Understanding the Importance of Dietary Fats in Liquid Feeds for Calves

J. N. Wilms

Trouw Nutrition Research and Development, P.O. Box 299, 3800 AG, Amersfoort, the Netherlands

Milk composition in mammals has likely evolved under evolutionary pressure to ensure the survival and optimal growth of offspring, who depend exclusively on milk during the early stages of life (Davis et al., 1994). These evolutionary adaptations have resulted in milk compositions that meets the specific nutritional requirements of neonates, addressing factors such as growth rate, body composition, and environmental conditions. In the dairy industry, calves are separated from the dam shortly after birth and half of calves are fed milk replacer (**MR**) or a combination of whole milk (**WM**) and MR. While substantial advances have been made in calf nutrition, MR formulations still differ significantly from WM in several key aspects, most notably in fat content, which is typically only half of that found in bovine WM (Wilms et al., 2022). This is counterintuitive as the logical starting point for creating a MR for any species would be to mimic the composition of its natural milk. As a result, nutrient imbalances in MR formulations may disrupt metabolic homeostasis, emphasizing the need to establish nutritional boundaries to support optimal calf development and health.

I) Implications of feeding milk replacers low in fat to calves

Feeding MR with a high fat content increased body fat in calves (Tikofsky et al., 2001). Likewise, a higher nutrient intake from enhanced plane of nutrition allows adipocyte to increase fat stores (Leal et al., 2018). Low-fat MR formulations are common due to the inclusion of dairy industry by-products and are often fed under the assumption that higher fat intake might impair mammary gland development. While fat accumulation in the mammary glands during the post-weaning phase has been linked to reduced milk production (Sejrsen and Purup, 1997; Van Amburgh et al., 2019), there is currently no evidence to suggest that fat deposition in the mammary glands during the pre-weaning phase negatively affects future milk production. In fact, a higher plane of nutrition during the pre-weaning phase has been associated with an increase in mammary parenchyma mass, which may contribute to improved future milk yield (Geiger, 2019). In a study by Soberon and Van Amburgh (2017), calves fed an enhanced plane of nutrition during the pre-weaning phase exhibited not only superior growth, but also increased development of the mammary gland, along with other organs such as the liver, kidneys, and parenchyma. In the same study, the gene expression profile across different tissues, including fat, liver, bone marrow, muscle, pancreas, and mammary gland, highlighted significant differences (Leal et al., 2018; Hare et al., 2019). This shows the need to take a whole-body approach when evaluating dairy calf development rather than solely focusing on mammary development. Calves fed enhanced plane of nutrition gained more fat, with gene expression suggesting increased fat deposition (Leal et al., 2018). In adipose tissues, the gene expression profile indicated a shift toward beige adipocytes (Leal et al., 2018), which is considered more metabolically favorable than white fat, as beige adipocytes are associated with improved energy regulation and health outcomes (Cannon and Nedergaard, 2004). The question of the ideal fat percentage for young calves remains unclear, especially in relation to its importance in calf development and future productivity.

