Rethinking Ruminal Acidosis in Dairy Calves

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▪ Take Home Messages

- Subacute ruminal acidosis is a costly disease in cows associated with extended bouts of low rumen pH; calves are assumed to be similarly responsive and susceptible to subacute ruminal acidosis.
- Little is known about rumen pH dynamics in calves.
- Calf rumens (pH dynamics) respond to increased diet fermentability differently than mature rumens do.
- In calves, low rumen pH does not appear to reduce growth, so increasing rumen pH may not be necessary.
- Low rumen pH may aid in development of the rumen papillae.
- Optimal rumen pH in calves is unknown but likely is different from that in adult cows.

▪ Introduction

Raising of replacement heifers represents 10–20% of all on-farm costs (Bailey and Cullin, 2009), yet performance in calf nutrition is poor. Morbidity rates before weaning remain stubbornly high at 20–25% of all calves (Windeyer et al., 2014), with gastrointestinal problems being the principal reason calves are treated with antibiotics. In a survey of Canadian dairy producers, researchers, and veterinarians, animal health was the top priority across all surveyed categories (Bauman et al., 2016). Therefore, looking at major gastrointestinal problems such as subacute ruminal acidosis (SARA) and evaluating them in calves is crucial.

In the last decade, research showed that calf nutrition and management impact lifetime performance of the animal. As a result, there has been a resurgence of interest in the young calf. Often, calves are treated as 'mini cows' as soon as they are weaned, and it is assumed that they will respond the same way to nutritional and management signals as mature cows do. Because calves undergo a massive transformation of their rumen, and gastrointestinal tract in general, in the first few months of life, assumptions that calves should be managed as though they are miniature cows require a re-evaluation.

The conundrum in calves is the high fermentability of calf starter and the drive to increase calf starter intake. Fermentation of calf starter drives rumen papillae development, so calf starters often have starch contents of 30% or more, very high by mature cow standards. High starch diets are a strong contributor to SARA and depressing health and productivity of cows (Plaizier et al., 2008). Though SARA is a complex disorder, one of the key indicators that a cow is experiencing SARA is an acidic rumen with pH below 5.8 (Aschenbach et al., 2011). Because our knowledge regarding SARA in calves is very limited, the same threshold of rumen pH 5.8 is used in calves. However, a rumen pH below 5.8 might not be a bad thing in calves whose rumens are undergoing rapid development.

▪ Rumen Development

The newborn calf has an undeveloped rumen that is non-functional. As the consumption of highly fermentable calf starter increases, butyrate produced from fermentation drives a strong increase in papillae development, which can be seen by the naked eye (Figure 1). For that reason, maximizing starter intake as a measure of readiness to wean is key to calf management. The NRC (2001) recommended weaning calves as soon as their starter intake is 680 g/day (1.5 lb/day), though this number has recently been revised to 1000 g/day (Stamey et al., 2012).

Figure 1. Development of the young calf's rumen via consumption of calf starter. At 28 days, calves fed milk only (LEFT) show little development, whereas calves fed milk and grain (RIGHT) show darker, more vascularized tissue with more prominent papillae. These papillae increase the absorptive surface area of the rumen. Modified from https://extension.psu.edu/photos-of-rumen-development

Increasing calf starter is primarily linked to decreased milk intake. In one study (de Passille et al., 2011), calves were fed a high plane of nutrition and a medium plane of nutrition and weaned at either 5 weeks or 8 weeks. Regardless of plane of nutrition, calf starter intake increased in earnest during the weaning transition when milk provision was reduced. When calves are fed a lower amount of milk replacer powder (~750 g/day), calves are so short on milk supply that they reach 680 g/day of calf starter intake by 7 weeks of age (Laarman and Oba, 2011). Limiting milk or milk replacer is therefore the most effective way of maximizing calf starter intake, and the reason why limit-fed programs were popular for decades.

In the past decade, this mantra has been overturned largely due to the discovered links between calf performance and lifelong productivity. In pre-weaned calves, average daily gain and body weight at weaning are associated with greater milk production in first lactation (Soberon et al., 2012). Recently, increases in calf starter intake were also linked to improved first lactation performance (Rauba et al., 2019). Specifically, for every Mcal of metabolizable energy intake from calf starter before weaning, cows will produce an extra 1.43 kg of milk in their first lactation (Rauba et al., 2019). Given the importance of early life nutrition and health, the current focus of calf management is on successful rumen development, driven by improving intakes of milk and calf starter.

