What Have We Learned About Fatty Acid Digestibility in Dairy Cattle?

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Introduction

Fats may be supplemented to cows to increase energy density of the diet, improve milk components, improve milk yield, and/or maintain or gain body condition. In order for a fat supplement to be able to accomplish all of those things in a dairy cow, the fat has to be digested. There is increased recognition that individual fatty acids (**FA**) have different bioactive properties, and not all FA or fat supplements are going to respond similarly in a cow. For instance, some FA more often increase milk fat production while others are a better FA to use for gaining body condition. A considerable amount of research has been conducted that increases our understanding of individual FA digestibility because of the specific roles that those FA play in the dairy cow. Understanding what factors impact FA digestibility will allow models to more accurately predict the energy and specific outcomes from fats. Currently, most ration balancing software treats FA as energy sources but does not necessarily discount their energy value based on differences in FA composition and differences in FA digestibility. We will discuss some of the fundamental information regarding FA digestibility as well as more recent research studies reporting individual FA digestibility. Work in this area has increased our understanding of how individual FA digestibility differs and also how individual FA interact with one another to impact digestibility.

How FA Are Altered in a Ruminant

The fat that ruminants consume is mostly unsaturated esterified fat (i.e. triglycerides or glycolipids) with a wide variety of fat supplements commercially available that include both saturated and unsaturated FA in multiple forms. The rumen converts esterified fats to FA and glycerol through hydrolysis, breaking the ester bond between the glycerol and FA. Hydrolysis of fats occurs quickly in the rumen from bacterial enzymes (Palmquist and Jenkins, 1980). These now un-esterified FA have a free carboxyl end, a requirement for biohydrogenation to occur. Due to unsaturated FA being toxic to certain rumen microbes, the rumen has developed an adaptation to hydrogenate the unsaturated FA into saturated FA. Saturated FA are considered mostly rumen inert and are therefore have little effect on rumen fermentation. An excess of H are present in the rumen due to anaerobic fermentation, therefore biohydrogenation occurs relatively rapidly. The FA leaving the rumen are mostly saturated FA, unlike in a monogastric where a considerable amount of monoglycerides and unsaturated FA are present leaving the stomach. Because of these changes in FA profile from intake FA to

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what is digested (or undigested), feed to feces estimates of FA are not accurate to estimate individual FA digestibility in ruminants. Although there are changes in the form of the fat in the rumen, FA that are commonly fed to dairy cattle are not extensively metabolized in the rumen.

Digestion of FA in The Small Intestine

The digesta leaving the rumen is at near neutral pH. At this pH, the free carboxyl end of the FA binds with salts (potassium, sodium, or calcium) to form salts of FA. However, the low pH in the abomasum causes dissociation of these salts from the FA. As digesta enters the duodenum, it now has a pH of < 3 (Moore and Christie, 1984). Any esterified fat that reach the duodenum are quickly hydrolyzed (Doreau and Ferlay, 1994) leaving FA with a free carboxyl end. However, there is evidence that triglycerides of saturated FA have reduced digestibility compared to nonesterified FA (de Souza and Lock, 2019) with hydrogenated fat supplements especially having reduced digestibility (Pantoja et al., 1996). Indicating that even with what is thought of as rapid hydrolysis both in the rumen and in the small intestine, triglycerides of saturated FA may have reduced digestibility. Bile salts and pancreatic phospholipase act on the FA to form micelles with increased surface area. The secretion of bile and pancreatic secretions is relatively constant regardless of flow rates of digesta (Noble, 1981). Bile salts in ruminants are mostly taurine-conjugated which are more effective at a low pH compared to monogastrics that are more glycine-conjugated and not as effective at a low pH.

In the duodenum, the low pH and bile containing increasing amounts of taurocholic acid increase the solubility of the FA. Pancreatic phospholipase acts upon lecithin to produce lysolecithin, a potent amphiphile. Amphiphiles contain both hydrophilic and lipophilic properties and help with micelle formation that is required to diffuse the FA across the enterocyte membrane. Lysolecithin is a potent emulsifier for stearic acid (Freeman 1969 and 1984) and contains a polar head group and a hydrocarbon tail generally in the form of lysophosphatidylcholine. However, feeding 10g/d of lysolecithin had modest to negative effects on production responses when feeding a higher fiber and lower unsaturated fat diet or a lower fiber and higher unsaturated fat diet, respectively (Rico et al., 2017a). Feeding de-oiled soy lecithin up to 0.36% of diet DM had no effect on 16 or 18-carbon FA digestibility (Fontoura et al., 2019; Rico et al., 2019). Feeding unprotected lysolecithin or lecithin may not be the solution to increase FA digestibility in the small intestine.