Calves are born with limited fat reserves with only about 3% of their BW as fat (McCance and Widdowson, 1977). Newborn calves rely on lipids and lactose from colostrum and WM to maintain body temperature and build energy stores. Body fat primarily serves as an energy reserve (Cahill, 1982; Norgan, 1997), and the accumulation of fat after birth prepares the animal for future energy challenges. The advantage of using triglycerides (**TG**) as energy storage rather than polysaccharides (glycogen) is due to the reduction level of carbon atoms of FA than those of carbohydrates (Nelson et al., 2008), allowing for more energy to be stored per molecule. In human infants, fat deposition supports the transition from breast milk to solid foods and aids the shift from maternal to endogenous immune protection (Kuzawa, 1998). Fat stores are mobilized during infections suggesting a link between nutritional status to disease outcomes in infants (Kuzawa, 1998). A parallel can be drawn with the early life of a calf, which is marked by numerous stressors, including separation from the dam shortly after birth and the frequent challenge of inadequate colostrum management leading to a dip in immunity during the second week of life. Additionally, calves are often fed low milk volumes (8-10% of birth BW as volume fed; 4-6 litres) (Leal et al., 2021), which is far below the 10-12 litres they would naturally consume when nursing from the dam (Reinhardt and Reinhardt, 1981). These factors likely contribute to the high morbidity observed during the second week of life (Urie et al., 2018). Moreover, many calves are weaned as early as 6-8 weeks of age, though naturally, they would remain with the dam for up to 10 months (Hall, 1979; Reinhardt and Reinhardt, 1981). These disruptions create significant challenges to calf health and may help explain why higher fat intake in liquid feeds was associated with reduced preweaning mortality (Urie et al., 2018). In addition, increasing the energy density of MR by supplementing fat allows calves to maintain BW gain during cold temperatures (Jaster et al., 1992). Calves fed MR high in fat also experience lower morbidity, with improved fecal scores (Amado et al., 2019) and reduced need for medical treatments (Berends et al., 2020). Thus, increasing fat content in MR not only supports energy needs but also enhances overall calf health and development, helping calves to better cope with the challenges of early life in modern dairy production systems.

An imbalanced nutrient profile in MR during early life can negatively affect calf metabolic health, potentially disrupting long-term metabolic homeostasis. Prolonged feeding of MR high in lactose (up to 55% DM) impaired glucose homeostasis and insulin sensitivity in veal calves (Hugi et al., 1997). While high-lactose MR reduced insulin sensitivity of calves in some studies, others found no significant differences (Stahel et al., 2019), suggesting that factors like feeding duration, lactose inclusion levels in MR, and plane of nutrition impact glucose-insulin metabolism. Likewise, calves fed MR high in protein required more insulin secretion after a meal compared to those on high-fat diets (Wilms et al., 2024a). This aligns with the higher serum insulin-like growth factor I (**IGF-I**) of calves fed MR high in proteins compared with MR high in fat (Bartlett et al., 2006; Wilms et al., 2022). High protein intake from infant formula increased the concentration of insulin-releasing amino acids, which stimulate the secretion of insulin and IGF-1 (Luque et al., 2015). This promotes accelerated growth during infancy (Koletzko et al., 2005), but also raises the risk of obesity and metabolic disorders later in life (Michaelsen and Greer, 2014). However, the long-term impact of early insulin and IGF-1 dynamics on the metabolic health of replacement heifers remains unclear. Since milk facilitates biochemical signaling between mother and offspring, it is crucial to carefully consider the metabolic signals transmitted to calves, particularly when feeding MR with significant macronutrient imbalances compared to WM.

II) Fat composition in milk replacer impacts lipid metabolism

Bovine milk fat exhibits unique complexity, containing over 400 different fatty acids (**FA**). The natural FA profile of WM, which shifts over the course of lactation, likely supports the evolving developmental needs of the calf. Fat plays a crucial role in the nutrition of calves, serving as a highly concentrated source of energy and providing essential FA critical for organ development, immune system development, metabolic regulation, and overall health. Yet, competition with the food industry limits the availability of milk fat for use in MR formulation, leading to reliance on alternative fat sources derived from vegetable or animal sources. These alternatives, while effective in providing energy and supporting growth, do not replicate the full nutritional profile of milk fat (Figure 1). Diarrhea in calves has been observed when the fat composition of MR significantly deviates from that of bovine milk fat (Jenkins et al., 1985,1988).

