness are two factors that increase the likelihood that a horse susceptible to ERS will develop muscle damage (MacLeay et al., 1999a).

Metabolic Effects of Fat or Oil Supplementation

The effect of fat or oil supplementation on resting muscle glycogen concentration and its subsequent rate of use during exercise is a controversial topic. Many researchers reported an increase in resting muscle glycogen concentration and subsequent utilization during moderate- to high-intensity exercise, despite a reduction in the nonstructural carbohydrate (NSC) content of the fat-supplemented versus control diets (Meyers et al., 1989; Oldham et al., 1990; Harkins et al., 1992; Scott et al., 1992). Equally, however, several authors have found no such increase in resting muscle glycogen concentration or subsequent utilization during exercise in horses fed diets providing comparable levels of fat (Pagan et al., 1987; Greiwe et al., 1989; Eaton et al., 1995; Orme et al., 1997; Hyyppa et al., 1999). In the former studies, the muscle glycogen concentrations measured were often very low in comparison to previously established levels and the effect of differences in the energy and protein content of the control and fat-supplemented diets, as well as the presence of any training effect, cannot be overlooked. Additionally, differences in the content and source of NSC in the fat- or oil-supplemented diets may also offer some explanation of the contradictory results reported between study groups. Prececal digestibility, glycemic response, and postprandial insulin concentration will affect glycogen synthesis.

Glycogen repletion rates following moderate-intensity exercise were reduced in horses fed a basal diet supplemented with rapeseed oil (7.5% of total DM, 14% DE) compared to the basal diet alone. However, this effect was abolished once these horses were adapted to an oil-supplemented diet (5% of total DM) for a period of three weeks (Hyyppa et al., 1999). Pre-exercise muscle glycogen concentrations were not significantly different when both normal horses and those suffering from recurrent equine rhabdomyolysis (RER) were fed either a high-oil diet (20% of total DE), a low-oil, low-carbohydrate control diet, or a high-carbohydrate diet. However, there was a trend towards lower muscle glycogen concentrations in the horses fed the high-oil diet and, in contrast, higher concentrations in the horses fed the high-carbohydrate diet compared to the control diet (MacLeay et al., 1999b).

It would seem that horses are able to maintain normal muscle glycogen levels in the face of moderate levels of fat supplementation (7.5% of total DM, 14% DE), despite reduced CHO-H intake, provided that a period of adaptation is undertaken. This has obvious advantages for certain types of performance horses in which muscle glycogen availability is important but high intake of grain rich in CHO-H is undesirable. In contrast, there is some suggestion that high intakes of supplemental oil may reduce muscle glycogen, which could be detrimental to performance in some instances but may be advantageous with respect to certain clinical conditions such as ERS.

Metabolic Adaptation

Fat or oil supplementation of the diet is characterized by an increase in plasma cholesterol and phospholipids and a reduction in plasma triglyceride (Orme et al., 1997; Geelen et al., 1999). Enzymatic studies suggest that the fat-adapted horse has an increased capacity for uptake of free fatty acids from circulating triglycerides into muscle (Orme et al., 1997; Geelen et al., 1999, 2000). Artificial elevation of plasma FFA prior to the onset of low-intensity exercise indicates that horses have the capacity to increase the contribution of fat to energy generation when substrate availability allows (Orme et al., 1995). Furthermore, it has been suggested by Orme et al. (1997) that the capacity for oxidation of FFA and carbohydrate may be increased in response to oil supplementation as indicated by an increase in the activity of key oxidative enzymes. However, this effect was not repeated in a similar study by Geelen et al. (2000).

This higher capacity for fat oxidation is confirmed by a lower observed respiratory exchange ratio in fat-adapted horses exercising at low to moderate intensities (Dunnett et al., 2002). This finding allows for a glycogen-sparing effect with a potentially positive outcome on performance during exercise, where the intensity and duration are compatible with increased fat utilization. Despite these treadmill-based studies, no endurance-type performance trials have been reported to date. However, fat supplementation (up to 20% of the total DE) is common in the diets of competitive endurance horses.

