



Invited review: Transitioning from milk to solid feed in dairy heifers

M. A. Khan,^{*1} A. Bach,^{†‡} D. M. Weary,^{*} and M. A. G. von Keyserlingk^{*2}

^{*}Animal Welfare Program, University of British Columbia, 2357 Mall, Vancouver, BC, Canada, V6T 1Z4

[†]Department of Ruminant Production, IRTA (Institut de Recerca i Tecnologia Agroalimentàries), 08140 Caldes de Montbui, Spain

[‡]ICREA (Institució Catalana de Recerca i Estudis Avançats), 08010 Barcelona, Spain

ABSTRACT

Calves are born with a physically and metabolically underdeveloped rumen and initially rely on milk to meet nutrient demands for maintenance and growth. Initiation of solid feed consumption, acquisition of anaerobic microbes, establishment of rumen fermentation, expansion of rumen in volume, differentiation and growth of papillae, development of absorption and metabolic pathways, maturation of salivary apparatus and development of rumination behavior are all needed as the calf shifts from dependence on milk to solid feed. In nature and some production systems (e.g., most beef calves), young ruminants obtain nutrients from milk and fresh forages. In intensive dairying, calves are typically fed restricted amounts of milk and weaned onto starter feeds. Here we review the empirical work on the role of feeding and management during the transition from milk to solid feed in establishing the rumen ecosystem, rumen fermentation, rumen development, rumination behavior, and growth of dairy calves. In recent years, several studies have illustrated the benefits of feeding more milk and group rearing of dairy calves to take advantage of social facilitation (e.g., housing with peers or dam), and this review also examines the role of solid feed on rumen development and growth of calves fed large quantities of milk and reared under different housing situations. We conclude that the provision of high-starch and low-fiber starter feeds may negatively affect rumen development and that forage supplementation is beneficial for promoting development of the gut and rumination behavior in young calves. It is important to note that both the physical form of starter diets and their nutritional composition affect various aspects of development in calves. Further research is warranted to identify an optimal balance between physically effective fiber and readily degradable carbohydrates in starter

diets to support development of a healthy gut and rumen, rumination behavior, and growth in young calves. **Key words:** calf starter feed, dietary transition, neonatal growth, rumen development

INTRODUCTION

On many dairy farms, calves are separated from their dams at birth and reared artificially. Unfortunately, dairy calves are at a great risk of morbidity and mortality, especially during the milk-feeding period and the weeks after weaning (USDA, 2009). Many producers wean calves at a young age to reduce costs associated with feeding milk or milk replacer, but calves are born with a nonfunctional rumen and must initially rely exclusively on milk to meet the nutrient demands of maintenance and growth. A smooth transition from liquid to solid feed allows calves to consume and digest sufficient solid feed to support growth during and after weaning; this transition requires the physical and metabolic development of the rumen and coincides with the development of the salivary apparatus, rumination behavior, and several physiological adjustments at the gut, hepatic, and tissue levels (Baldwin et al., 2004; Khan et al., 2011a).

The nature of solid feed and the amount consumed can influence rumen development. Highly palatable “starter” feeds, containing easily fermentable carbohydrates, are thought to stimulate rumen development, including changes in the epithelium of the forestomach (Baldwin et al., 2004; Drackley, 2008). In contrast, calves reared by their dams in extensive housing systems (e.g., cow-calf operations) and young ruminants artificially reared in pastoral systems would not typically have access to starter feeds. Under forage-based livestock production systems, forage quality and availability determines the need for supplementary feeds (e.g., concentrate through creep feeding) to support growth of young ruminants. However, in nature and where permitted (e.g., pastoral systems or cow-calf operations), milk and pasture provide the majority of the stimulants and nutrients required for development and growth to young ruminants.

Received June 16, 2015.

Accepted October 28, 2015.

¹Current address: Animal Nutrition and Physiology Team, Grassland Research Centre, AgResearch Limited, Palmerston North, 4442, New Zealand.

²Corresponding author: marina.vonkeyserlingk@ubc.ca

Table 1. List of fiber sources, their physical form, and inclusion levels in the diets of calves evaluated in some studies

Class	Forage	Inclusion rate, % of DM	Physical form of forage	Age of calves, d	Reference
Legume hay	Alfalfa hay	66.7	Pelleted	7	Addanki et al., 1966
	Alfalfa hay	Ad libitum	Chopped	10	Anderson et al., 1982
	Alfalfa hay	25–50	Ground, long	35	Bull et al., 1965
	Alfalfa hay	20–70			Žitnan et al., 1998
	Alfalfa hay	Ad libitum	Chopped	8	Castells et al., 2012
	Alfalfa hay	25			Beharka et al., 1998
Grass hay	Orchardgrass	Ad libitum	Chopped	3	Khan et al., 2011b
	Grass hay	15–30	Chopped		Suárez et al., 2006a,b
	Grass hay	5–15	Chopped	5 or 56	Hill et al., 2008a
	Ryegrass hay, oats hay	Ad libitum	Chopped	8	Castells et al., 2012, 2013
	Grass hay	Ad libitum	Chopped	6–8	Kosiorowska et al., 2011
	Bromegrass hay	7.5–15	Chopped	5	Coverdale et al., 2004
Grass and legume blend	Alfalfa and timothy hay	67		3	Hibbs et al., 1956
	Alfalfa and grass hay	15			van Ackeren et al., 2009
	Grass legume silage	67		3	Conrad and Hibbs, 1956
Silage	Corn silage	30–60			Suárez et al., 2006a,b
	Corn silage	33.7		Birth	Block and Shellenberger, 1980
Straw	Corn silage, triticale silage	Ad libitum		8	Castells et al., 2012
	Barley, rye, wheat	5–60			Jahn et al., 1970
	Barley straw	15–30	Chopped	10	Suárez et al., 2006a,b
Pasture/fresh grass	Barley straw	Ad libitum	Chopped	8	Castells et al., 2012
	Pasture	Ad libitum		4	Pounden and Hibbs, 1949
	Pasture	Ad libitum			Conrad and Hibbs, 1956
Other fiber sources	Ryegrass	Ad libitum		7	Phillips, 2004
	Beet pulp	66.7	Pelleted	7	Addanki et al., 1966
	Beet pulp	30.3–91.3	Ground		Suárez et al., 2006a,b
	Corn cobs	56.7	Ground		Conrad and Hibbs, 1956
	Cottonseed hull	5–10		5 or 56	Hill et al., 2008a,b
	Soybean hulls	15.5–46.4	Pelleted		Suárez et al., 2006a,b
	Wood pulp fines	11		Birth	Block and Shellenberger, 1980
	Cottonseed hull	15		2	Hill et al., 2009

To our knowledge, no review has summarized research on the role of forage, concentrate, and feeding management on rumen development and performance of dairy calves during the transition from milk to solid feed. The current paper has 3 aims; first, to review the available literature on the role of solid feed and feeding management in establishing rumen fermentation; second, to understand how solid feeds affect the development of the digestive tract and rumination behavior; and third, to discuss how the nature of solid feed (concentrate and forage) and feeding management affect growth of dairy calves.

