Metabolic and Production Responses to Increased Postruminal Starch Digestion in Cattle

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Introduction

In contrast to nonruminants, forage-fed ruminants normally absorb very little glucose from their feed. However, glucose supply is still crucial for maintenance and productive functions in ruminants, such as growing and lactating cattle. Glucose supply is especially important for the lactating dairy cow because of the demands of milk synthesis for glucose. Glucose requirements of ruminants are largely met through glucose synthesis, which predominantly occurs in the liver using glucose precursors absorbed following fermentation and digestion of the diet. Therefore, glucose metabolism in the lactating dairy cow represents a balance between glucose requirement for milk production and glucose carbon supply from the diet, which is integrated by the liver. As milk yield of the modern dairy cow increases, the glucose requirement of her mammary gland increases as well. Whilst ruminal fermentation typically limits the availability of starch for digestion in the small intestine, glucose absorption from the small intestine could benefit the glucose economy and production of both growing and lactating cattle. The present paper will consider the implications of high rates of milk yield for the glucose balance of the dairy cow in terms of:

1. Glucose requirements
2. The capacity for postruminal starch digestion and glucose absorption
3. The implications of increased glucose absorption for metabolism and production
4. The effect of transition on glucose balance of the high yielding dairy cow

Glucose Requirement

For lactating dairy cows, glucose requirement is often estimated using an equation reported by Elliot (1976) in a Cornell Nutrition Conference paper that is frequently cited in the scientific literature. This estimation was based on measurements of glucose supply and metabolism in lactating dairy cows obtained using isotopic labeling techniques (Annison et al. ,1974; Bickerstaff et al., 1974). In those studies, milk lactose output accounted for 69.4% of the total uptake of glucose by the mammary gland. While this value varied considerably (50 to 85%) across the cows studied (2 Jerseys, 2 British Friesians), the average agrees reasonably well with results from subsequent studies (62 to 83%; e.g. Davis et al., 1985, Hanigan et al., 1992). Assuming a milk lactose content of 4.8%, and that milk lactose output accounts for 70% of mammary glucose use, mammary glucose requirement can be readily calculated. For a cow producing 60 kg of milk daily, her mammary glucose requirement is over 4 kg/d.

In addition to the mammary gland, other tissues in the body use glucose, primarily through oxidation or triglyceride synthesis in adipose and other tissues. In the 2 highest yielding cows in

the study of Annison and colleagues (Bickerstaff et al., 1974), mammary glucose uptake accounted for nearly all of glucose supply, suggesting a minimal glucose requirement for other body tissues. Elliot (1976) suggested the amount of glucose not used by the mammary gland in these 2 cows (198 g/d) was the maintenance requirement for the rest of the body of high yielding dairy cows. This represents a 'bare bones' minimum amount of glucose use by nonmammary tissues, and would not include glucose which is used for body energy retention or maintenance (i.e. oxidized). In growing beef cattle weighing 400 kg at maintenance intakes, liver glucose production was about 500 g/d (Reynolds et al., 1991). This suggests that the glucose requirement for maintenance of nonmammary tissue in a 600 kg dairy cow may be greater than the 200 g/d suggested by the data of Bickerstaff et al. (1974). However, in high yielding dairy cows in early lactation body tissue energy balance would likely be negative, and the amount of glucose oxidized in nonmammary tissues would surely be minimal.

The data of Annison et al. (1974) also showed that as milk yield increased, mammary glucose use accounted for an increasing proportion of total glucose supply: from 20% at 6 kg milk/d to 90% at 25 kg milk/d. This decrease in the proportion of glucose supply used by nonmammary tissues at higher milk yields was not simply due to differences in total glucose availability, but must also reflect differences in the amount of surplus glucose oxidized and used to support body fat and protein synthesis in cows with lower milk yield. Previous studies have shown that the percentage of total glucose supply oxidized is reduced in lactating compared to dry cows (Bartley and Black, 1966; Bauman and Elliot, 1983). Similarly, glucose oxidation was reduced in cows treated with bST (Bauman et al., 1988). These observations suggest that as a cow progresses through lactation, a decline in milk yield and/or an increase in body tissue energy balance will be associated with an increase the amount of glucose used for maintenance functions or body fat synthesis.

