NUTRIENT REQUIREMENTS OF HORSES

SIXTH REVISED EDITION

Committee on Nutrient Requirements of Horses

Board on Agriculture and Natural Resources

Division on Earth and Life Studies

NATIONAL RESEARCH COUNCIL
OF THE NATIONAL ACADEMIES

THE NATIONAL ACADEMIES PRESS
Washington, D.C.
www.nap.edu

THE NATIONAL ACADEMIES PRESS • 500 Fifth Street, N.W. • Washington, DC 20001

NOTICE: The project that is the subject of this report was approved by the Governing Board of the National Research Council, whose members are drawn from the councils of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine. The members of the committee responsible for the report were chosen for their special competences and with regard for appropriate balance.

This study was supported by grants from the American Feed Industry Association, the American Paint Horse Association, the American Quarter Horse Association, the Equine Science Society, the North American Equine Ranching Information Council, general support of The Animal Nutrition Series provided by The Department of Health and Human Services (U.S. Food and Drug Administration) under Award No. 223-01-01-2460, and internal National Research Council funds. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the views of the organizations or agencies that provided support for the project.

Library of Congress Cataloging-in-Publication Data

Nutrient requirements of horses / Committee on Nutrient Requirements of Horses,
Board on Agriculture and Natural Resources, Division on Earth and Life Studies,
National Research Council of the National Academies. — 6th rev. ed.
p. cm.
Includes bibliographical references and index.
ISBN-10: 0-309-10212-X (cloth)
ISBN-10: 0-309-66096-3 (pdf)
ISBN-13: 978-0-309-10212-4 (cloth)
ISBN-13: 978-0-309-66096-9 (pdf)
1. Horses—Nutrition—Requirements. 2. Horses—Feeding and feeds. I. National Research Council (U.S.). Committee on Nutrient Requirements of Horses.
SF285.5.N37 2007
636.1′0852—dc22

2006030795

Additional copies of this report are available from the National Academies Press, 500 Fifth Street, N.W., Lockbox 285, Washington, DC 20055; (800) 624-6242 or (202) 334-3313 (in the Washington metropolitan area); Internet, http://www.nap.edu.

Printed in the United States of America

3

Fats and Fatty Acids

.INTRODUCTION

Fats or oils are generally used in equine diets to increase energy density and/or substitute for hydrolyzable and rapidly fermentable carbohydrates in the form of cereal grains. However, fat supplementation has other potential benefits, including improved energetic efficiency (Kronfeld, 1996), enhanced body condition, diminished excitability (Holland et al., 1996a), and metabolic adaptations that increase fat oxidation during exercise (Dunnett et al., 2002). Dietary fats also serve as carriers for fat-soluble vitamins and supply the essential fatty acids (EFAs) linoleic acid and α-linolenic acid that are not synthesized by the body, although an EFA requirement for horses has not been determined. All fatty acids serve structural functions, and several of the polyunsaturated fatty acids (PUFAs) are precursors of the prostaglandins and other eicosanoids, which are important for a host of cellular functions.

From a biochemical viewpoint, fats belong to a broad group of compounds known as lipids that can be glycerol or nonglycerol based. Glycerol-based lipids include the glycolipids, phospholipids, and triglycerides (also termed triacylglycerols). Triglycerides consist of three fatty acid molecules linked to a glycerol backbone. Cholesterol and its fatty acid esters are nonglycerol-based lipids. Included in this category of lipids are waxes, terpenes, cerebrosides, and various sterols.

Fatty acids may be designated on the basis of the number of carbon atoms they contain and the number of double bonds. Long-chain fatty acids contain 16 to 20 carbon atoms, medium-chain fatty acids contain 6 to 10 carbons, and short-chain or volatile fatty acids (VFAs), produced in the intestinal tract by bacterial fermentation, contain only 2 to 5 carbons. Saturated fatty acids (SFAs) contain no double bonds, monounsaturated (MUFAs) a single double bond, and PUFAs two or more double bonds. Fatty acids are also described by the position of the first double bond relative to the methyl end of the molecule (the omega [ω] end), in the form of A:Bω-C (or A:Bn-C), where A is the number of carbon atoms in the chain, B is the number of double bonds, and C is the position of the first double bond from the methyl terminus. For example, linoleic acid is referred to as 18:2n-6 because it contains 18 carbon atoms and 2 double bonds, the first between carbons 6 and 7 counted from the methyl terminus. Fatty acids with the first double bond in this position are commonly referred to as omega-6 fatty acids, whereas fatty acids with the first double bond between carbons 3 and 4 (e.g., α-linolenic, 18:3ω-3) are in the omega-3 series.

Triglycerides exist as fats or oils at room temperature according to their physical properties of the component fatty acids. Triglycerides with a high proportion of relatively short-chain fatty acids or unsaturated fatty acids tend to be liquid (oils) at room temperature. Saturated fatty acids have a higher melting point and exist as solids (fats) at room temperature.

SOURCES OF DIETARY FATS AND FATTY ACIDS

Both animal fats and vegetable fats or oils have been fed to horses, although use of vegetable sources is more prevalent in part due to superior palatability. In one study that examined the palatability of several animal and vegetable fats and oils, corn oil was the most palatable (Holland et al., 1998). In this study, diets containing up to 15 percent added fat as corn oil were readily accepted by horses. Several other vegetable sources, including seed and fruit oils (e.g., soy, canola, linseed [or flax], sunflower, safflower, coconut, and peanut) and other feed byproducts with relatively high fat content (e.g., lecithin, stabilized rice bran, wheat germ, and copra), appear to have acceptable palatability and are widely used in horse diets. Fish oil (menhaden) and medium-chain triglycerides (MCTs) also have been fed to horses. Use of these different fat and oil sources can be dictated by cost and

availability. Table 8-5 provides the fatty acid composition of some of the fats and oils added to horse diets.

DIGESTIBILITY AND ENERGY VALUE OF FATS

In general, there is an increase in the digestibility of fat when fats or oils are added to forages or grains (Potter et al., 1992). Mean estimates of apparent digestibilities of fats in horses and ponies are 42–49 percent for forages (Fonnesbeck et al., 1967; Bowman et al., 1979; Sturgeon et al., 2000), 55–76 percent for grains (Hintz and Schryver, 1989), and 88–94 percent for added fats and oils (Kane et al., 1979; McCann et al., 1987). Kronfeld et al. (2004) compiled published data from digestibility studies in which five basal (hay and grain mixes without added fats; 23–37 g fat/kg dry matter [DM]) and 18 test feeds with added fats (76–233 g fat/kg DM) were evaluated (Rich, 1980; Custalow, 1992; Holland, 1994; Bowman et al., 1979). This analysis demonstrated mean apparent digestibilities (D_a) of 55, 81, and 95 percent for fat in, respectively, forages, mixed feeds with added fat, and added fats. Encapsulation of fat within cereal grains or oilseeds may decrease the availability of these fats for digestion in the small intestine. The low true digestibility (D_t) of forage fat may be explained by the poor digestibility of waxes, pigments, and other non-triglyceride lipid components. Kronfeld et al. (2004) also reported that the true digestibility of added fats approached 100 percent with an endogenous fecal fat of 0.22 g/kg body weight (BW)/d. Maximal fat digestibility occurred between 100 and 150 g/kg DM and was sustained to 230 g/kg DM, suggesting high capacity for fat digestion in horses adapted to fat-supplemented rations. However, the results of other studies have suggested a lower upper limit in fat digestibility in horses. In an analysis of data from 225 digestion trials evaluating rations with varying amounts of partially hydrogenated soy oil, Zeyner (2002) reported a strong positive relationship between the D_a of fat and the amount of fat in the diet, but only up to approximately 7 percent DM. Assuming a gross energy value of 9.5 Mcal/kg for fat, caloric values for fat in forages, mixed feeds, and added vegetable fats have been estimated at 5.2, 7.7, and 9 Mcal/kg, respectively (Kronfeld et al., 2004). More precise digestible energy (DE) values can be calculated from measured fat content (g/kg) using the equation developed by Kronfeld et al. (2004): Energy value (Mcal/kg) = $0.095(92 - 92e^{(-\text{ether extract}/342)})$.