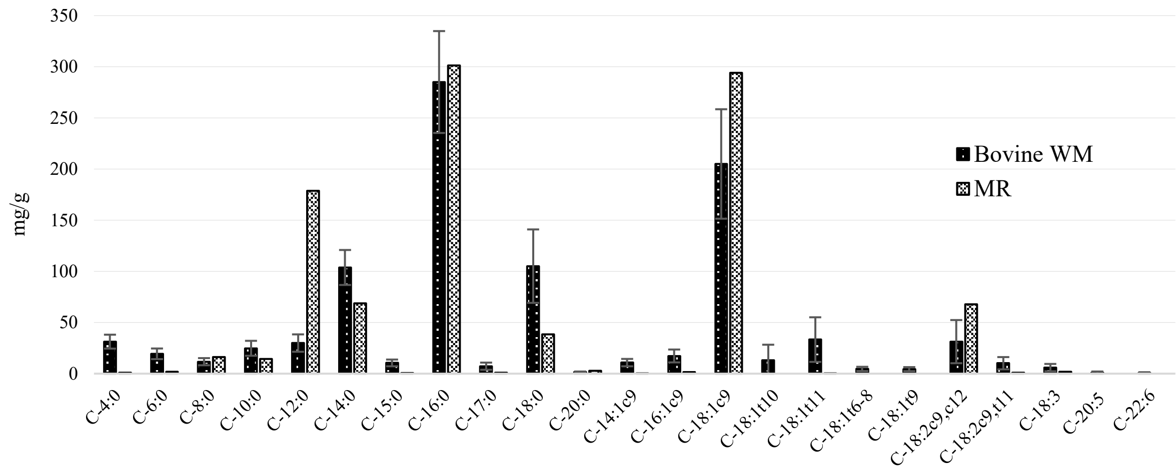

Figure 1. Fatty acid profile of bovine WM (Moate et al., 2007) and a MR containing 65% palm and 35% coconut fats.

Formulating the FA profile (and TG structure) of MR to more closely resemble that of bovine milk fat—by incorporating dairy cream—produced significant benefits, including increased voluntary MR intake in an ad libitum system, which led to enhanced preweaning growth (Wilms et al., 2024b). In contrast, in that same study, calves fed MR containing vegetable fats from rapeseed and coconut exhibited lower preweaning feed efficiency, along with reduced MR intake and preweaning growth (Wilms et al., 2024b). In addition, calves fed MR with rapeseed and palm fats had elevated plasma cholesterol compared to calves fed a MR with lard and dairy cream (Leite et al., 2024; Wilms et al., 2024b) (Figure 2). Notably, Wilms et al. (2024b) reported a shift from a high proportion of high-density lipoprotein (**HDL**) cholesterol, known as "good" cholesterol, to a higher proportion of low-density lipoprotein (**LDL**) cholesterol, often referred to as "bad" cholesterol, in calves fed ad libitum. A study by McNamara et al. (1987) showed that the quality of dietary fat is a more crucial factor in determining plasma cholesterol than dietary cholesterol intake. Indeed, cholesterol synthesis has a significantly greater impact on circulating cholesterol than intestinal absorption of cholesterol. It has been suggested that high cholesterol concentrations in calves fed MR with vegetable fats is related to high levels of polyunsaturated FA in rapeseed oil and to differences in C16:0 positioning on the glycerol backbone between palm oil and animal fats (Leite et al., 2024; Wilms et al., 2024b). Differences in total cholesterol concentration diminished during the weaning transition, suggesting that shifts in blood lipid profiles in response to animal or vegetable fat sources during early life are transient. Nevertheless, it remains unclear whether variations in fat composition and imbalances in lipid metabolism may have long-term consequences for the health and production of future dairy cows.