One of the principal outcomes of starter intake is morphological development of the rumen, which was long seen as synonymous with absorptive capacity of the rumen. As a result, starter intake is often used as an indicator of morphological development. The issue is that morphological development does not necessarily mean the rumen is capable of absorbing enough nutrients to meet the calf's energy needs post-weaning. Recent studies have shown that volatile fatty acid (VFA) absorption in the rumen can change independent of morphological changes (Laarman et al., 2016) and that pre-weaned calves with developed rumen papillae have the same VFA absorption rates as calves with an undeveloped rumen (Yohe et al., 2019). These results imply that rumen development includes more than just the morphological development (i.e., papillae formation) of the rumen epithelium. The cells that make up the rumen epithelium are also developing and may have a much larger impact on nutrient metabolism than previously thought.

▪ Regulation of Rumen pH in Calves

The rumen epithelium is continuously exposed to the rumen environment; therefore, fluctuations in rumen pH and the regulation of rumen pH are important to the barrier integrity and cellular survival of the rumen epithelium. Once rumination behaviour begins, rumen pH regulation is assumed to follow that of the mature cow: Increased fermentability in diets increases VFA production and rumen acidity, decreasing pH. Maximizing VFA production while mitigating pH drops is a decades-long effort that constantly requires research and updating (Plaizier et al., 2008). Underlying this research is the assumption that the relationship between diet fermentability, VFA concentrations, and rumen pH is constant, which may not be the case in young calves.

During the early phases of rumen development, rumen pH is considerably lower (more acidic) than that of a healthy rumen in a mature cow. For a long time, research on rumen fermentation dynamics in calves showed differences in rumen pH in calves fed starters using different starch sources (Khan et al., 2008). In many of these studies, calves younger than 50 days of age had rumen pH well below the threshold of SARA (in mature cows), despite having access to forage ad libitum (Table 1). These data suggest that optimal rumen pH in young calves may be lower than in adult cows, where a rumen pH above 5.8 is desirable for optimum feed digestion.

Table 1. Rumen pH in young calves at various ages

Calf Age (days)	Rumen pH	Forage	Source
35	5.19 – 5.49	Ad libitum	Khan et al., 2008
50	6.27 – 6.42	Ad libitum	Laarman and Oba, 2011
50	5.46 – 5.79	Ad libitum	Khan et al., 2008
64-69	5.72 – 5.83	Ad libitum	Laarman et al., 2012
70	5.66 – 6.16	Ad libitum	Khan et al., 2008
70	5.09 – 5.31	Variable	Suarez et al., 2007

Rumen pH is the product of several pressures that depress pH (e.g., increased dry matter intake and diet fermentability) and increase pH (e.g., increased inclusion of physically effective neutral detergent fibre (peNDF), and buffers, increased passage rate). In adult cows, managing forage intake to ensure inclusion of peNDF at levels above 12.5% (Plaizier et al., 2008) helps to keep rumen pH above the SARA thresholds. In calves, forage is generally fed either ad libitum (Laarman et al., 2012b, McCurdy et al., 2019) or not at all, despite calves being on bedding (Bach et al., 2007). In calves, the ability to regulate rumen pH is likely underdeveloped, leaving calves more vulnerable to an upset in rumen pH. Indeed, following a rapidly fermentable meal, rumen pH drops much more quickly in calves than it does in cows (Figure 2).

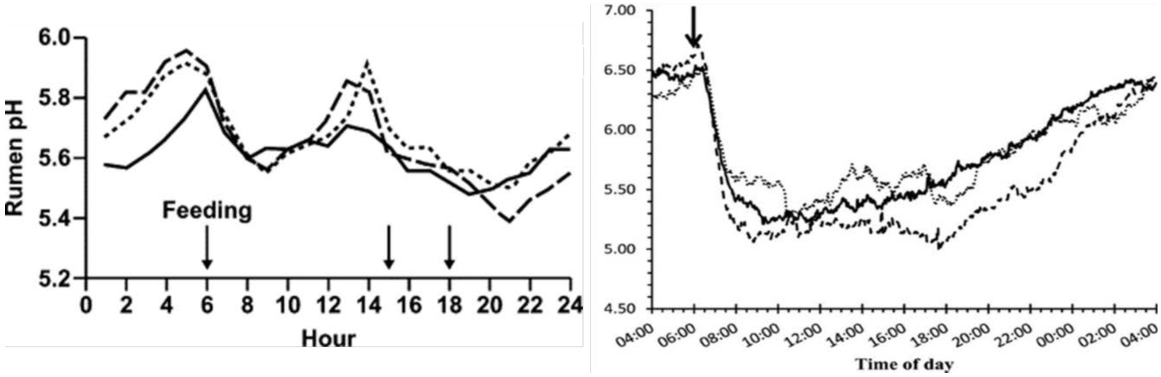

Figure 2. Changes in rumen pH following a rapidly fermentable meal (arrows) in cows (LEFT) and weaned calves (RIGHT). Cows reach their lowest pH point approximately 8 hours after a meal, whereas calves reach the lowest point in 2 hours. From Yang and Beauchemin (2006) and Laarman et al. (2012)