In other species, there is evidence that degree of saturation, melting point, and possibly fatty acid (FA) chain length affect the digestibility of added fats. Saturated fats are less digestible than unsaturated fats, while the digestibility is inversely related to the melting point of the FA. These factors are of minor importance in horse nutrition given the widespread use of vegetable oils containing predominantly unsaturated FAs. In two studies (McCann et al., 1987; Kronfeld et al., 2004), an effect of chain length or saturation of FAs on digestibility was not detected when comparing vegetable oils (corn, soy, soy lecithin, peanut), tallow, and vegetable-tallow blends.

In ruminants, the addition of oils to rations decreases ruminal fermentation of fiber (Coppock and Wilks, 1991), an effect not observed when encapsulated or protected fat is fed. There is conflicting evidence regarding the effects of added fat on the utilization of other nutrients in equine rations. The addition of corn oil at up to 15 percent of the total diet (DM basis) had no effect on fiber digestibility in three studies (Bowman et al., 1979; Kane et al., 1979; Bush et al., 2001). The digestibility of calcium, phosphorus, and magnesium also were largely unchanged in horses fed fat-supplemented diets (Bowman et al., 1979; Rich, 1980; McCann et al., 1987). The preileal digestibility of protein was slightly lower in horses fed coconut or soybean oils at 0.5 or 1 g/kg BW/d (Meyer et al., 1997). Kronfeld et al. (2004) reported that the addition of corn oil (up to 233 g/kg DM), tallow (up to 190 g/kg DM), or 50:50 soy lecithin and soy oil (100 g/kg DM) had no effect on DM, crude protein (CP), or acid detergent fiber (ADF) digestibility. Zeyner (2002) reported increased fiber digestibility of a mixed hay and concentrate ration with isoenergetic exchange of micronized corn (3 g starch/kg BW) by soy oil (up to 14 percent of DM). However, a further increase in the fat content of the ration (22 and 32 percent of DM) resulted in a statistically significant depression of gut microbial fermentative activity and decreased fiber digestibility. Jansen and co-workers reported a negative associative effect of soy oil on crude fiber (CF), neutral detergent fiber (NDF), ADF, and nitrogen-free extract (NFE) digestibility when horses were fed hay and isocaloric concentrates with different amounts of cornstarch, glucose, and soy oil (Jansen et al., 2000, 2001, 2002). In one of these studies (Jansen et al., 2001), CF digestibility was 71 percent and 55 percent in the control and fat-supplemented feeds (soybean oil 158 g/kg DM), respectively. Regression analysis of ether extract (EE) intake (as soybean oil) on CF digestibility showed that an increase of 10 g/kg DM of soybean oil resulted in a 0.9 percent decrease in apparent total tract digestibility (Jansen et al., 2001). The reason(s) for this apparent adverse effect of soy oil on fiber digestibility have not been elucidated. However, one possible explanation could be inadequate accommodation to the oil-supplemented ration. Zeyner (2002) reported decreased fiber digestibility with rapid substitution of cereal starch by soy oil (0.33 g soy oil/kg BW/d). This adverse effect was not evident after a 3-week accommodation period. Another explanation may be a specific negative effect of soybean oil at high levels of inclusion. Zeyner (2002) demonstrated no adverse effects in horses accommodated to soy oil-supplemented rations containing up to 0.7 g oil/kg BW/d. However, decreased fiber digestibility was observed in horses fed 1 g soy oil/kg/d. Therefore, at least for soy oil, 0.7 g/kg BW/d is suggested as an upper limit of fat inclusion.

Kronfeld et al. (2004) reported that rapid introduction of fat-supplemented diets is associated with greasy feces (steatorrhea) and increased fecal output, an indication that some fat has escaped digestion. These adverse effects are apparently avoided if fat is gradually introduced to the ration, with an accommodation period of 4 to 14 days depending on the level of fat supplementation.

PHYSIOLOGIC EFFECTS OF DIETARY FAT

Effects on Lipid and Carbohydrate Metabolism

Studies in humans and in rodent species have shown that high-fat diets result in enhanced capacity for fatty acid oxidation in skeletal muscle. Enhanced expression and activity of proteins and enzymes associated with the transport of free fatty acids (FFA) into muscle and β-oxidation underlie this increase in fat oxidation. There is some evidence that dietary fat supplementation results in similar adaptations in fat metabolism of horses, although some reports are conflicting and few studies quantitatively assessed fat oxidation. Fat supplementation has been demonstrated to increase post-heparin plasma hepatic and lipoprotein lipase (LPL) activities, decrease plasma triglyceride (TAG) concentrations by as much as 55 percent, and increase plasma cholesterol and phospholipid concentrations (Orme et al., 1997; Geelen et al., 1999). In Warmblood horses fed soy oil at 0, 0.33, 0.67, 1, and 1.33 g/kg BW/d, there were dose-dependent increases in serum VFA, phospholipids, and total cholesterol concentrations, as well as the proportion of α-lipoproteins (Zeyner, 2002). Serum TAG concentrations were decreased relative to the control diet at the 0.33 and 0.67 g/kg soy oil dosages, but significantly increased at the 1 and 1.33 g/kg dosages (Zeyner, 2002). In one study a dose-response relationship was detected between fat intake (3 to 10.8 percent fat, as soybean oil) and heparin-released plasma lipoprotein lipase activity (Geelen et al., 2001a). Specifically, an increase in fat intake by 1 g/kg DM was associated with an increase in LPL activity by 0.98 micromoles of fatty acid released per hour. As LPL is involved in the removal of FFA and glycerol from triglyceride-rich lipoprotein particles in tissue capillaries of skeletal muscle and adipose tissues, the increase in LPL activity with fat-supplementation indicates increased availability of FFA in these tissue beds. Geelen et al. (2001b) demonstrated decreases in the activities of acetyl-CoA carboxylase and fatty acid synthase in the liver of Shetland ponies on a high-fat diet (118 g/kg DM). Thus, the fat-induced decrease in plasma TAG concentrations may be due to a decrease in de novo fatty acid synthesis.

There is conflicting evidence regarding the effects of fat supplementation on the skeletal muscle activities of enzymes involved in oxidative metabolism. In Thoroughbred horses, 10 weeks of fat supplementation (soybean oil, 80 g/kg DM; control and fat-supplemented diets supplied 0.22 and 1 g/kg BW, respectively) resulted in increases in the activities of citrate synthase (CS) and β-hydroxyacyl CoA dehydrogenase (HAD) in skeletal (middle gluteal) muscle (Orme et al., 1997). On the other hand, the feeding of a high-fat diet (118 g/kg DM vs. control diet 15 g/kg DM) to Shetland ponies for 45 days was without effect on the activities of CS and HAD in gluteus and semitendinosus muscle, although an increase in CS activity was detected in the masseter muscle (Geelen et al., 2001b). Similarly, the activities of CS, HAD, hexokinase, and phosphofructokinase in middle gluteal muscle were unchanged in Standardbred horses fed a high-fat diet (Geelen et al., 2000).

The replacement of starch by fat or oils in concentrate feeds resulted in decreased blood glycemic and insulinemic responses to meal feeding (Williams et al., 2001; Zeyner et al., 2005). In mature Thoroughbred horses, the consumption of a fat and fiber supplement (approximately 10 percent nonstructural carbohydrates [NSC]; where NSC was determined by difference), when compared to a sweet feed supplement (approximately 50 percent NSC), resulted in a 65 percent and 85 percent decrease in, respectively, glycemic and insulinemic response (Williams et al., 2001). The feeding of a sweet feed (50 percent NSC, as determined by direct analysis) to mature Thoroughbred geldings maintained at pasture resulted in decreased insulin sensitivity when compared to the feeding of a high-fat, low-NSC (10 percent fat, 10 percent NSC in DM) feed or pasture alone (Hoffman et al., 2003).