ROLE OF CONCENTRATE AND FORAGE IN ESTABLISHING RUMEN FERMENTATION

A list of fiber sources, their physical form, and inclusion levels in the diets of calves evaluated in selected

studies is provided in Table 1. The effects of concentrate and forage on rumen development parameters (rumen weight and papillae growth, rumen motility and passage rate, rumen bacteria, rumen protozoa, fermentation end products, rumen pH, and buffering capacity) are summarized in Table 2.

Anaerobic Rumen Microbial System

At birth, young ruminants possess no anaerobic microbial population in the rumen. Establishment of rumen microbiota is necessary for the physiological development of the rumen and for the animal's ability to convert plant mass into products that can be utilized by the animal for maintenance and production (Jami et al., 2013). In adult ruminants, the rumen contains a complex anaerobic microbial ecosystem comprising various species of bacteria, protozoa, and fungi. During

the first hours of life, the forestomach is rapidly colonized by bacteria and the microbial density in the fluid fraction of the rumen quickly reaches concentrations as high as 10^9 cells/mL; strictly anaerobic bacteria become predominant by the second day after birth (Fonty et al., 1989). The establishment of a complex microbial ecosystem is, however, a long process and depends on many factors, including genetic background, age, management, and feeding conditions.

Under natural feeding conditions, when calves are nursed by their mothers, they start acquiring anaerobes from their dam, older peers, and the environment (e.g., contaminated pastures); in artificially reared calves, the acquisition and establishment of the anaerobic rumen ecosystem depends on the type of feed offered, housing, and handling situations (Fonty et al., 1988; Beharka et al., 1998). Previous literature has demonstrated that at early stages of life, anaerobic acidophiles, coliforms, lactobacilli, lactose fermenters, and some anaerobes predominate in the rumen, and, with age, there is a slow transition to the microflora typically found in the

fully developed rumen (Fonty et al., 1989). Major functional groups of ruminal bacteria including cellulolytic bacteria, sulfate-reducing bacteria, and other hydrogen-utilizing species such as methanogens can be found in the rumen within the first week of life (Anderson et al., 1987). Li et al. (2012a) characterized the rumen microbiota of preruminant calves fed milk replacer using metagenomic tools. Those authors reported that rumen microbiota of young calves (14 d of age) displayed a heterogeneous microbial composition and harbored more numerous bacterial species and genera than did older calves (42 d of age). Malmuthuge et al. (2014) investigated the composition of the bacteria along the gastrointestinal tract (**GIT**; e.g., rumen, jejunum, ileum, cecum, and colon) of 21-d-old preweaned bull calves using pyrosequencing to understand the segregation of bacteria between the mucosal surface and digesta. Those authors described the rumen as containing the most diverse bacterial population, consisting of 47 genera, including 16 rumen-specific genera, followed by the large intestine and then the small intestine. These

Table 2. Summary of the effects of dietary concentrate and forage on rumen development

Parameter ¹	Concentrate ²	Forage ³	References
Rumen weight	+	++	Tamate et al., 1962; Anderson et al., 1982; Suárez et al., 2006b; Khan et al., 2011b; Castells et al., 2013
Rumen volume/expansion	+	++	Tamate et al., 1962; Žitnan et al., 1998; Castells et al., 2013
Papillae differentiation/growth	++	+	Sander et al., 1959; Block and Shellenberger, 1980; Anderson et al., 1982; Lesmeister and Heinrichs, 2005; Hill et al., 2009; Laarman et al., 2012; Connor et al., 2013
Blood BHB/ketogenesis	+	+	Laarman et al., 2012; Castells et al., 2013
Rumen motility/passage rate	+	++	Tamate et al., 1962; Asai, 1973; Žitnan et al., 1998; Castells et al., 2013
Rumen bacteria	Amylolytic	Cellulolytic	Fonty et al., 1983; Anderson et al., 1987; Minato et al., 1992; Franzolin and Dehority, 1996; Beharka et al., 1998; Castells et al., 2013
Rumen protozoa	–	+	Eadie, 1962; Fonty et al., 1983; Anderson et al., 1987; Minato et al., 1992; Beharka et al., 1998
Total organic acids	++	+	Anderson et al., 1982; Coverdale et al., 2004; Suárez et al., 2006b, 2007; Hill et al., 2009
Acetate:propionate	–	+	Bull et al., 1965; Stobo et al., 1966; Coverdale et al., 2004; Hill et al., 2009; Terré et al., 2013
Butyrate	++	+	Stobo et al., 1966; Žitnan et al., 1998; Coverdale et al., 2004; Lesmeister and Heinrichs, 2005; Suárez et al., 2006b; van Ackeren et al., 2009; Terré et al., 2013
Lactate	+	–	Suárez et al., 2006b; Terré et al., 2013
Rumen pH	–	+	Kay et al., 1969; Kellaway et al., 1973; Greenwood et al., 1997; Vázquez-Añón et al., 1993; Lesmeister and Heinrichs, 2004; Suárez et al., 2006b; Khan et al., 2011b; Laarman and Oba, 2011; Terré et al., 2013; Castells et al., 2013
Buffering capacity/rumination	–	+	Kay, 1960; Phillips, 2004; van Ackeren et al., 2009; Laarman and Oba, 2011; Castells et al., 2012, 2013; Terré et al., 2013
Rumen health/parakeratosis	–	+	Bull et al., 1965; Kay et al., 1969; Hinders and Owen, 1965; McGavin and Morrill, 1976; Greenwood et al., 1997; Suárez et al., 2006b; Castells et al., 2013

¹Parameters were measured (within 3 mo of age) in developing calves fed different amounts of milk or milk replacer, weaned at different ages (4 to 8 wk of age) and housed on different bedding materials (no bedding, sawdust, and straw) individually or in groups. + = generally a positive effect on a parameter by a feed type; ++ = generally a more positive effect on a parameter by a feed compared with other feed (forage vs. concentrate); – = generally a negative effect on a parameter by feed type.

²Concentrate = grain-based mashed, pelleted, textured, and crumbed feeds.