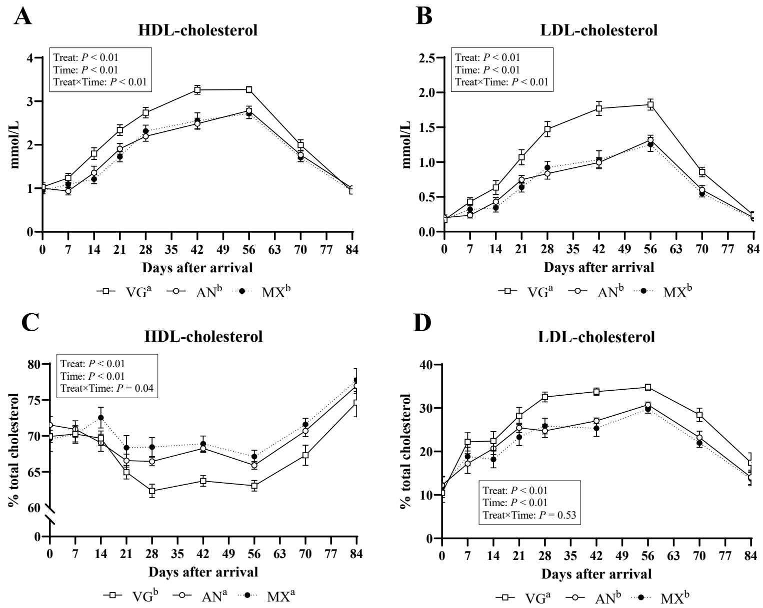

Figure 2. Plasma HDL-cholesterol (A) and LDL-cholesterol (B), as well as the proportion of HDL-cholesterol (C) and LDL-cholesterol (D) on total cholesterol (Wilms et al., 2024b). Treatments included an MR with only vegetable fats (VG, 80% rapeseed and 20% coconut fats, n = 19), an MR with only animal fats (AN, 65% lard and 35% dairy cream, n = 20), and an MR with a mix of 80% lard and 20% coconut fat (MX, n = 20). Means with a different superscript (a, b) in the figure legend are significantly different throughout the study period. Error bars indicate SEM.

III) Restoring butyric acid in milk replacer to promote health and growth

Formulating the FA profile of MR to more closely resemble that of milk fat by incorporating dairy cream has demonstrated significant benefits (Wilms et al., 2024b). However, adding dairy cream to MR formulations is not commercially viable due to its high cost. The positive effects of dairy cream may be partly due to the presence of short-chain FA and medium-chain FA, specifically butyric acid (**C4:0**) and caproic acid (**C6:0**), which are natural components of mammalian milk, but absent in MR. Butyric acid plays a crucial role in promoting gut development and metabolic regulation (Guilloteau et al., 2010). Although C6:0 has received less attention, experiments by Aurousseau et al., (1984, 1988) showed that calves and lambs fed MR with a blend of tallow and coconut fats, along with tricaproin, had higher growth rates and feed efficiencies. Incorporating tributyrin and tricaproin into MR enhanced digestive health, leading to better fecal scores and improved apparent total-tract fat digestibility (Wilms, 2024). These improvements may also be linked to enhanced ileal development and a healthier gut microbiota (Liu et al., 2022; Wilms, 2024). Additionally, tributyrin in MR seemed to promote rumen development in 5-week-old calves (Wilms, 2024), a key factor in the successful transition from a milk to solid feed. Remarkably, enhanced rumen development was observed in calves fed MR with tributyrin and tricaproin although solid feed was not available (Wilms, 2024). This early development likely enabled the calves to consume more starter feed at weaning, resulting in improved growth performance (Figure 3). This suggests that tributyrin and possibly tricaproin play a systemic role in gastrointestinal maturation, as MR bypasses the rumen and is directed to the abomasum through the closure of the esophageal groove. Facilitating the weaning transition through enhanced rumen development reduces stress, a major welfare concern for calves. Conflicting findings between studies regarding growth performance may be related to different MR feeding regimes, the type and method of C4:0 supplementation, the timing of C4:0 introduction, the time of treatment exposure, and the C4:0 inclusion levels in MR. Differences in growth may only become apparent during the late weaning and early post-weaning phases. In a study by Wilms (2024) where calves were fed ad libitum, calf health was also improved, with a 50% reduction in treatment days for illness when tributyrin and tricaproin were included in MR. Improvements in health are likely due to reduced diarrhea severity, stronger gut development, and a smoother weaning transition, all contributing to more resilient calves.