Substrate Storage

There is conflicting information on the effects of dietary fat supplementation on muscle glycogen storage. In several studies, muscle glycogen content was increased after oil or fat supplementation, while other studies reported no change or a moderate decrease in muscle glycogen content. Five different studies from a single laboratory examined the effects of feeding a fat-supplemented concentrate (100 g tallow/kg DM in a grain-based concentrate) for 3–4 weeks (Meyers et al., 1987; Oldham et al., 1990; Jones et al., 1991; Scott et al., 1992; Julen et al., 1995). In these studies, (the concentrates were fed) with hay in a ratio of 65:35 to 75:25 such that the concentration of fat in the total diet was approximately 6–7 percent. A consistent finding was increased glycogen storage, with muscle glycogen content increasing by as much as 50 percent. In another study, Harkins et al. (1992) measured muscle glycogen in Thoroughbred horses fed a control diet of hay and a pelleted concentrate for 3 weeks followed by a fat-supplemented diet (corn oil, 3 percent DM) for a further 3 weeks, and mean muscle glycogen was 15.8 percent higher after oil supplementation. However, as hay was not fed with the fat-supplemented diet, absolute starch intake was higher for the fat-supplemented diet when compared to the control diet. These differences in fiber and starch intake confounded interpretation of the apparent change in muscle glycogen content. Hambleton et al. (1980)

measured muscle (quadriceps femoris m.) glycogen in horses conditioned for 3 weeks and fed diets containing 4 percent, 8 percent, 12 percent, or 16 percent soybean oil. Muscle glycogen content was measured before and after 6 hours of exercise (trotting interspersed with walking). Although mean values for muscle glycogen were higher in the 8 percent and 12 percent diets when compared to the other diets, statistically significant differences were not detected. This study has been consistently misquoted in the literature as demonstrating an effect of dietary fat on muscle glycogen content.

Other investigators have reported either no change (Essen-Gustavsson et al., 1991; Eaton et al., 1995; Orme et al., 1997; Hyyppa et al., 1999; MacLeay et al., 1999) or a moderate decrease (Pagan et al., 1987; Geelen et al., 2001b) in muscle glycogen storage following 3–10 weeks of fat supplementation. In two studies, liver glycogen content also decreased after oil supplementation (Pagan et al., 1987; Geelen et al., 2001b). A fat-supplemented diet (5 percent DM) slowed the rate of muscle glycogen replenishment in horses not accommodated to fat feeding (Hyyppa et al., 1999). However, the rate of post-exercise muscle glycogen resynthesis was not different from the control diet after an adaptation period of 3 weeks. In summary, there is no consensus on the effects of dietary fat supplementation on muscle glycogen storage in horses. The variability in results between the different studies could be due to differences in diet composition, duration of fat supplementation, muscle sampling and analysis techniques, and breed, age, and training state of the horses studied.

There is also conflicting information regarding the effects of a fat-supplemented diet on muscle triglyceride content. Essen-Gustavsson et al. (1991) demonstrated no change in the triglyceride content of middle gluteal muscle from Standardbred horses fed a fat-supplemented diet (60 g/kg DM) for 5 weeks. Orme et al. (1997) also reported no change in middle gluteal muscle triglyceride content of Thoroughbred horses provided oil supplementation (80 g soybean oil/kg DM) for 10 weeks. On the other hand, Geelen et al. (2001b) found an 80 percent increase in the semimembranosus triglyceride content of ponies fed a diet that provided 118 g soybean oil/kg DM.

Metabolic Responses to Exercise

Several studies have assessed the effects of fat supplementation on metabolic responses to exercise. The focus of earlier studies was the effects of fat supplementation on the concentrations of various plasma substrates or metabolites (e.g., glucose, FFA, TAG, and lactate) during exercise (Slade et al., 1975; Hintz et al., 1978; Hambleton et al., 1980; Hintz et al., 1982; Duren et al., 1987; Ferrante et al., 1994). More recent studies sought to obtain quantitative measures of substrate oxidation (Pagan et al., 1987, 2002; Dunnett et al., 2002). In general, fat supplementation (animal or vegetable fat at 8 percent or more of total DM) has been associated with mitigation of exercise-associated decreases in plasma glucose concentrations and increased TAG and FFA during prolonged, low-intensity exercise (Slade et al., 1975; Hintz et al., 1978; Hambleton et al., 1980; Hintz et al., 1982; Duren et al., 1987). Maintenance of higher plasma glucose concentrations has been taken as evidence of a glucose-sparing effect of fat supplementation. This hypothesis was supported by a recent study in which tracer-determined blood glucose utilization during 90 minutes of exercise at 30 percent of maximum aerobic capacity ($V_{O_2}max$) was lower after 5 weeks adaptation to a diet providing 29 percent DE from fat (corn oil) (Pagan et al., 2002).

In a small group (n = 4) of conditioned Thoroughbred horses, supplementation with soybean oil (20 percent of DE from oil) resulted in a decrease in respiratory exchange ratio (RER) during low- (trot at 3.2 m/s) and medium- (canter at 7 m/s) intensity treadmill (0° incline) exercise (Dunnett et al., 2002). This metabolic response during low-intensity exercise was apparent after 3 weeks of oil supplementation, but was not evident at higher workloads (canter at 10 m/s), perhaps reflecting greater dependence on carbohydrate metabolism during intense exercise. Two other studies have also reported a fat supplementation-induced decrease in the RER of horses during low-intensity exercise (Pagan et al., 1987, 2002). Overall, these findings suggest an increase in the utilization of fat, with a concomitant decrease in carbohydrate utilization, during low- and moderate-intensity exercise following oil supplementation. However, oil supplementation does not appear to alter substrate oxidation at high exercise intensities (> 50–60 percent $V_{O_2}max$). The increase in fat oxidation during low-intensity exercise may be related to changes in plasma lipase activity and mechanisms for fat utilization in skeletal muscle. In the study by Dunnett et al. (2002), parallel increases in plasma total lipase activity, circulating FFA during exercise, and activity of CS in skeletal muscle were detected. However, whereas the fat-supplementation–induced decrease in RER was correlated to the increase in muscle CS activity (r^2 = 0.95), there was no relationship to changes in FFA concentrations or to total lipase or β-hydroxyacyl CoA dehydrogenase activities.

The length of time required for expression of these metabolic adaptations to dietary oil has been debated. Some nutritionists have advocated that a minimum of 10–12 weeks is required for full adaptation (Kronfeld and Harris, 2003). However, metabolic adaptations to oil supplementation have been observed as early as 3–5 weeks after the start of supplementation (Pagan et al., 1987, 1995; Orme et al., 1997; Pagan et al., 2002). Thus, whereas a 2–3 month period may be required for complete adaptation to an oil-supplemented diet, some of the metabolic responses are evident much earlier. Importantly, the metabolic response to oil supplementation is apparently transient and dependent on its continued use. In one study, the effects on RER were abolished within

5 weeks of withdrawal of the oil-supplemented diet (Dunnett et al., 2002).

Whereas the aforementioned adaptations in lipid metabolism (e.g., decreased RER during low-intensity exercise) might imply a sparing of muscle glycogen, the available data do not support this view. Essen-Gustavsson et al. (1991) and Pagan et al. (1987) reported no effect of fat supplementation (approximately 7 percent of total DM intake) on muscle glycogen utilization of Standardbred horses during 60–100 minutes of submaximal exercise. Similarly, Harkins et al. (1992) and Eaton et al. (1995) reported no change in net muscle glycogen utilization in fat-supplemented Thoroughbred horses undertaking exercise that simulated race performance. Other researchers (Oldham et al., 1990; Jones et al., 1991; Scott et al., 1992; Hughes et al., 1995) have reported higher net muscle glycogen utilization and plasma lactate concentrations and improved performance during exercise tests consisting of multiple sprints (e.g., 4×600 m). The improved performance was attributed to the higher glycogen stores and maintenance of anaerobic energy transduction during sprint exercise.

