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Effects of replacing lactose from milk replacer by glucose, fructose, or glycerol on energy partitioning in veal calves

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ABSTRACT

Calf milk replacers contain 40 to 50% lactose. Fluctuating dairy prices are a major economic incentive to replace lactose from milk replacers by alternative energy sources. Our objective was, therefore, to determine the effects of replacement of lactose with glucose, fructose, or glycerol on energy and protein metabolism in veal calves. Forty male Holstein-Friesian calves (114 ± 2.4 kg) were fed milk replacer containing 46% lactose (CON) or 31% lactose and 15% of glucose (GLUC), fructose (FRUC), or glycerol (GLYC). Solid feed was provided at 10 g of dry matter (DM)/kg of metabolic body weight ($BW^{0.75}$) per day. After an adaptation of 48 d, individual calves were harnessed, placed in metabolic cages, and housed in pairs in respiration chambers. Apparent total-tract disappearance of DM, energy, and N and complete energy and N balances were measured. The GLUC, FRUC, and GLYC calves received a single dose of 1.5 g of [U-^{13}C]glucose, [U-^{13}C]fructose, or [U-^{13}C]glycerol, respectively, with their milk replacer at 0630 h and exhaled $^{13}CO_2$ and ^{13}C excretion with feces was measured. Apparent total-tract disappearance was decreased by 2.2% for DM, 3.2% for energy, and 4.2% for N in FRUC compared with CON calves. Energy and N retention did not differ between treatments, and averaged 299 ± 16 kJ/kg of $BW^{0.75}$ per day and 0.79 ± 0.04 g/kg of $BW^{0.75}$ per day, respectively, although FRUC calves retained numerically less N (13%) than other calves. Recovery of ^{13}C isotopes as $^{13}CO_2$ did not differ between treatments and averaged 72 ± 1.6%. The time at which the maximum rate of $^{13}CO_2$ production was reached was more than 3 h delayed for FRUC calves, which may be explained by a conversion of fructose into other substrates before being oxidized. Recovery of ^{13}C in feces was greater for FRUC calves (7.7 ± 0.59%) than for GLUC (1.0 ± 0.27%) and GLYC calves (0.5 ± 0.04%), indicating incomplete absorption of fructose from the small intestine resulting in fructose excretion or fermentation. In conclusion, energy and N retention was not affected when replacing >30% of the lactose with glucose, fructose, or glycerol. Increased fecal losses of DM, energy, and N were found in FRUC calves compared with CON, GLUC, and GLYC calves. Postabsorptive losses occurred with the urine for glucose and glycerol, which caused a lower respiratory quotient for GLUC calves during the night. Fructose was oxidized more slowly than glucose and glycerol, probably as a result of conversion into other substrates before oxidation.
Key words: veal calf, glucose, fructose, glycerol, energy retention

INTRODUCTION

Calf milk replacers (**MR**) contain 40 to 50% lactose. Apparent ileal lactose disappearance is high in milk-fed calves, up to or exceeding 97% of intake (Coombe and Smith, 1974; Gilbert et al., 2015a). High and fluctuating dairy prices are a major economic incentive to replace lactose from MR by alternative energy sources. It has been recently demonstrated that starch products are not suitable for replacing lactose, as maltase activity likely limits starch digestion and the vast majority of ingested starch products from MR disappears from the intestinal tract by fermentation rather than after hydrolysis by animal enzymes and subsequent absorption of glucose (Gilbert et al., 2015a,b). Therefore, energy sources that do not require enzymatic hydrolysis before absorption from the intestinal lumen might be more suitable lactose replacers. Glucose, fructose, and glycerol are potential lactose replacers. The small intestinal lumen absorbs glucose and fructose by specific carriers [i.e., glucose by Na^+-dependent glucose transporter (SGLT1; Hediger and Rhoads, 1994; Zhao et al., 1998)

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and fructose by the facilitative glucose transporter GLUT5 (Burant et al., 1992; Zhao et al., 1998)]. Glycerol is easily absorbed from the small intestinal lumen, with 78% of the glycerol absorbed within 25 min after infusion in isolated loops of the small intestine of rats (Höber and Höber, 1937). There are indications that Na^+-dependent carriers are also involved in the absorption of glycerol (Kato et al., 2005).