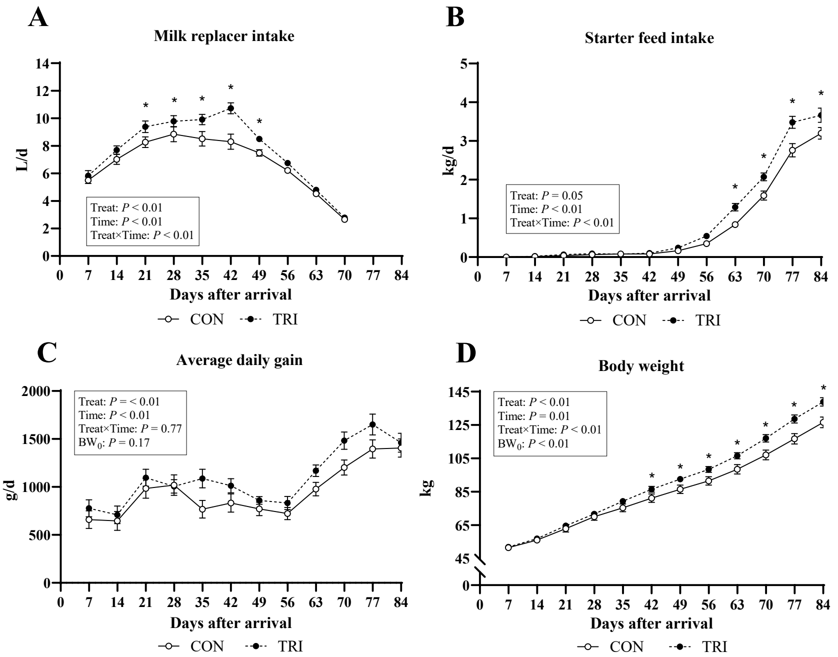

Figure 3. Intakes of milk replacer (A), starter feed (B), and growth (C: ADG, D: BW) in calves (Wilms, 2024b). Milk replacer (13.5% solids) was fed ad libitum from arrival to 42 d after arrival, weaning took place between d 43-70 after arrival, and from d 71-84, calves were fed exclusively solid feeds. Treatments included an MR with vegetable fats (palm, coconut, and linseed, CON, n = 22) and a MR with the same fat blend to which tributyrin and tricaproin were incorporated (TRI, n = 24).

Calves fed MR with tributyrin and tricaproin required significantly less insulin to regulate postprandial blood glucose compared to those fed MR with dairy cream (**MF**) or a control diet, suggesting enhanced insulin sensitivity (Wilms, 2024) (Figure 5). The role of butyric acid in enhancing insulin-glucose metabolism has also drawn attention in human nutrition, particularly for its potential therapeutic benefits in managing diabetes and metabolic syndromes (van Deuren et al., 2022). Furthermore, calves fed TRI displayed lower postprandial TG than those fed a control MR. Calves fed TRI also had lower plasma cholesterol and non-esterified FA concentrations (Wilms, 2024). This was also observed within rodent models and individuals with metabolic syndrome suggesting improved lipid metabolism and liver function (van Deuren et al., 2022). However, while these so called “enhanced lipid markers” are beneficial in humans suffering from metabolic disorders associated with obesity, their relevance to young calves remains uncertain.