A single study has examined the effects of dietary fish (menhaden) oil supplementation on metabolic response to incremental treadmill exercise in horses (O'Connor et al., 2004). Horses were assigned to either a fish oil (n = 6) or corn oil (n = 4) treatment in which the oil (324 mg/kg BW) was supplemented to a hay and concentrate ration for 63 days. The horses underwent moderate physical conditioning 5 days/week and completed an incremental exercise test after 63 days. During the test, horses that received fish oil had significantly lower heart rate and serum free fatty acid, glycerol, and cholesterol concentrations when compared to the corn oil treatment. The physiological importance of these findings remains to be determined.

Acid-Base Responses

Adaptation to a fat-supplemented diet influences blood acid-base responses to exercise. During a treadmill exercise test, venous pH was higher (~ 7.44–7.46) in Arabian horses fed a diet supplemented with corn oil (100 g/kg DM) when compared to the control diet (~ 7.40–7.42) at speeds between 3 and 6 m/s (Taylor et al., 1995; Kronfeld et al., 1998). There also was a decrease in venous blood pCO_2 during repeated sprints, which was attributed to a lower RER associated with enhanced fat oxidation, although RER was not measured (Kronfeld et al., 1998). Graham-Thiers et al. (2001) showed that dietary protein restriction (crude protein 7.5 g/100 g with supplemental L-lysine [0.5 percent] and L-threonine [0.3 percent]) had an additive effect with fat supplementation (corn oil, 100 g/kg DM) in the mitigation of the acidogenic effects of exercise. The biological significance of these small alterations in acid-base response to exercise is unclear.

This research group (Ferrante et al., 1994; Taylor et al., 1995) also reported higher plasma lactate concentrations during repeated sprints or incremental exercise in horses fed an oil-supplemented diet. The mechanism of this response is unclear. One hypothesis is that "fat adaptation" confers improved metabolic regulation of glucose utilization in muscle, with glycogen sparing at work of low intensity but enhanced glycolysis and lactate production during exercise requiring higher power output (Kronfeld et al., 1998). An alternative explanation is down regulation in the activity of skeletal muscle pyruvate dehydrogenase in response to oil feeding, as has been observed in humans (Spriet and Watt, 2003). It should also be noted that other researchers have reported lower plasma lactate accumulation during submaximal incremental exercise when horses are fed an oil-supplemented (11.8 percent fat, DM basis) diet (Sloet van Oldruitenborgh-Oosterbaan et al., 2002).

Athletic Performance

A number of researchers have attempted to determine the effects of fat supplementation on athletic performance. It has been hypothesized that adaptation to fat supplementation results in an improvement in the athletic performance of horses. Several theoretical explanations have been put forth as explanations for enhanced athletic performance with the feeding of higher-fat diets, including: (1) an improved power-to-weight ratio due to a reduction in DM intake and bowel ballast; (2) decreased metabolic heat production associated with feeding and exercise (Kronfeld, 1996); (3) enhanced stamina as a result of muscle glycogen sparing (Kronfeld et al., 1998); (4) improved sprint performance due to increased energy transduction from anaerobic glycolysis (Oldham et al., 1990; Kronfeld et al., 1998); and (5) mitigation of acidemia during high-intensity exercise (Kronfeld et al., 1998). However, the results of studies examining the effects of fat supplementation in horses on athletic performance are equivocal. Some authors have reported improved performance (Oldham et al., 1990; Harkins et al., 1992; Eaton et al., 1995), while others have found no change (Topliff et al., 1983; Pagan et al., 1987; Essen-Gustavsson et al., 1991; Hyyppa et al., 1999). Harkins et al. (1992) reported that 14 of 15 horses ran a 1,600-m simulated race faster when fed a fat-supplemented diet (corn oil, 3 percent DM for 3 weeks) compared to the control ration. Mean race time improved 2.5 s (2.1 percent) after consuming the fat-added diet. However, as discussed above, this experiment was inappropriately designed. A longitudinal design was used with all horses completing the control-diet race first, with the fat-diet race undertaken after a further 3 weeks of training. It is possible, therefore, that the observed decrease in simulated race time was due to training rather than oil supplementation. Furthermore, as the horses were not fed hay during the second diet period, it is possible the faster race time was associated with a reduction in gut weight.

Four weeks of fat supplementation (12 percent DE from corn oil) was associated with a small but statistically significant increase in run time to fatigue in Thoroughbred horses undertaking treadmill exercise at an intensity equivalent to 120 percent of VO_2max (Eaton et al., 1995). Earlier studies of the effects of fat supplementation found enhanced performance during exercise protocols consisting of repeated sprints (Meyers et al., 1987; Oldham et al., 1990; Scott et al., 1992) or efforts during protocols that simulated exercise undertaken by cutting horses (Webb et al., 1987). Improved work performance during high-intensity exercise was attributed to increases in resting muscle glycogen content and the rate of glycogen utilization. However, in the study by Eaton et al. (1995), there was no effect of diet on glycogen utilization rate during exercise.

Several factors could account for the variability in results between studies, including the type and amount of fat supplemented, duration of fat feeding, variation in the intensity and duration of exercise tests, small number of horses per treatment (most often fewer than six), and differences in the conditioning status of the horses.

Behavior

There are limited published data on the effects of fat supplementation on behavior of horses. Holland et al. (1996a) evaluated the effects of fat supplementation on spontaneous activity (distance moved per day, measured by use of a pedometer) and reactivity (responses to pressure, loud noise, and sudden visual stimuli) in eight horses. The control diet (CON) contained chopped hay, corn, oats, beet pulp, and molasses, while the three test diets contained an additional 10 percent (by weight) corn oil (CO), soy lecithin-corn oil (SL-CO), or soy lecithin-soy oil (SL-SO), with small decreases in hay, grains, and molasses. Horses were fed each diet in random order for four 3-week periods. When compared to CON, spontaneous activity was less in horses fed SL-CO (~ 4 km/day vs. ~ 5 km/day in CON) but unaffected by the CO or SL-SO diets. Similarly, there was no consistent effect of fat supplementation on measures of reactivity, although startle response to the sudden opening of an umbrella was decreased in all three diets. In studies examining the effect of dietary energy source on the clinical expression of recurrent exertional rhabdomyolysis in Thoroughbreds, researchers have reported decreased excitability, nervousness, and resting heart rate when the horses were consuming a fat-supplemented ration when compared to a high-grain ration (MacLeay et al., 2000; McKenzie et al., 2003). These authors suggested that the effect of fat supplementation on the behavior of RER-affected horses was due to the exclusion of dietary starch rather than a specific effect of dietary fat. Other researchers have reported a reduction in the exercise-associated increase in plasma cortisol concentration in horses fed a fat-supplemented ration (Crandell et al., 1999; Graham-Thiers et al., 2001).

Holland et al. (1996b) found lower plasma cortisol concentrations in 4- to 5-month-old foals fed a fat-and-fiber supplement when compared to a starch and sugar (sweet feed) supplement. Subjectively, the foals fed the fat-and-fiber supplement were less stressed after weaning. In a longitudinal study of growing horses, supplementation with a fat and fiber concentrate was associated with lower apparent distress at weaning and diminished responses to standardized temperament tests when compared to a starch-and-sugar concentrate (Nicol et al., 2005).

Lactation, Reproductive Performance, and Growth

Davison et al. (1987, 1991) added 5 percent animal fat to concentrates fed to pregnant and lactating Quarter horse mares. Feed consumption was lower during gestation, while growth rate tended to be higher in foals of mares fed the supplemented diet compared to mares and foals fed the unsupplemented diet (Davison et al., 1987, 1991). Fat supplementation increased milk fat concentration at days 10 and 60 of lactation, but protein and total solids content were unaffected. The feeding of fat to mares during late gestation and early lactation did not affect reproductive performance (Davison et al., 1991). Growth of Thoroughbred weanlings kept at pasture and fed a 10-percent fat supplement was not different when compared to weanlings fed an isocaloric supplement rich in starch and sugar (Hoffman et al., 1999).