A recent study showed that the differences between cows and calves in terms of rumen pH dynamics are much greater than the rate of decrease only. In a recent study (McCurdy et al., 2019), calves were divided into pre-weaning and post-weaning groups (Figure 3). The pre-weaning group was fed either milk replacer only (PRE-M) or milk replacer, starter and hay (PRE-S). The post-weaning group was weaned during weeks 7 and 8 by reducing milk replacer provision to 900 g/day and 600 g/day, respectively. In week 9, milk replacer was cut-off completely and calves were harvested (slaughtered) one week later. During weeks 7 and 8, calf starter was either not supplemented (POST-B) or supplemented with butyrate at 1% w/w (POST-S). In week 9, all calves were fed non-supplemented calf starter and calves were harvested at the end of week 9.

Figure 3. Schematic of milk feeding and weaning in a recent study (McCurdy et al., 2019) examining the effects of calf starter intake on VFA concentrations, rumen pH, and growth; each box represents one week of life. Two groups of calves were harvested before the start of the weaning transition (PRE-M & PRE-S), with PRE-M being fed milk only, and PRE-S being fed milk, starter, and hay. Two additional groups were harvested one week after completion of weaning (POST-S & POST-B), with both being fed milk, starter, and hay before the weaning transition and starter and hay. During weeks 7 and 8 (yellow boxes), POST-B calf starter was supplemented with butyrate at 1% inclusion, while POST-S calf starter was not supplemented.

Prior to the beginning of the weaning transition, increased calf starter intake tended to increase VFA concentrations but did not impact rumen pH (Table 2), in line with other studies (Laarman and Oba, 2011; Yohe et al., 2019). During the weaning transition, calf starter intakes increased by 2000 g/day and VFA concentrations increased 4-fold, yet rumen pH remained unchanged (Table 2). After weaning, the POST-B calves (received butyrate during the 2-week weaning transition only) had a calf starter intake 800 g/day higher than POST-S calves (did not receive supplemented calf starter during weaning transition). Post-weaning, one week after POST-B calves were returned to their non-supplemented calf starter, ruminal VFA concentrations tended to be lower and the POST-B calves had a strong drop in rumen pH (McCurdy et al., 2019). Despite these variable responses to rapidly fermentable diets, average daily gain was not adversely impacted. On the contrary, the POST-B group with the highest starter intake and lowest rumen pH had the highest average daily gain (McCurdy et al., 2019).

This study suggests calf rumen pH dynamics behave differently than in adult cows. Increased intake of calf starter did not impact rumen pH until after calves were weaned. Further, increased calf starter intake did not increase VFA concentrations after weaning. Lastly, productivity in calves appears to be linked to starter intake, not rumen pH. Higher calf starter intake caused lower pH and higher average daily gain, suggesting that, unlike cows, calves are able to thrive despite low rumen pH. Altogether, these findings paint a picture of rumen pH regulation in young calves that is distinct from mature cows and changing in various phases of life. A freshly weaned calf is not yet a mature ruminant in terms of its ability to regulate rumen pH. When rumen pH dynamics in calves begin to resemble those of a mature cow is unclear but appears to be well after dairy calves are typically weaned.

Table 2. Changes in rumen pH pre-weaning ((PRE), 42 days of age) or post-weaning ((POST), 63 days of age). Calves were fed milk only (PRE-M) or milk, starter and hay (PRE-S) and slaughtered at 42 days of age; or were fed milk, starter and hay, then weaned over a period of 14 days from 42 until 56 days of age, with either no supplementation during the two-week weaning transition (POST-S) or supplementation with sodium butyrate (POST-B). From McCurdy et al., 2019.