Oleic acid also acts as an amphiphile to increase stearic acid digestibility (Freeman 1969 and Freeman 1984). Typically, due to extensive biohydrogenation of unsaturated FA the amount of oleic acid reaching the duodenum may not be sufficient to improve stearic acid digestibility. However, feeding protected oleic acid may improve digestibility of saturated FA. de Souza et al. (2018) reported increased 16 and 18-carbon digestibility when a fat supplement blend containing 35% oleic acid mostly as a calcium salt compared to a blend of palmitic and stearic acid. Calcium salts of palm FA containing 38% oleic acid increased digestibility of 16-carbon FA compared to a palmitic acid triglyceride supplement (de Souza and Lock, 2018). A calcium salt of FA containing oleic acid appears to have the ability to improve both 16 and 18-carbon digestibility, likely due to its amphiphilic properties, which increases emulsification and helps with micelle formation required for FA absorption.

Fat Sub-Model

Moate (2004) developed a fat sub-model to describe intestinal digestibility of long chain fatty acids in dairy cattle. To quantify the amount of FA available at the small intestine available for digestion, the model considers intake of dietary FA, ruminal lipolysis of dietary FA, biohydrogenation of long chain FA, de novo production of long-chain FA in the rumen, ruminal passage of FA, and ultimately intestinal absorption of those FA. All of those steps have inherent error associated with them. However, if our ultimate goal is to provide accurate FA digestibility measurements, we need accurate estimates of all of these factors that will change the composition and amount of FA available for absorption. Moate (2004) reported a linear relationship between duodenal flow of long-chain FA and absorbed total long-chain FA, with an increase in the amount of FA reaching the duodenum resulting in more FA being absorbed. The form of the fat was also a consideration for digestibility and provided a foundation for understanding individual FA digestibility.

Measuring Individual FA Digestibility

Due to the change in FA from intake to feces, duodenally cannulated animals are required for individual FA digestibility estimates. The large intestine can also hydrogenate unsaturated FA (Pantoja et al., 1996) and most FA absorption occurs in the jejunum, therefore samples of the contents of the ilium would be optimal to measure small intestinal digestibility of FA. Alternatively, difference from duodenal to fecal FA can be used to estimate individual FA digestibility, with a potential bias against stearic acid digestibility, as 18-carbon unsaturated FA could be biohydrogenated to stearic acid, increasing the amount of stearic acid in feces. There are a limited number of published studies reporting individual FA digestibility from measurements in the duodenum and ileum. Therefore, we combined both methods and found negligible differences between methods for individual FA digestibility. To better understand both dietary factors and FA profile factors that impact individual FA digestibility, we combined 15 research trials, including 61 treatment means, that measured individual FA digestibility and conducted a meta-analysis to increase our scope and increase our number of observations (Boerman et al., 2015).

As mentioned above, due to extensive biohydrogenation in the rumen, more unsaturated FA are consumed and more saturated FA are present at the duodenum (**Figure 1**). As there is minimal digestion of FA in the rumen, a positive relationship exists between duodenal flow of total FA and total FA intake. When duodenal flow of total FA increased, the total FA digestibility is reduced (**Figure 2**). We compared all individual FA to stearic acid (C18:0), because palmitic acid (C16:0) is a saturated FA and oleic (C18:1), linoleic (C18:2) and linolenic (C18:3) are all unsaturated 18-carbon FA, making stearic acid a logical comparison. Mean apparent intestinal digestibility is not different between palmitic and stearic acid. Whereas, oleic and linolenic acid had increased apparent intestinal digestibility compared to stearic acid. However, making those same comparisons for diets with no added fat in the diets, stearic acid digestibility was not different from any FA and stearic acid digestibility was significantly greater than when fat supplements were included in the diet. At lower levels of stearic acid reaching the duodenum, digestibility of stearic acid is high, this increases the mean stearic acid digestibility. However, as duodenal flow of stearic acid increases, intestinal digestibility of stearic acid is reduced. Reductions in stearic acid digestibility with increasing amounts of stearic acid reach the duodenum are consistent with other studies that reported reduced stearic acid digestibility in fat supplemented diets compared to control diets with no added fat (e.g. Pantoja et al., 1996).

