

# Dynamics of ruminant fat digestion: Part 1

Currently, a major area of interest is the biology and dynamics of fatty acid digestion in ruminants, especially related to the issue of the digestibility of individual fatty acids in the small intestine.

By **A.L. LOCK, K.J. HARVATINE, I. IPHARRAGUERRE, M. VAN AMBURGH, J.K. DRACKLEY** and **D.E. BAUMAN\***

**O**UR understanding of fat and fatty acid digestion and metabolism in ruminants has advanced significantly over the last decade, and these advances were the focus of our review at the Cornell Nutrition Conference in 2003 (Bauman et al., 2003).

In particular, we now recognize that fatty acids, both of dietary and rumen origin, can have specific and potent effects on ruminant metabolism and human health. Furthermore, the use of dietary fat supplements has increased and will continue to do so as nutritionists strive to increase the energy density of diets to meet requirements of the high-producing dairy cow.

Both of these areas have driven recent efforts to include lipid metabolism in models of ruminant digestion (e.g., Moate et al., 2004), which may potentially be useful in diet formulations and decision-making processes and recommendations.

Currently, a major area of interest is the biology and dynamics of fatty acid digestion. This relates to the contentious issue of the digestibility of individual fatty acids in the small intestine. In particular, there is confusion regarding the digestibility of stearic acid in dairy cows and the extent to which its digestibility differs from other fatty acids.

Consequently, there is also debate on the effects of different fat supplements on fat digestibility.

In the following sections, we will review the biology of digestion and absorption of fatty acids in the lactating dairy cow and highlight differences between ruminants and non-ruminants. We will also provide a summary of the available literature regarding the digestibility of individual fatty acids in lactating

dairy cows. Finally, implications of these findings with regard to the effects of different fat supplements on fat digestibility will be discussed.

## Biology of absorption

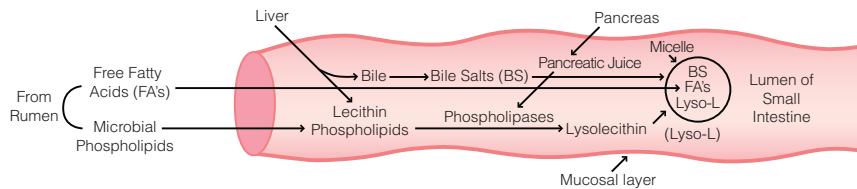
In a previous presentation, we reviewed in detail the metabolism of dietary fats and fatty acids in the rumen (Bauman et al., 2003). In brief, bacterial enzymes hydrolyze the dietary glycerides and hydrogenate

the unsaturated free fatty acids. Thus, the lipid material leaving the rumen consists primarily of highly saturated free fatty acids, with the saturated fatty acids being about one-third palmitic and two-thirds stearic.

Because there is no significant absorption or modification of long- and medium-chain fatty acids in the omasum or abomasum, the lipid material available for absorption in the small intestine is similar to that leaving the rumen (Moore and Christie, 1984). This lipid material consists of approximately 80-90% free fatty acids attached to feed particles (Doreau and Chilliard, 1997).

The remaining lipid components are microbial phospholipids plus small amounts of triglycerides and glycolipids from residual feed material.

## Fat digestion in the small intestine of ruminants (reproduced from Davis, 1990)



## 1. Differences between ruminant and non-ruminant digestive tract pH (adapted from Moore and Christie, 1984)

	Sheep	Pigs
Abomasum/stomach	2.0	2.4
Proximal duodenum	2.5	6.1
Distal duodenum	3.5	6.8
Proximal jejunum	3.6-4.2	7.4
Distal jejunum	4.7-7.6	7.4
Ileum	8.0	7.5

## 2. Amphiphilic properties of some polar lipids (adapted from Freeman, 1969 and 1984)

Amphiphile	Amphiphilic index <sup>1</sup>	% increase or decrease in Km/o of stearic acid <sup>2</sup>
Oleic acid	0.138	-11
Monoglyceride (1-Monoolein)	0.138	+37
Linoleic acid	0.154	—
Lauric acid	0.164	—
Lysolecithin	0.280	+115

<sup>1</sup>The amphiphilic index is defined as the increase in stearic acid solubility in bile salt solution per unit increase in amphiphilic concentration.

<sup>2</sup>Distribution coefficient describing the distribution of stearic acid between the particulate oil phase and the micellar phase; a positive (+) value indicates that an amphiphile increases the distribution of stearic acid into the micellar phase, which would favor absorption.

These esterified fatty acids are hydrolyzed by intestinal and pancreatic lipases (Doreau and Ferlay, 1994).

