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Chapter **2**

DIETARY FATS AND LIPID METABOLISM IN RELATION TO EQUINE HEALTH, PERFORMANCE AND DISEASE

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Summary

A review is given of the role of fats in equine nutrition. The issues addressed are palatability of fat-supplemented rations, fat digestibility, requirement of essential fatty acids and the impact of amount and type of dietary fat on plasma lipid metabolism. Applications of high-fat diets are discussed with regard to athletic performance, recurrent rhabdomyolysis, growth, and reduced intake of carbohydrate or protein.

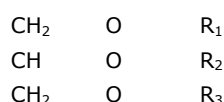
Introduction

Fat in the diet provides energy and essential fatty acids. Horses, especially when they are intensively exercised, may be fed high-fat diets not only to meet their energy requirements, but also to enhance athletic performance. It is well-known that the amount and type of dietary fat are important determinants of lipid metabolism. However, in horses, the relation between dietary fats and lipid metabolism has not been as extensively studied as in man and experimental animals. In this review, attention is given to the digestibility of fat, the requirement of essential fatty acids and the metabolic responses to high-fat diets or diets with different fat sources. In addition, practical information on the formulation and the use of high-fat diets is given.

Fats and fatty acids

Fats, also called lipids, are substances that are insoluble in water, but soluble in organic solvents such as ether and chloroform. The fat content of feedstuffs of either plant or animal origin or that of concentrates or whole rations is generally expressed as crude fat, i.e. the total amount of fat that can be extracted with a defined solvent. Based on their chemical structure, lipids are divided into triacylglycerols, phospholipids, glycolipids and steroids. Triacylglycerols are the major dietary fats and they constitute the most important energy reservoir of the body. In triacylglycerols a glycerol molecule is esterified with three fatty acids (acyl groups). In natural occurring triacylglycerols, the fatty acids usually have different chain length. Most of the fatty acids have an even number of carbon atoms. They contain a single carboxyl group and have an unbranched carbon chain which may be saturated or either mono- or poly-unsaturated. Figure 1 shows the general structure of a triacylglycerol and also the structures of the common fatty acids palmitic acid (C16:0), oleic acid (C18:1, n-9), linoleic acid (C18:2, n-6) and alpha-linolenic acid (C18:3, n-3). The shorthand notation of the fatty acids, as given in parentheses, indicates the number of carbon atoms, the number of double bonds behind the colon and the location of the first double bond on the carbon atom closest to the methyl group.

Triacylglycerol



Fatty acids

Palmitic acid	$\text{CH}_3(\text{CH}_2)_{14}\text{COOH}$
Oleic acid	$\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$
Linoleic acid	$\text{CH}_3(\text{CH}_2)_4(\text{CH}=\text{CHCH}_2)_2(\text{CH}_2)_6\text{COOH}$
Alpha-linolenic acid	$\text{CH}_3\text{CH}_2(\text{CH}=\text{CHCH}_2)_3(\text{CH}_2)_6\text{COOH}$

Figure 1

General structure of triacylglycerol and structures of palmitic acid, oleic acid, linoleic acid and alpha-linolenic acid.

Fats and fatty acids in feedstuffs

Table 1 shows the contents of crude fat and of selected fatty acids in common feedstuffs used in equine rations. Grass contains little fat, but has a high relative percentage of alpha-linolenic acid. Barley, oats, corn and rye have a high relative percentage of linoleic acid and linseed particularly has a high content of alpha-linolenic acid. Coconut oil is an exception in having the saturated lauric acid (C12:0) as its major fatty acid. Palm oil contains a relatively large proportion of long chain saturated fatty acids, especially palmitic acid, but also is rich in oleic acid.

Fat levels in equine rations

The amount and type of fat in horse rations is determined by the roughage:concentrate ratio and by the type of roughage and concentrate. In general, the fat content of horse diets is about 5% in the dry matter (Meyer, 1992, Van 't Klooster, 1999). Commercial concentrates typically contain 3 - 6 % crude fat in the dry matter. Muesli's may contain 9 - 10 % crude fat. For satisfactory pelleting performance, the amount of fat in concentrates is 2 - 3 %. However a level of up to 7 % may be achieved by spraying fat onto the pellets (Atkinson, 1980). Pellet firmness declines progressively with increasing fat addition.

Table 1
Contents of crude fat and that of selected fatty acids in common equine feedstuffs.

Feedstuff	Dry Matter (DM)	Crude fat (CF)	FA ¹ in CF %	C12:0	C16:0	C18:1 n-9	C18:2 n-6	C18:3 n-3
	g/kg prod.			g/kg dry matter				
Barley	870	17	70	-	3.1	1.8	7.7	0.8
Oats	885	49	90	-	9.5	17.4	19.4	1.0
Corn	864	38	90	0.08	4.8	11.1	21.8	0.4
Rey	863	16	70	-	2.3	1.9	7.1	0.9
Wheat	863	14	70	-	2.2	1.7	6.5	0.6
Linseed	910	351	95	-	25.7	66.0	58.6	197.9
Soybean meal, fat extracted	876	19	65	-	1.6	3.1	7.6	1.1
Wheat bran	869	35	70	-	5.4	4.2	16.1	1.4
Coconut expeller	914	82	75	32.3	6.1	4.7	1.3	-
Grass	150	5	50	-	0.4	0.1	0.3	1.5
Palm oil	1000	1000	100	1.0	435	366	91	2.0
Coconut oil	1000	1000	100	446	82	58	18	-
Soybean oil	1000	1000	100	-	103	228	510	68

¹ FA= fatty acids

New techniques make it possible to produce fat-rich feed. Abrasion-resistant pellets were reliably obtained from fat-rich mixtures when prior pressure conditioning, like expanding, was used (Heidenreich, 1997). According to Reinbek (1989) up to 20% fat can be added to mixtures when an expander is incorporated before pelleting.

Fat sources in concentrates are cereals, added linseed and vegetable oils like soybean oil and palm oil. For pelleting, palm oil, which has a relatively high melting point, is preferred above other vegetable oils. A disadvantage of feeding a diet with a high fat content is the limited tenability because unsaturated fatty acids oxidize rapidly. To prevent oxidation, antioxidants can be added to the diet, but it should be noted that after these compounds have been oxidized into in-active free radicals, the unsaturated fatty acids will still be oxidized (Meyer, 1992). The most commonly used anti-oxidant in horse concentrates is vitamin E. The requirement of vitamin E by horses may be increased when a high amount of unsaturated fat is added to the diet. However, adding 6.4% soybean oil to the total ration of 2-year old horses fed recommended amounts of vitamin E, did not

alter serum vitamin E per gram of total serum lipids, and thus did not appear to increase their vitamin needs (Lewis, 1995). It is possible that the requirement of vitamin E is raised with higher fat contents in rations, like in other species (Grant, 1961; Blaxter, 1962). It thus can be usefull to increase the anti-oxidant content of a high fat concentrate (> 8%), especially when poly-unsaturated fatty acids are used.

The fat content of the whole ration is related to the amount of hay or roughage. Table 2 gives examples of how the fat intake can be modulated. The daily rations shown provide an amount of energy required by a 600 kg horse with 1 hour of excercise each day. With a low-fat concentrate (3% fat) the proportion of the total net energy provided by fat (NE) is 10 % when feeding hay and concentrate in a 1:1 ratio on NE basis. Using a high-fat concentrate (8% fat) this proportion will be 25%. Dietary fat levels higher than 8 % in the dry matter can be achieved only when pure oils are added to the diet. It should be stressed that extra fat in the ration raises its energy density and that less dietary dry matter is required to satisfy the energy need of the horses. High-fat rations by definition are rations that are low in carbohydrates and/or protein when expressed as percentage of dietary energy.

Table 2
Examples of fat-rich rations

	<i>Concentrate :hay ratio on energy basis</i>		
	1:1	1:1	3:1
	Fat content of total ration (g/kg DM		
	30	80	80
<u>Ingredient</u>			
Hay, kg/d	7.3	7.3	4
Concentrate (3% crude fat/kg), kg/d	4.3	2.7	-
Muesli (8% crude fat/kg), kg/d	-	-	5
Vegetable oil, ml/d	-	500	180
Dry matter intake, kg/d	10.0	9.1	8.0
Vitamin E, mg/d ¹		± 700	± 700
Total NE, MJ/d	69	69	69
NE % of fat	10	25	25

¹ Amount of extra vitamin E depends on the contribution of the feedstuffs

NE = Net Energy

Palatability and preferences

Because of a decrease in palatability, more than 10-15% fat in the diet is not advisable under practical conditions. Under experimental conditions high-fat concentrates containing either soybean oil, palm oil or medium chain triacylglycerols were accepted for periods up to at least 3 months ([Hallebeek and Beynen, 2001a; 2002a; 2002b; 2002c](#)). The concentrates had fat levels of 12-18%, and fed in a 3:1 ratio of concentrate:hay so that whole-ration fat levels were 11-16 %. We have frequently observed that the time of feed intake was increased when horses were fed high-fat diets (12 %) when compared to low-fat diets (3 %). Likewise, Landes and Meyer (1998) saw an increase in time of feed intake by 58% when horses were fed high-fat diets containing 10% sunflower oil. Oxidation of unsaturated fatty acids and consequent rancidity makes the feed unpalatable. We have observed that when concentrates have a rancid odour, they may be rejected by horses.

[Holland et al \(1998\)](#) compared the acceptance of fats and lecithin containing diets by horses. In different feeding trials, 15% fat was included in concentrates. Horses could choose freely, twice daily for 20 minutes, from four adjacent feed compartments in a stall. During the feeding trials the diets were randomly rotated among compartments. The amount of each concentrate eaten was measured. The fats used, apart from corn oil, were three blends of vegetable and animal fats, three animal fats (hydrolyzed tallow, inedible tallow and fancy bleached tallow), and four vegetable fats (cottonseed oil, peanut oil, and safflower oil) and mixtures of corn- or soy oil with lecithin. In different trials, corn oil concentrate was the most palatable when offered together with other concentrates. If corn-oil rich concentrate was left out, the concentrate with a corn oil mixture, like one of the animal-vegetable oil blends or corn lecithin with corn oil, was preferred. The relative acceptance of each fat was calculated by comparison with the acceptability of corn oil for each trial (Figure 2). When compared to corn oil, peanut oil and safflower oil were moderately accepted and cottonseed oil and tallow were considered unpalatable by horses. Coconut oil and soybean oil (10%) when incorporated into horse feed were generally well accepted ([Pagan et al., 1993; Flothow, 1994](#)).