The concentration of insulin, a potent antilipolytic hormone, has been reported to be lower both postprandially (Williams et al., 2001) and during exercise following oil supplementation (Pagan et al., 1994). The metabolic response to oil supplementation, in terms of FFA oxidation, increase in lipoprotein lipase activity, and muscle oxidative capacity, could be mediated in part via characteristic changes in postprandial and exercise-induced insulin concentrations. In other words, these adaptive effects may not be directly attributable to the oil supplementation per se. They may simply reflect differences in the hormonal response to test and control diets, changes in the level of CHO-H, and any associative effects of the oil on the rates of gastric emptying and transit time.

The metabolic response to oil supplementation occurs rapidly and is apparent after just three weeks of supplementation (Hughes et al., 1995; Orme et al., 1997).

These supplementation effects are, however, transient and dependent on continued use, with the response being abolished within five weeks of withdrawal of the oil-supplemented diet (Orme et al., 1997). The response to oil supplementation may also vary between individual horses, depending on their inherent ability to utilize fat as a fuel source during exercise (Dunnett et al., 2002).

Performance Effects

The effect of fat or oil supplementation on exercise performance is not unequivocal. Some researchers report improvements and others indicate no changes (Topliff et al., 1983; Essen-Gustavsson et al., 1991; Moser et al., 1991). It was expected that any positive effect of fat or oil supplementation would be dependent on the intensity and duration of exercise as well as the training status of the horses. Improvement in performance in response to fat or oil supplementation is feasible where either a glycogen-sparing effect occurs, mediated by an increase in fat oxidation either during training or during the competition, or where resting muscle glycogen concentration is increased by an unidentified mechanism. Meyers et al. (1989) and Oldham et al. (1990) reported a greater capacity for exercise during a standardized treadmill exercise test, and Harkins et al. (1992) demonstrated improved racetrack performance. These performance effects were suggested to have been mediated via an observed increase in resting muscle glycogen concentration and associated increase in glycogen utilization rates during exercise. Latterly, however, Eaton et al. (1995) reported an increased capacity for high-intensity exercise and a greater mean accumulated oxygen debt in fat-supplemented horses with no corresponding change in resting muscle glycogen concentration or subsequent utilization during exercise. It is unlikely that any positive effect on high-intensity exercise is due to increased fat oxidation during exercise because the contribution of FFA oxidation to energy generation during this type of exercise is likely to be low. An increased flux through glycolysis, characteristic of high-intensity exercise, would lead to an accumulation of acetyl CoA, which may inhibit the carnitine transport system needed for FFA uptake into mitochondria. It is, however, possible that chronic fat supplementation may lead to improvements in carbohydrate oxidation rates due to increases in key Krebs cycle enzymes such as citrate synthase (Orme et al., 1997).

Thermal Load

A further advantage to fat or oil supplementation is a reduction in thermal load. Physiological processes including ingestion, fermentation, and assimilation, as well as the metabolic process of energy generation, are not completely efficient and heat is produced as a consequence, giving rise to a thermal load. The total amount of heat produced as a consequence of maintenance processes is referred to as the heat of maintenance (Hm), and additional heat produced as a consequence of exercise or work is known as heat of work (Hw). A horse's thermal load is equivalent to the total of Hm and Hw, which must be dissipated in order to maintain normal body temperature. Exercise in hot environments presents a greater challenge to the horse's thermoregulatory system, and measures that are effective in reducing the thermal load could confer a performance advantage.

Diets supplemented with fats or oil have been suggested to reduce thermal load by a number of different mechanisms. An increase in the energy density of the diet (e.g., through the addition of fat or oil) reduces the work of feeding or the heat of ingestion, and when accompanied by a lowered forage to concentrate ratio, this would be additive to a reduced heat of fermentation. Reduced gut fill or ballast as a result of the increase in energy density may also have an effect on Hw. In addition, the heat produced per molecule of ATP generated was calculated to be least during the direct oxidation of long-chain fatty acids (stearic and linoleic acids) compared to carbohydrates (glucose), amino acids (leucine), or volatile fatty acids (propionic or acetic acid) (Kronfeld, 1996). This premise is also apparent when each of these energy sources is oxidized indirectly following storage as glycogen, triglyceride, or lactate in the case of glucose or as triglyceride in the case of stearic acid or acetic acid.