³Forage = fresh, dried, or fermented grasses and legumes, fibrous crop residues (hulls, straw, cobs).

results were similar to those of Li et al. (2012a), who reported 45 bacterial genera belonging to 15 different phyla in the rumen of milk-fed calves. Jami et al. (2013) also reported a diverse rumen bacterial community in 1- to 3-d-old calves, which was dominated by *Streptococcus* species. Although the rumen contents of adult cattle fed a grain-based diet were reported to contain more *Prevotella* than *Bacteroides* (Li et al., 2012b), young calves fed whole milk or milk replacer mainly contained *Bacteroides* (Li et al., 2012a; Jami et al., 2013). Malmuthuge et al. (2014) reported similar levels of *Prevotella* (15.1%) and *Bacteroides* (15.8%) in 21-d-old dairy calves and suggested that starter feed intake contributes to the development of the rumen microbiome that adult cattle need to ferment plant polysaccharides. Most studies undertaken on the rumen microbiome of young calves do not evaluate the different fractions of the rumen contents; however, Malmuthuge et al. (2014) provided a comparison between the rumen digesta- and mucosa-associated communities. These authors argued that studies based only on rumen contents fail to adequately describe the rumen microbiome of calves. For example, they and others have described more *Bacteroidetes* and fewer *Firmicutes* in the rumens of preweaned calves than in adult ruminants (Chen et al., 2011; Li et al., 2012b; Malmuthuge et al., 2014). Collectively, the above literature indicates that younger calves harbor a more diverse microbial population in the rumen than older calves, and age, weaning, and initiation of solid feed consumption affect the composition of rumen microbes. Furthermore, understanding the rumen digesta- and mucosa-associated microbial communities is needed to define the establishment and role of rumen microbiota in developing calves.

Advances in microbiology, molecular and genomic tools offer an opportunity to study the development of microbiome (digesta plus epimural) in young calves under different management, housing and dietary conditions. The effect of weaning strategies, nature (physical form and chemical composition), and amount of solid feed eaten may be particularly important. For instance, the type of solid feed and feeding regimen are important factors influencing the rumen microbiome. In isolated calves, some rumen microorganisms typically found in adult cattle fail to become established for many weeks and even months after birth (Anderson et al., 1982; Minato et al., 1992; Franzolin and Dehority, 1996). Under many commercial dairying conditions, the transition from milk to solid feed (weaning) typically occurs before the full microbial colonization of the rumen is complete (Fonty et al., 1983). A gradual decline in facultative anaerobic population and a slow increase in the number of anaerobic bacteria in early-weaned

calves has been attributed to increased consumption of starter feed and starch (Anderson et al., 1987). Greater amylolytic and lower cellulolytic bacterial counts in calves (Table 2) fed a ground diet (1 mm) compared with those fed diets containing long particles (0.64-cm-long forage and rolled grains) was reported by Beharka et al. (1998). Depressed cellulolytic bacterial counts in calves fed a ground high-starch diet could be attributed to a low ruminal pH (Franzolin and Dehority, 1996). More recent work from our own laboratories conducted over the last 5 yr has indicated that dietary (i.e., provision of a forage source) and management factors (e.g., gradual weaning, grouping, social learning, and social facilitation) can promote solid feed intake (e.g., Bach et al., 2010; Khan et al., 2011b; de Paula Vieira et al., 2012; Costa et al., 2015) in young calves. For example, provision of chopped grass hay improves solid feed intake during weaning and stabilizes the rumen pH in young calves (Khan et al., 2011b; Castells et al., 2012, 2013). Pair-housed calves begin to ingest solid feed sooner and eat more solid feed during the milk-feeding phase compared with calves housed individually (de Paula Vieira et al., 2010), and individually housed calves that are commingled preweaning (when milk is decreased) have higher solid feed consumption than calves that remain isolated (Bach et al., 2010). Furthermore, calves paired soon after birth began to consume solid feed earlier than late-paired (43 d of age) and individually housed calves, likely contributing to the increased weight gains (Costa et al., 2015). Greater solid feed intake and decreased latency to eat novel feeds was found in calves reared in complex social housing (calves housed with cows and other calves) versus those reared individually (Costa et al., 2014). These dietary and management factors that affect the solid feed consumption in developing calves likely also affect the establishment of the rumen microbiome. Social housing conditions, where calves are kept with older peers or their dams (de Paula Vieira et al., 2010; Costa et al., 2014), may also affect the rumen microbiome directly through inoculation. Some European work (Abecia et al., 2014) has assessed the effects of natural rearing (with mother) versus artificial feeding (milk replacer) in goat kids on colonization of the rumen by the 3 main microbial groups over the first 4 wk of life. Those authors reported that feeding management before weaning (natural vs. artificial) had a pronounced effect on microbial colonization and rumen fermentation. The same research group demonstrated that feeding forage versus concentrate around weaning modified the rumen bacterial population of lambs and that the effect persisted for more than 4 mo (Yáñez-Ruiz et al., 2010), even after all lambs were on the same diet. A recent review (Yáñez et al., 2015) further describes

potential mechanisms involved in establishing rumen microbiota early in life. From the above literature, we can conclude that the nature of solid feed (e.g., forage and concentrate), weaning method, and management factors (e.g., grouping with peers or dam) may affect foraging skills, feeding behavior, and inoculation of the GIT, and promote initiation of solid feed consumption, all of which could affect the microbiome in developing calves. We encourage integrated research efforts involving animal management, nutrition, and microbiology to more clearly elucidate the factors affecting the rumen microbiome in calves.

Acquisition and establishment of anaerobic protozoa and fungi have received little or no attention in young ruminants. Below, we provide a summary of the work conducted in developing calves to study establishment of anaerobic protozoa during transition. Anaerobic protozoa are far less numerous than bacteria in the rumen, but due to their greater size they represent a volume nearly equal to that of bacteria in the mature rumen. Minato et al. (1992) reported that protozoa colonized the rumen of calves about 8 wk of age. Numbers and types of protozoa are markedly affected by diet (Table 2), and the variability among protozoa populations tends to be greater than that of bacterial populations. Ciliate protozoa fail to establish unless bacterial communities had previously colonized the rumen (Fonty et al., 1988). Rumen protozoa were absent in individually housed calves weaned at different ages (Anderson et al., 1987) and fed diets differing in particle size (Beharka et al., 1998). Low rumen pH was largely responsible for the failure of ciliates to become established in calves provided all-concentrate diets (Eadie, 1962). Thus, delayed establishment of protozoa in the rumen of calves may be partly attributed to high grain feeding (no forage) and an acidic environment of the rumen (Beharka et al., 1998; Minato et al., 1992; Franzolin and Dehority, 1996). We encourage further studies to understand the establishment of anaerobic protozoa and fungi in developing calves under different management and dietary situations.

Recent studies on the rumen microbiome in adult cattle have demonstrated that the rumen “core microbiome” is variable among animals and remains stable regardless of the differences in adult diets or host genetics (Jami and Mizrahi, 2012; Petri et al., 2012). Others have shown that despite swapping of ruminal contents (Weimer et al., 2010) or inducing acidosis in cows (Petri et al., 2013), the core microbiome is resistant to change. Collectively, these studies demonstrate that the core rumen microbiome is variable across animals and surprisingly stable within an animal tested under different diets and feeding situations. We suggest that the period when calves transition from liquid to solid

feed may provide a window for microbial programming to manipulate the core rumen microbiome.