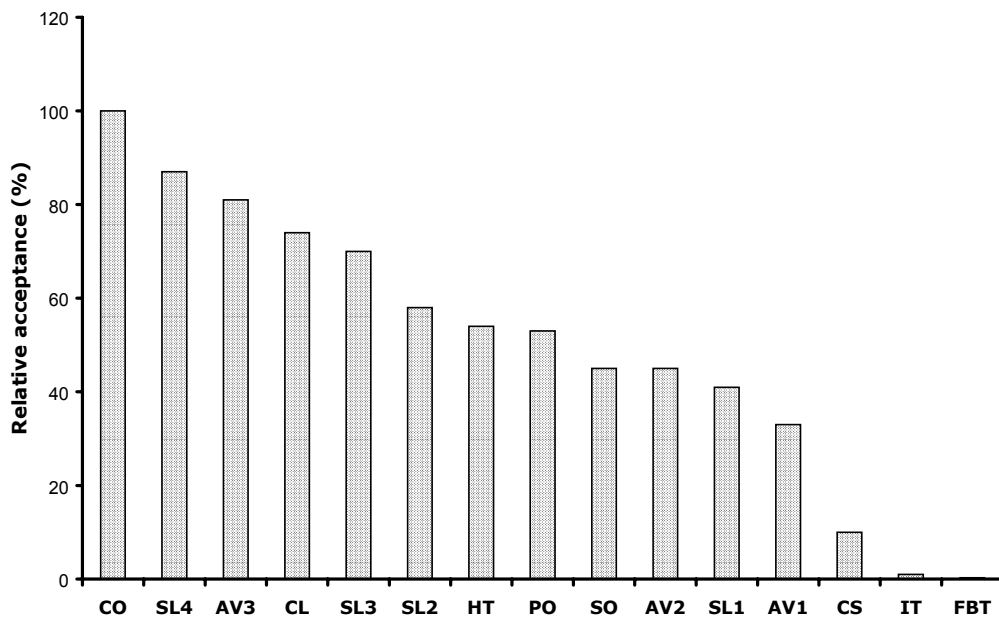


Figure 2

Relative acceptance of fats compared to corn oil.

Description of abbreviations: CO = corn oil, CS = cottonseed oil, PO = peanut oil, SO = safflower oil, CL = corn oil and corn lecithin, SL1 and SL4 = corn oil and soy lecithin (different manufacturer), SL2 = soy oil and soy lecithin, SL3 = corn oil, soy oil and soy lecithin, FBT = fancy bleached tallow, IT = Inedible tallow, HT = Hydrolyzed tallow flakes, AV1, AV2 and AV3 = animal/vegetable oil blends

Requirement of essential fatty acids

The requirement of dietary fat relates to that of essential fatty acids. Linoleic and alpha-linolenic acid are essential fatty acids for mammals and it can be assumed that they are so for the horse as well. The essential fatty acids are important structural components of biomembranes and serve as precursors for prostaglandines, thromboxanes and leukotrienes. The National Research Council (1989) advises to include at least 0.5 % linoleic acid in the dietary dry matter. Grazing and browsing horses are consuming a diet with oils derived from

grasses and leaves and have an intake of alpha-linolenic acid that is much greater than that in horses receiving a cereal-based diet that is typically rich in linoleic acid ([Frape, 1998](#)). On a grass ration with a dry matter intake of 2% of body weight, a 500-kg horse will consume approximately 3 g linoleic acid and 15 g alpha-linolenic acid per day. For a horse eating 7 kg hay and 3 kg of a cereal-based concentrate, the daily intakes of linoleic and alpha-linolenic acid are in the order of 70 and 4 g, respectively.

In non-ruminants including the horse, the intake of essential fatty acids determines the fatty acid composition of adipose tissue. Adipose tissue of grass-fed horses contains 17% of total fatty acids as alpha-linolenic acid and 4% as linoleic acid, as compared to 2% alpha-linolenic acid and 22% linoleic acid in the adipose tissue of horses fed oats ([Shorland et al., 1952](#)). Similar results in shoulder and perinephric fat of grass-fed horses, 10 % alpha-linolenic acid and 6 % linoleic acid, are published by [Bowland and Newell \(1974\)](#). A diet with as little fat as 0.04% in the dry matter and only 0.02% linolenic acid did not lead to clinical signs ([Grunwald, 1991](#)) such as scaly appearance of the skin which is seen in rats given diets extremely low in fat. Maybe the feeding period of seven months was too short to deplete the stores of essential fatty acids in tissues of the horses. Likewise, no deficiencies occurred when a diet with 10% of coconut oil was fed to horses for 16 months ([Harris et al., 1999](#)). The horses were fed an amount of concentrates (1.5 - 3 kg/d) fortified with either soybean oil or coconut oil. For a period of 10 months, 12% of the energy intake came from either coconut or soybean oil, this level being increased to 20% for another 6 months. Coconut oil is poor in linoleic acid, but the high inclusion level plus the intake of an additional 3 kg sweet feed per day led to a linoleic acid level of 1% in the total dietary dry matter, which is more than the requirement of linoleic acid for horses. Thus, in that trial ([Harris et al., 1999](#)), no fatty acid deficiency would be expected.

Above the requirement levels of essential fatty acids, there may be beneficial effects. Linoleic acid is a precursor of arachidonic acid (C20:4 n-6), which is used for the synthesis of eicosanoids such as thromboxane A₂ and prostacyclin, both affecting the pathogenesis of endotoxemia ([Bottoms et al., 1982](#), [Templeton et al., 1985](#)). High intakes of alpha-linolenic acid change arachidonic acid metabolism. Conversion of alpha-linolenic acid yields eicosapentaenoic (EPA) and docosahexaenoic acids (DHA) and inhibits the conversion of linoleic acid into arachidonic acid through competition for the same enzymes. In humans and laboratory animals, it has been found that the reduction of thromboxane A₂ synthesis by consuming a diet rich in n-3 fatty acids is beneficial during endotoxemia ([Sanders and Roshanai, 1983](#); [Magrum](#)

and Johnston, 1983; Marshall and Johnston, 1985; Van Dias et al., 1982). The in-vitro, endotoxin-induced thromboxane A₂ and prostacyclin production by peritoneal macrophages was reduced when donor horses were fed a diet containing 8% linseed oil as compared to a control diet without linseed oil (Morris et al., 1989). Also the release by equine macrophages of tumor necrosis factor, an important mediator of endotoxin-induced morbidity and mortality, in response to endotoxin administration to horses was reduced when their diet was rich in linseed oil (Morris et al., 1991). The in-vivo responses of horses to endotoxin infused into the jugular vein resulted in an inflammatory response, but there was no diet effect. Horses fed the linseed oil ration were found to have improved anticoagulant properties (Henry et al., 1991). The dietary concentrations of linoleic and alpha-linolenic acid were estimated to be 2.9 and 0.4 g/kg DM, respectively, for the control ration and 25 and 5.5 g, respectively, for the linseed-ration. Before the experiments (Morris et al., 1989; Morris et al., 1991; Henry et al., 1991), the horses were fed grass hay (2% DM of the body weight per day), followed by 8 weeks of complete, pelleted rations. The test diet was formulated by adding 8% linseed oil to the control diet so that the two diets differed in many respects. Thus, the data obtained cannot be unequivocally interpreted as effects of different fatty acid intake.

Digestion and absorption

Fat digestion involves hydrolyses of dietary triacylglycerols into fatty acids and mono-acylglycerols, which together with bile acids, cholesterol and phospholipids, form micelles. The micelles diffuse through the small intestinal contents and the unstirred water layer of the villi and their constituents are taken up by the enterocytes. In the epithelial cells of the small intestine, triacylglycerols, phospholipids, cholesterol esters and apoproteins are combined to form chylomicrons. The chylomicrons (diameter > 75 nm) are released into the lymphatic system which drains into the main circulation. Attempts to isolate chylomicrons from adult ponies following an oral fat load have been unsuccessful as the animals showed no evidence of post-prandial lipaemia (Watson, 1991). None of the authors that examined plasma from non-fasted horses using electrophoresis (Campbell, 1963; Robie et al., 1975; Leat et al., 1979) or density gradient ultracentrifugation (Terpstra et al., 1982; Hollanders et al., 1986; Le Goff et al., 1987) mention a chylomicron fraction. Marchello (2000) and Kurzt (1991) mention a change in the lipid content of lipoproteins due to fat supplementation, but only trace amounts of chylomicrons were present in the plasma of horses on a diet of alfalfa and corn or alfalfa and corn oil. In horses fed high-fat diets either rich in MCT or soybean oil we did not find a postprandial

increase in plasma triacylglycerols in plasma taken 4 hours after feed intake (Table 3).

Table 3.

Plasma triacylglycerols (TAG) before (t=0) and 4 hours (t=4) after feed intake in horses fed either a diet with MCT or soybean oil.

	% of NE intake	TAG, mmol/l	
		t=0	t=4
MCT	± 25	0.42 ± 0.09	0.38 ± 0.08
Soybean oil	± 25	0.17 ± 0.03	0.16 ± 0.03

Values are mean ± SE, n = 6
(Hallebeek and Beynen, 2002b)

Lecithin (5.6%), cholesterol (4.4%), and conjugated bile salts (90%) are the major lipid constituents of equine bile (Engelking et al., 1989), which is secreted into canaliculi and directly passes into the duodenum as equine do not possess a gallbladder. Pony bile is found to be supersaturated with cholesterol, because of its low bile salt content (Engelking et al., 1989). The pool size of total bile acids in ponies is small, but the high rate of enterohepatic cycling probably enables ponies to maintain intestinal bile acid concentrations needed for lipid digestion and absorption. Fat feeding stimulates the secretion of bile (Kolb and Guntler, 1971; Meyer et al., 1997). However, the faecal excretion of bile acids was not enhanced after feeding high fat ration to ponies (Jansen et al., 2001). Assuming that there is indeed little absorption of bile acids in the large intestine (Swinney et al., 1995) this implicates that the extra secretion of bile is reabsorbed further down the small intestine.

Standard horse rations are low in fat (2-5% in the dry matter), but horses are capable to efficiently digest fat in diets with fat levels as high as 20% fat (Potter et al., 1992). Fat source does not have a big influence on the digestibility (Table 4). Preileal digestibility of coconut fat and soybean oil was measured in ponies with a permanent fistula at the end of the jejunum (Meyer et al., 1997). After fat supplementation (1 or 2 g fat/kg body weight per day), preileal fat digestibility increased from ± 75% towards ± 85%, without a difference between the fat sources. The apparent digestibility on low fat diets is much influenced by metabolic or endogenous fat. Endogenous fat is considered to be constant. On high fat diets the apparent digestibility is relatively less influenced by metabolic fat. The differences of the true digestibilities between

high- and low-fat diets can be much smaller than the apparent digestibilities. Apparent digestibility increases with the amount of fat ingested ([Hughes et al., 1995](#); [Jansen et al., 2001](#); [Julen et al., 1995](#); [Kane and Baker, 1977](#); [Kane et al., 1979](#); [McCann et al., 1987](#); [Meyers et al., 1987](#); [Rich et al., 1981](#); [Scott et al., 1987](#); [Swinney et al., 1995](#); [Webb et al., 1987](#)).

Table 4.
Apparent digestibility of different dietary fats.

<i>Fat source</i>	<i>Numbers of experiments</i>	<i>Fat intake g/kg body weight/ day</i>	<i>Apparent digestibility %</i>
Corn oil	8	0.8 - 2.5	83 (70 - 91)
Soybean oil	8	0.6 - 1.5	74 (61 - 85)
Peanut oil	2	1.0 - 2.5	89 (83 - 89)
Animal fat	9	0.6 - 2.5	74 (56 - 87)

According to [Bowman et al., 1977](#); [Kane et al., 1979](#); [Rich et al., 1981](#); [Snyder et al., 1981](#); [Coenen 1986](#); [Davidson et al., 1987](#); [McCann et al., 1987](#); [Meyers et al., 1989](#); [Eilmans 1991](#); [Hollands and Cuddeford, 1992](#); [Holland et al., 1995](#)

Feeding a high-fat ration (8%) to horses showed no changes in the activity of pancreatic lipase when compared to a low-fat ration ([Landes and Meyer, 1998](#)). It appears that horses digest fat rather efficiently when fat is fed at 5-15% of the diet, however the upper limit of fat digestion in the equine small intestine has yet to be determined. According to [Meyer and Sallmann \(1996\)](#) disturbances of microbial flora in the large intestine are to be expected when horses are fed more than 75-100 g fat/100 kg bodyweight per meal. [Jansen \(2001\)](#) determined in vitro gas production of isolated intestinal contents of ponies fed either a low- or a high-fat (2% versus 9% in dry matter) after incubation with various substrates. It was concluded that fat feeding in ponies inhibits microbial activity in the caecum.