Across a broad range of intakes and physiological states, including growth, lactation and dry periods, there is a very good relationship between glucose supply and energy (DE or ME) intake (e.g. Leng, 1970; Lomax and Baird, 1983; Reynolds, 1995). This likely reflects a relationship between glucose requirement and metabolizable energy (ME) supply, and effects of glucose demand on liver glucose production. In growing animals, glucose requirement will be determined by growth rate, which is set by ME intake. In lactating cows glucose requirement will be determined by milk yield, which is highly correlated with ME intake, except in very early lactation. In periods of under nutrition, as occurs during fasting, in late pregnancy in sheep, or perhaps in very early lactation, the relationship between glucose supply and ME is altered because of the dominant effect of glucose requirement on glucose synthesis. However, in most circumstances glucose requirement can be predicted reasonably well from ME intake (e.g. Reynolds, 1995), or on the basis of milk yield (milk lactose yield/0.7) and an estimate of the amount of glucose used by nonmammary tissues (minimally 200 g/d), as described previously. In pregnant animals, glucose requirement of the uterus and fetus can also be estimated on the basis of previous measurements of glucose uptake per unit mass and an estimate of utero-placental and fetal tissue mass (see Drackley et al., 2001).

Postruminal Starch Digestion And Glucose Absorption

Although ruminants normally absorb little glucose, considerable research attention has been given to the extent to which glucose supply in cattle could be met by increasing starch flow

to the small intestine. Without the use of rumen protection technology, this is achieved in practice by feeding high levels of starch that is resistant to rumen degradation, such as dry shelled corn or sorghum grain. One concern is that the capacity for starch digestion in the small intestine may be limited, such that with greater starch flow to the intestines the fraction digested may decrease and significant amounts of starch appear in the feces (Elliot, 1976). There is a large amount of published data describing total postruminal starch digestion, which includes both the small intestine and hindgut (cecum and large intestine), where considerable amounts of starch fermentation can occur (for reviews see Nocek and Tamminga, 1991; Reynolds et al., 1997; Mills et al., 1999; Firkins et al., 2001). While starch digestion is affected by a number of factors (processing, maturity, genetics, etc.), in a summary of published data from lactating dairy cows total postruminal starch digestion averaged 95% (Reynolds et al., 1997). Over a range of duodenal starch flows up to 5 kg/d there was no indication of a limitation to starch digestion. Because starch digestion was incomplete (95%), fecal starch output increases slightly with increased postruminal digestion, but there was no indication that fractional digestibility was reduced at higher starch flows to the small intestine. However, it is impossible to know from these data the extent to which total postruminal starch digestion occurred in the small intestine or hindgut.

Considering the implications for the glucose economy of the lactating dairy cow, there are remarkably few published measurements of starch digestion in the small intestine of the lactating dairy cow (Reynolds, 2006). For the measurements available, fractional starch digestion in the small intestine averaged 70%, with no concrete evidence of variation due to grain type or processing. In these studies fractional digestion was lower in the hindgut (59%), reflecting the increasing resistance of residual starch to further digestion as it progressed through the digestive tract (Reynolds et al., 1997). When the amount of starch digested postruminally was increased by increasing the particle size of ground corn (Remond et al., 2004), fractional starch digestibility in the small intestine was markedly reduced such that a greater proportion of postruminal starch digestion occurred in the hindgut. While starch digestion in the small intestine will provide glucose for absorption, starch fermentation in the hindgut will yield volatile fatty acids (VFA) for absorption, as well as microbial protein which is unavailable for further digestion. Thus it appears that there is considerable capacity for small intestinal starch digestion in the lactating dairy cow. However, any increase in starch flow to the small intestine will be accompanied by an unavoidable increase in hindgut starch fermentation and microbial protein excretion in the feces, even if starch digestibility remains constant. In nonlactating cattle, a recent summary of published data suggests that with increasing starch flow to the duodenum (from 250 to 1800 g/d), starch digestibility in the small intestine decreased from 80 to 50%, respectively (Matthé et al., 2001).