Health Effects of Dietary (n-3) vs. (n-6) Fatty Acids

In other species, the two recognized EFAs are linoleic acid (18:2, n-6) and α-linolenic acid (18:3, n-3), both of which are PUFAs. Mammals lack the desaturase enzymes necessary to introduce double bonds into fatty acid chains that are more than nine carbons from the carboxyl terminus. Therefore, mammals are unable to synthesize n-3 and n-6 fatty acids, and they must be supplied in the diet (Dunbar and Bauer, 2002).

Soy, corn, sunflower, and safflower oils are rich in linoleic acid, while α-linolenic acid is the major fatty acid in linseed and flaxseed oils. Soy and canola oils also contain α-linolenic acid. The fatty acids in oils obtained from cold-water fish (e.g., menhaden oil) are rich in the n-3 fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). When supplied in the diet, EFAs can be converted to long-chain PUFAs by desaturase and chain-elongation enzymes located in the cellular endoplasmic reticulum. Linoleic acid is desaturated and elongated to yield arachidonic acid (20:4, n-6) and other long-chain PUFAs that are incorporated into cell membrane phospholipids, while metabolism of α-linolenic acid yields eicosapentaenoic acid (EPA; 20:5, n-3) and docosapentaenoic acid (22:5, n-3). Docosapentaenoic acid may be retroconverted to EPA (20:5, n-3) or further metabolized to DHA (22:6, n-3).

In human and animal nutrition there is interest in the potential health benefits of n-3 fatty acid supplementation (or alterations in the dietary n-6:n-3 ratio). The dietary n-6 vs. n-3 PUFA ratio affects the fatty acid composition of cell membranes (Simopoulos, 1999). When the diet of humans is supplemented with fish oil, the ingested EPA and DHA partially replace n-6 fatty acids (especially arachidonic acid) in cell membranes, particularly those of platelets, erythrocytes, neutrophils, and monocytes. This alteration in membrane fatty acid composition reduces the quantity of arachidonic acid available for eicosanoid synthesis, alters the spectrum of eicosanoids synthesized, and lessens the inflammatory and prothrombotic responses to physical or chemical stimuli (Hulbert et al., 2005). In addition, EPA competitively inhibits the activity of the enzyme cyclooxygenase, which is necessary for eicosanoid synthesis (Weber et al., 1986).

Several studies in horses have examined the effects of n-3 fatty acid supplementation on plasma fatty acid composition and various physiologic responses. Henry et al. (1990) fed horses a complete pelleted ration containing 8 percent (by weight) raw linseed oil vs. a control ration without added linseed oil. After 8 weeks on the ration, the mean procoagulant activity and thromboxane B_2 production by endotoxin-stimulated monocytes from horses consuming the linseed oil ration decreased by 51 percent and 71 percent, respectively, compared with cells from horses consuming the control ration. Fatty acid analysis of membrane phospholipids demonstrated a decrease in the n-6:n-3 ratio in monocytes from horses fed the linseed oil ration (Henry et al., 1990). In a companion study (Morris et al., 1991), it was shown that endotoxin-induced synthesis of tumor necrosis factor by peritoneal macrophages was lower in horses fed the linseed oil ration when compared to cells from horses fed the control ration. This research group also demonstrated that intravenous administration of a single dose of a 20 percent lipid emulsion enriched with n-3 fatty acids to healthy horses resulted in decreased inflammatory mediator synthesis (thromboxane, TNF-alpha) by monocytes and a lower n-6:n-3 fatty acid ratio in cell membranes when compared to the infusion of a lipid emulsion enriched with n-6 fatty acids (McCann et al., 2000). However, the feeding of an 8 percent linseed oil ration for 8 weeks did not alter the in vivo response of horses to the infusion of *Escherichia coli* 055:B5 endotoxin (0.03 mg/kg BW, infused over 30 minutes) (Henry et al., 1991). In another study, there were statistically significant increases in the plasma concentrations of α-linolenic acid (18:3, n-3) and EPA, but not DHA, in horses fed a 10 percent flaxseed oil-enriched complete pellet (80 percent of the ration) and hay (20 percent) for 16 weeks. However, in vitro measures of platelet aggregation were not altered by the supplementation of flaxseed oil (Hansen et al., 2002). More marked increases in plasma concentrations of EPA and DHA were observed when healthy horses were fed ration supplemented with fish (menhaden) oil. Hall et al. (2004a) fed horses diets supplemented with either 3 percent (by weight) corn oil or fish oil for 14 weeks. At 12 weeks, horses fed fish oil had increased plasma concentrations of EPA (27-fold; 8.5 vs. 0.3 g/100g fatty acids), DHA (34-fold; 5.1 vs. 0.1 g/100 g fatty acids), and arachidonic acid (8.3-fold; 4.1 vs. 0.5 g/100 g fatty acids). Neutrophils from horses fed fish oil produced 17.6-fold more leukotriene B_5 (LTB_5) compared with horses fed corn oil, and the ratio of LTB_5 to leukotriene B_4 was 4-fold high in horses fed fish oil. In addition, the quantity of prostaglandin E_2 by endotoxin-stimulated bronchoalveolar fluid (BALF) cells was lower in fish oil-fed when compared to corn oil-fed horses. However, the production of TNF-alpha by BALF cells did not differ between diets and cell- mediated immunity, assessed by the skin response to injection of the key-hole limpet hemocyanin, was similar in the corn oil- and fish oil-fed horses (Hall et al., 2004b).

Supplementation of horses with recurrent seasonal pruritis ("sweet itch") with large amounts of flaxseed (454 g flaxseed/450 kg BW) was associated with a significant decrease in the allergic skin response to *Culicoides* extract, suggesting a possible benefit of flaxseed in the management of horses with this condition. However, in another study, supplementation with flax oil did not alter clinical signs in horses with *Culicoides* hypersensitivity (Friberg and Logas, 1999).

In summary, the data from studies in which horses were fed diets enriched with omega-3 (n-3) fatty acids (linseed, flaxseed, or fish oils) have demonstrated modulation of inflammatory mediator synthesis by cells harvested from blood, peritoneal fluid, or respiratory secretions. However, physiological importance of these findings is unclear, and further research is needed to determine the effects of n-3 fatty acid supplementation in the treatment and prevention of inflammatory diseases in horses (e.g., recurrent airway obstruction) (McCann and Carrick, 1998).

REQUIREMENTS, DEFICIENCIES, AND EXCESSES

Dietary fats or oils are required to facilitate absorption of the fat-soluble vitamins A, D, E, and K, and as a source of the EFAs, linoleic and α-linolenic. There have been no reports of EFA deficiency in horses. In other species, an EFA deficiency causes dry coat, scaly skin, hair loss, and, with prolonged deficiency, development of exudative dermatitis (Connor, 2000). Decreased reproductive efficiency and fetal abnormalities are other potential consequences of an EFA deficiency. No clinical abnormalities were observed in ponies fed extremely low-fat diets (0.05 percent and 0.22 percent total fat containing, respectively, 0.03 and 0.14 percent linoleic acid) for 7 months (Sallmann et al., 1991). However, a substantial decrease in plasma and tissue vitamin E concentration was observed in ponies fed the 0.05 percent fat diet, suggesting that there was inadequate intestinal absorption of this fat-soluble vitamin.