Fat intake and digestibility of macronutrients other than fat

When going through literature, there is controversy about the influence of high fat intakes on apparent crude fiber digestibility in horses. Studies on the influence of high-fat intakes on total tract digestibility of crude fibre in horses have yielded conflicting results. Several researchers reported that the addition of fat to the diet did not affect the apparent digestibility of cell wall contents ([McCann et al., 1987](#); [Rich et al., 1981](#)), neutral detergent fiber ([Davidson et](#)

al., 1987; Kane and Baker, 1977; Kane et al., 1979; McCann, 1987; Meyers et al., 1987; Rich et al., 1981) or acid detergent fiber (McCann et al., 1987).

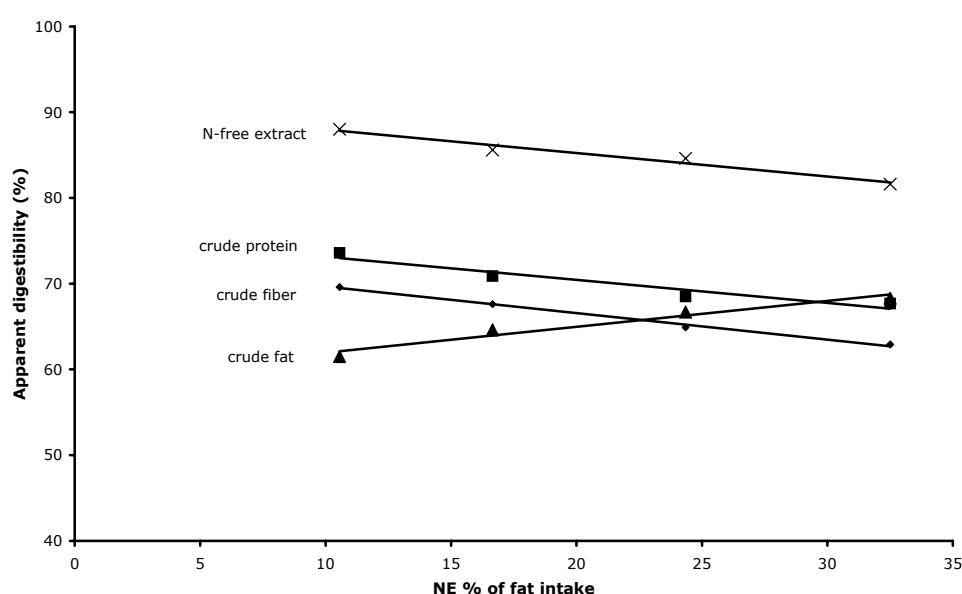


Figure 3

Apparent digestibilities of macronutrients (crude protein, crude fat, crude fiber and N-free extract) when dietary fat content of the ration increases (3.0, 5.0, 7.7 and 10.8 % in dry matter) in horses.

Others reported an increase in apparent digestibility of either neutral-detergent fibre (Hughes et al., 1995; Julen et al., 1995; Scott et al., 1987; Webb et al., 1987) or acid detergent fibre (Rich et al., 1981) after the feeding of fat-supplemented diets. In contrast, it has been reported that administration of a high-fat diet lowered the digestibility of neutral-detergent fiber (Rich et al., 1981; Worth et al., 1987). The conflicting results probably relate to the fact that the low-fat and high-fat diets used in the various studies differed with respect to multiple components, including the amount of crude fiber. A change in fibre intake by itself may affect the percentage of apparent fibre digestibility, as

digesta passage rate may be altered and the microflora will be exposed to a change in the amount of fermentable substrates. In order to maintain energy balance, the intake of extra fat must be associated with less energy intake in the form of other nutrients. In some studies fat was provided as a supplement ([Kane and Baker, 1977](#); [Rich et al., 1981](#); [Snyder et al., 1981](#)) so that the intake of extra fat coincided with lower intakes of carbohydrates, crude fibre and crude protein. In other studies, up to 162.5 g fat/kg of diet was isoenergetically substituted for hay ([Hughes et al., 1995](#); [Julen et al., 1995](#); [Scott et al., 1987](#); [Swinney et al., 1995](#)) or one ([Davidson et al., 1987](#)) or more ([McCann et al., 1987](#); [Meyers et al., 1987](#); [Webb et al., 1987](#)) other feed ingredients with complex compositions, such as grains.

[Jansen et al. \(2001\)](#) substituted soybean oil isoenergetically with non-structural carbohydrates. Figure 3 shows the effect of increasing dietary fat levels on the apparent digestibility of the macronutrients. As mentioned above, increasing fat intakes are associated with increased apparent digestibilities of fat. The intake of extra fat also changed the apparent total tract digestibility of macronutrients other than fat in a statistically significant, dose-dependent fashion. An increase in dietary fat concentration by 10 g/kg dry matter was associated with a decrease in crude fibre digestion by 0.9 percentage units, a decrease in protein digestibility of 0.7 percentage units and an increase in fat digestibility by 0.9 percentage units. The effects have been repeated in further experiments in which non-structural carbohydrates were isoenergetically replaced by soybean oil ([Jansen, 2001](#)). The observed interaction between fat content of the diet and macronutrient utilization could have consequences for practical horse feeding in that calculating the energy content of high-fat diets on the basis of feedstuffs tables will lead to over- or underestimating the amount of energy provided by the ingredients of the diets. However, the impact is negligible. It can be calculated that, as a result of changes in macronutrient digestibilities, with an increase in fat intake by 25 g/ kg dry matter the net energy value of the ration will be about 4% lower than that expected.

Lipid metabolism

Lipoprotein metabolism

Triacylglycerols are transported in plasma with chylomicrons and very low- density lipoproteins (VLDL). In the fed state, chylomicrons are secreted by the small intestine into the lymph and via the ductus thoracicus they reach the circulation. Long-chain fatty acids in the form of triacylglycerols have to be

released by pancreatic lipase and incorporated into micelles as described above. Medium-chain fatty acids from the diet are taken up by the mucosa cells as such and carried via the portal system to the liver. VLDLs are secreted by the liver and they contain either de-novo synthesized fatty acids or fatty acids taken up from the blood. Through the action of lipoprotein lipase (LPL), chylomicrons and VLDL are rid off their esterified fatty acids which are taken up by tissues. In case of energy shortage, e.g. during exercise or fasting, fatty acids are released from the adipose tissue for utilization by muscle. The liver takes up fatty acids and esterifies them into triacylglycerols for assembly into VLDL which in turn deliver the constituent fatty acids to muscle tissue with a high activity of LPL (Barton et al., 1998; Johnston, 1968). LPL is bound to capillary endothelial cells. In the fed state, the high activity of LPL in adipose tissue ensures that triacylglycerol-fatty acids are directed towards this tissue, whereas during energy shortage the fatty acids will be oxidized by muscle (Newsholme and Start, 1973). An enzyme with the typical characteristics of LPL has been isolated from post-heparin plasma in horses. A dose of 70 IU heparin per kg body weight is required for maximum recovery of LPL, its activity peaking at 5 min after the injection of heparin (Watson et al., 1991; Watson and Packard, 1993).

Equine plasma contains lipoproteins that can be classified as VLDL, low-density (LDL) and high-density lipoproteins (HDL). VLDL is converted into LDL during the action of LPL. HDL accounts for approximately 60% of plasma lipoprotein mass. HDL play an important role in reverse cholesterol transport, i.e. the transport of cholesterol from peripheral tissues to the liver (Swenson, 1992). Unesterified cholesterol from peripheral tissues can be taken up by HDL and be esterified by the enzyme lecithin:cholesterol acyltransferase (LCAT). Humans and most animal species have plasma cholesterol ester transfer protein (CETP) activity (Ha and Barter, 1979) so that HDL cholesterol esters generated by LCAT can be transferred to VLDL and LDL and be cleared from the plasma by the liver. Cholesterol in LDL taken up by the liver can be secreted into bile as such or in the form of bile acids and then leave the body with faeces. Animal species such as the rat, the pig (Ha and Barter, 1979) and the horse (Watson et al., 1993) lack plasma CETP activity. Geelen et al. (2001a) have shown that in the pony there is cholesterol ester transfer from HDL to LDL. Thus, it appears that ponies have an alternative, CETP-independent pathway for the transfer of HDL cholesterol esters to the lower density lipoproteins so that reverse cholesterol transport can take place. Feeding extra fat to ponies lowered the transfer rate which was associated with an increase in HDL cholesterol esters (Geelen et al., 2001a). The horse appears unique in that its HDL is composed of

a single population of small particles with high density that have characteristics similar to those of human HDL₃ ([Watson et al, 1991](#)).

Hyperlipoproteinaemia

Hyperlipaemia, or called hyperlipoproteinaemia, is a disorder of lipid metabolism peculiar to the pony breeds and donkeys. The excess of triacylglycerols and cholesterol is mainly located in VLDL. Hyperlipaemia arises from the mobilization of fatty acids from adipose tissue in response to a negative energy balance. A greater flux of fatty acids to the liver increases the synthesis of triacylglycerols and the production of VLDL. VLDLs in ponies with hyperlipaemia are enriched in triacylglycerol and depleted of protein ([Watson et al., 1992](#)). LPL and hepatic lipase activity are increased in ponies with hyperlipaemia ([Watson et al., 1992](#)). Hyperlipaemia is caused by anorexia, but is associated with stress, pregnancy, lactation and obesity. Treatment of ponies with hyperlipaemia usually consists of intravenous administration of heparin, insulin, and glucose (Beynen and Wensing, 1985; Naylor, 1982). The aim is to promote the degradation of the accumulated VLDL particles by heparin-mediated stimulation of LPL. At the same time, lipolysis in adipose tissue is depressed by the administered insulin. Glucose is given to prevent insulin-induced hypoglycaemia. The treatment rapidly lowers plasma triacylglycerol concentrations in hyperlipaemic ponies, but in spite of this many patients do not start eating again and die (Beynen and Wensing, 1985 ; [Gay et al., 1978](#)).

Nutritional support of hyperlipaemic patients can reverse the negative energy balance, increase serum glucose concentrations, promote endogenous insulin release, and inhibit mobilization of fatty acids from peripheral adipose tissue ([Rush Moore et al., 1994](#)). Moreover, nutritional support prevents the further tissue breakdown. The total amount of nutrients that can be force-fed with gruels prepared from dried grass and mixed feed is often less than that required by the patient (Naylor and Freeman, 1987). Hallebeek and Beynen (2001b) formulated a fat-free liquid diet and used this in combination with regular therapy for hyperlipaemic ponies. Elevated plasma triacylglycerol levels decreased within several days, but this was not always accompanied by spontaneous eating so that nutritional support had to be continued. The duration of nutritional supplementation in the patients that recovered ranged from 3 to 17 days.