Ruminal Fermentation End Products

Acquisition of microbial populations and the presence of suitable substrates (i.e., liquid and solid organic matter) triggers fermentation activity in the rumen. Fermentation end products can be found in the rumen of calves as early as the second week of age (Beharka et al., 1998). Suárez et al. (2006b) reported that ruminal VFA concentrations in calves (8 wk of age) fed concentrate diets were close to the range normally observed in adult ruminants (120 to 160 mM, Bergman, 1990) and to those observed in roughage-supplemented calves (~120 mM, Vázquez-Añón et al., 1993; ~150 mM, Žitnan et al., 1998). However, after calves start consuming solid feed, the level and physical-chemical nature of available substrate affects rumen microbial diversity and subsequent fermentation patterns (Lesmeister and Heinrichs, 2004). Concentrate diets generally favor starch digesters in the rumen and tend to result in increased butyrate and propionate molar proportions at the expense of acetate (Schwartzkopf-Genswein et al., 2003; Table 2). In contrast, forage intake promotes cellulolytic microbial growth and results in increased molar proportions of acetate in the rumen (Žitnan et al., 1998). In summary, rumen fermentation starts at a very young age and VFA concentrations increase with increasing solid feed intake. Rapidly fermentable dietary carbohydrates (e.g., sugars and starch) yield more butyrate and propionate at the expense of acetate in the rumen, whereas the incorporation of slowly degradable carbohydrate (e.g., fiber) reverses this effect. It is important to note that the effect of various carbohydrate fractions (sugars, starch, forage fiber, or nonforage fiber) on rumen VFA concentration or composition in young calves is not clearly described in the literature. Furthermore, it has been argued that the concentration of VFA in the rumen is not appropriate for use as an indicator of ruminal fermentation, given the great variability in volume of rumen digesta liquid (Hall et al., 2015). We urge additional research focused on defining the requirements of various carbohydrate and protein fractions needed within calf starter diets, considering both dietary (e.g., nutrient fractionation) and animal factors (e.g., absorption and passage rate), on rumen fermentation and animal performance.

Starch sources, their dietary level, and type of processing affect rumen VFA yield and composition. Amount of starch eaten, starch granule size (1 to 38 μm), shape (lenticular, polyhedral, or spherical), and interactions between amylose and surface compounds can alter the rate of enzymatic digestion of cereals, consequently af-

fecting VFA concentration in mature (Bergman, 1990) and developing (Hill et al., 2008a,b; Khan et al., 2008) ruminants. Processing of grains (e.g., steam flaking, steam-rolling, dry-rolling, and grinding) can fracture the seed pericarp, disrupt the starch-protein matrix, and increase the surface area for enzymatic action and enhance fermentation rate (Huntington, 1997), likely reducing rumen pH in calves (Lesmeister and Heinrichs, 2004). Although the available literature indicates that processing can be used to vary the rate of starch fermentation in the rumen, it is not clear how different starch sources and processing affect starch digestion and contribute to meeting the energy requirements of developing calves.

Rumen fermentation patterns in developing calves can be affected by source, level, and processing of dietary forage (Suárez et al., 2006b; Castells et al., 2013; Terré et al., 2013) and grains (Lesmeister and Heinrichs, 2004; Khan et al., 2008). Terré et al. (2013) found higher molar proportions of acetate and propionate and lower butyrate and valerate in the rumen of forage-fed calves compared with calves that received no forage. Previously, Cline et al. (1958) described a positive relationship between microbial growth and an increase in the rate of valerate utilization. The lower rumen valerate molar proportion observed by Terré et al. (2013) in forage-supplemented calves may indicate cellulolytic bacterial proliferation. Suárez et al. (2006b) demonstrated greater acetate and lower propionate concentrations with the inclusion of straw in the diet. Others (Žitnan et al., 1998) reported similar shifts in rumen fermentation pattern with the inclusion of dietary forage. It is not clear whether the increased acetate molar proportions in the rumen are due to the inclusion of dietary forage or an increase in rumen pH, but work on continuous culture fermentors indicated that a combination of both pH and type of substrate were responsible for the fermentation pattern and concentration of particular VFA in the rumen (Calsamiglia et al., 2008). Accumulation of ruminal fermentation end products increases osmolality, causing the death of certain bacteria and inhibiting feed intake (Carter and Grovum, 1990). Thus, feeding diets to young calves that result in a vigorous fermentation (i.e., highly fermentable carbohydrates) may compromise intake and ultimately performance.

Ruminal pH

Ruminal pH is crucial for normal rumen development, rumen fermentation, and overall calf health. Generally, rumen fluid pH is influenced by the rate of fermentation and absorption of VFA, which in turn are affected by passage rate of digesta and the buffering

capacity of the rumen contents (Williams et al., 1987). General effects of concentrate and forage on rumen pH and buffering capacity are described in Table 2. In artificially reared calves, rumen pH is highly variable, influencing the rumen microbial ecosystem (Penner and Oba, 2009; Laarman and Oba, 2011). Increased acidity has a detrimental effect on certain rumen microorganisms. Low pH has important implications for the composition of the microbial community, often resulting in an undesired population shift and inefficient digestion of feed (Penner and Oba, 2009). Low pH also decreases rumen motility (Krause and Oetzel, 2005) and increases keratinization of the papillae (Bull et al., 1965), resulting in decreased blood flow to the rumen mucosa and reduced VFA absorption (Hinders and Owen, 1965). Ruminal acidosis can also cause liver abscesses in calves (Bull et al., 1965; Kay et al., 1969) and may lead to permanent damage to the rumen wall. Available studies demonstrate the negative effects of low rumen pH on performance and health of developing calves. However, the severity of rumen acidosis caused by different types of solid feeds, weaning method, and feeding management is not yet clear.

Subacute ruminal acidosis (pH <5.8 for 3 h/d) is well studied in feedlot cattle (e.g., Schwartzkopf-Genswein et al., 2003) and dairy cows (e.g., Krause and Oetzel, 2005) but has received scant attention in the young calf. Many dietary factors, including source of grain cereal, level and processing, roughage source, feed particle length, feeding method, intake level, protein quality and level, postprandial time, and dietary buffers, affect the ruminal pH (Williams et al., 1987; Krause and Oetzel, 2005). Ruminal acidosis is perhaps more likely in young calves due to their relatively low production of saliva (Kay 1960), a natural buffer for the rumen. Furthermore, when the rumen epithelium is still underdeveloped, production of VFA may exceed the absorptive capacity of the epithelium, causing the rumen pH to fall (Williams et al., 1987). This is likely exacerbated in calves consuming concentrate diets containing processed grains (Lesmeister and Heinrichs 2004; Laarman and Oba, 2011). Rapid fermentation of processed cereal grains may also result in high proportions of lactate (a much stronger acid than VFA) in the rumen. A negative correlation between rumen VFA concentration and rumen pH in developing calves has been reported (Castells et al., 2013; Terré et al., 2013). Interestingly, Terré et al. (2013) found a stronger negative correlation between rumen VFA and rumen pH in forage-supplemented calves than in those fed starter feed only. Those authors showed that when rumen pH was >5.1, rumen VFA concentrations and rumen pH were linearly correlated; however, when rumen pH was <5.1, this relationship waned, implying that other fac-

tors such as lactic acid may be influencing rumen pH at that stage.