While there appears to be considerable capacity for starch digestion in the small intestine of the dairy cow, numerous studies have shown that the net absorption of glucose into the portal vein is near zero, or negative, even when starch is infused postruminally. Generally, the recovery of purified starch infused into the abomasum or duodenum as increased net glucose absorption into the portal vein ranges from 19 to 46% (Reynolds, 2006). This low recovery of starch as glucose absorbed into blood suggests a limitation of glucose absorption, a substantial utilization of glucose during absorption by the small intestine, or increased utilization of glucose from arterial blood by portal-drained viscera (PDV) tissues. The small intestinal enterocytes

represent a small proportion of the total PDV, but any increase in glucose use from arterial blood by other PDV tissues would negate, on a net basis, any increase in glucose absorption into the portal vein. Early studies in sheep found as much as 25% of whole body glucose utilization occurred in the PDV (Bergman et al., 1974). Isotopic labeling studies in catheterized steers (Harmon et al., 2001) suggest that the low recovery of starch infused into the abomasum as increased net glucose absorption across the PDV is to a large extent due to an increase in glucose use from arterial blood, rather than a catabolism of glucose during absorption. In this study, increases in true glucose absorption into the portal vein accounted for 70% of the glucose in the starch infused, but increased use of arterial glucose by the PDV equaled 20% of those glucose equivalents. Assuming that starch digestibility was only 75% in the small intestine, then most of the starch digested could be accounted for as increased glucose absorption into blood. As the PDV can include as much as 25%, or more, of body fat, then a part of the increase in PDV glucose use with increased postruminal starch digestion may well reflect an increase in glucose use for fat retention in PDV adipose tissue.

In summary, it appears that there is a reasonable capacity for small intestinal digestion of starch in lactating dairy cows, and increased glucose absorption, although increased small intestinal starch digestion is invariably accompanied by increased starch fementation in the hindgut. However, increases in glucose absorption into the portal vein are accompanied by increased utilization of arterial blood glucose by tissues drained by the portal vein, such as mesenteric and omental fat deposits.

Implications Of Increased Glucose Absorption

In the early 1990's, an extensive review of published studies concluded that 'production studies provide no clear evidence that site of starch digestion enhances milk yield or changes composition' (Nocek and Tamminga, 1991), suggesting no benefit of greater, or less, postruminal starch digestion. In contrast, other studies have suggested a benefit of increased ruminal starch digestion on milk and or milk protein yield (Theurer et al., 1999), perhaps as a consequence of increased microbial protein supply. However, these conclusions were based largely on effects of steam flaking on corn or sorghum grains, which also improved total tract starch digestibility and increased ME supply. In early lactation dairy cows, incremental starch infusion into the abomasum at relatively low rates (up to 2 kg/d) increased milk yield, but decreased milk fat concentration in a quadratic manner such that there was little change in milk energy output except at the highest level of infusion (Reynolds et al., 2001). A similar response was observed when glucose was infused into the duodenum of early lactation cows (Hurtaud et al., 1998). This suggests that the increased ME supplied as absorbed glucose (or VFA) was either oxidized or used to support greater tissue energy balance. Rigout et al. (2003) summarized a number of predominantly French or Finnish studies in lactating dairy cows where glucose was infused at varying levels into the abomasum or propionate, a glucose precursor, was infused into the rumen. Across these studies increased supply of glucose equivalents was associated with a curvilinear increase in milk yield (maximally 2.5 kg/d at 10 Mcal/d), a linear increase in milk protein concentration (.3 percentage units at 13 Mcal/d) and a curvilinear decrease in milk fat concentration (maximally 1.4 percentage units at 13 Mcal/d).

In a calorimetry trial in the UK, energy and nitrogen balance were measured in late lactation, pregnant dairy cows which received abomasal infusions of 1200 g starch per day for 14 days (Reynolds et al., 2001). Abomasal starch infusion did not alter fecal starch excretion, but increased fecal protein and decreased fecal pH, suggesting at least a part of the starch infused was fermented in the hindgut. The resulting decrease in apparent nitrogen digestion contributed to a decrease in urinary nitrogen excretion, which was also due to a large increase in nitrogen retention in body tissues. Milk energy and nitrogen production was not affected, but tissue energy retention increased, accounting for 85% of the increase in ME measured when starch was infused. This suggests that the energy absorbed as glucose or VFA from starch digestion postruminally is used with a very high efficiency for body tissue protein and fat deposition. The increase in body protein retention was likely a consequence of an insulin response to increased glucose absorption from the small intestine. Similarly, increased insulin and glucose use for body tissue energy may explain the relatively small increase in milk energy yield in cows infused postruminally with starch or glucose in early lactation (Reynolds et al., 2001; Hurtaud et al., 1998; Rigout et al., 2003).