Influence of amount of dietary fat

The feeding of extra fat generally is associated with a decrease in the intake of nonstructural carbohydrates. The effects on lipoprotein metabolism

seen after giving a high-fat diet to horses and ponies are caused by the combination of consuming more fat and less carbohydrates. The feeding of high-fat diets causes pronounced changes in equine lipid metabolism. Fat feeding in the form of soybean oil lowered the concentration of plasma triacylglycerols and raised heparin-released LPL activity, pointing at an increased flux of triacylglycerol-fatty acids (Orme et al., 1997; Geelen et al., 1999). The fat-induced metabolic adaptations are comparable to those described as induced by training (McMiken, 1983; Hodgson et al., 1986). The relationship between fat intake and LPL activity is linear (Figure 4). An increase in fat intake by 1 g/kg dry matter was associated with an increase in LPL activity by 0.98 μmol free fatty acids released per ml plasma per hour (Geelen et al., 2001b).

The fat-induced lowering of plasma triacylglycerols may be secondary to the increase in LPL activity and thus to an increased removal of lipoprotein particles. However, a diminished production rate of triacylglycerols could also be involved. as well. Geelen et al. (2001c) have shown that the fat-induced reduction of plasma triacylglycerols in ponies was associated by a decrease in de novo fatty acid synthesis as evidenced by decreased activities of acetyl-CoA carboxylase and fatty acid synthase in liver. The rates of hepatic de novo fatty acid synthesis is directly related with the rate of VLDL secretion (Beynen et al., 1981). Furthermore, fat feeding in ponies rendered hepatic carnitine palmitoyltransferase-I less sensitive to inhibition by malonyl-CoA, which could result in an increased fatty acid oxidation rate (Geelen et al., 2001c). In addition, dietary fat supplementation caused enhancement of carnitine palmitoyltransferase-I and citrate synthase activity in the masseter muscle which is highly oxidative (Geelen et al., 2001c).

In the steady state, the rate of input of triacylglycerols into plasma must equal the output. When assuming that the output is determined by LPL activity, then fat-feeding raises triacylglycerol output and thus should also lead to more input of plasma triacylglycerols. Triacylglycerol production can be measured indirectly by using a non-ionic detergent such as Triton WR 1339 (oxyethylated t-octyl-phenol polymethylene polymer). The Triton-induced block of lipoprotein lipase causes triacylglycerol accumulation in plasma which has been used as an index of triacylglycerol secretion rates in rodents (Borensztajn et al., 1976; Nicolosi et al., 1976). When horses were fed a high-fat diet, they had significantly less triacylglycerol production rates than when they were fed a low-fat diet (Geelen et al., 2002). The unexpected result was explained by Triton administration being less effective when the horses were given a high-fat diet because their post-heparin LPL activity was increased. The amount of Triton used was too low to completely block LPL activity, but higher dosages were

avoided as they can be toxic ([Scanu et al., 1961](#); [Sato et al., 1997](#)). Post-heparin LPL activity measured 5 hours after Triton administration was still 50-60% of the baseline activity ([Geelen et al., 2002](#)).

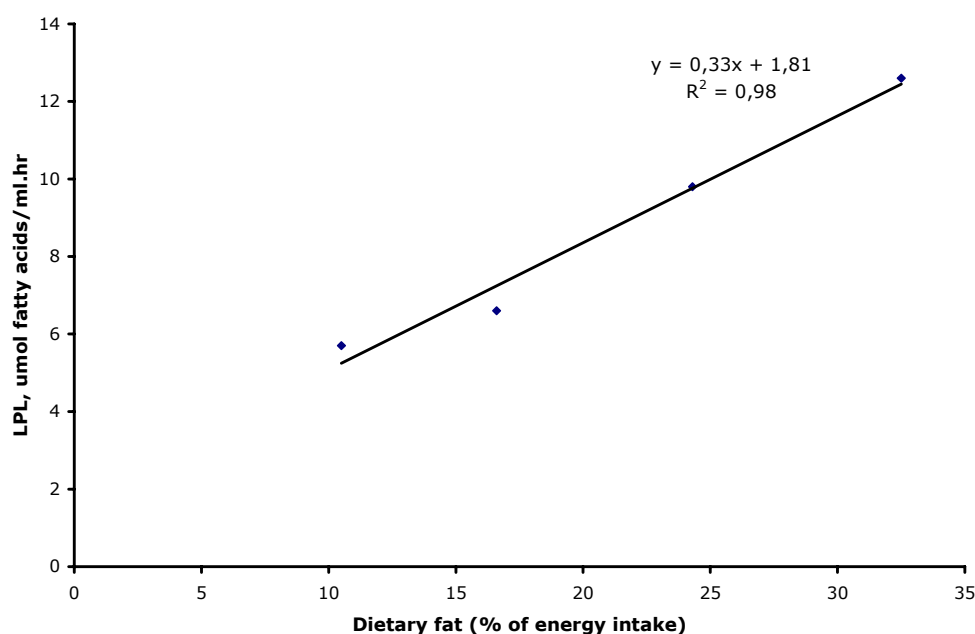


Figure 4

Heparin-released LPL activity in plasma prepared from blood collected 5 min after heparin injection (70 IU/kg body weight) in horses fed different amounts of fat.

Fat feeding is associated with lower post-prandial plasma insulin concentrations in the horse ([Pagan et al., 1995](#), [Stull et al., 1987](#)). Possibly, on a high-fat diet the insulin-mediated down-regulation of muscle LPL activity ([Kiens and Lithell, 1989](#)) is diminished. The fat-induced increase in heparin-released LPL in the fasting state could reflect LPL from muscle ([Mackie et al., 1980](#); [Terjung et al., 1982](#)). The feeding of extra fat to horses did not increase fasting plasma FFA concentrations ([Orme et al., 1997](#); [Geelen et al., 2001c](#)). Thus, horses fed a high-fat diet may not have enhanced mobilisation of fatty acids from adipose tissue. However, the noradrenaline-induced stimulation of lipolysis in adipose tissue biopsies tended to be higher when the donor horses had been

fed a fat-rich diet. When fat feeding inhibits de-novo fatty acid synthesis, but stimulates the turnover of triacylglycerol-fatty acids, fatty acid turnover and thus fatty acid mobilization should be increased which might be associated with an unaltered concentration of free fatty acids.

Influence of type of fat

There are limited studies on the influence of different dietary fats on lipid metabolism in horses. It is well known that in man the replacement of dietary saturated fatty acids by either mono-or polyunsaturated fatty acids has a cholesterol lowering effect. The mechanism underlying the hypocholesterolaemic effect of polyunsaturated fatty acids still remains obscure (Beynen and Katan, 1985). When isoenergetic diets high in polyunsaturated instead of saturated fat are fed to healthy men, serum triacylglycerol also drop (Beynen and Katan, 1989). The fall is not associated with a change in post-heparin lipolytic activity (Chait et al, 1974). Hallebeek and Beynen (2002a) showed that in horses there was no triacylglycerol lowering effect of dietary polyunsaturated fatty acids in the form of soybean oil when compared to saturated fatty acids fed as palm oil. The activity of heparin-released lipoprotein lipase was not influenced by the type of dietary fat. The feeding of soybean oil versus palm oil did not affect plasma cholesterol (Hallebeek and Beynen, 2002a). Harris et al. (1999) reported a significant increase in the plasma levels of cholesterol and triacylglycerols when Thoroughbred horses were fed a concentrate supplemented with 15% coconut oil when compared to soybean oil. Pagan et al. (1993) also fed horses a fat-supplemented concentrate with either 10% coconut oil or soybean oil, but the plasma levels of triacylglycerols were not significantly different between treatment groups.

Diets containing MCT produced marked changes in lipid metabolism in horses. Medium chain fatty acids generally refer (C8:0) and (C10:0). These fatty acids are absorbed as free fatty acids and transported as such to the liver via the portal vein. In the liver they undergo β -oxidation in the mitochondrial matrix, yielding acetyl-CoA (Bach and Babayan, 1982). The acetyl-CoA produced can enter the Krebs cycle or ketogenesis within the mitochondria, or its C₂ units can be transported to the cytosol and be used for de-novo synthesis of fatty acids. The ketogenic effect of MCT feeding in horses is indicated by a rise in serum β -hydroxybutyrate (Hallebeek and Beynen, 2002b; 2002c; Zeyner and Lengwenat, 1997) but acetyl-CoA may also be used for de-novo synthesis of fatty acids. Horses fed MCT-rich diets show a marked increase in plasma triacylglycerol levels, irrespective of MCT was substituted for an isoenergetic amount of either soybean oil, (Table 3), glucose plus starch or cellulose

(Hallebeek and Beynen, 2001a; 2002b; 2002c; Zeyner and Lengwenat, 1997). The increase in plasma triacylglycerols in rats seen after MCT feeding instead of corn oil feeding is explained by the observed MCT-induced stimulation of hepatic de-novo fatty acid synthesis (Geelen et al., 1995). There is evidence that in horses the consumption of MCT stimulates the production of plasma triacylglycerols (Hallebeek and Beynen, 2001a; 2002b; 2002c). When compared to a diet rich in poly unsaturated fatty acids the activity of LPL was either left unchanged or lowered by MCT feeding in horses (Hallebeek and Beynen, 2001a; 2002b; 2002c).

Free fatty acids and ketone bodies

Triacylglycerols, free fatty acids and ketone bodies are three forms of lipid fuels in the blood for use by various tissues. The free fatty acids arise from hydrolysis of triacylglycerol within adipose tissue and are released into the bloodstream, this process being enhanced during starvation. Food deprivation raises the plasma concentration of free fatty acids in horses, whereas after 96 hours of fasting there is only a small increase in β -hydroxybutyrate (Fig. 5). In the horse, ketosis might not be a feature of fasting due to the ability of the liver to maintain glycogenolysis and/or gluconeogenesis and hence the supply of carbohydrate for the citric acid cycle. Likewise, in ponies with anorexia-induced hyperlipaemia there is no increase in plasma ketone bodies (Naylor et al., 1980; Rose and Sampson, 1982). The suggestion of adequate gluconeogenesis during food deprivation is supported by the maintenance of glucose concentrations (Fig. 5) albeit at relatively low values similar to those in ruminants (Ford and Evans, 1982). During fasting, insulin concentrations do not fall (Fig.5), which may relate to the rather constant glucose concentrations.

Fat-supplemented diets for horses

Performance

The increased activity of post-heparin lipoprotein lipase activity and decreased plasma level of triacylglycerol concentrations in horses fed a high-fat diet points at a rise in the flux of fatty acids in the form of triacylglycerols. It could be suggested that preferential and more use of fatty acids for generation of energy utilization has advantageous effects on other aspects of intermediary metabolism.