At the amount of individual FA reaching the small intestines reported in the studies included in the meta-analysis, stearic acid is the only FA that had reduced digestibility as the amount reaching the duodenum increased (**Figure 3**). Comparatively, unsaturated FA appear to have a neutral to positive effect as more reaches the duodenum and palmitic acid digestibility is changed to smaller extent than stearic acid. It is important to point out that stearic acid is by far the greatest FA reaching the duodenum and that some of the unsaturated FA represent < 10 grams of FA. The reduction in total FA digestibility observed in **Figure 2** is primarily from the reduction in C18:0 digestibility as more FA reaches the small intestine.

A FA digestibility meta-analysis utilizing individual cow observations rather than treatment means, reported similar reductions in total FA digestibility as flow of FA leaving the rumen increased (de Souza et al., 2018). Stearic acid was the major FA leaving the rumen and was the FA that had the largest reduction in digestibility as the amount increased. Palmitic acid digestibility remained unchanged across the range FA leaving the rumen and entering the rest of the digestive tract. Therefore, comparing both treatment means and individual cow data points showed similar reductions in stearic acid digestibility as duodenal flow of stearic acid increased.

A dosing study of a highly pure stearic acid supplement reported reduced digestibility of total FA when increasing amounts of stearic acid was supplemented (Boerman et al., 2017). Increasing amounts of stearic acid reduced the digestibility of both 16 and 18-carabon FA, however it reduced 18-carbon digestibility to a greater extent. However, still more 18-carbon FA were absorbed when intake of stearic acid was increased. The more stearic acid that was fed, the more was absorbed but the efficiency of absorption is greatly reduced (Boerman et al. 2017). In this instance, if digestibility of this supplement was considered constant, there would be a reduction in energy available to the cow because of the reduction in 18-carbon FA digestibility.

A dosing study of a highly pure palmitic acid supplement utilized two different basal diets, one with lower total FA content and one with added cottonseed and higher total FA content (Rico et al., 2017b). Overall, increasing palmitic acid reduced 16-carbon FA digestibility, however there was a difference between the lower and higher fat diets. The higher fat diet had less of a reduction in 16-carbon FA digestibility and total FA digestibility. These results may be surprising, as we would likely see more stearic acid reaching the duodenum with a higher fat diet, which from research discussed above reduces total FA digestibility. However, the additional fat in the form of cottonseed may have offered some protection from biohydrogenation leading to more unsaturated FA that may improve digestibility compared to more saturated FA at the duodenum. Compared to the stearic acid supplemented study, dosing a highly pure source of palmitic acid reduced total FA digestibility less. The differences between digestibility of FA based on basal diet FA content indicates that not just amount of FA but, also profile likely influences FA digestibility.

Form of FA Impacts Digestibility

Daley et al. (2018) analyzed 31 studies and 142 treatments means for total tract FA digestibility across 11 different categories of fat supplements. Total tract digestibility coefficients of FA are influenced by the source of the dietary fat. Fat supplements with high levels of palmitic, stearic or hydrogenated triglycerides have lower FA digestibility than those with higher amounts of unsaturated FA. Results from Daley et al. (2018) provide further evidence that the form of the fat supplement impacts digestibility. We utilized meta-regression to determine which dietary factors impact individual FA digestibility (Boerman et al., 2015). Fat type impacted the individual digestibility of palmitic acid, oleic acid and linoleic acid, with calcium salts and vegetable oils having numerically higher digestibilities. Specifically, whole seeds had lower FA digestibility, while whole seeds may offer some protection from biohydrogenation, they also have reduced intestinal digestibility. For saturated FA, increasing dry matter intake (**DMI**) negatively impacted palmitic and stearic acid digestibility. Potentially, increasing the passage rate of feedstuffs would negatively impact saturated FA digestibility due passage of FA too fast to allow for absorption in the small intestine.

Profile of FA Impacts Digestibility

Duodenal flows of FA influence individual FA digestibility (Boerman et al., 2015). For stearic acid, total flow of FA as well as the proportion of stearic acid and oleic acid negatively impacted digestibility. The proportion of stearic acid reaching the duodenum also negatively impacted the digestibility of all unsaturated 18-carbon FA. These results indicate that the profile that reaches the duodenum in addition to the amount of individual FA likely influences digestibility. Because of difference in digestibility between individual FA, the amount of digestible energy available to the cow differs based on fatty acid flow and profile. These changes in digestible energy between individual FA influences production responses observed when supplementing fat.