One concern with increasing glucose absorption through greater postruminal starch digestion is that increased glucose absorption may be negated by decreased endogenous glucose synthesis such that there is little benefit in terms of total glucose supply (Elliot, 1976). This concern is based on infusion studies where increased exogenous glucose supply achieved through intravenous or intraduodenal glucose infusion caused a decrease in endogenous glucose synthesis (e.g. Bartley and Black, 1966; Leng, 1970). However, in most cases these studies employed short-term infusions, with little time for metabolic adaptation. With longer term infusions, allowing time for metabolic adaptations, total glucose use increases, and the suppression in endogenous synthesis abates such that total glucose supply is increased (Reynolds et al., 1994). The long term extent of the suppression in glucose synthesis, and ultimate increase in supply, will of course depend on the amount of exogenous glucose supplied and the capacity of the cow to utilize the additional glucose for milk or body tissue synthesis, or maintenance functions. In general, it appears that increased glucose absorption will increase glucose supply to the lactating dairy cow, but even in early lactation the primary metabolic response appears to be an increase in body tissue energy balance, rather than an increase in milk energy yield. This effect on insulin status and body energy balance may have important implications for the reproductive success of the cow (Gong et al., 2002).

Glucose Synthesis

The liver is the predominant site of glucose synthesis in the ruminant, although 10 to 15% of total glucose synthesis occurred in the kidneys of sheep (Bergman et al., 1974). The relative contribution of the kidneys increased to 25% when sheep were fasted, reflecting an increase in the use of glucose precursors from the breakdown of body tissues. The contribution of the kidneys to total glucose synthesis in lactating dairy cows has never been measured, but it is conceivable that it would be greater in very early lactation. Precursors for glucose synthesis include propionate, glucogenic amino acids, lactate, glycerol, i-butyrate and n-valerate (Leng, 1970). On a quantitative basis, propionate accounts for the largest amount of glucose synthesis, maximally accounting for up to 76% of liver glucose synthesis (Reynolds et al., 1994). Propionate represents an important metabolic link between ME intake and liver glucose

production. Propionate supply is dictated by dietary intake, and is itself an important regulator of voluntary intake. Nearly all of the propionate absorbed into the portal vein is removed by the liver, and virtually all the propionate taken up by the liver is used for glucose synthesis.
In conditions of undernutrition, the contribution of propionate and other precursors derived from the diet decreases, while the relative contributions of lactate, glycerol and amino acids from body tissues increase, albeit at a reduced rate of glucose synthesis (Lomax and Baird, 1983). The use of lactate from body tissues represents 'Cori Cycling' of glucose carbon between the liver and peripheral tissues, such as the muscle or adipose. However, substantial amounts of lactate can be absorbed across the PDV, which to a large extent represents dietary contributions (van der Walt et al., 1983). Nearly all the amino acids can contribute their carbon to glucose synthesis, and in total they are considered the second most important glucose precursor. Of all the amino acids, alanine represents the greatest potential contributor, and is absorbed into the portal vein in the greatest amount. However, like lactate, a part of the alanine released by the PDV and removed by the liver is a product of glucose metabolism, thus represents a recycling of glucose carbon.
Unlike propionate and alanine, whose rate of removal by the liver appears to be dictated by their supply from the PDV, lactate removal by the liver is sensitive to the supply of other glucose precursors (Reynolds, 1995). As such, lactate's contribution to glucose balance across the liver represents a point of metabolic flexibility which reflects body energy status. At a given level of intake, increasing the appearance of propionate or alanine in the portal vein increases their removal by the liver, but this is often accompanied by a concomitant reduction in lactate removal. This reduction in liver lactate removal increases its supply to peripheral tissues, where it can be used for adipose synthesis and thus tissue energy retention. In periods of body tissue energy loss, lactate removal by the liver increases, in part as a consequence of increased lactate flow from peripheral muscle and adipose to the liver (Benson et al., 2002).

In summary, propionate supply from the diet is by far the most important component of glucose balance in the lactating dairy cow, with amino acids and lactate making important contributions which, in the case of lactate, vary with the energy status of the cow. For the dairy cow in very early lactation, the state of negative body energy balance is often compared to the undernutrition which occurs in fasting, thus it is assumed that lactate, glycerol and amino acids from the body will make a greater relative contribution to glucose synthesis in the liver.