Unfortunately, the majority of studies to date (Tables 1 and 2) evaluating rumen pH in calves have sampled rumen fluid at only a single time point between 1 and 12 h after feeding; this approach does not take into consideration diurnal variation or the length and extent of ruminal acidotic conditions. Continuous measurement of ruminal pH in developing calves provides a much clearer picture. Laarman and Oba (2011), using electronic probes that enabled continuous monitoring, reported rumen pH <5.8 for approximately 4 h/d in calves fed milk and a starter feed. Similarly, Kristensen et al. (2007) fed varying amounts of milk (3.1 to 3.8 L/d) to 5-wk-old rumen-cannulated calves and reported that, regardless of treatment, the duration of ruminal pH <6.2 exceeded 12 h/d, and found no correlation between a barley-based concentrate and severity of ruminal pH depression with concentrate intakes above 20 g of DM/d. Recently, Wood et al. (2015) reported that the duration of rumen pH <5.5 increased after weaning relative to preweaning, possibly contributing to increased permeability in the rumen. They also argued that higher intake of rapidly fermentable carbohydrates at weaning can induce ruminal acidosis and may increase the concentration of antigens such as LPS in the digesta and challenge the integrity of the rumen epithelium. When taken together, these studies provide some evidence that weaning method and consumption of rapidly fermentable carbohydrates before weaning can dispose calves to rumen acidosis and associated anomalies. We suggest more work to understand the dynamics of rumen pH in developing calves and its association with the type of solid feed consumed, weaning method, and feeding management using continuous measurement methods.

Inclusion of forage or fibrous materials that do not ferment rapidly (e.g., soyhulls) may be beneficial in raising and stabilizing pH in the rumen. Dietary fiber buffers the gastrointestinal tract via the fiber matrix and the stimulatory effect of fiber on rumination and salivation (McBurney et al., 1983). The inclusion of dietary fiber through forage supplementation increases rumen pH in both preweaned and weaned calves (Khan et al., 2011b; Castells et al., 2012). Laarman and Oba (2011) reported that hay intake was negatively correlated with the severity of SARA with a breakpoint of 0.080 kg/d, suggesting that consumption of even small amounts of hay mitigates rumen acidosis in calves. Castells et al. (2013) also reported increased expression of a VFA transporter (mono-carboxylate transporter 1) in the rumen epithelium of milk-fed calves that had access to forage compared with calves fed pelleted starter

feed only. The increased expression might aid in the maintenance of rumen pH by promoting absorption of protonated VFA (Graham et al., 2007). The effects of the physical form of starter diets and inclusion of various fiber sources (e.g., forage and nonforage) to increase dietary NDF contents on rumen pH and fermentation profile have been examined in several studies (Suárez et al., 2006a,b; Porter et al., 2007; Hill et al., 2009). Collectively, the results indicate that the physical form and particle size distribution of the starter are more important than fiber level in improving rumen fermentation and initiating rumination (Porter et al., 2007). However, this finding has now been questioned by Terré et al. (2013), who found that forage provision, not just increased fiber content in the concentrate, was required to increase rumen pH around weaning. It is important to note that fiber sources, whether of forage or nonforage origin, differ in their effectiveness at stimulating chewing activity and saliva production in adult cattle (Allen, 1997; Mertens, 1997; Zebeli et al., 2012). Unfortunately, for calf diets, the amount of forage or nonforage NDF required to develop and stimulate rumination, saliva production, and stabilizing rumen pH is not clearly defined. Although the association between rumen fermentation acid load and the requirement for fiber has been extensively reviewed (see Mertens, 1997; Zebeli et al., 2012) and requirements for physically effective NDF (peNDF) are well defined for adult cattle, an optimal balance between physically effective fiber and readily degradable carbohydrates to support healthy rumen development and fermentation in the young calf is not yet clear. The above literature collectively demonstrates that forage provision positively affects rumen functions and rumen pH in calves; however, available studies are inconclusive in defining the exact amount, source, method, and timings of forage provision to calves.

Rumen Buffering and Salivary Functions

The salivary gland in ruminants provides continuous fluid and buffering for normal rumen function. Saliva flow is affected by eating and chewing, but the parotid gland has little ability to produce saliva in calves before 4 wk of age (Kay, 1960). Dietary concentrates are often eaten at a faster rate, require less chewing and regurgitation, and thus foster less saliva compared with forages (Yang and Beauchemin, 2006). Jasaitis et al. (1987) demonstrated that the buffering capacity of feeds varies considerably; grains have low capacity, low-protein grass roughages have intermediate capacity, and high-protein roughages, such as legumes, have the greatest buffering capacity. Suárez et al. (2006a,b) ex-

amined the inclusion of different roughages in veal calf diets; these diets failed to maintain rumen buffering, even at pH values close to optimal buffering capacity (pH 5.0). The authors partly attributed this failure to low saliva secretion because of underdeveloped salivary glands in calves. In summary, it appears that both age and dietary factors (e.g., initiation of feed intake, feed particle size, and associated regurgitation) affect the development of the salivary gland and saliva production in young calves.

The particle size of forage or feed sorting can play role in ruminal pH dynamics; increased particle size length will increase time spent eating and time spent ruminating (van Ackeren et al., 2009). Large particle size promotes salivary flow to the rumen through greater mastication and rumination (Hibbs et al., 1956). Given that, in mature dairy cows, salivary buffer flow is estimated to neutralize 30% of all protons produced in the rumen (Allen, 1997), changes in salivary buffer flow rate caused by variable hay consumption (Laarman and Oba, 2011) or feed sorting (Costa et al., 2016a) likely play an important role in influencing rumen pH in calves. Furthermore, domestic ruminants balance their intake of high-energy grain components with forage that helps buffer the rumen against the acidic by-products of carbohydrate fermentation (Krause and Oetzel, 2006). Miller-Cushon and DeVries (2011) found that calves fed either concentrate or hay during weaning selectively consumed the familiar feed when switched to a mixed ration. Provision of solid feed during pre-weaning to calves as separate components (forage and concentrate) compared with that offered as a mixed ration reduces the extent of feed sorting after weaning (Miller-Cushon et al., 2013). In a recent study, Costa et al. (2016a) demonstrated that calves offered TMR and concentrate throughout the milk-feeding period preferentially consumed long particles from the TMR after weaning. When offered only TMR postweaning, calves preferentially consumed fine particles contained within the TMR. These results indicate that young calves are able to sort a TMR and can modify their sorting behavior in response to changes in feed offered. Costa et al. (2016a) also argue that sorting for longer particles is evidence that calves are motivated to consume forage when offered supplementary concentrate. Calves provided forage have increased rumination times (Phillips, 2004; Castells et al., 2012); however, feed sorting might affect the development of rumination behavior and could challenge the developing calves to stabilize their rumen pH. The available literature provides little guidance in terms of understanding the effects of various types of forages and amount of fiber on the development of rumination, salivary function, and rumen buffering.