Fatty acid absorption occurs predominantly in the jejunum region of the small intestine. Prior to reaching the jejunum, two secretions — bile and pancreatic juice — are added to the digesta in the duodenum. Because of the continuous flow of digesta entering the small intestine in the ruminant, the secretion of bile and pancreatic juices is continuous and not subject to large cyclic changes, like in non-ruminants (Noble, 1981).

Before fatty acid absorption can occur, it is necessary for the lipid material absorbed into the feed particles to be solubilized into the aqueous environment. In ruminants, as in all species, micelle formation is the key to this process and, therefore, key to efficient fatty acid absorption (Davis, 1990).

The essential and physiologically important feature of micellar solutions is their ability to dissolve (solubilize) the water-insoluble fatty acids by incorporating appropriately shaped and charged molecules either into the core or the outer sheath of the bile salt molecules that comprise the micellar matrix (Freeman, 1984).

In ruminants, both the bile and pancreatic secretions are required for this process. Bile supplies bile salts and lecithin, and pancreatic juice provides enzymes to convert lecithin to lysolecithin and bicarbonate to raise the pH. Lysolecithin, together with bile salts, desorbs the fatty acids from feed particles and bacteria, allowing the formation of the micelle (Figure).

The critical role of lysolecithin and bile salts in this process is illustrated in studies with sheep where fatty acid absorption was virtually eliminated when bile secretion into the duodenum was blocked (Moore and Christie, 1984).

Once micelles are formed, they facilitate transfer of water-insoluble lipids across the unstirred water layer of intestinal epithelial cells of the jejunum, where the fatty acids and lysolecithin are absorbed. The fatty acids are re-esterified into triglycerides and then packaged into chylomicrons for transport in blood.

The manner of presentation of lipids in the digesta of the small intestine together with the environment in which the lipid material exists differ markedly in ruminants and non-

ruminants (Noble, 1981).

In ruminants, the majority of lipid material entering the small intestine is in the free fatty acid form (80-90%) in contrast to non-ruminants, where the majority is esterified (> 90%). Also, the degree of neutralization of the acid digesta as it passes through the duodenum of the ruminant is significantly less than it is in non-ruminants, a consequence of the low concentration and rate of secretion of bicarbonate in ruminant pancreatic secretions (Moore and Christie, 1984).

Differences in the pH of the digestive tract between ruminants and non-ruminants are illustrated in Table 1. In reviewing the available literature, it is evident that the ruminant has evolved a number of key differences and features in fatty acid absorption compared with non-ruminants that allow for efficient absorption of fatty acids under the prevailing conditions.

First, ruminant bile is characterized by an excess of taurine-conjugated bile acids compared to glycine-conjugated bile acids. In most herbivores, glycine-conjugated bile acids predominate, but in the mature ruminant, taurine-conjugates exceed glycine-conjugates about 3:1 (Noble, 1981).

This is significant because under the acidic conditions of the ruminant upper small intestine (Table 1), taurine-conjugated bile acids remain in a partially ionized condition. Thus, taurine-conjugated bile acids are mainly in the micellar phase, where they are able to affect solubilization of fatty acids (Noble, 1981).

Even at pH 2.5, taurine-conjugates remain soluble and partly ionized, while glycine-conjugates are insoluble in much less acidic conditions (pH 4.5) and unable to affect solubilization (Moore and Christie, 1984).

The most significant difference in micelle formation between ruminants and non-ruminants is the source of amphiphile or "swelling agent" that promotes micelle formation. In non-ruminants, monoglycerides plus bile salts interact with the fatty acids to form the micelle, and the bile salt/monoglyceride complex serves as the stabilizer of the micelle (Davis, 1990).

Monoglycerides, short-chain saturated fatty acids, unsaturated fatty acids and phospholipids are able to infiltrate and increase the size (swell) of the bile salt micelle, in particular increasing the capacity of its hydrophobic core.

This is significant as non-polar solutes (i.e., long-chain saturated fatty acids) have non-amphiphilic characteristics and must be solubilized in the hydrophobic interior of the mixed micelle. Therefore, increasing the capacity of the micelle's hydrophobic core significantly enhances the solubility of long-chain saturated fatty acids with a consequent improvement in their absorption (Freeman, 1984).

In contrast to non-ruminants, ruminants have a low pH in the small intestine, and they form a bile salt/lysolecithin complex, as discussed earlier. Freeman (1969) examined the amphiphilic properties of polar lipid solutes and found that lysolecithin had a pronounced effect on the micellar solubility of stearic acid (Table 2).