Glucose Balance In Transition Dairy Cows

In a recent study (Reynolds et al., 2003), liver metabolism was measured in transition dairy cows using catheterization procedures. Measurements of blood flow and net nutrient flux across the PDV and liver (together called the 'total splanchnic tissues') were obtained at 10 day intervals before and after calving, and some of those measurements are presented in tables 1 and 2. After calving, dramatic increases in metabolic activity (blood flow and oxygen use) of the PDV and liver accompanied increases in milk yield and liver glucose production, but as in numerous other studies there was no net glucose absorption across the PDV. Estimates of glucose requirements of these cows based on their milk yield and gestational and maintenance requirements, as described previously (Drackley et al., 2001; Elliot, 1976), are compared to measured glucose production by the liver in figure 1. In late gestation, liver glucose production was slightly greater than estimated glucose requirement, without any contribution from the kidneys or additional use of glucose for maintenance or tissue energy retention. As lactation

progressed after calving, liver glucose production was progressively greater than estimated requirement. This may reflect an underestimation of requirement, or more likely an increasing use of glucose for maintenance and tissue energy retention, as discussed previously. As we have observed in previous studies in growing and lactating cattle (Reynolds, 1995; Benson et al., 2002), increases in body tissue energy balance were accompanied by an increase in total splanchnic flux of lactate (PDV plus liver flux). In early lactation splanchnic flux of lactate was negative (liver removal greater than PDV release), representing glucose carbon cycling between the liver and non-PDV tissues, but as lactation progressed splanchnic flux became more positive, which likely reflects use of lactate derived from the diet for tissue energy retention as body fat.

Except for measurements of alanine, amino acid removal by the liver was not measured in this study, but the minimal required contribution of amino acid carbon for glucose synthesis can be estimated as the difference between glucose released by the liver and the maximal potential contribution of the other precursors removed (Table 2). During transition, the percentage contribution of propionate to liver glucose synthesis remained fairly constant, but was greatest at 12 weeks after calving, when dry matter intake was maximal. The total amount of lactate, alanine and glycerol removed by the liver were all greatest 11 days after calving, which likely reflects an increase in the activity of the gluconeogenic enzyme pyruvate carboxylase (Greenfield et al., 2000), but the relative rate of removal of lactate was far greater than for alanine (Table 1). As a proportion of the glucose synthesized, the contributions of alanine and glycerol were greatest at the first measurement after calving, but the required contribution of other amino acids was, surprisingly, lowest at this point in transition (11%; Table 2).

The relative contribution of amino acids, and other endogenous precursors, to glucose synthesis in the liver may well have been greater in the first days of lactation, but by day 11 of lactation a minimal contribution was observed. In these cows, who had a relatively smooth transition, increases in liver removal of measured glucose precursors between 9 days before calving and 11 days after calving accounted for 100% of the increase in liver glucose release. An increase in the removal of other amino acids may well have occurred, but it was not required to balance changes in glucose carbon production across the liver. This suggests that in early lactation a priority for amino acid usage for milk protein synthesis, or the growth of splanchnic tissues, may direct amino acid carbon away from liver catabolism and towards anabolic functions which establish lactation. Other than the contribution of alanine, the contributions of other amino acids to glucose synthesis may, in total, reflect obligatory catabolic processes, rather than a metabolic priority for lactation.

Conclusions

Glucose requirements of the dairy cow are dominated by the requirements of the mammary gland for milk synthesis and set by ME intake during growth. With greater milk yield, glucose requirements increase, but they are largely met through glucose synthesis in the liver. There appears to be considerable capacity for starch digestion in the small intestine and subsequent increases in glucose supply to the lactating dairy cow, but the increased glucose supply appears to be used primarily to support body fat and protein retention, and not greater milk energy production. This response is accompanied by changes in insulin status, and may have important implications for the metabolic health and reproductive success of the early

lactation cow. However, greater starch digestion in the small intestine will be accompanied by greater starch fermentation in the hindgut, and fecal protein loss. The contribution of propionate dominates the budget of glucose precursors, and represents an important integration of ME intake and liver glucose synthesis. In transition dairy cows, the contributions of lactate, alanine and glycerol to liver glucose synthesis were greatest at 11 days postpartum, reflecting negative body energy balance, but the required contribution of other amino acids to glucose synthesis in early lactation was minimal. Lactate represents an important component of glucose balance in cattle. Lactate exchange across the PDV and liver reflects shifts in body energy status, with lactate flowing to the liver in early lactation and flowing to peripheral tissues later in lactation when body energy balance and fat synthesis is greater.

Table 1. Dry matter Intake (DMI), milk yield, liver blood flow and net portal-drained visceral (PDV) and liver metabolism in transition dairy cows (Reynolds et al., 2003).