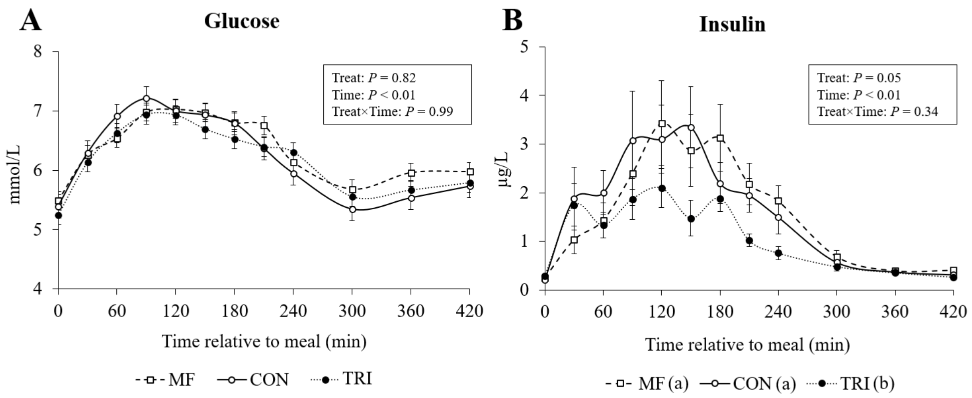

Figure 4. Postprandial glucose (A) and insulin dynamics (B) in calves. Treatments (n = 15 per treatment group) included an MR with dairy cream (MF), an MR with a blend of vegetable oils (palm, coconut, and linseed, CON), and an MR with the same oil blend than CON to which tributyrin and tricaproin were incorporated (TRI). [a,b]Means with a different superscript in the legend are significantly different ($P \leq 0.05$).

Conclusion

Taken together, these findings highlight the critical importance of dietary fats in calf nutrition. Higher fat intake from liquid feed is beneficial for calves as it allows them to build energy stores that can be mobilized during energetic challenges (e.g. low nutrient intake, weaning) and diseases. This likely explains the lower morbidity and mortality in calves fed high fat liquid feeds. When considering fat composition, MR formulations often rely on vegetable or animal fats, which differ from bovine milk fat in terms of FA profile and TG structure. Balancing individual FA by incorporating tributyrin and tricaproin into MR improved digestive health. In addition, tributyrin in MR enhanced rumen development allowing for a substantial increase in starter feed intake, which likely reduces weaning stress. In conclusion, increasing fat inclusion in MR and carefully balancing fat composition to closely resemble WM led to substantial improvements in calf welfare while supporting optimal growth.

Literature cited

Amado, L., H. Berends, L. N. Leal, J. Wilms, H. Van Laar, W. J. J. Gerrits, and J. Martín-Tereso. 2019. Effect of energy source in calf milk replacer on performance, digestibility, and gut permeability in rearing calves. J. Dairy Sci. 102(5):3994-4001.

Aurousseau, B. 1988. Effects of substitution of tricaproin for tallow and of protein concentration in milk substitutes on nitrogen and energy balance in the preruminant lamb. Br. J. Nutr. 60(3):525-538.

Aurousseau, B., P. Thivend, and M. Vermorel. 1984. Influence du remplacement d'une partie du suif d'un aliment d'allaitement par de la tricaproïne ou de la tricapryline en association à de l'huile de coprah sur la croissance du jeune veau préruminant. Ann. Zootech. 33(2):219-234.

Bartlett, K. S., F. K. McKeith, M. J. VandeHaar, G. E. Dahl, and J. K. Drackley. 2006. Growth and body composition of dairy calves fed milk replacers containing different amounts of protein at two feeding rates. J. Anim. Sci. 84(6):1454-1467.

Berends, H., H. van Laar, L. N. Leal, W. J. J. Gerrits, and J. Martín-Tereso. 2020. Effects of exchanging lactose for fat in milk replacer on ad libitum feed intake and growth performance in dairy calves. J. Dairy Sci. 103(5):4275-4287.

Cahill GC Jr (1982) Starvation. Trans. Am. Clin. Climatol. Assoc. 94:1–21.

Cannon, B. and J. Nedergaard. 2004. Brown Adipose Tissue: Function and Physiological Significance. Physiol. Rev. 84(1):277-359.

Davis, T. A., H. V. Nguyen, R. Garcia-Bravo, M. L. Fiorotto, E. M. Jackson, D. S. Lewis, D. R. Lee, and P. J. Reeds. 1994. Amino acid composition of human milk is not unique. J. Nutr. 124(7):1126-1132.

Geiger, A. J. 2019. Review: The pre-pubertal bovine mammary gland: unlocking the potential of the future herd. Animal. 13(S1):s4-s10.