A suggested dietary minimum for linoleic acid is 0.5 percent of DM. This minimum is easily achieved when supple-

mental fat is fed, as fats and oils added to equine rations are high in linoleic acid (see Table 8-5). Because fat is energy dense, one concern with the feeding of fat-supplemented diets is weight gain associated with the provision of DE in excess of needs. The promotion of weight gain in hard keeper horses is a common rationale for the addition of fat to equine diets. For less active or easy keeper horses, however, use of fat-supplemented energy concentrates may lead to undesirable weight gain. Metabolic utilization of absorbed fat is highly efficient. In ponies fed supplemental corn oil, the DE to net energy (NE) conversion efficiency was about 85 percent (Kane et al., 1979). The comparative efficiency for a hay/grain diet is less than 60 percent. Accordingly, the NE of fat-supplemented feeds is higher than is predicted by estimation of the DE content.

In Shetland ponies, there is evidence that fat supplementation (soybean oil, 10 percent DM) results in glucose intolerance (Schmidt et al., 2001). When ponies were fed to meet DE requirement (15.5 MJ DE/100 kg BW), mean plasma glucose concentrations during an oral glucose tolerance test (1 g/kg BW) were approximately 40 percent higher in the fat-supplemented diet when compared to the control diet. Furthermore, the feeding of a hypercaloric (18.5 MJ DE/100 kg BW) fat-enriched diet resulted in a 25-fold increase in plasma insulin concentrations after oral glucose loading. Thus, glucose intolerance and insulin resistance may occur in ponies fed fat-supplemented diets, particularly when energy intake exceeds requirements. As insulin resistance is considered a risk factor for laminitis in ponies, some caution in the feeding of fat-supplemented diets is warranted.

Most of the studies evaluating the effects of fat supplementation in horses have been of short duration (less than 3 months). However, Pagan et al. (1995) observed no adverse effects in 2-year-old Thoroughbreds fed supplemental fat (soybean oil, 12 percent DE) for 7 months. Harris et al. (1999) reported no apparent adverse effects of feeding a diet supplemented with either an unsaturated or saturated vegetable oil for 6 months at 20 percent DE after 10 months at 12 percent DE. In Warmblood-type horses, no detrimental effects on blood biochemical variables were observed after feeding a mixed diet containing 14 percent and 16.3 percent partially hydrogenated soy oil for, respectively, 168 (Zeyner and Dittrich, 2003) and 390 (Zeyner et al., 2002) days.

REFERENCES

Bowman, V. A., J. P. Fontenot, T. N. Meacham, and K. E. Webb. 1979. Acceptability and digestibility of animal, vegetable and blended fats by equine. Pp. 74–75 in Proc. 6th Equine Nutr. Physiol. Soc. Symp., College Station, TX.

Bush, J. A., D. E. Freeman, K. H. Kline, N. R. Merchen, and G. C. Fahey, Jr. 2001. Dietary fat supplementation effects on in vitro nutrient disappearance and in vivo nutrient intake and total digestibility by horses. J. Anim. Sci. 79:232–239.

Connor, W. E. 2000. Importance of n-3 fatty acids in health and disease. Am. J. Clin. Nutr. 71(suppl):171S–175S.

Coppock, C.E., and D. L. Wilks. 1991. Supplemental fat in high energy rations for lactating cows: effects on intake, digestion, milk yield and composition. J. Anim. Sci. 69:3826–3837.

Crandell, K. G., J. D. Pagan, P. Harris, and S. E. Duren. 1999. A comparison of grain, oil and beet pulp as energy sources for the exercised horse. Equine Vet. J. Suppl. 30:485–489.

Custalow, S. E. 1992. Lactate and Glucose Responses to Exercise in the Horse: Influence of Interval Training and Dietary Fat. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Davison, K. E., G. D. Potter, J. W. Evans, L. W. Greene, P. S. Hargis, C. D. Corn, and S. P. Webb. 1987. Growth and nutrient utilization in weanling horses fed added dietary fat. Pp. 95–100 in Proc. 11th Equine Nutr. Physiol. Soc. Symp., Stillwater, OK.

Davison, K. E., G. D. Potter, L. W. Greene, J. W. Evans, and W. C. MacMullan. 1991. Lactation and reproductive performance of mares fed added dietary fat during late gestation and early lactation. J. Equine Vet. Sci. 11:111–115.

Dunbar, B. L., and J. E. Bauer. 2002. Metabolism of dietary essential fatty acids and their conversion to long-chain polyunsaturated metabolites. J. Am. Vet. Med. Assoc. 220:1621–1626.

Dunnett, C. E., D. J. Marlin, and R. C. Harris. 2002. Effect of dietary lipid on response to exercise: relationship to metabolic adaptation. Equine Vet. J. Suppl. 34:75–80.

Duren, S. E., S. G. Jackson, J. P. Baker, and D. K. Aaron. 1987. Effect of dietary fat on blood parameters in exercised Thoroughbred horses. Pp. 674–685 in Equine Exercise Physiology 2, J. R. Gillespie and N. E. Robinson, eds. Davis, CA: ICEEP Publications.

Eaton, M. D., D. R. Hodgson, and D. L. Evans. 1995. Effect of diet containing supplementary fat on the effectiveness for high intensity exercise. Equine Vet. J. Suppl 18:353–356.

Essen-Gustavsson, B., E. Blomstrand, K. Karlstrom, A. Lindholm, and S. G. B. Persson. 1991. Influence of diet on substrate metabolism during exercise. Pp. 288–298 in Equine Exercise Physiology 3, S. G. B. Persson, A. Lindholm, and L. B. Jeffcott, eds. Upsala: ICEEP Publications.

Ferrante, P. L., D. S. Kronfeld, L. E. Taylor, and T. N. Meacham. 1994. Blood lactate concentration during exercise in horses fed a high-fat diet and administered sodium bicarbonate. J. Nutr. 124:2738S–2739S.

Fonnesbeck, P. V., R. K. Lydman, G. W. Vander Noot, and L. D. Symons. 1967. Digestibility of the proximate nutrients of forage by horses. J. Anim. Sci. 26:1039–1045.

Friberg, C. A., and D. Logas. 1999. Treatment of culicoides hypersensitive horses with high-dose n-3 fatty acids: a double-blinded crossover study. Vet. Dermatol. 10:117–122.

Geelen, S. N. J., M. M. Sloet van Oldruitenborgh-Oosterbaan, and A. C. Beynen. 1999. Dietary fat supplementation and equine plasma lipid metabolism. Equine Vet. J. Suppl. 30:475–478.

Geelen, S. N. J., W. L. Jansen, M. J. H. Geelen, M. M. Sloet van Oldruitenborgh-Oosterbaan, and A. C. Beynen. 2000. Lipid metabolism in equines fed a fat-rich diet. Int. J. Vitam. Nutr. Res. 70:148–152.

Geelen, S. N. J., W. L. Jansen, M. M. Sloet van Oldruitenborgh-Oosterbaan, H. J. Breukink, and A. C. Beynen. 2001a. Fat feeding increases equine heparin-released lipoprotein lipase activity. J. Vet. Int. Med. 15:478–481.

Geelen, S. N. J., C. Blazquez, M. J. H. Geelen, M. M. Sloet van Oldruitenborgh-Oosterbaan, and A. C. Beynen. 2001b. High fat intake lowers fatty acid synthesis and raises fatty acid oxidation in aerobic muscle in Shetland ponies. Br. J. Nutr. 86:31–36.

Graham-Thiers, P., D. S. Kronfeld, and D. J. Sklan. 2001. Dietary protein restriction and fat supplementation diminish the acidogenic effect of exercise during repeated sprints in horses. J. Nutr. 131:1959–1964.

Hall, J. A., R. J. Van Saun, and R. C. Wander. 2004a. Dietary (n-3) fatty acids from menhaden fish oil alter plasma fatty acids and leukotriene B synthesis in healthy horses. J. Vet. Int. Med. 18:871–879.

Hall, J. A., R. J. Van Saun, S. J. Tournquist, J. L. Grandin, E. C. Pearson, and R. C. Wander. 2004b. Effect of type of dietary polyunsaturated fatty acid supplement (corn oil or fish oil) on immune responses in healthy horses. J. Vet. Int. Med. 18:880–886.