					P Value[1]		
	PRE-M	**PRE-S**	**POST-S**	**POST-B**	**PRE-M vs. PRE-S**	**PRE-S vs. POST-S**	**POST-S vs. POST-B**
Age, days	42	42	63	63	N/A[2]	N/A[2]	N/A[2]
Starter intake, g/day	0	77 ± 165	2247 ± 171	3102 ± 171	N/A[2]	< 0.01	< 0.01
Total VFA[3], mM	11.9 ± 11.8	35.6 ± 11.4	154.4 ± 11.8	131.0 ± 11.8	0.08	< 0.01	0.09
Mean pH	6.17 ± 0.21	6.25 ± 0.22	6.40 ± 0.22	5.83 ± 0.21	0.78	0.66	0.05
Duration pH < 5.8, min/d	485 ± 188	280 ± 178	209 ± 201	730 ± 188	0.44	0.79	0.07

[1]P value of 0.05 or less indicates significant difference
[2]No statistical comparison was made
[3]Ruminal volatile fatty acid concentration

▪ How Does pH Affect Papillae Development?

Rumen epithelial development and the formation of papillae are the result of division and differentiation of cells that make up the rumen epithelium. Over time, papillae become visible as cell division continues. The primary driver of cell division and papillae development is butyrate, which is a bioactive molecule produced by ruminal fermentation of carbohydrates. Part of the reason calf starter is a great nutritional stimulus is its propensity to raise butyrate concentration in the rumen (Laarman and Oba, 2011, Yohe et al., 2019). Cell division is then increased, leading to increased development of the rumen epithelium, which becomes visible as papillae begin to develop.

Butyrate is a bioactive VFA involved in many processes critical to rumen development, including VFA transport (Laarman et al., 2012a), and cellular changes involved in epithelial development (Baldwin et al., 2012). Butyrate, however, has different effects in the lab than it does in an animal. In calves, supplementing butyrate appears to be effective only in the first week of life and during the weaning transition (Górka et al., 2018). We don't know why. Since butyrate is bioactive, the impact of butyrate on calf performance is likely involved in the functioning of the cells that make up the rumen epithelium.

Cells in the rumen epithelium must tightly regulate homeostasis, the maintenance of intracellular conditions that allow them to function. In much the same way that the rumen only functions effectively in a certain pH range, so too do epithelial cells only function in a narrow pH range. However, the physiological pH range in epithelial cells is extremely narrow, from 7.0–7.4, whereas the physiological pH in the rumen ranges from 5.8–6.8, considerably lower than the intracellular pH of the epithelial cells.

By itself, low rumen pH is not a problem for the rumen epithelium. In a recent study, rumen tissue that was exposed to pH of 5.2 without VFA present did not exhibit breakdown of the rumen epithelium that occurs in cows with rumen pH of 5.2 (Meissner et al., 2017). Only when VFA was added at 100 mM did the integrity of the rumen epithelium break down (Meissner et al., 2017). At low pH, passive diffusion of VFA increases (Sehested et al., 1999), which represents an unregulated flow of VFA into the cells, acidifying the interior of the cells. Therefore, the production of VFA during the fermentation of calf starter puts a constant acidotic pressure on cells in the calf's ruminal epithelium.

Acidotic pressure may be a good thing for the developing rumen through the promotion of epithelial remodelling, which is what turns the undeveloped rumen at birth into the developed rumen with papillae at weaning (Figure 1). Epithelial remodelling requires a breakup of the bonds that hold cells to each other, normally preventing cells from floating away and preventing bacteria from passing around the cells and into the bloodstream. When the cell interior acidifies, the bonds that hold cells to one another to form a protective barrier, the backbone of epithelial integrity, begin to come apart (Duffy et al., 2004). The breaking of these bonds allows the cells to migrate to new positions (Streuli, 1999), allowing for the development of rumen papillae. Once the cells have migrated, the bonds holding cells together will re-form, and epithelial integrity will be re-established. In other words, low intracellular pH in calves may boost the epithelial remodelling process that forms papillae in early life.

▪ Is SARA a Problem in Calves?

In calves, the impact of SARA may be different than in cows. In cows, SARA is a well-studied problem where rapid increases in non-fibre carbohydrate intake is linked to reduced rumen pH, gut inflammation, epithelial barrier breakdown, and reduced productivity (Plaizier et al., 2008; Aschenbach et al., 2011). In calves, that linkage is not established; however, in the absence of studies on SARA in calves, the impact of low rumen pH on gut health and animal productivity is assumed to be the same in calves as in cows. Calf research in the past 10 years casts doubt on that assumption.

In young calves, SARA does not necessarily happen when calves eat large amounts of non-fibre carbohydrates (Figure 4). Before and during weaning, increases in non-fibre carbohydrates intake do not appear to impact rumen pH (McCurdy et al., 2019; Yohe et al., 2019). Likewise, the microbiome, responsible for the actual fermentation, is also developing and changes dramatically over the course of weaning (Meale et al., 2016), and through 1 year of age (Li et al., 2012). The young rumen's microbiome may therefore be a contributor to the uniqueness of rumen pH dynamics in young calves, though the linkage between rumen microbiome and rumen pH in young calves requires more research.