In fact, lysolecithin's ability to increase the solubility of stearic acid is about twofold greater than that of other amphiphiles, including oleic acid that has been quoted recently as having important amphiphilic properties when fed as a calcium salt to ruminants (Moate et al., 2004; Block et al., 2005). Lysolecithin was, furthermore, the only amphiphile examined shown to significantly increase the distribution of stearic acid into the micellar phase and away from the particulate phase (Table 2).

Considering that most fatty acids leaving the rumen are saturated and the predominant fatty acid available for absorption is stearic acid, perhaps it is not surprising that the ruminant has evolved such an efficient system involving lysolecithin for solubilizing this fatty acid.

## References

The complete list of references can be found at [www.feedstuffs.com](http://www.feedstuffs.com) or by e-mailing [tlundeen@feedstuffs.com](mailto:tlundeen@feedstuffs.com).

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# Dynamics of ruminant fat digestion: Part 2

Currently, a major area of interest is the biology and dynamics of fatty acid digestion, especially relating to the issue of the digestibility of individual fatty acids in the small intestine.

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In our previous Cornell Nutrition Conference publication, we provided a brief overview of the digestibility of individual fatty acids (Bauman et al., 2003). In the following section, we have collated available data and summarized the 20 trials in which total and individual fatty acid intakes and duodenal flows were measured, 14 of which had calculations of intestinal digestibility of individual fatty acids (Bauchart et al., 1987; Murphy et al., 1987; Klusmeyer and Clark, 1991; Wu et al., 1991; Weisbjerg et al., 1992; Ferlay et al., 1993; Wonsil et al., 1994; Tice et al., 1994; Pantoja et al., 1996; Enjalbert et al., 1997; Pires et al., 1997; Kalscheur et al., 1997a and b; Christensen et al., 1998; Avila et al., 2000; Loor et al., 2002, 2004 and 2005; Shingfield et al., 2003; Lundy et al., 2004).

All studies involved lactating dairy cows, and estimates of digestibility were based on measurements either between the duodenum and ileum or between the duodenum and feces. Studies based on whole tract disappearance of lipids were not used because they do not account for the extensive shift in fatty acid composition that occurs in the rumen. The Table provides a descriptive summary of these investigations.

The data set clearly shows the extensive microbial metabolism of dietary unsaturated fatty acids in the rumen, which, as summarized in the Table, results in stearic acid being the major fatty acid entering the duodenum.

The Figure illustrates this on an individual treatment basis for the data set and compares changes in intake and duodenal flow (i.e., rumen output) of linoleic and stearic acids.

Linoleic acid (18:2) is typically the most common fatty acid present in diets in U.S. dairy cows, and the intake varies widely; however, only a fraction of the linoleic acid consumed (mean: 272 g per day) is actually available for absorption (mean duodenal flow: 56 g per day).

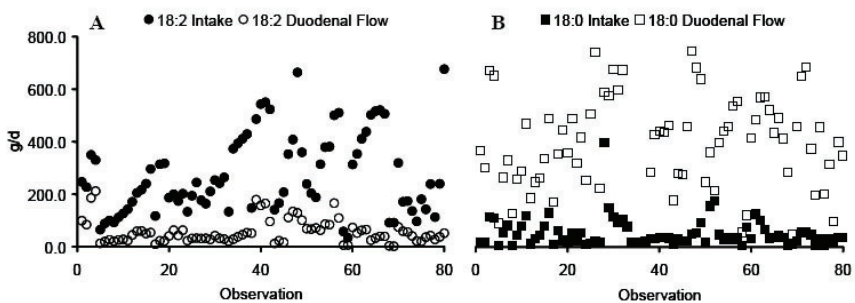
On the other hand, very little stearic acid (18:0) is typically consumed (mean: 52 g per day), but

we see a reciprocal increase in stearic acid flow to the duodenum (mean: 397 g per day) as a result of it being the end product from biohydrogenation of all 18-carbon poly-unsaturated fatty acids. In this data set, several studies measured more than 500 g per day of stearic acid leaving the rumen and being available for absorption.

Despite the dramatic changes that occur in the rumen, rumen outflow of total fatty acids is very similar to dietary intake of fatty acids; this is true across a wide range of diets with different fatty acid intakes (data not shown).

In some instances, the total amount of fatty acids entering the duodenum

Relationship between linoleic acid (18:2) intake and duodenal flow (Panel A) and stearic acid (18:0) intake and duodenal flow (Panel B). (Data from references listed in Table 3 of Part 1, *Feedstuffs*, Feb. 13.)