Hambleton, P. L., L. M. Slade, D. W. Hamar, E. W. Kienholz, and L. D. Lewis. 1980. Dietary fat and exercise conditioning effect on metabolic parameters in the horse. J. Anim. Sci. 51:1330–1339.

Hansen, R. A., C. J. Savage, K. Reidlinger, J. L. Traub-Dargatz, G. K. Ogilvie, D. Mitchell, and M. J. Fettman. 2002. Effects of dietary flaxseed oil supplementation on equine plasma fatty acid concentrations and whole blood platelet aggregation. J. Vet. Int. Med. 16:457–463.

Harkins, J. D., G. S. Morris, R. T. Tulley, A. G. Nelson, and S. G. Kamerling. 1992. Effect of added dietary fat on racing performance in Thoroughbred horses. J. Equine Vet. Sci. 12:123–129.

Harris, P. A., J. D. Pagan, K. G. Crandell, and N. P. Davidson. 1999. Effect of feeding Thoroughbred horses a high unsaturated or saturated vegetable oil supplemented diet for 6 months following a 10 month fat acclimation. Equine Vet. J. Suppl. 30:468–474.

Henry, M. M., J. N. Moore, E. B. Feldman, J. K. Fischer, and B. Russell. 1990. Effect of dietary alpha-linolenic acid on equine monocyte procoagulant activity and eicosanoid synthesis. Circ. Shock 32:173–188.

Henry, M. M., J. N. Moore, and J. K. Fischer. 1991. Influence of an omega-3 fatty acid-enriched ration on in vivo responses of horses to endotoxin. Am. J. Vet. Res. 52:523–527.

Hintz, H. F., and F. F. Schryver. 1989. Digestibility of various sources of fat by horses. Pp. 44–48 in Cornell Nutr. Conf. for Feed Manuf., Syracuse, NY.

Hintz, H. F., M. W. Ross, F. R. Lesser, P. F. Leids, K. K. White, J. E. Lowe, C. E. Short, and H. F. Schryver. 1978. The value of dietary fat for working horses. 1. Biochemical and hematological evaluations. J. Equine Med. Surg. 2:483.

Hintz, H. F., J. E. Lowe, K. K. White, C. E. Short, and M. Ross. 1982. Nutritional value of fat for exercising horses. Unpublished data, Cornell University.

Hoffman, R. M., L. A. Lawrence, D. S. Kronfeld, W. L. Cooper, D. J. Sklan, J. J. Dascanio, and P. A. Harris. 1999. Dietary carbohydrates and fat influence radiographic bone mineral content of growing foals. J. Anim. Sci. 77:3330–3338.

Hoffman, R. M., R. C. Boston, D. Stefanovski, D. S. Kronfeld, and P. A. Harris. 2003. Obesity and diet affect glucose dynamics and insulin sensitivity in Thoroughbred geldings. J. Anim. Sci. 81:2333–2342.

Holland, J. L. 1994. Lecithin Containing Diets for the Horse: Acceptance, Digestibility and Effects on Behavior. M.S. Thesis. Virginia Polytechnic Institute and State Univ., Blacksburg.

Holland, J. L., D. S. Kronfeld, and T. N. Meacham. 1996a. Behavior of horses is affected by soy lecithin and corn oil in the diet. J. Anim. Sci. 74:1252–1255.

Holland, J. L., D. S. Kronfeld, R. M. Hoffman, and K. M. Griewe-Crandell. 1996b. Weaning stress is affected by nutrition and weaning methods. Pferdeheilkunde 12:257–260.

Holland, J. L., D. S. Kronfeld, G. A. Rich, K. A. Kline, J. P. Fontenot, T. N. Meacham, and P. A. Harris. 1998. Acceptance of fat and lecithin containing diets by horses. Appl. Anim. Behav. Sci. 56:91–96.

Hughes, S. F., G. D. Potter, L. W. Greene, T. W. Odom, and M. Murray-Gerzik. 1995. Adaptation of Thoroughbred horses in training to a fat supplemented diet. Equine Vet. J. Suppl. 18:349–352.

Hulbert, A. J., N. Turner, L. H. Storlein, and P. L. Else. 2005. Dietary fats and membrane function: implications for metabolism and disease. Biol. Rev. 80:155–159.

Hyyppa, S., M. Saastamoinen, and A. R. Poso. 1999. Effect of a post exercise fat-supplemented diet on muscle glycogen repletion. Equine Vet. J. Suppl. 30:493–498.

Jansen, W. L., J. van der Kuilen, S. N. J. Geelen, and A. C. Beynen. 2000. The effect of replacing nonstructural carbohydrates with soybean oil on the digestibility of fiber in trotting horses. Equine Vet. J. 32:27–30.

Jansen, W. L., J. van der Kuilen, S. N. Geelen, and A. C. Beynen. 2001. The apparent digestibility of fiber when dietary soybean oil is substituted for an iso-energetic amount of glucose. Arch. Tierernahr. 54:297–304.

Jansen, W. L., S. N. J. Geelen, J. van der Kuilen, and A. C. Beynen. 2002. Dietary soyabean oil depressed the apparent digestibility of fibre in trotters when substituted for an iso-energetic amount of corn starch or glucose. Equine Vet. J. 34:302–305.

Jones, D. L, G. D. Potter, L. W. Greene, and T. W. Odom. 1991. Muscle glycogen concentrations in exercised miniature horses at various body conditions and fed a control or fat-supplemented diet. P. 109 in Proc. 12th Equine Nutr. Phys. Soc. Symp., Calgary, Alberta.

Julen, T. R., G. D. Potter, L. W. Greene, and G. G. Stott. 1995. Adaptation to a fat-supplemented diet by cutting horses. Pp. 56–61 in Proc. 14th Equine Nutr. Physiol. Soc. Symp., Ontario, CA.

Kane, E. J., J. P. Baker, and L. S. Bull. 1979. Utilization of a corn oil supplemented diet by the pony. J. Anim. Sci. 48:1379–1383.

Kronfeld, D. S. 1996. Dietary fat affects heat production and other variables of equine performance under hot and humid conditions. Equine Vet. J. Suppl. 22:24–34.

Kronfeld, D. S., and P. A. Harris. 2003. Equine grain-associated disorders. Comp. Contin. Educ. Pract. Vet. 25:974–983.

Kronfeld, D. S., S. E. Custalow, P. L. Ferrante, L. E. Taylor, J. A. Wilson, and W. Tiegs. 1998. Acid-base responses of fat-adapted horses: relevance to hard work in the heat. Appl. Anim. Behav. 59:61–72.

Kronfeld, D. S., J. L. Holland, G. A. Rich, S. E. Custalow, J. P. Fontenot, T. N. Meacham, D. J. Sklan, and P. A. Harris. 2004. Fat digestibility in *Equus caballus* follows increasing first-order kinetics. J. Anim. Sci. 82:1773–1780.

MacLeay, J. M., S. J. Valberg, J. D. Pagan, F. de laCorte, J. Roberts, J. Billstrom, J. McGinnity, and H. Kaese. 1999. Effect of diet on thoroughbred horses with recurrent exertional rhabdomyolysis performing a standardised exercise test. Equine Vet. J. Suppl. 30:458–462.

MacLeay, J. M., S. J. Valberg, J. Pagan, J. A. Billstrom, and J. Roberts. 2000. Effect of diet and exercise intensity on serum CK activity in Thoroughbreds with recurrent exertional rhabdomyolysis. Am. J. Vet. Res. 61:1390–1395.

McCann, J. S., T. N. Meacham, and J. P. Fontenot. 1987. Energy utilization and blood traits of ponies fed fat-supplemented diets. J. Anim. Sci. 65:1019–1026.

McCann, M. E., and J. B. Carrick. 1998. Potential uses of ω-3 fatty acids in equine diseases. Comp. Cont. Educ. Pract. Vet. 20:637–641.