The amount of FA included in diets is relatively small compared to other nutrients; however, as cows are genetically capable of making more milk, we are looking for every opportunity to increase milk production and/or milk components. Another important consideration is the effect of fat supplements on DMI and digestibility of other nutrients. Reducing DMI and reducing fiber digestibility may have more negative effects on digestible energy rather than modest reductions in FA digestibility. In order to accurately predict digestibility of FA and digestible energy from FA, we need to not only treat individual FA as unique when it comes to predicting their digestibility but also consider their interactions with other FA and their effect on digestibility of other nutrients. Cows consume blends of FA and because of the difficulty in predicting biohydrogenation rates and passage rates of FA, accuracy of individual FA reaching the duodenum will be challenging. However, a first step is accounting for differences in digestibility as flow of FA increases to better account for individual FA available for the cow.

Conclusions

Stearic acid is the FA in the greatest quantity reaching the small intestine and available for absorption. Increasing the amount of stearic acid, reduces the digestibility of stearic acid as well as reducing the digestibility of other 18-carbon FA. Improving the ability of FA to emulsify and form a micelle is a logical place to try to improve stearic acid digestibility. Thus far, rumen protected oleic acid appears to have the most positive effect on increasing stearic acid digestibility. The form of the fat, the profile FA reaching the duodenum, and the amount of fat all impact digestibility of individual FA. Although relatively little fat is supplemented to dairy cows, maximizing the amount of FA digested increases digestible energy as well as the increasing the specific FA available for bioactive properties.

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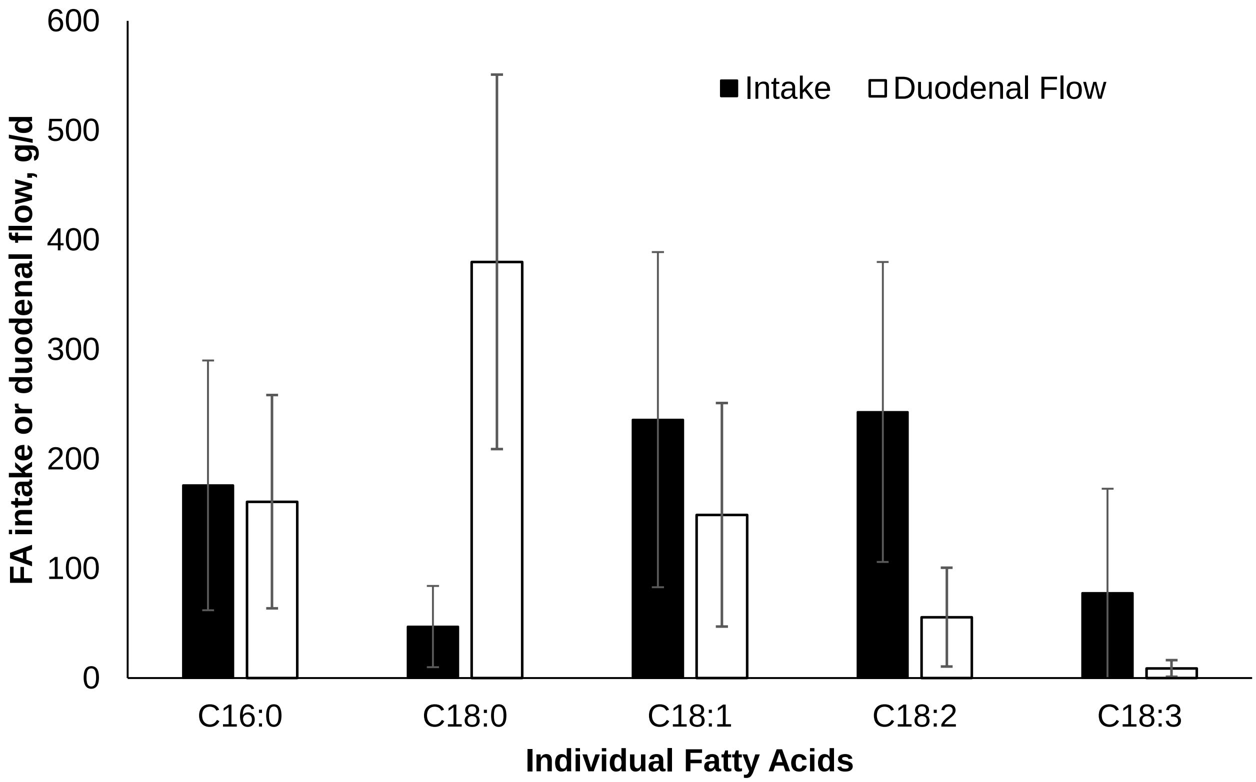

Figure 1. Mean and standard deviation reported from 15 studies of individual FA intake and duodenal flow. Adapted from Boerman et al. (2017). Due to extensive biohydrogenation, there are a reduction in unsaturated FA reaching the duodenum and an increase in stearic acid.