ROLE OF CONCENTRATE AND FORAGE IN GUT DEVELOPMENT

The reticulorumen is underdeveloped at birth and requires extensive morphological changes and physiological adjustments before a calf is able to thrive on solid feed (Baldwin et al., 2004). Rumen development involves acquisition and establishment of a microbial ecosystem, muscularization, and vascularization of the wall, papillary development, and initiation of rumination and rumen motility. In the milk-fed calf, this process has received considerable interest. Early work investigated the effects of providing different diets on ruminal development (see Brownlee, 1956) and, in the years following, several studies recognized that initiation of solid feed intake and composition could affect various aspects of development (Tamate et al., 1962; Sutton et al., 1963). Since then, numerous studies have explored the relationship between rumen development and the physical-chemical nature of solid feeds (e.g., Suárez et al., 2006a,b; Hill et al., 2009). One study (Connor et al., 2013) showed that transition from liquid to solid feed alters the expression of more than 900 gene transcripts. These gene transcripts are involved in lipid metabolism, cell morphology and death, cellular growth and proliferation, molecular transport, and the cell cycle.

Generally, the start of anaerobic fermentation triggers metabolic development of the rumen. The presence of fermentation end products (i.e., VFA) in the rumen provides chemical stimuli required for epithelial proliferation (Flatt et al., 1958; Sander et al., 1959). Sutton et al. (1963) proposed that low rumen pH affects VFA absorption and acts as a catalyst inducing papillae differentiation. Differentiation and growth of squamous epithelial cells promotes papillae length and width and thickness of the interior ruminal wall (Baldwin et al., 2004). The rank of growth stimulatory activity of VFA (butyrate > acetate > propionate) follows the order in which they are metabolized by the rumen epithelium (Bergman, 1990). Increased blood flow through the rumen wall (Sander et al., 1959), along with a direct effect of butyrate and propionate (Galfi et al., 1991) on gene expression, is proposed to trigger papillae differentiation. Ruminal VFA concentrations, as well as early and extended exposure to VFA, are thought to induce the expression of genes (acetoacetyl-CoA thiolase; 3-hydroxy-3-methylglutaryl-CoA synthase; β -hydroxybutyrate dehydrogenase) responsible for rumen epithelial cell differentiation and metabolic activity (Baldwin et al., 2004; Connor et al., 2013).

Butyrate is believed to be the main stimulatory VFA for ruminal epithelial development (Flatt et al., 1958; Sander et al., 1959; Baldwin et al., 2004), and this is

the main reason why grain-based starter feeds are often recommended for the milk-fed calf. Extensive efforts have focused on improving ruminal starch digestibility by grain processing methods (e.g., cracking, crimping, and flaking). Unfortunately, consuming starter feeds containing a high proportion of grains with small particle sizes increases lactic acid production, lowers rumen pH, and reduces rumen microbial diversity (Kay et al., 1969; Greenwood et al., 1997). The development of the rumen mucosa is positively affected by rumen VFA concentrations but negatively by rumen lactate concentrations (Suárez et al., 2006b). Other negative effects (including clumping of papillae, acidosis, rumenitis, and parakeratosis of rumen epithelium) of providing grain-based feeds have been reported in calves (Kay et al., 1969; Suárez et al., 2006a,b; Castells et al., 2013). Increased keratinization, in conjunction with low pH, reduces the activity of rumen papillae needed to absorb VFA (McGavin and Morrill, 1976; Greenwood et al., 1997).

It is important to note that under natural rearing conditions, particularly when young ruminants are kept on pasture with their dams, most nutrients and stimulants for rumen development are derived from fresh forages and milk. For example, Knott et al. (2005) demonstrated a functional and well-developed rumen at 60 d of age in both muskoxen and reindeer calves consuming arctic plants. Large particle size and bulk of forage provide physical stimuli to enhance rumen motility, muscularization, and rumen volume in calves (Table 2). Physical stimulation through forage consumption has been shown to result in increased rumen weight (Tamate et al., 1962; Khan et al., 2011b; Kosiorowska et al., 2011). Other work has shown that calves fed chopped hay had 10% more muscle and 10% less mucosa in the rumen wall than calves fed concentrate only (Nocek et al., 1984). The benefits of feeding forage on total rumen weight and gene expression were shown by Castells et al. (2013), who reported increased expression of mono-carboxylate transporter isoform 1 (*MCT1*) in calves provided forage; *MCT1* is involved in the absorption of lactate, acetate, and protons from the rumen epithelium into the bloodstream (Graham et al., 2007). Castells et al. (2013) further explained that due to the enhanced proton export, intracellular pH likely increased, and *MCT1* may have improved absorption of VFA from the lumen into the epithelium by simple diffusion of protonated short-chain fatty acids and the short-chain fatty acids/ HCO_3 exchange. Similarly, increased expression of *MCT1* and decreased expression of Na^+/H^+ exchanger, isoform 3 (*NHE3*) was reported by Laarman et al. (2012) in calves fed a starter feed, hay, and milk. Connor et al. (2014) demonstrated that grain feeding at weaning activates molecular pathways

in rumen epithelium primarily related to the cell cycle, which appear to be regulated by transcription factors, including forkhead box protein O1 (FOXO1) and transforming growth factor- β 1 (TGFB1). Hay feeding at weaning activates gene pathways participating in energy production, in which estrogen-related receptor α (ESRRA), likely in conjunction with peroxisome proliferator-activated receptors (PPAR), may play a prominent role in fatty acid absorption and metabolism. Furthermore, TGFB1 and ESRRA were identified as likely transcriptional regulators of rumen epithelial development and energy metabolism, respectively, and are potential targets for modulation of rumen development and function in the growing calf. These studies provide evidence that rumen metabolic development is driven by the provision of both dietary forage and concentrates, and dietary forage is important to promote the physical development of the rumen. It is important to mention here that most of the studies illustrating molecular changes in the rumen and gut of developing calves have studied only a limited number of genes of interest; evaluation of global changes in gene expression occurring in the rumen and gut during transition to solid feed is required to better understand mucosal development, epithelial cell proliferation, cell metabolism, and gut functions (see Connor et al., 2014).