McCann et al. (1987) reported that heat production, expressed as a percentage of total DE, was lower for three types of fat-supplemented diets in comparison to a control diet. Calculation of energy balance (ME - heat production) by calorimetry revealed a significant increase over the control diet. Using a model to compare energetic efficiencies and heat production of three diets that provided varying proportions of fermentable carbohydrate (CHO_f), hydrolyzable carbohydrate (CHO_h), fat, and protein, Kronfeld (1996) calculated that the high-fat diet (which also provided the lowest levels of CHO_f and CHO_h) would result in the lowest total heat production, equivalent to the sum of Hm and Hw.

Fatty Acid Chain Length

Little work has been carried out to investigate the effect of fatty acid chain length or degree of saturation on exercise metabolism. Oils such as coconut and palm contain a high proportion of medium-chain fatty acids (MCFA) (C6-C10). The mechanism by which these fatty acids are absorbed from the intestinal lumen is somewhat different than their long-chain counterparts. As a result of their greater solubility in water, MCFA are absorbed much more quickly from the small intestine and unlike long-chain fatty acids are not re-esterified in the intestinal epithelial cells. MCFA are absorbed intact and are transported from the intestine to the liver, via the portal circulation, in association with albumin. Furthermore, oxidation of the former can occur either with or without the involvement of the carnitine-dependent mitochondrial transport system. These differences in the mechanism of absorption and oxidation for MCFA make their metabolism more rapid than long-chain sources. There has been a suggested beneficial effect of MCFA on performance reported in horses fed coconut oil (10% of a grain-based concentrate pellet) during exercise of moderate speed and duration (8-9 m/s, 8 minutes) (Pagan et al., 1993). Horses exhibited lower plasma lactate or ammonia concentrations in response to this exercise when fed the coconut oil in comparison to a traditional grain-based control diet or a soya oil-supplemented diet, respectively. The authors suggest that the fatty acid composition of the coconut oil may have allowed more rapid mobilization and oxidation of fatty acids, permitting a significant contribution to energy release during moderately intense exercise. However, subsequent trials have failed to support these findings. A field-based trial by Jackson et al. (2001) failed to repeat these observed changes in lactate response to exercise when feeding MCFA; however, an increase in pre-exercise plasma betahydroxybutyrate concentration was observed. As these authors suggest, this may provide evidence of increased oxidation of medium-chain fatty acids to ketones in the group supplemented with MCFA. A subsequent long-term fat acclimation trial, which involved horses being fed a diet supplemented with predominantly saturated (MCFA) or unsaturated oils, revealed no significant change in insulin or lactate response to exercise. This was apparent following the first nine months of the trial, where the saturated or unsaturated supplemental oil contributed 12% of the total DE, and following a further six months of supplementation, where the level of oil fed was increased to provide a total of 20% of DE (Harris et al., 1999). There is no clear evidence to support the use of MCFA in performance horses.

Vitamin E

Supplementation of the equine diet with oil may bring with it an increased requirement for antioxidant provision, including vitamin E, because enhanced fat oxidation increases the production of peroxyl free radicals. This may in part be satisfied by the natural tocopherol content of the oil, which is dependent on its source and is related to its polyunsaturated fatty acid content.

The term vitamin E refers to a group of compounds known as tocopherols, with the most biologically active form being alpha-tocopherol. Vegetable oils are the richest dietary sources of natural vitamin E, a fat-soluble vitamin that functions as a membrane-bound antioxidant. Vitamin E traps lipid peroxyl free radicals produced from unsaturated fatty acids when oxidative stress arises. The orientation of vitamin E within cell membranes appears to be critical to its functionality. Vitamin E is an amphipathic molecule, a structure that incorporates hydrophobic (water-hating) and hydrophilic (water-loving) properties. This characteristic facilitates its orientation and retention within the lipid bilayer of cell membranes, probably giving it an ideal position for free-radical scavenging and thus protection of cell membranes.