Guilloteau, P., L. Martin, V. Eeckhaut, R. Ducatelle, R. Zabielski, and F. Van Immerseel. 2010. From the gut to the peripheral tissues: the multiple effects of butyrate. Nutr. Res. Rev. 23(2):366-384.

Hall, S. 1979. Studying the Chillingham wild cattle [UK]. Ark.
Hare, K. S., L. N. Leal, J. M. Romao, G. J. Hooiveld, F. Soberon, H. Berends, M. E. Van Amburgh, J. Martín-Tereso, and M. A. Steele. 2019. Preweaning nutrient supply alters mammary gland transcriptome expression relating to morphology, lipid accumulation, DNA synthesis, and RNA expression in Holstein heifer calves. J. Dairy. Sci. 102(3):2618-2630.
Hugi, D., S. H. Gut, and J. W. Blum. 1997. Blood metabolites and hormones--especially glucose and insulin--in veal calves: effects of age and nutrition. Zentralbl. Veterinarmed. A 44(7):407-416.
Jaster, E. H., G. C. McCoy, N. Spanski, and T. Tomkins. 1992. Effect of extra energy as fat or milk replacer solids in diets of young dairy calves on growth during cold weather. J. Dairy Sci. 75(9):2524-2531.
Jenkins, K. J. 1988. Factors affecting poor performance and scours in preruminant calves fed corn oil. J. Dairy Sci. 71(11):3013-3020.
Jenkins, K. J., J. K. Kramer, F. D. Sauer, and D. B. Emmons. 1985. Influence of triglycerides and free fatty acids in milk replacers on calf performance, blood plasma, and adipose lipids. J. Dairy Sci. 68(3):669-680.
Koletzko, B., I. Broekaert, H. Demmelmair, J. Franke, I. Hannibal, D. Oberle, S. Schiess, B. T. Baumann, and S. Verwied-Jorky. 2005. Protein intake in the first year of life: a risk factor for later obesity? The E.U. childhood obesity project. Adv. Exp. Med. Biol. 569:69-79.
Kuzawa, C. W. 1998. Adipose tissue in human infancy and childhood: An evolutionary perspective. Am. J. Phys. Anthropol. 107(S27):177-209.
Leal, L. N., J. Doelman, B. R. Keppler, M. A. Steele, and J. Martín-Tereso. 2021. Preweaning nutrient supply alters serum metabolomics profiles related to protein and energy metabolism and hepatic function in Holstein heifer calves. J. Dairy Sci. 104(7):7711-7724.
Leal, L. N., J. M. Romao, G. J. Hooiveld, F. Soberon, H. Berends, M. V. Boekshoten, M. E. Van Amburgh, J. Martín-Tereso, and M. A. Steele. 2018. Nutrient supply alters transcriptome regulation in adipose tissue of pre-weaning Holstein calves. PLoS One. 13(8):e0201929.
Leite, G. B. C., J. N. Wilms, I. R. R. Castro, M. I. Marcondes, and L. N. Leal. 2024. Fat composition in milk replacer modulates plasma cholesterol of dairy calves. JDS Communications.
Liu, S., J. Wu, Z. Wu, G. M. Alugongo, M. Zahoor Khan, J. Li, J. Xiao, Z. He, Y. Ma, S. Li, and Z. Cao. 2022. Tributyrin administration improves intestinal development and health in pre-weaned dairy calves fed milk replacer. Anim. Nutr. 10:399-411.
Luque, V., R. Closa-Monasterolo, J. Escribano, and N. Ferré. 2015. Early Programming by Protein Intake: The Effect of Protein on Adiposity Development and the Growth and Functionality of Vital Organs. Nutr. Metab. Insights 8(Suppl 1):49-56.
McCance, R. and E. Widdowson. 1977. Fat. Pediatric research 11(10 Pt 2):1081-1083.
McNamara, D. J., R. Kolb, T. S. Parker, H. Batwin, P. Samuel, C. D. Brown, and E. H. Ahrens, Jr. 1987. Heterogeneity of cholesterol homeostasis in man. Response to changes in dietary fat quality and cholesterol quantity. J. Clin. Invest. 79(6):1729-1739.
Michaelsen, K. F. and F. R. Greer. 2014. Protein needs early in life and long-term health. Am. J. Clin. Nutr. 99(3):718s-722s.