Dietary forage likely contributes to the development of the digestive tract more than just by providing bulk and scratch to increase physical capacity, volume, and motility. For example, providing roughage to calves can reduce plaque formation, improving the macroscopic appearance of the rumen wall (Suárez et al., 2006b). Anomalies (e.g., ruminal acidosis, depressed intake, papillae branching, and parakeratosis of the rumen) associated with high grain feeding in young calves can be avoided by feeding forage (Greenwood et al., 1997; Laarman and Oba, 2011). Kristensen et al. (2007) suggested that digestible fiber in a calf diet can replace barley and wheat starch, and this approach can prevent SARA. Intestinal inflammation associated with dietary adaptation in ruminants is well documented and attributed to increased VFA production, SARA, and LPS from gram-negative bacteria in the rumen (Gozho et al., 2006; Penner et al., 2011). Connor et al. (2013) proposed that solid feed, particularly hay, stimulates *TRIM40* (tripartite motif containing 40) mRNA expression, protecting the epithelial mucosa from inflammation via inhibition of NF- κ B (nuclear factor kappa-light-chain-enhancer of activated B cells) activity. Taken together, these studies indicate that dietary forage can promote rumen development and help maintain gut health in developing calves.

It is important to note that almost all studies to date on GIT development in calves have been focused

primarily on promoting solid feed intake at the expense of milk allowance (Khan et al., 2011a). However, improved development of the small intestine in calves fed whole milk (versus those fed a milk replacer) and positive correlations between small intestine and reticulorumen weights were reported by Górká et al. (2011). Furthermore, both the quality and amount of liquid feeds appear to affect gastrointestinal development in calves (Górká et al., 2011; Naeem et al., 2012). For example, provision of more nutrients through liquid feed to developing calves induced changes in mRNA expression of proteins (e.g., peroxisome proliferator-activated receptor- δ) involved in promoting growth of ruminal epithelium (Naeem et al., 2012). This study also found that the expression of genes involved in cellular proliferation (*INSR*, *FOXO1*, and *AKT3*) was greater in calves fed high amounts of liquid feed and corresponded to increased serum insulin concentrations. Shen et al. (2004) found greater IGF-1 concentrations in plasma, increased papillae size and surface area of rumen epithelium, and an enhanced net flux of Na^+ across the isolated rumen epithelium in goat kids fed high energy levels. Thus, we conclude from the evidence presented above that rumen development is driven not only by the presence of VFA and bulk in the rumen, but also by the nutrients supplied from liquid feed, and that the development of the rumen and the small intestine are linked. Therefore, it is important to adequately balance the provision of liquid and solid feed (both from concentrate and roughage) to maximize nutrient intake and gut development.

ROLE OF DIET IN THE DEVELOPMENT OF RUMINATION BEHAVIOR

Rumination refers to a process of regurgitation of ingested feed from the reticulorumen into the mouth, where the bolus is masticated, mixed with saliva for 30 to 60 s, and then swallowed again. Rumination is absent in newborn ruminants and development of rumination behavior is critical in stabilizing rumen fermentation (rumen pH and particle size of digesta) and rumen emptying (Baldwin et al., 2004). Generally, rumination increases the surface area of ingested feed by decreasing the particle size and thus reduces the lag time to fermentation, and increases the digestion and passage rate of digesta from the rumen. Furthermore, rumination results in a continuous supply of fluids and buffers (sodium bicarbonate) into the rumen that aid in neutralizing the acid produced during the fermentation process and thus helps to maintain rumen pH required for normal rumen function.

Development of rumination in calves is affected by age and solid feed consumption (Asai, 1973; Quigley

et al., 1992). Once solid feed consumption is initiated, calves start ruminating, as young as 3 wk of age (Quigley et al., 1992; Morisse et al., 2000; Khan et al., 2008). Development of rumen motility is essential for the initiation and regulation of regurgitation. Calves display weak reticulorumen movements before the initiation of solid feed intake, but regular, strong cyclic contractions increase as calves age and begin to consume solids (Asai, 1973). Calves fed both concentrates and roughage were shown by Asai (1973) to have active biphasic movements of the reticulorumen beginning between 6 and 8 wk of life. The available literature indicates that the presence of forage bulk and fermentation end products in the rumen is needed to initiate the development of these biphasic movements essential for regurgitation, digesta flow, and removal of fermentation waste from rumen.

Rumination time and solid feed intake are highly correlated for young dairy calves (Swanson and Harris, 1958), with rumination time increasing after weaning with increasing solid feed intake (Hepola et al., 2008). Rumination time tends to level out at approximately 5 h/d (Swanson and Harris, 1958; Margerison et al., 2002; Hepola et al., 2008). Longer and more frequent rumination was observed in calves raised in groups compared with those individually housed (Phillips, 2004), likely due to earlier initiation and greater consumption of solid feed in the grouped calves (Hepola et al., 2008; Bach et al., 2010; de Paula Vieira et al., 2010). In summary, the available literature to date indicates that initiation of solid feed and the amount eaten are the primary factors in initiating rumen motility and thereby regurgitation in calves.

Carbohydrate fractions (starch and fiber) and particle length of the diet are considered important factors affecting rumination in cattle (Schadt et al., 2012). Porter et al. (2007) demonstrated that calves fed a texturized calf starter feed began ruminating by 4 wk of age and spent 21% of their time ruminating. In comparison, calves fed a pelleted starter feed did not begin ruminating until wk 6 and spent only 9% of the time ruminating. Hodgson (1971) reported that 12-wk-old calves fed dried long grass alone ruminated about 7.5 h/d compared with only 2 h/d in calves fed pelleted grass. van Ackeren et al. (2009) found that calves receiving a low-fiber TMR (26.2% NDF) spent less time chewing compared with calves fed a high-fiber TMR (31.3% NDF). Moreover, in the same study, a tendency was noted for a reduced number of rumination chews and rumination bouts for calves fed low-fiber diets. The stimulation of rumination associated with forage intake (Table 2) may also promote and accelerate rumen development (Williams et al., 1987; Williams and Frost, 1992), allowing calves to make use

of forages at an earlier age. Two recent studies (Castells et al., 2012; Terré et al., 2013) have reported increased rumination time in calves fed a pelleted starter feed plus a forage source compared with those fed a pelleted starter feed alone, regardless of the amount of fiber in the pelleted starter feed. Previous work has shown that the time spent ruminating is greater in calves provided grass compared with those provided only starter feed (~5.5 vs. 4.2 h/d) at 7 wk of age (Phillips, 2004). These results indicate that solid feed consumption, feed particle size, and type of solid feed (e.g., concentrate, forage, TMR) all affect the development of rumination behavior. Management decisions (e.g., weaning age and method, amount of milk, and social facilitation) that affect solid feed intake, including the provision of forage (Khan et al., 2012; Costa et al., 2014), can affect the development of rumination behavior. Dairy cattle are eventually transitioned to high-forage diets, and delays in the ability of calves to process these diets may result in poor performance.