	Average day relative to calving						
Item	-19	-9	11	21	33	83	SEM
DMI, kg/d	9.6	9.6	14.7	17.1	19.5	22.1	0.7
Milk yield, kg/d			36.4	41.3	43.1	40.7	1.2
Liver blood flow, L/h	1121	1147	2187	2222	2247	2437	119
PDV flux, mmol/h							
Oxygen	-1505	-1682	-3108	-3296	-3425	-3911	214
Glucose	-24.6	-30	3.6	-25.8	-1.3	-4.7	12.1
Lactate	96.6	94.7	134.0	182.3	203.1	208.1	21.5
Alanine	23.3	24.0	74.1	73.3	91.8	80.5	8.6
Liver flux, mmol/h							
Oxygen	-1505	-1682	-3108	-3296	-3425	-3911	214
Glucose	294	317	627	777	810	840	45
Lactate	-112	-145	-266	-265	-254	-140	32
Alanine	-18.3	-14.6	-60.9	-45.4	-24.9	-28.5	6.1
Glycerol	-13.8	-18.7	-44.8	-39.0	-25.0	-9.3	7.8

Table 2. Maximal net contributions of glucose precursors removed to glucose released (% of total) by the liver of transition dairy cows (Reynolds et al., 2003).

	Average day relative to calving						
Item	-19	-9	11	21	33	83	SEM
Propionate	55.2	43.5	55.8	49.0	57.6	66.4	7.0
Lactate	18.5	22.7	21.1	16.9	15.6	8.0	2.7
Alanine	3.1	2.3	5.5	3.0	1.5	1.7	0.6
Glycerol	2.3	3.0	3.6	2.4	1.5	0.4	0.7
Triglyceride glycerol	-0.2	1.5	0.2	0.0	0.1	-0.1	0.5
i-Butyrate	1.7	1.4	1.3	1.1	1.4	1.6	0.5
n-Valerate	2.8	2.4	3.3	2.3	2.8	3.0	0.6
Total	83.4	76.8	88.9	74.7	80.5	81.8	7.5

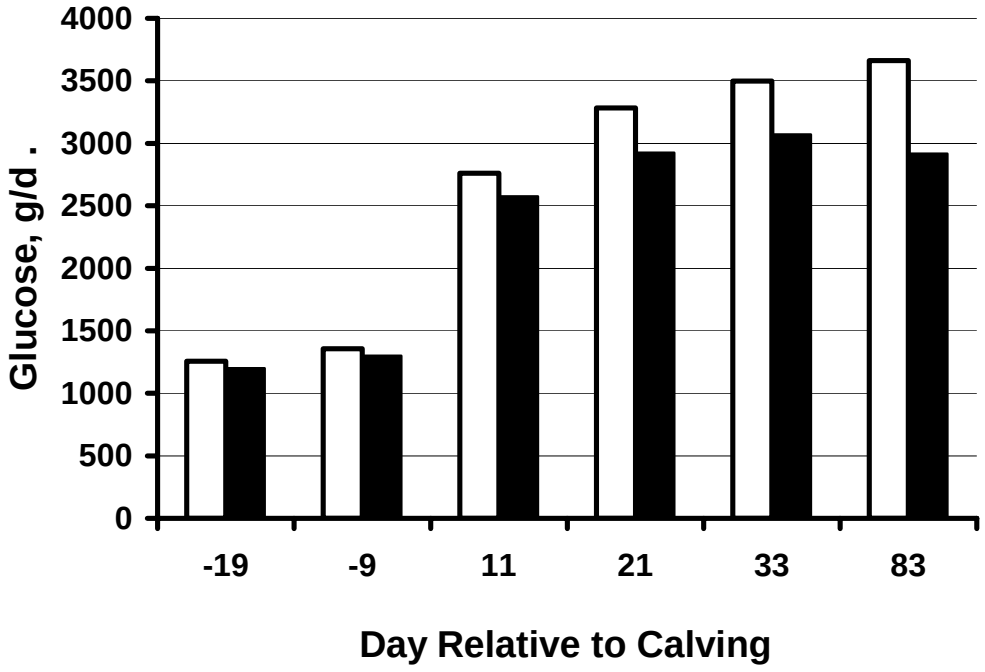

Figure 1. Liver glucose release (open bars) and estimated glucose requirement (solid bars) in transition dairy cows (Reynolds et al., 2003).

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