Ingestion of glucose, fructose, or glycerol by milk-fed calves results in the luminal presence of different (ratios of) monosaccharides and glycerol compared with the ingestion of lactose. Lactose is split into equimolar amounts of glucose and galactose by the brush-border enzyme lactase (Coombe and Smith, 1973). Lactase activity is high in milk-fed calves (Toofanian et al., 1973; Le Huerou et al., 1992; Gilbert et al., 2015a). Glucose is preferentially absorbed from the small intestine over galactose (Coombe and Smith, 1973), and replacing lactose with glucose might result in a greater postprandial blood glucose concentration, which could result in an increased excretion of glucose via urine when the renal threshold is exceeded (Hostettler-Allen et al., 1994; Vicari et al., 2008a). Feeding a fructose solution to milk-fed calves results in a low reducing sugar response in blood sampled from the jugular vein (Velu et al., 1960; Siddons et al., 1969). This result suggests either a rapid uptake of fructose by the liver from hepatic portal blood, as seen in rats and humans (as reviewed by Mayes, 1993), and subsequent postabsorptive conversion of fructose into products other than reducing sugars (i.e., glycogen, lactate, CO_2), or a low absorption of fructose from the intestinal lumen. The latter might result in incomplete disappearance of fructose from the small intestine, resulting in substrate fermentation. Almost no increase in plasma glucose was found after feeding glycerol with an oral rehydration solution to 3-wk-old Swedish Red calves (Werner-Omazic et al., 2013). Feeding fructose or glycerol, therefore, probably results in a lower postprandial increase in glucose compared with lactose feeding. Also, fructose does not elicit insulin release (Curry, 1989). Feeding glycerol or glucose to 3-wk-old Swedish Red calves resulted in similar increases in plasma insulin, whereas plasma glucose levels were lower after glycerol feeding (Werner-Omazic et al., 2013). Glycerol or fructose feeding might, therefore, affect the insulin-to-glucose ratio and, consequently, alter glucose metabolism compared with lactose feeding. Also, heavier milk-fed calves often develop insulin resistance (Hostettler-Allen et al., 1994; Hugi et al., 1997) and replacing lactose might affect the development of insulin resistance.

Replacing lactose with glucose, fructose, or glycerol not only results in the luminal presence of different (ratios of) monosaccharides and glycerol, but could potentially alter glucose homeostasis and, thereby, energy partitioning. The objective of our study was to determine the effects of replacement of lactose with glucose, fructose, or glycerol on energy and protein metabolism in veal calves. The effects on glucose homeostasis and insulin sensitivity are presented elsewhere [A. Pantophlet, M. Gilbert, J. van den Borne, W. Gerrits, H. Roelofsen (Medical Biomics, University Medical Centre Groningen, Groningen, the Netherlands), M. Priebe (Department of Pediatrics; Center for Liver, Digestive and Metabolic Diseases, University Medical Centre Groningen, Groningen, the Netherlands), and R. Vonk (Medical Biomics, University Medical Centre Groningen, Groningen, the Netherlands), unpublished data].

MATERIALS AND METHODS

This experiment was approved by the Animal Care and Use Committee and conducted at the research facilities of Wageningen University.

Animals and Experimental Design

Forty male Holstein-Friesian calves were selected from 1 farm based on BW, age, and clinical health. Calves arrived at the research facilities in 3 batches and were equally divided over 5 blocks of 8 calves based on BW. Within each block, pairs of calves were assigned to 1 of 4 MR treatments (n = 10 per treatment, n = 2 per treatment per block). Each block was separated by 1 wk, which was required because of the capacity of the respiration chambers. At the start of the experiment, weight and age of the calves (mean ± SE) were 114 ± 2.4 kg and 97 ± 1.4 d, respectively.

After arrival, calves received the control MR for 11 d; thereafter, the adaptation period started and calves were assigned to 1 of 4 MR. The control treatment (**CON**) contained 46.2% lactose as the only source of carbohydrates. In the other MR treatments, 15.0% of 1 of 3 lactose replacers [glucose (**GLUC**), fructose (**FRUC**), or glycerol (**GLYC**)] was included in the MR at the expense of lactose. Calves were fed these MR for 48 d before the experimental period started in which measurements on energy and protein metabolism were performed. This long adaptation period was applied to determine the long-term effects of these lactose replacers on energy and protein metabolism.

Housing

During the first 42 d of the adaptation period, calves were housed in groups of 5 on wooden, slatted floors without bedding material. Per calf, 2.0 m^2 was available. Each group received the same MR, but the MR