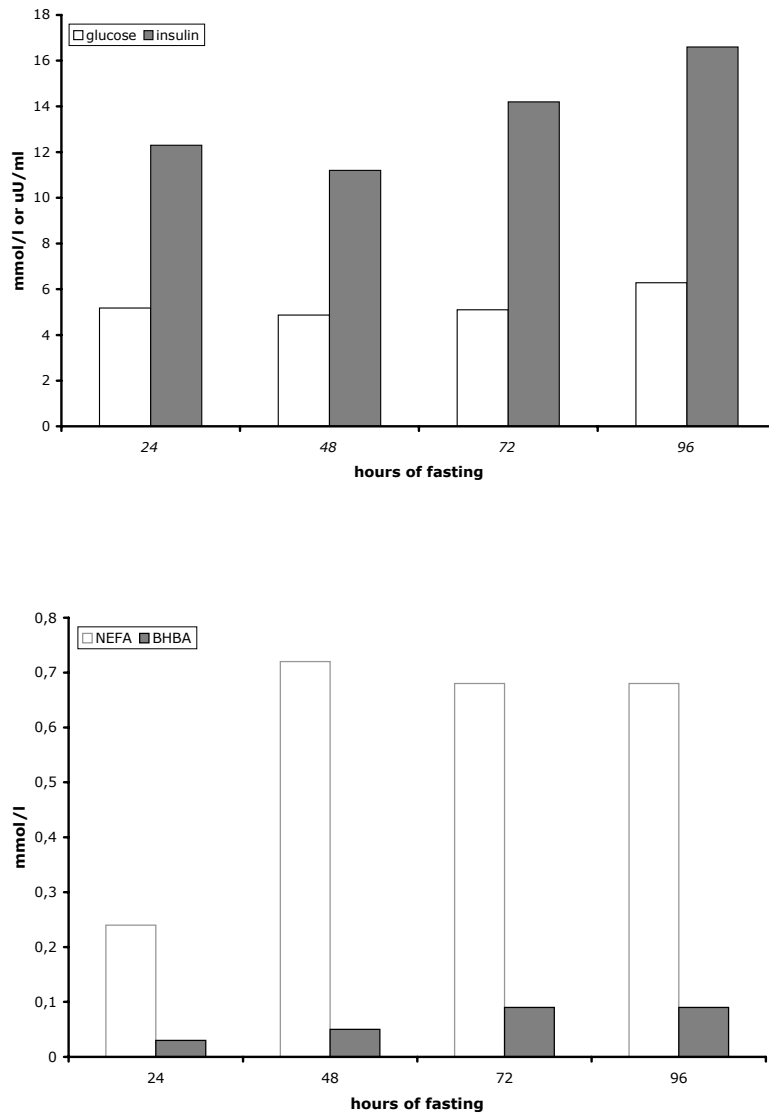


Figure 5
Changes in plasma concentrations of non-esterified fatty acids (NEFA),
betahydroxybutyrate (BHBA), glucose and insulin in horses during food deprivation from
24 to 96 hours. (Rose and Sampson, 1982)

Enhanced oxidation of fatty acids during aerobic exercise might lead to a sparing of glucose and thus to less lactate accumulation which in turn could extend the onset of fatigue (Frape, 1994). In addition, enhanced fatty acid oxidation could spare glycogen, which could increase the potential of sprinting (Oldham et al., 1990; Scott et al., 1992; Hughes et al., 1995).

In non-trained ponies there was a decrease in muscle glycogen in various muscle types when a high-fat diet was fed (Geelen et al., 2001c). This outcome is in line with results of Pagan et al. (1987), but most reports describe an increase in resting muscle glycogen following supplementation of the diet with fat (Meyers et al., 1989; Oldham et al., 1990; Harkins et al., 1992; Jones et al., 1992; Scott et al., 1992; Julen et al., 1995; Hughes et al., 1995). In the studies showing a fat-induced increase in glycogen, the horses were intensively trained during the period of fat feeding. The decrease in muscle glycogen found by Pagan et al. (1987) was in horses doing a long, slow work test. It would appear that a glycogen-sparing effect of high-fat diets is seen only with simultaneous exercise. The mobilization of glycogen during anaerobic exercise was increased in fat-supplemented horses (Table 6) but, in horses performing a 1600-m race, the rate of glycogen utilization was not increased (Harkins et al., 1992).

In sprint-trained horses fed a diet with 10% corn oil instead of a diet without added fat, there was increased lactate accumulation during repeated sprints (Ferrante et al., 1993; Taylor et al., 1995; Kronfeld et al., 1994). No effect of fat feeding on blood lactate concentrations was seen when horses completed either a simulated cutting test (Julen et al., 1995), a 1600-m race (Harkins et al., 1992) or repeated sprints (Scott et al., 1992). When performing a standardised sub-maximal exercise test, horses fed a high-fat (11.8% in the dietary dry matter) instead of a low-fat (1.5% fat) diet showed lower blood lactate accumulation (Sloet van Oldruitenborgh-Oosterbaan, 2002). Clearly, the anticipated decrease in lactate accumulation in exercising horses fed a high-fat diet was not observed in most experiments.

The discrepancies in the outcome of the above-mentioned studies could not relate to the type of dietary fat used. Pagan et al. (1993) fed to horses hay and a concentrate without added fat or a concentrate containing either 10% soybean oil, coconut oil or a 50:50 mixture of the two oils. The velocity achieved at a heart rate of 200 bpm (V200) was higher when the diet with soybean oil diet was fed instead of the diets with coconut oil or the mixed oil. Plasma free fatty acids concentrations were highest in horses fed the diet containing coconut oil. The velocity at which blood lactate reached 4 mmol/l was lowest in the horses fed the low-fat control diet. Plasma lactate after an 8 minute gallop was

Table 6
Crude fat intake and changes in muscle glycogen in horses and ponies.

Reference	Fat source	Exercise test ¹	Crude fat in total dry matter (%)		Significant change in muscle glycogen in high-fat diet versus control diet	
			Control	High-fat	Resting	Disappearance after exercise
Pagan et al., 1987	soybean oil	LSD	3	12	↓	↑
Meyers et al., 1989	animal fat	SET	4.4	8.2		
			4.4	12.1	↑	
Oldham et al., 1990	animal fat	ET	4	8.4	↑	↑
Essen-Gustavsson et al., 1991	vegetable oil	SEF	2.8	6.9	=	↑
Harkins et al., 1992	corn oil	#	2.5	8.7	↑	↓
Jones et al., 1992	?	SET	4.3	11.8	↑	↑
Scott et al., 1992	animal fat	*	4.3	10.9	↑	↑
Julen et al., 1995	animal fat	SET	4.2	11.1	↑	↑
Hughes et al., 1995	animal fat	*	4.9	12.8	↑	↑
Geelen et al., 2001c	soybean oil	-	1.5	11.8	↓	

¹ LSD, SET, ET, SEF are all different standardised exercise tests; # race 1600 m; * sprint

lowest in horses supplemented with coconut oil. The authors concluded that the medium chain fatty acids in coconut oil are oxidized quickly and thus spare glucose (Pagan et al, 1993). Ingested MCT may not deliver fatty acids to the exercising muscle for oxidation (Berning, 1996), but are preferentially oxidized in the liver so that the ketone bodies formed may be used for oxidation in muscle. However, most published studies do not support the use of MCTs to spare muscle glycogen and thus improve exercise performance (Berning, 1996).

Recurrent rhabdomyolysis

Exertional rhabdomyolysis represents a number of muscle diseases with common clinical signs. The diagnosis is made on the basis of a history of muscle cramping and stiffness following exercise and moderate to marked elevations in serum myoglobin, creatine kinase, lactate dehydrogenase and aspartate aminotransferase. Certain horses have recurrent episodes of rhabdomyolysis (RER). Two specific causes have been identified, including a disorder of muscle contractility and a disorder of carbohydrate storage and utilization, the so-called polysaccharide storage myopathy (PSSM).

Management of horses affected with RER is based on decreasing carbohydrate ingestion and thus feeding a high-fat diet combined with regular exercise (Beech, 97). In a controlled study of MacLeay et al. (1999) the effects of a low carbohydrate-, a high-carbohydrate- and a high-fat diet were tested in Thoroughbred horses with RER. The carbohydrate diets were composed of molasse-supplemented grains, 2.5 kg or 4.6 kg per day. The high-carbohydrate diet provided 135% more energy than the other two diets. The high-fat diet was composed of 2.3 kg rice-bran and contained 9% fat on a dry matter basis. Forage was provided with alfalfa/timothy hay cubes. The horses were rotated between the three diets for periods of three weeks and exercised. At the end of the feeding periods, blood and muscle samples were taken before and after a standardised exercise test. The results showed very little effect of the three diets on the metabolic responses to exercise. Serum creatine kinase (CK) activity showed no significant diet-induced changes. There was a trend towards higher glycogen concentrations in muscles when the horses were fed the high-carbohydrate-diet. Maybe the feeding period of three weeks was too short to produce clear effects. In a case study of Valentine et al. (1998), 19 horses with RER were fed a high-fat diet for 3-6 months. The diets used were different combinations of timothy or alfalfa hay with a fat-supplement, like vegetable oil, rice bran or a high-fat feed. All diets were supplemented with vitamin E and selenium and a trace mineral salt block. The fat content in the diets were estimated to be 9-11% in the dietary dry matter. All horses had abnormal

glycogen accumulation and serum CK and aspartate transaminase (AST) values four hours after exercise. Post-exercise CK and AST activities after feeding the high-fat diet were significantly lower than the initial post-exercise values. When fed the high-fat diet, sixteen horses did not have any episodes of exertional rhabdomyolysis. Thus, the feeding of a diet with low-carbohydrate and high-fat content may reduce the severity of exercise-induced injury in horses with exertional rhabdomyolysis.

De La Corte et al. (1999) have suggested that Quarter horses with PSSM have enhanced uptake of glucose that may be related to an increased sensitivity to insulin. To decrease glycogen accumulation in skeletal muscle, diets low in soluble carbohydrates might be most effective.

Horses fed on the high-carbohydrate diet in the study of MacLeay et al. (1999) were more reactive in their stalls, difficult to catch and to lead. Conversely, when fed a high-fat diet the same horses were regarded as more docile. An association between anxiety or nervousness and the onset of episodes has been observed in Thoroughbreds with RER. Management of horses with RER should include strategies to minimise stress and excitability and involve regular exercise. The diet should contain approximately 10% fat in the dietary dry matter and be low in nonstructural carbohydrates.

Growing horses

To sustain the rapid growth rates in foals, nutrient and energy intakes have to be high. Traditionally, the amount of concentrate in the ration is increased. With extra concentrate, large quantities of soluble carbohydrates may be ingested, which could enhance insulin-mediated conversion of thyroxine (T_4) to triiodothyronine (T_3), which in turn influences growth and maturation (Davison et al., 1991). Elevated levels of blood glucose and insulin and the subsequent increase in T_3 concentration have been implicated as factors contributing to developmental orthopedic diseases (DOD). In this light, fat supplementation could be considered in feeding programs for young horses. Fat intake instead of carbohydrate will reduce postprandial blood insulin concentrations but does not influence blood glucose. The insulin lowering could decrease the risk of skeletal problems in growing foals (Ott and Kivipelto, 1989). Davidsson et al (1991) used Quarter horses, 19 weeks of age, to compare the effect of fat-supplemented and conventional diets on growth, nutrient utilization and post-prandial thyroid hormone concentrations. The horses were fed fat-supplemented (10% animal fat) or conventional diets. There were no clear diet effects, including on radiographic evidence for any abnormalities in the physes.

Thus, so far there is no experimental support for the notion that high-fat diets may reduce the risk of DOD.