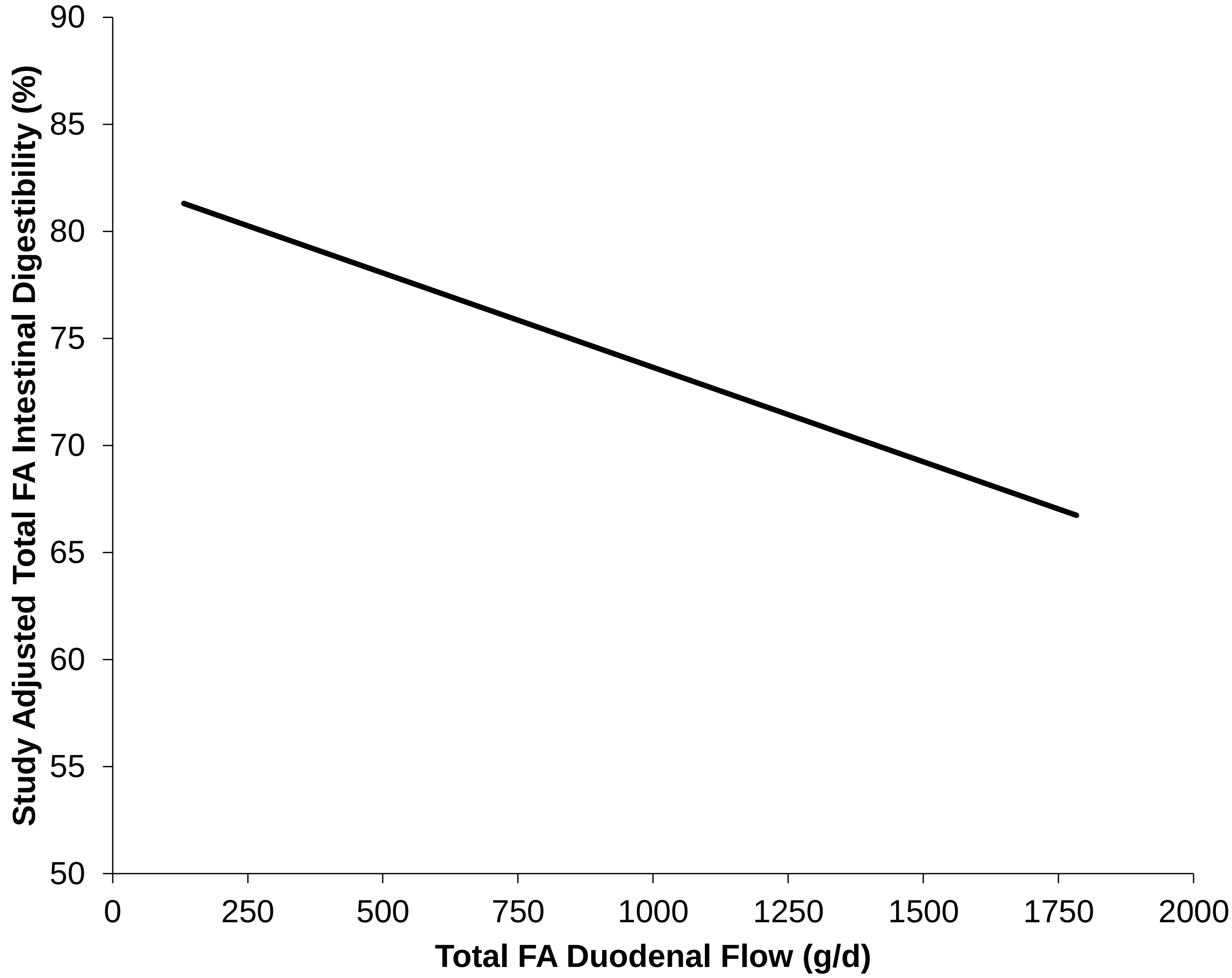

Figure 2. Best-fit line for study adjusted total FA digestibility from 61 observations from 15 studies reporting individual and total FA digestibility measured from duodenal to ileal or fecal disappearance of FA. Adapted from Boerman et al. (2015).