## Descriptive statistics of the duodenal fatty acid flow data set involving lactating dairy cows<sup>1</sup>

Variable	n <sup>2</sup>	Range		Mean
		5th percentile	95th percentile	
<b>Fatty acid intake (g per day)</b>				
Total	80	315	1,293	865
C16:0	76	47	351	170
C18:0	80	8	130	52
<sup>3</sup> C18:1	80	56	532	229
C18:2	80	92	524	272
C18:3	75	29	138	77
<b>Duodenal fatty acid flow (g per day)</b>				
Total	80	34	1,444	858
C16:0	76	54	307	161
C18:0	75	113	675	397
C18:1	75	44	375	162
C18:2	80	10	165	56
C18:3	75	1	25	9

<sup>1</sup>All data were taken or calculated from experiments reported in 20 independent studies.

<sup>2</sup>Total number of treatments within the data set contributing to each variable.

<sup>3</sup>Includes all 18:1 fatty acid isomers. For intake, this is predominately oleic acid, but in the duodenal flow, this consists of a range of trans 18:1 fatty acids and some oleic acid.

can exceed fatty acid intake, and this most often occurs when lipid intake is low, e.g., with high forage-based diets.

In this case, the increase is a result of bacterial lipid synthesis in the rumen. However, the contribution of microbial lipids is extremely variable as a result of the associative effects of different diets on microbial synthesis (Noble, 1981). An accurate determination of fatty acid intake will allow for a reasonable approximation of duodenal flow of total fatty acids, although it must be remembered that the profile of this lipid material is vastly different.

However, it is important to note that accurate determination of fatty acid intake can present some challenges, often due to the overestimation of total fatty acid content of forages and the difficulty in obtaining a complete recovery of highly saturated fat supplements (Palmquist and Jenkins, 2003).

In the current data set, fatty acid absorption was relatively constant with no significant decline when fatty acid duodenal flow was high. Total fatty acid digestibility averaged 74%, resulting in a mean absorption of 628 g per day.

The range (95% confidence interval) for total fatty acid digestibility and total fatty acid absorption was 58-86% and 247-1,102 g per day, respectively.

These data are in agreement with Doreau and Ferlay (1994), who carried out an extensive review of the literature in all ruminant species and reported values for fatty acid digestibility ranging from 55 to 92%. Again, this range was not related to fatty acid intake.

Of particular interest is whether differences exist in the digestibility of individual fatty acids. Specifically, there is disagreement regarding the digestibility of stearic acid in dairy cows and whether its digestibility differs substantially from other fatty acids.

In general, the ability of ruminants to absorb fatty acids is much higher than non-ruminants (Noble, 1981). In non-ruminants, there is a wide divergence in the digestibility of fatty acids (Freeman, 1984) with the digestibility of individual fatty acids — decreasing when chain length increases and increasing as the number of double bonds increases (Lessire et al., 1992). In particular, free palmitic and stearic acids are poorly absorbed in non-ruminants (Noble, 1981).

Although similar patterns are observed in ruminants, relative differences in the digestibility of

individual fatty acids are modest; mean digestibilities for 16:0, 18:0, 18:1, 18:2 and 18:3 were 75, 72, 80, 78 and 77%, respectively.

These data are in agreement with the review of Doreau and Ferlay (1994), which reported that mean digestibilities were 77, 85, 83 and 76% for 18-carbon fatty acids with zero, one, two and three double bonds, respectively.

A number of reasons may explain this highly efficient absorption. The slow and continuous release of relatively small amounts of fatty acids into the duodenum of the ruminant and the role of the lysolecithin-bile salt complex are both key components facilitating the solubility of the highly saturated lipid material and its incorporation into micelles and subsequent absorption.

With recent improvements in analytical techniques, differences in the digestibilities of individual fatty acids and fatty acid isomers can be more thoroughly examined, but application in feeding systems still requires accurate information on the profile of fatty acids leaving the rumen.

The overall conclusion is that differences in digestibility among individual fatty acids contribute very little to the extensive variation reported in the literature (range: approximately 60-90%). Rather, the majority of this variation reflects differences among individual experiments, and, thus, relates to experimental approaches and analytical techniques as well as differences in diets and specific feed components.

It is important to note that in the current data set, all 18:1 fatty acids are grouped together; for intake, this will primarily be oleic acid, but following rumen metabolism, this will consist predominantly of a number of trans 18:1 fatty acids and a lesser amount of cis 18:1 fatty acids.

There are limited data as to whether differences exist in the digestibility of individual 18:1 fatty acids, with some studies showing that trans 18:1 fatty acids have higher digestibilities compared to cis 18:1 fatty acids and some studies reporting the opposite.