The level and type of tocopherol in vegetable oil vary among different oil sources. Natural tocopherols largely act as an internal antioxidant to prevent oxidation of unsaturated fatty acids that make up the constituent triglyceride and hence prevent rancidity of the oil. The level of vitamin E in an oil appears to be related to its polyunsaturated fatty acid content, specifically the combined amounts of linoleic and alpha-linolenic fatty acids. Horses appear to absorb natural forms of vitamin E to a much greater extent than synthetic versions (Gansen et al., 1995). Additionally, when the absorption of different sources of vitamin E was compared in Thoroughbred yearlings, higher plasma concentrations were reported with the d-forms compared to equivalent amounts of the dl-form (Wooden et al., 1991).

Early studies in human subjects suggested that requirement for vitamin E increased with increasing dietary polyunsaturated fatty acid content (Wardlaw, 1999). Looking at both human and animal studies, the requirement for vitamin E was estimated to be 0.6 mg of alpha-tocopherol per gram of linoleic acid, which equates to an additional 36 mg of vitamin E per 100 g of vegetable oil added. For most animal species 3 mg of alpha-tocopherol is recommended for each 1 g of omega-3 polyunsaturated fatty acid (Vitec, 1987). For soya or corn oil, this would equate to 180 mg per 100 g of oil. However, both soya and corn oil have an endogenous tocopherol content of about 60 mg per 100g, leaving a net requirement for 120 mg per 100g of oil or 108 mg vitamin E per 100 ml of oil. Care should, however, be taken to ensure that vitamin E levels are adequate to take into account the shelf life of the product as endogenous tocopherol levels may be substantially reduced during storage without additional antioxidant support.

Table 2. Typical vitamin E content of fats and oils (mg/100 g oil). Total tocopherol is the sum of alpha-tocopherol and gamma-tocopherol (Dupont et al., 1990).

Oil or fat	*α-tocopherol*	*γ-tocopherol*	*Total*
Lard	1.20	0.70	1.90
Olive	7.94	trace	7.94
Sunflower	48.70	5.10	53.80
Rapeseed	25.82	30.01	55.83
Soybean	10.25	50.48	60.73
Corn	11.28	50.76	62.04

Horses fed a diet supplemented with 6.4% soya oil and containing current NRC recommended levels of vitamin E (80 IU/kg DM) showed no significant change in the ratio of alpha-tocopherol to total lipid (serum cholesterol and triglyceride) compared to an isoenergetic control diet (Siciliano and Wood, 1993). This may indicate that either the current requirements for vitamin E were high enough to cope with the level of addition of PUFA-containing oil or that the endogenous tocopherol content of the oil itself diminished the need for further supplementation. Likewise, McMeniman et al. (1992) reported no reduction in plasma or muscle vitamin E status in ponies fed a diet in which 10% of the total DE was provided in the form of corn oil. However, in the same study plasma thiobarbituric acid reactive substances (TBARS) and breath pentone, which are indicative of "oxidative stress," were increased during exercise, especially in those horses with a relatively low plasma vitamin E concentration.

Added vegetable oils and animal fats have previously been used in the commercial manufacture of horse feed. Additionally, ingredients such as linseed meal, soya, rice bran, peanuts, and sunflower meal have been utilized for their endogenous oil content. In the post BSE era, however, it is now the vegetable oils and oilseed products which largely prevail as raw materials. Supplementation of the equine diet with fat or oil offers many potential advantages, ranging from effects on behavior to those on performance. Oil is readily accepted by horses; however, care should be taken in introducing it into the diet and the level of supplementation should be increased gradually in order to avoid digestive problems. For performance effects, the adaptive response to fat supplementation is long-term and measured in weeks rather than days. Care should also be taken to provide an overall balance of protein as well as minerals and trace elements when integrating oil into the diet, as oil will not contribute to the provision of these latter nutrients.

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