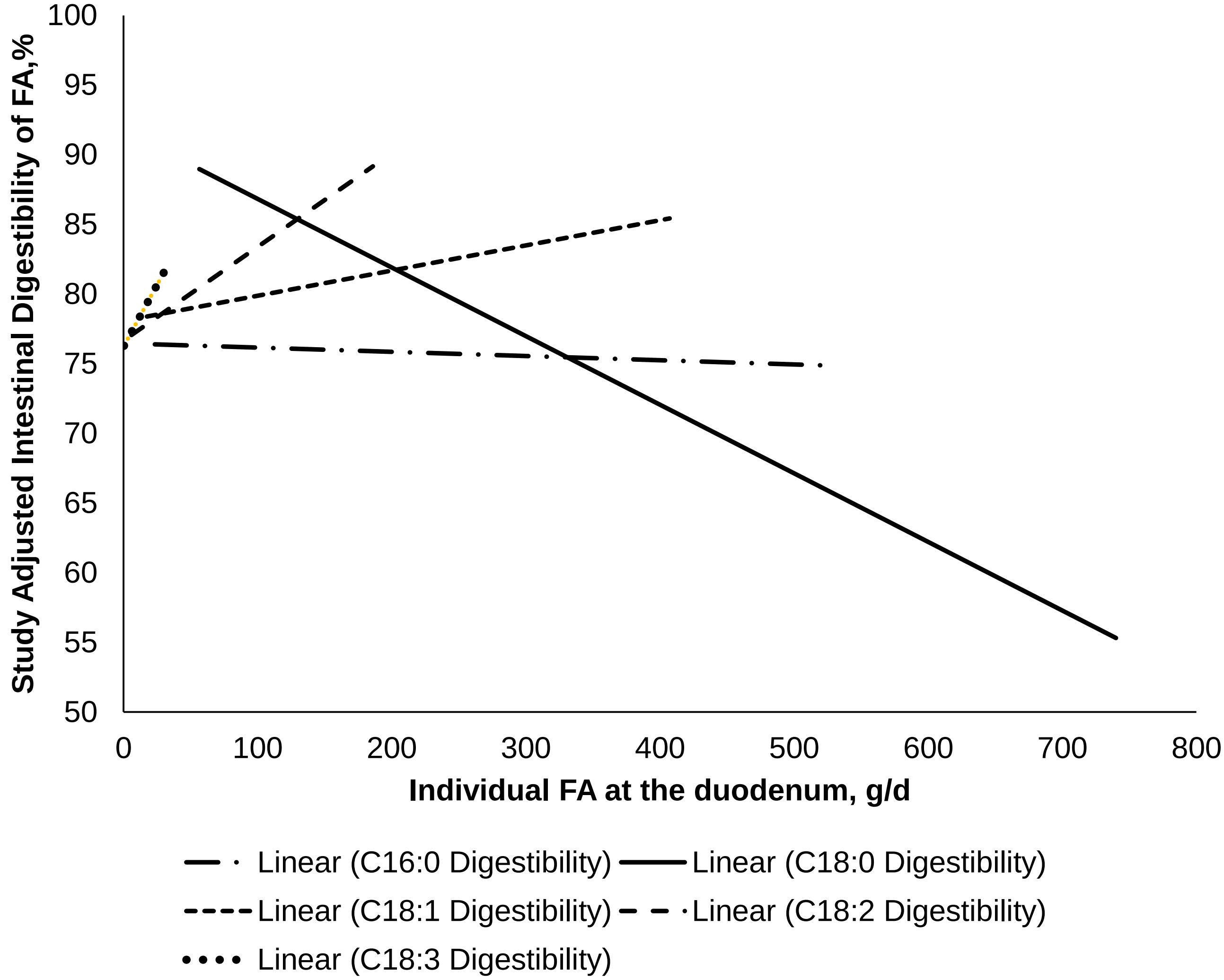

Figure 3. Best-fit lines for study adjusted intestinal digestibility of individual FA by grams of individual FA at the duodenum reported from 61 treatment means from 15 studies. Adapted from Boerman et al. (2015).

SESSION NOTES