McCann, M. E., J. N. Moore, J. B. Carrick, and M. H. Barton. 2000. Effect of intravenous infusion of omega-3 and omega-6 lipid emulsions on equine monocytes fatty acid composition and inflammatory mediator production in vitro. Shock 14:222–228.

McKenzie, E. C., S. J. Valberg, S. Godden, J. D. Pagan, J. M. MacLeay, R. J. Geor, and G. P. Carlson. 2003. Effect of dietary starch, fat and bicarbonate content on exercise responses and serum creatine kinase activity in equine recurrent exertional rhabdomyolysis. J. Vet. Int. Med. 17:693–701.

Meyer, H., C. Flothow, and S. Radicke. 1997. Preileal digestibility of coconut 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., G. D. Potter, L. W. Greene, S. F. Crouse, and J. W. Evans. 1987. Physiological and metabolic response of exercising horses to added dietary fat. Pp. 107–113 in Proc. 10th Equine Nutr. Physiol. Soc. Symp., Fort Collins, CO.

Morris, D. D., M. M. Henry, J. N. Moore, and J. K. Fisher. 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.

Nicol, C. J., A. J. Badwell-Waters, R. Rice, A. Kelland, A. D. Wilson, and P. A. Harris. 2005. The effects of diet and weaning method on the behavior of young horses. Appl. Anim. Behav. Sci. 95:205–221.

O'Connor, C. I., L. M. Lawrence, A. C. St. Lawrence, K. M. Janicki, L. K. Warren, and S. Hayes. 2004. The effect of dietary fish oil supplementation on exercising horses. J. Anim. Sci. 82:2978–2984.

Oldham, S. L., G. D. Potter, J. W. Evans, S. B. Smith, T. S. Taylor, and W. S. Barnes. 1990. Storage and mobilization of muscle glycogen in exercising horses fed a fat-supplemented diet. J. Equine Vet. Sci. 10:353–359.

Orme, C. E., R. C. Harris, D. J. Marlin, and J. Hurley. 1997. Metabolic adaptation to a fat-supplemented diet by the Thoroughbred horse. Br. J. Nutr. 78:443–458.

Pagan, J. D., B. Essen-Gustavsson, A. Lindholm, and J. Thornton. 1987. The effect of dietary energy source on exercise performance in Standardbred horses. Pp. 686–799 in Equine Exercise Physiology 2, J. R. Gillespie and N. E. Robinson, eds. Davis, CA: ICEEP Publications.

Pagan, J. D., I. Burger, and S. G. Jackson. 1995. The long term effects of feeding fat to 2-year-old Thoroughbreds in training. Equine Vet. J. Suppl. 18:343–348.

Pagan, J. D., R. J. Geor, P. A. Harris, K. Hoekstra, S. Gardner, C. Hudson, and A. Prince. 2002. Effects of fat adaptation on glucose kinetics and substrate oxidation during low-intensity exercise. Equine Vet. J. Suppl. 34:33–38.

Potter, G. D., S. L. Hughes, T. R. Julen, and S. L. Swinney. 1992. A review of research on digestion and utilization of fat by the equine. Pferdeheilkunde Sonderheft 1:119–123.

Rich, V. A. B. 1980. Digestibility and Palatability of Animal, Vegetable and Animal-Vegetable Blended Fats by the Equine. Ph.D. Diss., Virginia Polytechnic Institute and State Univ., Blacksburg.

Sallmann H. P., E. Kienzle, H. Fuhrmann, D. Grunwald, I. Eilmans, and H. Meyer. 1991. Metabolic consequences of feeding ponies with marginal amounts of fat. Pp. 81–82 in Proc. 12th Equine Nutr. Physiol. Soc. Symp., Calgary, Alberta.

Schmidt, O., E. Deegen, H. Fuhrmann, R. Duhlmeier, and H. P. Sallmann. 2001. Effects of fat feeding and energy level on plasma metabolites and hormones in Shetland ponies. J. Vet. Med. 48A:39–49.

Scott, B. D., G. D. Potter, L. W. Greene, P. S. Hargis and J. G. Anderson. 1992. Efficacy of a fat-supplemented diet on muscle glycogen concentrations in exercising Thoroughbred horses maintained in varying body conditions. J. Equine Vet. Sci. 12:105–109.

Simopoulos, A. P. 1999. Essential fatty acids in health and chronic disease. Am. J. Clin. Nutr. 70 (Suppl):560S–569S.

Slade, L. M., L. D. Lewis, C. R. Quinn, and M. L. Chandler. 1975. Nutritional adaptations of horses for endurance performance. Pp. 114–128 in Proc. 4th Equine Nutr. Physiol. Soc. Symp., Pomona, Calif.

Sloet van Oldruitenborgh-Oosterbaan, M. M., M. P. Annee, E. J. M. M. Verdegaal, A. G. Lemens, and A. C. Beynen. 2002. Exercise and metabolism-associated blood variables in Standardbreds fed either a low- or a high-fat diet. Equine Vet. J. Suppl. 34:29–32.

Spriet, L. L., and M. J. Watt. 2003. Regulatory mechanisms in the interaction between carbohydrate and lipid oxidation during exercise. Acta. Physiol. Scand. 178:443–452.

Sturgeon, L. S., L. A. Baker, J. L. Pipkin, J. C. Haliburton, and N. K. Chirase. 2000. The digestibility and mineral availability of matua, bermuda grass, and alfalfa hay in mature horses. J. Equine Vet. Sci. 20:45–48.

Taylor, L. E., P. L. Ferrante, D. S. Kronfeld, and T. N. Meacham. 1995. Acid-base variables during incremental exercise in sprint-trained horses fed a high-fat diet. J. Anim. Sci. 73:2009–2018.

Topliff, D. R., G. D. Potter, T. R. Dutson, J. L. Kreider, and G. T. Jessup. 1983. Diet manipulation and muscle glycogen in the equine. Pp. 224–229 in Proc. 8th Equine Nutr. Physiol. Soc. Symp., Lexington, KY.

Webb, S. P., G. D. Potter, and J. W. Evans. 1987. Physiologic and metabolic response of race and cutting horses to added dietary fat. P. 115 in Proc. 10th Equine Nutr. Physiol. Soc. Symp., Fort Collins, CO.

Weber, P. C., S. Fischer, C. von Schacky, R. Lorenz, and T. Strasser. 1986. Dietary omega-3 polyunsaturated fatty acids and eicosanoid formation in man. Pp. 49–60 in Health Effects of Polyunsaturated Fatty Acids in Seafoods, A. P. Simipoulos, R. R. Kifer, and R. E. Martin, eds. Orlando, FL: Academic Press.

Williams, C. A., D. S. Kronfeld, W. B. Staniar, and P. A. Harris. 2001. Plasma glucose and insulin responses of Thoroughbred mares fed a meal high in starch and sugar or fat and fiber. J. Anim. Sci. 79:2196–2200.

Zeyner, A. 2002. Ernährungsphysiolische Wirkungen eines Austusches von starker-eichen Konponenten durch Sojaöl in der Reitpferdeernährung. Göttingen: Georg-August-University, Habilitation thesis.

Zeyner, A., and A. Dittrich. 2003. Digestibility of energy, proximate nutrients and minerals and indicators of gut microbial activity in horses fed a moderate amount of soybean oil over 168 days. Proc. Soc. Nutr. Physiol. 12:98.

Zeyner, A., J. Bessert, and J. M. Gropp. 2002. Effect of feeding exercised horses on high starch or high fat diets for 390 days. Equine Vet. J. Suppl. 34:50–57.

Zeyner, A., C. Hoffmeister, A. Einspanier, and O. Lengwenat. 2005. Glycemic and insulinemic response of Quarter horses to concentrates high in fat and low in soluble carbohydrates. P. 312 in Proc. 19th Equine Sci. Soc., Tucson, AZ.