Reduce intake of carbohydrate rich concentrate

Adult, non-exercising and non-lactating horses can be adequately fed on diets consisting of roughage only. However, in order to meet their energy requirements, intensively exercising horses have to be fed on diets with concentrates. High concentrate diets have been associated with laminitis, gastric ulcers, colic and diarrhoea ([Garner et al., 1978](#), [Rowe et al., 1994](#), [Clarke et al., 1990](#), [Coenen, 1990](#)). Reducing dry matter intake in combination with that of highly fermentable carbohydrates can help to prevent these disorders. In a controlled study with ponies, [Coenen \(1990\)](#) found significantly more gastric ulcers in animals fed a concentrate diet only when compared to a hay diet.

The intake of large amounts of starch and sugars with concentrates has been suggested to cause so-called "hot" or excitable behaviour ([Greiwe et al., 1989](#); [Kohnke, 1992](#)), but the suggestion is not based on controlled experiments. As mentioned above ([MacLeay et al., 1999](#)), found differences in behaviour when horses were fed either a carbohydrate-rich or a fat-rich concentrate. According to results of [Holland et al. \(1996\)](#) dietary fat reduces the activity and reactivity of horses. Horses fed diets containing 10% fat in the form of either soy lecithin plus corn oil, soy lecithin plus soybean oil or corn oil showed less reactivity in visual stimulus, noise, and pressure tests when compared to control horses fed a low-fat diet. The horses given the high-fat diet also showed less spontaneous activity as measured with a pedometer.

Reduce intake of protein

Chronic renal failure sometimes occurs in older horses as a result of glomerular or interstitial disease. For such patients, a diet low in protein, phosphorus and calcium is recommended, which can be accomplished by adding up to 20% vegetable oil to a grain-forage ration ([Lewis, 1995](#)). The digestibility of fat can be depressed in liver-diseases because production and excretion of bile can be disturbed ([Zeyner, 1995](#)). For patients with liver disease and cholestasis, a low-protein, low-fat diet is considered suitable. There may be a contra-indication for MCT in the diet. Although no bile is required for the digestion and absorption of MCT, which may be beneficial for liver patients, the oxidation by the liver may be diminished, leading to the accumulation of octanoic acid. There is evidence that octanoic acid contributes to the development of encephalopathy. Thus, for liver patients with cholestasis, a low-protein, low-fat, high-carbohydrate diet may be advised.

Conclusions

The fat content of horse diets generally is about 5% in the dry matter. With the commercially available high-fat concentrates, fat levels higher than 8% in the total dietary dry matter can be achieved only when pure oils are added to the diet. Vegetable oils, especially corn oil, are more palatable to horses than animal fats. Horses are capable to adequately digest fat in diets with fat levels as high as 20%. An increase in dietary fat concentrations is associated with a decrease in apparent crude fiber digestibility. The feeding of extra fat diet to horses, in the form of soybean oil, causes a decrease in the level of plasma triacylglycerols and an increased flux of plasma triacylglycerol-fatty acids. A high-fat diet produces an increase in plasma levels of cholesterol. The degree of saturation of the dietary fatty acids may not affect the plasma levels of cholesterol and triacylglycerols in horses. Diets with medium-chain triacylglycerols (MCT) stimulate the production of plasma triacylglycerols, leading to an elevation of plasma triacylglycerols. Fat-supplemented diets may be advantageous for the athletic performance of horses, in the treatment of horses with recurrent rhabdomyolysis and may serve to reduce the intake of carbohydrates and/or protein. So far there is no experimental support that high-fat diets may reduce the risk of DOD in growing horses.

References

- Atkinson, R.E. (1980) Adding fat to animal feed. *Milling Feed and Fertiliser*. 163: 2, 14-18.
- Bach, A.C. and Babayan, V.K. (1982) Medium-chain triglycerides: an update. *American J. Clin. Nutr.* 36: 950-962.
- Barton, B.M. and Morris, D.D. (1998) Diseases of the liver. In: *Equine Internal Medicine*. Eds. Reed, S.M. and Bayly, W.M., W.B.Saunders Company, Philadelphia. pp: 707-738.
- Beech, J. (1997) Chronic exertional rhabdomyolysis. *Vet. Clin. North Am. Equine Pract.* 13: 145-168.
- Berning, J.R. (1996) The role of medium-chain triglycerides in exercise. *Int. J. Sport Nutr.* 6: 121-133.
- Beynen, A.C. and Katan, M.B. (1985) Why do polyunsaturated fatty acids lower serum cholesterol? *American J. Clin. Nutr.* 42: 560-563.
- Beynen, A.C. and Katan, M.B. (1989) Impact of dietary cholesterol and fatty acids on serum lipids and lipoproteins in man. In: *The role of fats in human nutrition*. Academic Press Limited.
- Beynen, A.C. and Wensing, Th. (1985) Fasting-induced hyperlipoproteinemia in ponies.

- Cholesterol Metabolism in Health and Disease: Studies in the Netherlands. ed by A.C. Beynen, M.J.H. Geelen, M.B. Katan and J.A. Schouten. Ponsen & Looijen. Wageningen, The Netherlands.
- Beynen, A.C., Haagsman, H.P., Van Golde L.M.G. and Geelen, M.J.H. (1981) The effects of insulin and glucagon on the release of triacylglycerols by isolated rat hepatocytes are mere reflections of the hormonal effects on the rate of triacylglycerol synthesis. *Biochimica et Biophysica Acta* 665: 1-7.
- Blaxter, K.L. (1962) Muscular dystrophy in farm animals: Its cause and prevention. *Proc. Nutr. Soc.* 21: 211-220.
- Borensztajn, J., Rone, S.J., Kotlar, T.J., (1976) The inhibition of lipoproteinlipase (Clearing-Factor Lipase) activity by Triton WR-1339. *Biochem. J.* 156: 539-54
- Bottoms, G.D., Templeton, C.B., Fessler, J.R., Johnson, M.A., Roesel, O.F., Ewart, K.M. and Adams, S.B. (1982) Thromboxane, prostaglandine I₂ (epoprostenol) and the haemodynamic changes in equine endotoxin shock. *Am. J. Vet. Res.* 43: 999-1002.
- Bowland, J.P. and Newell, J.A. (1974) Fatty acid composition of shoulder fat and perinephric fat from pasture-fed horses. *Can. J. Anim. Sci.* 54: 373-376.
- Bowman, V.A. Fontenot, J.P., Webb, K.E., and Meacham.T.N., (1977) Digestion of fat by equine. *Proc. 5th Equine Nutr. Physiol. Soc.* p: 40.
- Cambell, E.A. (1963) The serum lipoproteins of the domestic animal. *Res. Vet. Sci.* 4: 56-63.
- Clarke, L.L., Roberts, M.C. and Argenzio, R.A. (1990) Vet. Clinics of North Am. Equine Pract. 6: 433-450.
- Chait, A., Onitiri, A., Nicoll, A., Rabaya, E., Davies, J and Lewis, B. (1974) Reduction of serum triglyceride levels by polyunsaturated fat. Studies on the mode of action and on very low density lipoprotein composition. *Artherosclerosis* 20: 347-374.
- Coenen, M. (1986) Beiträge zur Verdauungsphysiologie des Pferdes. Verdaulichkeit und praececale Passage einer, suspendierfähigen Diät in Abhängigkeit von der Applikationsform. *Z. Tierphysiol. Tierernährg. Futtermittelk.* 56: 104-117.
- Coenen, M. (1990) Beobachtungen zum vorkommen fütterungsbedingter magenulcera beim pferd. *Schweiz. Arch. Tierheilk.* 132: 121-126.
- Davison, K.E., Potter, G.D., Evans, J.W., Greene, L.W., Hargis, P.S., Corn, C.D. and Webb, S.P. (1991) Growth, utilization, radiographic bone characteristics and postprandial thyroid hormone concentrations in weanling horses fed added dietary fat. *Equine Vet. Sci.* 11: 119-125.
- Davidson, K.E., Potter, G.D., Greene, L.W., Evans, J.W. and McMullan, W.C. (1987) Lactation and reproductive performance of mares fed added dietary fat during late gestation and early lactation. *Proc. 10th Equine Nutr. Physiol. Soc.* p: 87-92.
- De La Corte, F.D., Valberg, S.J., MacLeay, J.M., Williamson, S.E. and Mickelson, S.R. (1999) Glucose uptake in horses with polysaccharide storage myopathy. *AJVR* 60: 458-462.
- Eilmans, I. (1991) Fettverdauung beim Pferd sowie die Folgen einer marginalen Fettversorgung. Hannover. Tierärztl. Hochsch., Diss.
- Engelking, L.R., Anwer, M.S. and Hofmann, A.F. (1987) Basal and bile salt-stimulated bile flow and biliary lipid excretion in ponies. *Am. J. Vet. Res.* 50:578-582.
- Essén-Gustavsson, B., Blomstrand, E., Karlström, K., Lindholm, A. and Persson, S.G.B. (1991) Influence of diet on substrate metabolism during exercise. *Proc. 3rd Int. Conf. Equine Exercise Physiology*, pp: 288-298.

- Ferrante, P.L., Taylor, L.E., Meacham, T.N., Kronfeld, D.S. and Tiegs, W. (1993) Evaluation of acid-base status and strong ion difference (SID) in exercising horses. *Proc. Equine Nutr. Physiol. Symp.* 13: 123-124.
- Flothow, C. (1994) Einfluss von kokosfett und Sojaöl auf Preileale Verdauungsvorgänge beim Pferd. *Hannov. Tierärztl. Hochsch. Diss.*
- Ford, J.H. and Evans, J. (1982) Glucose utilization in the horse. *Br. J. Nutr.* 48: 111-117.
- Frape, D.L. (1994) Diet and exercise performance in the horse. *proc. Nutr. Soc.* 53: 189-206.
- Frape, D. (1998) *Equine Nutrition and Feeding*. 2nd ed. Blackwell Sciences. London.
- Garner, H.E., Moore, J.N., Johnson, J.H., Clark, L., Amend, J.F., Tritschler, L.G. Coffmann, J.R., Sprouse, R.F., Hurcheson, D.P. and Salem, C.A. (1978) Changes in the caecal flora associated with the onset of laminitis. *Equine Vet. J.* 10: 249-252.
- Gay, C.C., Sullivan, N.D., Wilkinson, J.S., McLean, J.D. and Blood, D.C. (1978) Hyperlipaemia in ponies. *Austr. Vet. J.* 52: 459 - 462.
- Geelen, M.J.H., Schoots, W.J., Bijleveld, C. & Beynen, A.C. (1995) Dietary medium-chain fatty acids raise and (n-3) polyunsaturated fatty acids lower hepatic triacylglycerol synthesis in rats. *Journal of Nutrition* 125: 2449-2456.
- Geelen, S.J.N., Lemmens, A.G., Terpstra, A.H.M., Wensing, Th. and Beynen, A.C. (2001a) High density lipoprotein cholesteryl ester metabolism in the pony, an animal species without plasma cholesteryl ester transfer protein activity: transfer of high density lipoprotein cholesteryl esters to lower density lipoproteins and the effect of the amount of fat in the diet. *Comp. Biochem Physiol. B. Biochem. Mol. Biol.* 130: 145-154.
- Geelen, S.N.J., Jansen, W.L., Sloet van Oldruitenborgh-Oosterbaan, M.M., Breukink, H.J. and Beynen, A.C. (2001b). Fat feeding increases equine heparin-released lipoprotein lipase activity. *J. Vet. Intern. Med.* 15: 478-481.
- Geelen, S.N.J., Blázquez, C., Geelen, M.J.H., Sloet van Oldruitenborgh-Oosterbaan, M.M. and Beynen, A.C. (2001c) High fat intake lowers hepatic fatty acid synthesis and raises fatty acids oxidation in aerobic muscle in Shetland ponies. *Brit. J. Nutr.* 86: 31-36.
- Geelen, S.N.J., Sloet van Oldruitenborgh-Oosterbaan, M.M. and Beynen, A.C. (1999) Dietary fat supplementation and equine plasma lipid metabolism. *Equine Vet. J. suppl.* 30: 475-478.
- Geelen, S.N.J., Sloet van Oldruitenborgh-Oosterbaan, M.M. and Beynen, A.C. (2002) Indirect measurement of the production of plasma triacylglycerols by horses given a high fat diet. *Int. J. Vitam. Nutr. Res.* in press.
- Grant, C.A. (1961) Morphological and etiological studies of dietetic microangiopathy in pigs. *Acta Scand.* 2 (suppl 3): 1.
- Greiwe, K.M., Meacham, T.N., Fregin, G.F. and Waldberg, J.L. (1989) Effect of added dietary fat on exercising horses. *Prc. 11th Equine Nutr. Physiol. Symp.* pp: 101-106.
- Grunwald, D. (1991) Marginale Linolsäureversorgung und Parameter des Lipidstoffwechsels in Plasma und Organen beim adulten Pony. *Hannover, Tierärztl. Hochsch., Diss.*
- Ha, Y. C. and Barter, P.J. (1979) Differences in plasma cholesteryl ester transfer activity in sixteen vertebrate species. *Comp. Biochem. Physiol.* 71B: 265-269.
- Hallebeek, J.M. and Beynen, A.C. (2001a) Effect of dietary medium chain triacylglycerols on plasma triacylglycerol levels in horses. *Arch. Anim. Nutr.* 54, 159-171.