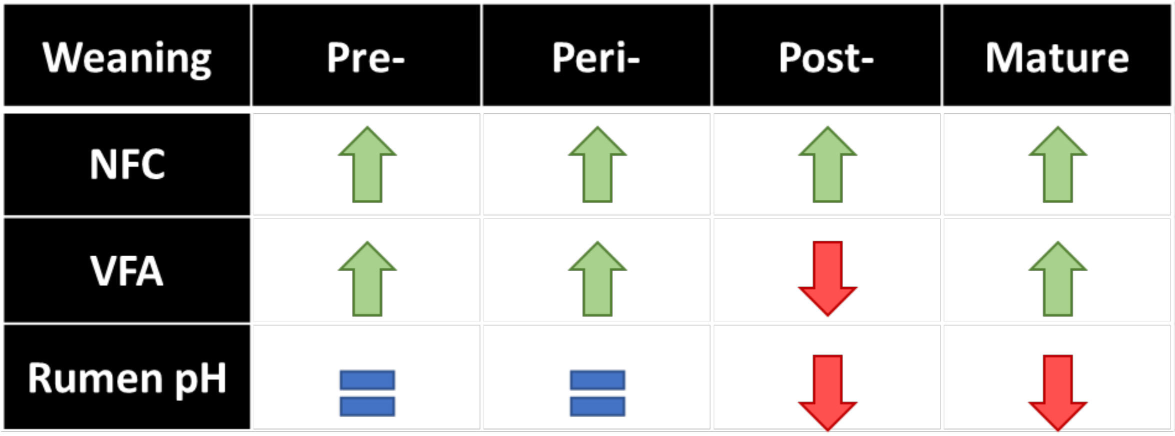

Figure 4. Impact of changes in non-fibre carbohydrate (NFC) intake on VFA concentration and rumen pH in calves pre-weaning (Pre-), during weaning (Peri-) and post-weaning (Post-), compared with that in a mature cow. Until completion of weaning, calves are highly able to manage rumen pH despite drastic changes in NFC intake, whereas weaned calves and mature cows are far less able to. Based on Laarman and Oba (2011), McCurdy et al. (2019), and Plaizier et al. (2008).

While calf rumen pH prior to weaning is not impacted by calf starter intake, it is impacted by forage intake. In a recent study (McCurdy and Laarman, unpublished), our team fed calves 1200 g/day of milk replacer, unlimited calf starter, and either unlimited long-stem forage or limited (90 g/day) long-stem forage. All calves were housed on sand to limit fibre intake to the forage source only. While there was no difference in starter intake between the two treatments, calves fed limited amounts of forage tended to have a lower rumen pH (5.98 ± 0.23 vs. 6.38 ± 0.16, P = 0.09). The duration of SARA, where rumen pH fell below 5.8, increased from 261 min/day to 796 min/day (P = 0.03; Table 3). Despite these differences in rumen pH, no difference in average daily gain was noted. The similar growth rates in all these studies suggests that the performance of these calves is unaffected when rumen pH drops.

Table 3. Performance of pre-weaned calves, housed on sand, fed high amounts of milk replacer, unlimited calf starter, and a long-stem forage source either free-choice or limited to 90 g/d.

	Free Choice	Limited Forage Provision	*P* Value
Starter intake, g/d	617 ± 90	763 ± 106	0.33
Average daily gain, kg/day	0.91 ± 0.03	0.89 ± 0.04	0.61
Total VFA, mM	87.7 ± 13.1	62.1 ± 16.7	0.16
Average pH	6.38 ± 0.16	5.98 ± 0.23	0.09
Duration pH <5.8, min/day	261 ± 133	796 ± 145	0.03

▪ Conclusion

In the young calf, the immature rumen is physiologically distinct from that of a mature cow, where an increase in rapidly fermentable carbohydrates increases fermentation rates, leading to increased VFA concentrations and a decreased rumen pH. The young calf, however, responds quite differently, and rumen pH appears much more stable through weaning with ad libitum feeding of calf starter and forage. Rumen pH can be manipulated before and immediately after weaning without compromising productivity, and inducing SARA in young calves may be a useful tool for promoting gut development. At this stage, our team is working on research to define the conditions and timeframe under which SARA may have beneficial effects on rumen development in young animals. Despite uncertainty regarding optimal rumen pH in calves, recent research results indicate optimal rumen pH in calves is likely to be very different from that of mature cows.

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