Again, these differences would appear to be minor compared to the extensive variation in overall fatty acid digestibility across studies. Further investigation into whether differences in the digestibility of different 18:1 fatty acids exist is warranted.

As emphasized earlier, stearic acid is the predominant fatty acid in the digesta and, consequently, is the

major contributor to total absorbed fatty acids. Therefore, any discrimination against the absorption of stearic acid relative to the other fatty acids may be hardly noticeable since this is the predominant component in the digesta and more is absorbed than of any other fatty acid (Noble, 1981).

Consequently, the composition of absorbed fatty acids is close to the composition of fatty acids entering the duodenum.

In compiling the current data set from available lactating dairy cow studies, a number of considerations became apparent that should be taken into account before formulating any rigid rules with regard to the digestibility of individual fatty acids.

First, the majority of studies investigating individual fatty acid digestibility use data calculated by difference between duodenal and fecal samples. An often overlooked consideration is the rate and extent of fatty acid biohydrogenation in the large intestine that would result in an over-prediction of unsaturated fatty acid digestibility and an under-prediction of saturated fatty acid digestibility.

Biohydrogenation in the large intestine may be small in quantity, but the amount of unsaturated fatty acids reaching the lower tract is also small, so the error could be significant. Unfortunately, there are only very limited data available in which sampling from the duodenum and ileum was carried out, thereby avoiding this bias.

Second, the extent of oxidation of unsaturated fatty acids during storage and sample preparation should be considered, which would also bias results.

Last, following the secretion of bile and pancreatic juices into the duodenum, there is a significant influx of both free and esterified unsaturated fatty acids into the lipid material in the small intestine (Noble, 1981).

There are limited data on the quantitative significance of this influx in dairy cows, but again, this may bias results regarding individual fatty acid digestibility. Moreover, this influx of unsaturated fatty acids is important in further facilitating micelle formation and absorption of saturated fatty acids.

Bearing these considerations in mind, differences observed in the digestibility of individual fatty acids in the current data set are minor.

Many of the treatments in the current data set used lipid supplements of various types. A key question, therefore, is whether

different lipid supplements significantly alter fatty acid digestibility. However, the consistency of the data showing little or no difference in the absorption of individual fatty acids indicates that there is no reason to believe that different fat supplements will markedly affect overall fatty acid digestibility.

An exception to this statement is that there is sufficient evidence to indicate that saturated triglyceride supplements made from hydrogenated animal fats are poorly digested (e.g., Pantoja et al., 1996), which is probably not related to the amount fed but, rather, to the physical nature of the product limiting ruminal hydrolysis and resulting in increased duodenal flow of triglyceride.

## Conclusions

The objective of this paper was to summarize the biology of fatty acid digestion and review the available literature as to the digestibility of individual fatty acids in ruminants. The lipid material leaving the rumen consists predominantly of saturated free fatty acids, and before absorption can take place, these must be released from their intimate association with the particulate matter of the digesta.

This is overcome by solubilization of the fatty acids into the aqueous

environment, with micelle formation key to this process. Ruminants have evolved a number of key differences and features in fatty acid absorption compared with non-ruminants that allow for efficient absorption of fatty acids under the prevailing conditions, and these include differences in both bile salt composition and the amphiphile involved in micelle formation.

Consequently, in general, the ability of ruminants to absorb fatty acids, particularly saturated fatty acids, is much higher than that of non-ruminants.

The available data from lactating dairy cow studies indicate that relative differences in the digestibility of individual fatty acids are modest and contribute very little to the extensive variation reported in the literature. Rather, this variation likely reflects differences in diets, specific feed components and methodology among individual experiments.

The data also clearly show that any discrimination against the absorption of stearic acid relative to other fatty acids may be hardly noticeable since this is the predominant component in the digesta and more is absorbed than of any other fatty acid. Therefore, with the exception of saturated triglyceride supplements, there is no reason to believe that

different fat supplements will markedly affect overall fatty acid digestibility.

Our review of the available literature is in its early stages, and further analysis of the current data set are planned that will include the use of meta-analytic techniques (St-Pierre, 2001; Ipharraguerre and Clark, 2005) and a thorough examination of the effects of different fat supplements on fatty acid digestibility using both the current data set and a data set using the available literature from studies in which total tract lipid digestibility has been reported for diets containing different fat supplements.

## References

The complete list of references for this article can be found at [www.feedstuffs.com](http://www.feedstuffs.com) or by e-mailing [tlundeen@feedstuffs.com](mailto:tlundeen@feedstuffs.com).

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