- [Hallebeek, J.M. and Beynen, A.C. \(2001b\) A preliminary report on a fat-free diet formula for nasogastric enteral administration as treatment for hyperlipaemia in ponies. Vet. Quart. 23: 201-205.](#)
- [Hallebeek, J.M. and Beynen, A.C.\(2002a\) Dietary soybean oil versus palm oil does not influence the level of plasma triacylglycerols in the horse. Anim. Nutr. a. Anim. Physiol. accepted](#)
- [Hallebeek, J.M. and Beynen, A.C.\(2002b\) Production and clearance of plasma triacylglycerols in ponies fed diets containing either medium-chain triacylglycerols or soybean oil. submitted](#)
- [Hallebeek, J.M. and Beynen, A.C.\(2002c\) The concentration of plasma triacylglycerols in horses fed diets containing either medium chain triacylglycerols or an isoenergetic amount of starch or cellulose. Arch. Anim. Nutr. Accepted](#)
- [Harkins, J.D., Morris, G.S., Tulley, R.T., Nelson, A.G. and Kamerling, S.G. \(1992\) Effect of added dietary fat on racing performance in Thoroughbred horses. Equine Vet. Sci. 12: 123-129.](#)
- [Harris, P.A., Pagan, J.D., Crandell, K.G. and Davidson, N. \(1999\) Effect of feeding Thoroughbred horses a high unsaturated or saturated vegetable oil supplement diet for 6 month following a 10 month fat acclimation. Equine vet. J. Suppl. 30: 468-474.](#)
- [Heidenreich, E. \(1997\) Abriefefeste Pellets fur fettreiche Futtermischungen. Kraftfutter 12: 506-516.](#)
- [Henry, M.M., Moore, J.N. and Fischer, K. \(1991\) Influence of an w-3 fatty acid-enriched ration on in vivo responses of horses to endotoxin. Am J Vet Res 52: 523-527.](#)
- [Hodgson, D.R., Rose, R.J., Dimauro, J. and Allen, J.R. \(1986\) Effects of training on muscle composition in horses. Am. J. Vet. Res. 47: 12-15.](#)
- [Holland, J.L., Kronfeld, D.S., Rich, G.A., Kline, K.A., Fontenot, J.P., Meacham, T.N. and Harris, P.A. \(1998\) Acceptance of fat and lecithin containing diets by horses. Appl. Anim. Behaviour Sci. 56: 91-96.](#)
- [Holland, J.L., Kronfeld, D.S. and Meacham, T.N. \(1996\) Behavior of horses is affected by soy lecithin and corn oil in the diet. J. Anim. Sci. 74: 1252-1255](#)
- [Holland, J., Meacham, T. and Kronfeld, D. \(1995\) Digestibility of lecithin containing diets by horses. Proc. 14th Equine Nutr. Physiol. Soc. pp: 80-81.](#)
- [Hollanders, B., Mougin, A., N'Diaye, F, Hentz, E., Aude, X. and Girard, A. \(1986\) Comparison of the lipoprotein profiles obtained from rat, bovine, horse, dog, rabbit and pig serum by a new two step ultracentrifugal gradient procedure. Comp. Biochem. Physiol. 84B; 83-89.](#)
- [Hollands, T. and Cuddeford, D. \(1992\) Effect of supplementary soya oil on the digestibility of nutrients contained in a 40:60 roughage/concentrate diet fed to horses. Pferdeheilkunde, Sonderheft: 128-132.](#)
- [Hughes, S.J., Potter, G.D., Greene, L.W., Odom, T.W. and Murray-Gerzik, M. \(1995\) Adaptation of Thoroughbred horses in training to a fat supplemented diet. Equine Vet. J. 18: 349-352.](#)
- [Jansen, W.L. \(2001\) Fat intake and apparent digestibility of fibre in horses and ponies. Thesis, University of Utrecht, Utrecht, The Netherlands.](#)
- [Johnston, J.M. \(1968\) Mechanism of fat absorption. In: Handbook of Physiology: alimentary canal. American Physiology Society. Washington. pp: 1323-1340.](#)
- [Jones, D.L., Potter, G.D., Greene, L.W. and Odom, T.W. \(1992\) Muscle glycogen in exercised miniature horses at various body conditions and fed a control or fat-supplemented diet. Proc. 12th Equine Nutr. Physiol. Symp. Equine Vet. Sci. 12: 287-291.](#)

- Julen, T.R., Potter, G.D., Greene, L.W. and Stott, G.G. (1995) Adaptation to a fat-supplemented diet by cutting horses. Proc. 14th Equine Nutr. Physiol. Soc. pp: 56-61.
- Kane, E. and Baker, J.P. (1977) Utilization of an corn oil supplemented diet by the horse. Proc. 5th Equine Nutr. Physiol. Soc. p. 41.
- Kane, E., Baker, J.P. and Bull, L.S. (1979) Utilization of a corn oil supplemented diet by the pony. J. Anim. Sci. 48: 1379.
- Kiens, B. and Lithell, H. (1989) Lipoprotein metabolism influenced by training-induced changes in human skeletal muscle. J. Clin. Invest. 83: 558-564.
- Kohnke, J.B. (1992) Feeding and Nutrition. The making of a champion. Birubi Pacific, Rouse Hill, NSW, Australia. pp: 25.
- Kolb, E. and Günthler, H. (1971) Ernährungsphysiologie der landwirtschaftlichen Nutztieren. VEB Gustav Fischer Verlag, Jena.
- Kronfeld, D.S., Ferrante, P.L. and Granjean, D. (1994) Optimal nutrition for athletic performance, with emphasis on fat adaptation in dogs and horses. J.Nutr. 124 (suppl): 2745s-2753s.
- Kurcz, E.V., Schurg, W.A., Marchello, J.A. and Cuneo, S.P. (1991) Dietary fat supplementation changes lipoprotein composition in horses. Proc. 12th Equine Nutr. Physiol. Symp. Calgary. pp253-254.
- Landes, E. and Meyer, H. (1998) Einfluss von Fetten auf die Futteraufnahme sowie mikrobielle Umsetzungen im Magen und Dunndarm des Pferdes. Pferdeheilkunde 14: 51-58.
- Leat, W.M.F., Northorp, C.A., Buttress, N. and Jones, D.M. (1979) Plasma lipids and lipoproteins of some members of the order Perissodactyla. Comp. Biochem. Physiol. 63B: 275-281.
- Le Goff, D., Nouvelot, A., Fresnel, J. and Silberzahn, P. (1987) Characterization of equine plasma lipoproteins after separation by density gradient. Comp. Biochem. Physiol. 87B: 501-506.
- Lewis, L.D. (1995) Feeding and care of horses for athletic performance. In: Equine clinical nutrition: feeding and care. Eds. Williams and Wilkins. Waverly Company, Baltimore, pp: 239-281, 412-413.
- Mackie, B.G., Dudley, G.A., Kaciuba-Uscilko and Terjung, R.L. (1980) Uptake of chylomicron triglycerides by contracting skeletal muscle in rats. J. Appl. Physiol. 49: 851-855.
- MacLeay, J.M., Valberg, S.J., Pagan, J.D., De La Corte, F., Roberts, J., Billstrom, J., McGinnity, J. and Kaese, H. (1999) Effect of diet on Thoroughbred horses with recurrent exertional rhabdomyolysis performing a standardised exercise test. Equine vet. J. Suppl. 30: 458-462.
- Magrum, L.J. and Johnston, P.V. (1983) Modulation of prostaglandin synthesis in rat peritoneal macrophages with w-3 fatty acids. Lipids 19: 514-521.
- Marchello, E.V., Schurg, W.A., Marchello, J.A. and Cuneo, S.P. (2000) Changes in lipoprotein composition in horses fed a fat-supplemented diet. J. Eq. Vet. Sci. 20:453-458.
- Marshall, L.A. and Johnston, P.V. (1985) The influence of dietary essential fatty acids on rat immunocompetent cell prostaglandin synthesis and mitogen-induced blastogenesis. J. Nutr. 115: 1572-1580.
- McCann, J.S., Maecam, T.N. and Fontenot, J.P. (1987) Energy utilization and blood traits of ponies fed fat-supplemented diets. J. Anim. Sci. 65: 1019-1026.
- McMiken, D.F. (1983) An energetic basis of equine performance. Equine Vet. J., 15: 123-133.
- Meyer, H. (1992) Energie-, Nährstoff- und Ballastbedarf. In: Pferdefütterung. Ed.