Moate, P. J., W. Chalupa, R. C. Boston, and I. J. Lean. 2007. Milk fatty acids. I. Variation in the concentration of individual fatty acids in bovine milk. J. Dairy Sci. 90(10):4730-4739.

Nelson, D. L., A. L. Lehninger, and M. M. Cox. 2008. Lehninger principles of biochemistry. Macmillan. Noble, R. C. 1980. Lipid metabolism in the neonatal ruminant. Prog. Lipid Res. 18:178.

Norgan N (1997) The beneficial effects of body fat and adipose tissue in humans. Int. J. Obes. 21:738–754.

Reinhardt, V. and A. Reinhardt. 1981. Cohesive relationships in a cattle herd (Bos indicus). Behaviour. 77:121-151.

Sejrsen, K. and S. Purup. 1997. Influence of prepubertal feeding level on milk yield potential of dairy heifers: a review. J. Anim Sci. 75(3):828-835.

Soberon, F. and M. E. Van Amburgh. 2017. Effects of preweaning nutrient intake in the developing mammary parenchymal tissue. J. Dairy Sci. 100(6):4996-5004.

Stahel, P., H. Berends, L. N. Leal, and J. Martin-Tereso. 2019. Effect of replacing lactose with fat in milk replacer on abomasal emptying and glucose–insulin kinetics in male dairy calves. AAS. 35(6):586-595.

Tikofsky, J. N., M. E. Van Amburgh, and D. A. Ross. 2001. Effect of varying carbohydrate and fat content of milk replacer on body composition of Holstein bull calves. J. Anim Sci. 79(9):2260-2267.

Urie, N. J., J. E. Lombard, C. B. Shivley, C. A. Kopral, A. E. Adams, T. J. Earleywine, J. D. Olson, and F. B. Garry. 2018. Preweaned heifer management on US dairy operations: Part V. Factors associated with morbidity and mortality in preweaned dairy heifer calves. J. Dairy Sci. 101(10):9229-9244.

Van Amburgh, M. E., F. Soberon, M. J. Meyer, and R. A. Molano. 2019. Symposium review: Integration of postweaning nutrient requirements and supply with composition of growth and mammary development in modern dairy heifers. J. Dairy Sci. 102(4):3692-3705.

van Deuren, T., E. E. Blaak, and E. E. Canfora. 2022. Butyrate to combat obesity and obesity-associated metabolic disorders: Current status and future implications for therapeutic use. Obes. Rev. 23(10):e13498.

Wilms, J. N. R. 2024. Unlocking the Potential of Fat in Milk Replacer for Calves. PhD Thesis. University of Guelph, Ontario, Canada.

Wilms, J. N., M. H. Ghaffari, P. S. Darani, M. Jansen, H. Sauerwein, M. A. Steele, J. Martín-Tereso, and L. N. Leal. 2024a. Postprandial metabolism and gut permeability in calves fed milk replacer with different macronutrient profiles or a whole milk powder. J. Dairy Sci. 107(1):184-201.

Wilms, J. N., M. H. Ghaffari, M. A. Steele, H. Sauerwein, J. Martín-Tereso, and L. N. Leal. 2022. Macronutrient profile in milk replacer or a whole milk powder modulates growth performance, feeding behavior, and blood metabolites in ad libitum-fed calves. J. Dairy Sci. 105(8):6670-6692.

Wilms, J. N., V. van der Nat, M. H. Ghaffari, M. A. Steele, H. Sauerwein, J. Martín-Tereso, and L. N. Leal. 2024b. Fat composition of milk replacer influences growth performance, feeding behavior, and plasma fatty acid profile in ad libitum-fed calves. J. Dairy Sci. 107(5):2797-2817.