- Paul Parey, Berlin und Hamburg, pp: 45-81.
- Meyer, H. and Sallmann, H.P. (1996) Organische Säuren und pH-Wert im Jejunal- und Ilealchymus des Pferdes in Abhängigkeit von der Fütterung. *Pferdeheilkunde* 10; 381-392.
- Meyer, H., Flothow, C. and Radicke, S. (1997) [Preileal digestibility of coconut fat and soybean oil in horses and their influence on metabolites of microbial origin of the proximal digestive tract.](#) *Arch. Anim. Nutr.* 50: 63-74.
- Meyers, M.C., Potter, G.D., Evans, J.W., Greene, L.W. and Crouse, S.F. (1989) Physiological and metabolic response of exercising horses to added dietary fat. *J. Equine Vet. Sci.* 9: 218-223.
- Meyers, M.C., Potter, G.D., Greene, L.W. Crouse, S.F. and Evans, J.W. (1987) Physiological and metabolic response of exercising horses to added dietary fat. *Proc. 10th Equine Nutr. Physiol. Soc.* pp:107-113.
- Morris, D.D., Henry, M.M., Moore, J. N. and Fischer, K. (1989) [Effect of dietary linolenic acid on endotoxin-induced thromboxane and prostacyclin production by equine peritoneal macrophages.](#) *Circulatory Shock* 29:311-318.
- Morris, D.D., Henry, M.M., Moore, J.N. and Fischer, K. (1991) [Effect of dietary \$\alpha\$ -linolenic acid on endotoxin-induced production of tumor necrosis factor by peritoneal macrophages in horses.](#) *Am J Vet Res* 52: 528-532.
- National Research Council (1989) Nutrient Requirements of horses. Fifth revised edition. National Academy Press, Washington, D.C.
- Naylor, J.M. (1982) Proceedings of the 27th Annual Convention American Association of Equine Practitioners: 323.
- Naylor, J.M. and Freeman, D.E. (1987) Nutrition of the sick horse. In: Robinson NE, ed. Current therapy in equine medicine, 2nd ed. Philadelphia: WB Saunders Co. p: 426.
- Naylor, J.M., Kronfeld, D.S. and Acland, H. (1980) [Hyperlipaemia in horses: effects of undernutrition.](#) *Am. J. Vet. res.* 41: 899-905.
- Newsholme, E.A. and Start, C. (1973) Regulation of fat metabolism in liver. In: Regulation in Metabolism. John Wiley and Sons, London.
- Nicolosi, R.J., Herrera, M.G., Lozy, M. and Hayes, K.C. (1976) [Effect of dietary fat on hepatic metabolism of \$^{14}\text{C}\$ -oleic acid and very low density lipoprotein triglyceride in the gerbil.](#) *J. Nutr.* 106: 1279-1285.
- Oldham, S.L., Potter, G.D., Evans, J.W., Smith, S.B., Taylor, T.S. and Barnes, W.S. (1990) [Storage and mobilization of muscle glycogen in exercising horses fed a fat-supplemented diet.](#) *Proc. 11th Equine Nutr. Physiol. Symp. Equine Vet. Sci.* 10:353-355, 358,359.
- Orme, C.E., Harris, R.C., Marlin, D.J. and Hurley, J. (1997) [Metabolic adaptation to a fat-supplemented diet by the thoroughbred horse.](#) *Brit. J. Nutr.* 78: 443-58.
- Ott, E.A. and Kivipelto, J. (1998) [Influence of dietary fat and time of hay feeding on growth and development of yearling horses.](#) *J. Equine Vet. Sci.* 18: 254-259.
- Pagan, J.D., Burger, I. and Jackson, S.G. (1995) [The long term effects of feeding fat to 2 year old thoroughbreds in training.](#) *Equine Vet. J.* 18, suppl: 343-348.
- Pagan, J.D., Essén-Gustavson, B., Lindholm, A. and Thornton, J. (1987) [The effect of dietary energy source on exercise performance in Standardbred horses.](#) In: *Equine exercise physiology 2. Proceedings 2nd Intern Conf. Equine Exercise Physiology.* Eds: Gillespie, J.R. and Robinson, N.E. pp: 686-700.
- Pagan, J.D., Tiegs, W., Jackson, S.G. and Murphy, H.Q. (1993) [The effect of different fat sources on exercise performance in thoroughbred racehorses.](#) *Proc. 13th Equine Nutr. and Phys. Symp.* pp.125-129.

- Potter, G.D., Hughes, S.L., Julen, T.R. and Swinney, D.L. (1992) A review of research and utilization of fat by the equine. Proc. 1. Europäischen Konferenz über die Ernährung des Pferdes. pp. 119-123.
- Reinbek, G.F. (1989) Pelletierung fettreicher Mischungen. Mühle- und Mischfuttertechnik. 126: 53-55.
- Rich, G.A., Fontenot, J.P. and Meacham, T.N. (1981) Digestibility of animal, vegetable and blended fats by equine. Proc. 7th Equine Nutr. Physiol. Soc. pp.30-36.
- Robie, S.M., Janson, C.H., Smith, S.C. and O'Connor, J.T. (1975) Equine serum lipids: lipid composition and electrophoretic mobility of equine serum lipoprotein fractions. Am. J. Vet. Res. 36: 1715-1717.
- Rose R.J. and Sampson, D. (1982) Changes in certain metabolic parameters in horses associated with food deprivation and endurance exercise. Res. Vet. Sci. 32: 198-202.
- Rowe, J.B., Lees, M.J. and Pethick, D.W. (1994) Prevention of acidosis and laminitis associated with grain feeding in horses. J.Nutr.124: 2742S-2744S.
- Rush Moore, B., Abood, S.K. and Hinchcliff, K.W. (1994) Hyperlipaemia in 9 miniature horses and miniature donkeys. J. Vet. Int. Med. 8: 376-381.
- Sanders, T.A., Roshanai, F. (1983) The influence of different type of w3 polyunsaturated fatty acids on blood lipids and platelet function in healthy volunteers. Clin. Sci 64: 91-99.
- Sato, K. Akiba, Y. and Horiguchi, M. (1997) Species differences between chickens and rats in chemical properties of adipose tissue lipoprotein lipase. Comp. Biochem. Physiol. 118: 855-858.
- Scanu, A., Oriente, P., Szajewski, J.M., Lawrence, J., McCormack, M.D. and Page, I.H. (1961) Triton hyperlipemia in dogs. J. Exp. Med. 114: 279-293.
- Scott, B.D., Potter, G.D., Evans, J.W., Reagor, J.C., Webb, G.W. and Webb, S.P. (1987) Growth and feed utilization by yearling horses fed added dietary fat. Proc. 10th Equine Nutr. Physiol. Soc. pp: 101-105.
- Scott, B.D., Potter, G.D., Greene, L.W., Hargis, P.S. and Anderson, J.G. (1992) Efficacy of a fat-supplemented diet on muscle glycogen concentrations in exercising Thoroughbred horses maintained in various body conditions. Proc. 12th Equine Nutr. Physiol. Symp. Equine Vet. Sci. 12: 109-113.
- Shorland, F.B., Bruce, L.W., Jessop, A.W. (1952) The component fatty acids of lipids from fatty tissues, muscle and liver. Biochem. J. 52: 400-407.
- Sloet van Oldruitenborgh-Oosterbaan, M.M., Annee, M.P., Verdegaal, E.J.M.M., Lemmens, A.G. and Beynen, A.C. (2002) Blood metabolic profile in exercising horses fed either a low- or high-fat diet. submitted.
- Snyder, J.L., Meacham, T.N., Fontenot, J.P. and Webb jr., K.E. (1981) Heat production in pony geldings fed fat supplemented diets. Proc. 7th Equine Nutr. Physiol. Soc. pp:144-148.
- Stull, C.L., Rodiek, A.V. and Arana, M.J. (1987) The effects of common equine feeds on blood levels of glucose, insulin and cortisol. Proc. 10th Equine Nutr. Physiol. Symp.. pp: 61-66.
- Swenson, T.L. (1992) Transfer proteins in reverse cholesterol transport. Current Opinion in Lipidology 3: 67-74.
- Swinney, D.L., Potter, G.D., Greene, L.W., Schumacher, J. Murray-Gerzik, M. and Goldy, G. (1995) Proc. 14th Equine Nutr. Physiol. Soc. pp: 30-35.
- Taylor, L.E., Ferrante, P.L., T.N., Kronfeld and Meacam, , D.S. (1995) Acid-base variables during incremental exercise in sprint-trained horses fed a high-fat diet. J. Anim. Sci. 73: 2009-2018.

- [Templeton, C.B., Bottoms, G.D., Fessler, J.F., Turek, J.J. and Boon, G.D. \(1985\) Effects of repeated endotoxin injections on prostanoids, hemodynamics, endothelial cells and survival in ponies. *Circ. Shock* 16: 253-264.](#)
- [Terjung, R.L., Budohoski, L., Nazar, K., Kobryn, A. and Kaciuba-Uscilko, H. \(1982\) Chylomicron triglyceride metabolism in resting and exercising fed dogs. *J. Appl. Physiol.* 52: 815-820.](#)
- [Terpstra, A.H.M., Sanchez-Muniz, F.J., West, C.E. and Woodward, C.J.H. \(1982\) The density profile and cholesterol concentrations of serum lipoproteins in domestic and laboratory animals. *Comp. Biochem. Physiol.* 71B: 669-673.](#)
- [Valentine, B.A., Hintz, H.F., Freels, K.M., Reynolds, A.J. and Thompson, K.N. \(1998\) Dietary control of exertional rhabdomyolysis in horses. *JAVMA* 212: 1588-1593.](#)
- [Van Dias, F.W., Gibney, M.T. and Taylor, T.G.F. \(1982\) The effect of polyunsaturated fatty acids of the n-3 and n-6 series on platelet aggregation and platelet and aortic fatty acid composition in rabbits. *Artherosclerosis* 43: 245-257.](#)
- [Van 't Klooster, A.Th., Hallebeek, J.M. and Beynen, A.C. \(1999\) Voeding van paarden: vertering, energie- en eiwitwaardering en voedernormen. *Tijdsch Diergeneeskd* 124: 401-405](#)
- [Watson, T.D.G. \(1991\) Lipoprotein metabolism in the horse. Ph. D. Thesis, University of Glasgow.](#)
- [Watson, T.D.G. and Packard, C.J. \(1993\) Plasma lipid transport in the horse. *Comp. Biochem. Physiol.* 106: 27-34.](#)
- [Watson, T. D. G., Burns, L., Freeman, D.J., Packard, C.J. and Shepherd, J. \(1993\) High-density lipoprotein metabolism in the horse \(*Equus caballus*\). *Comp. Biochem. Physiol.* 104B: 45-53.](#)
- [Watson, T.D., Burns, L., Love, S., Packard, C.J. and Shepherd J. \(1991\) The isolation, characterisation and quantification of the equine plasma lipoproteins. *Equine Vet. J.* 23: 353-359.](#)
- [Watson, T.D.G., Burns, L., Love, S., Packard, C.J. and Shepherd, J. \(1992\) Plasma lipids, lipoproteins and post-heparin lipases in ponies with hyperlipaemia. *Equine Vet.J.* 24: 341-346.](#)
- [Webb, S.P., Potter, G.D. and Evans, J.W. \(1987\) Physiology and metabolic response of race and cutting horses to added dietary fat. *Proc. 10th equine Nutr. Physiol. Soc.* pp: 115-120.](#)
- [Worth, M.J., Fontenot, J.P. and Meacham, T.N. \(1987\) Physiological effects of exercise and diet on metabolism in the equine. *Proc. 10th Equine Nutr. Physiol. Soc.* p: 145.](#)
- [Zeyner, A. \(1995\) Diätetik beim Pferd. Gustav Fischer Verlag Jena, Stuttgart, Germany.](#)
- [Zeyner, A. and Lengwenat, O. \(1997\) Untersuchungen zur oralen gabe von mittelkettigen triglyceriden und sojalecithin sowie von L-carnitin an galoprennpferde. In: Vitamine und weitere Zusatzstoffe in der Ernährung von Mensch und Tier \(Hrsg.: R. Schubert, G. Flachowsky, R.Bitsch & G. Jahreis\). 304-309.](#)