GROWTH PERFORMANCE OF CALVES

Effect of Composition and Physical Form of Starter Feed

Commercial starter feeds are pelleted, mashed, or textured, with the latter consisting of a mix of coarsely rolled or ground grains, whole grains, and some pellets. Collectively, these ingredients are intended to provide the energy, protein, minerals, and vitamins needed to meet the nutrient requirements of the young calf. Special attention is placed on the palatability of starter feeds to foster intake (Sander et al., 1959; Tamate et al., 1962; Montoro and Bach, 2012). Research on improving starter feeds has focused on different sources and inclusion levels of carbohydrates (e.g., Maiga et al., 1994; Khan et al., 2008; Hill et al., 2008a,b), processing techniques (e.g., Abdelgadir and Morrill 1995; Lesmeister and Heinrichs, 2005; Bateman et al., 2009), their physical form (e.g., Franklin et al., 2003; Coverdale et al., 2004; Bach et al., 2007), and the potential benefits of including feed additives in starter feeds (e.g., Bunting et al., 2000; Górka et al., 2011; Terré et al., 2015).

Corn, rice, barley, wheat, oats, and sorghum are commonly used as starch sources in calf starter feeds. Maiga et al. (1994) fed calves pelleted diets containing corn, barley, and whey, and found the highest BW gains in calves fed corn. Khan et al. (2007) fed calves pelleted starter feeds containing equal amounts of starch from corn, oats, barley, or wheat and reported that calves on the corn diet consumed more solid feed (starter feed and hay) and gained more weight than calves fed the barley, oats, or wheat diet. Replacing corn in starter

feeds with molasses, sucrose, or soybean hulls reduced postweaning BW gain by 10 to 14% (Hill et al., 2008b), but replacing corn with whole oats did not reduce BW gain, suggesting that oats may be an acceptable substitute for corn. Differences in physical-chemical attributes of corn, barley, oats, and wheat could alter the rate of enzymatic digestion (Svihus et al., 2005). Slow rates of digestion increase the proportion of starch bypassing the rumen (Svihus et al., 2005), and the site of starch digestion along the gastrointestinal tract may affect performance and feed efficiency. The available information to date indicates that starch sources and how they are processed can change the rate of starch fermentation and site of starch digestion; however, further studies are required to quantify such effects and how they affect calf performance.

Soybean meal, canola meal, cottonseed meal, sunflower seed meal, linseed meal, and corn gluten meal are commonly used as protein sources in calf starter diets. Commercial calf starter feeds are recommended to contain 18% CP on a DM basis (NRC, 2001) with no apparent growth advantage observed when protein levels were increased above 22% (Akayezu et al., 1994; Hill et al., 2007). Soybean meal is the most commonly used protein source in calf starter feed (Drackley, 2008). Other vegetable protein sources such as rapeseed meal (Schrama et al., 1986), cottonseed meal (Hollon et al., 1958), sunflower meal (Stake et al., 1973), and corn gluten meal (Terui et al., 1996) have also been studied; however, in general, replacement of soybean meal with other protein sources reduces intake and BW gain (Schrama et al., 1986), likely due to the presence of antinutritional factors, relatively poor amino acid profiles, and lower palatability of different oilseed meals compared with soybean. Suarez-Mena et al. (2011) evaluated corn dried distillers grains with solubles (DDGS) in starter diets and reported decreased BW gain (6 to 10%) and decreased DM digestibility by 10% in 7-wk-old calves with the inclusion of 39 to 49% DDGS in their diets. Whether lower inclusion rates (e.g., <20% DDGS) might be more safely included in starter feeds remains to be seen.

In general, the fat content of starter feeds is low (~3–4%); higher levels are generally associated with reduced intake and depressed weight gains (Doppenberg and Palmquist, 1991). However, Hill et al. (2009) found that supplementing ruminally inert fat to a corn and soybean meal-based diet resulted in increased weight gain and improved feed efficiency. Recently, Araujo et al. (2014) compared the performance of calves offered either restricted amounts (4 L/d) of milk replacer or 6 L/d along with either a low-fat (4.1%) or a high-fat (11.2%) starter feed. The authors reported that, when offering 6 L/d of milk replacer, feeding a high-fat

starter feed was beneficial for BW gain after weaning, mainly due to higher energy intakes after weaning.

Processing of ingredients can alter the rumen fermentation pattern and passage rate of digesta (Huntington, 1997), thereby affecting solid feed consumption in young calves (Lesmeister and Heinrichs, 2004; Bateman et al., 2009). Mechanical and chemical modifications during feed processing increase the surface area for fermentation and improve starch digestibility of grains (Huntington, 1997; Lesmeister and Heinrichs, 2004). Starch availability is typically greatest when adult cattle are provided steam-flaked grains, followed by finely ground, and then dry-rolled grains, and is lowest in whole grains (Huntington, 1997); no information is available for calves although feed intake is generally depressed in calves offered starter feeds with fine particles (Kertz et al., 1979; Bateman et al., 2009). Results from Porter et al. (2007) and Hill et al. (2008a) suggest that starter feeds should contain more than 75% of particles >1,190 μm in length, and there is evidence that starter feeds with large amounts of fine particles depress solid feed intake and BW gain relative to feeding textured starter feeds (Bateman et al., 2009). Unfortunately, “textured” is poorly defined in the literature and it is not clear what specific attributes of textured feed are beneficial.

Many studies (e.g., Owen and Larson, 1986; Bach et al., 2007; Porter et al., 2007; Hill et al., 2008a) have evaluated the effects of the physical form (e.g., mashed, pelleted, and textured) of the starter feed on intake and growth, but results of these studies have been inconsistent for young calves. For example, Bach et al. (2007) and Porter et al. (2007) reported greater solid feed consumption in calves fed coarse versus pelleted starter feeds. In contrast, Bateman et al. (2009) observed no differences in intake when comparing a pelleted starter feed with a textured starter feed. Such differences among studies may be attributed to the differences in processing methods and variation in the physical-chemical structure of starter feeds among studies.

Effect of Forage Supplementation

For the past 2 decades, forage feeding has not been recommended for dairy calves during the preweaning period. However, when allowed access to pasture, calves begin nibbling grass within the first few weeks of life (Tedeschi and Fox, 2009). Herbivores use sight, smell, and taste to locate nutritious plants (Mirza and Provenza, 1990, 1994). Interactions with the mother (Mirza and Provenza, 1990) and peers combined with the consequences of feed ingestion (Mirza and Provenza, 1994) help young ruminants select forage efficiently at an early age. Studies on beef calves have

shown that forage consumption is influenced by the amount of suckled milk and by the availability and quality of available forage (Wright and Russel, 1987). As occurs with starter feeds, forage intake per unit of BW is greater for calves receiving reduced quantities of milk (Tedeschi and Fox, 2009). The above literature indicates that young calves can start consuming forage at a very young age, they learn foraging skills from their peers, and intake of forage increases with reduced milk supply around weaning.

On many commercial dairy farms, calves are provided ad libitum access to starter feed during the first few months of life with little or no access to forage. Calves are then typically switched to restricted starter feed and free-choice forage in the weeks after weaning (Drackley, 2008). In pastoral systems, dairy calves are fed a variety of solid feeds during milk-feeding phase and then weaned onto pasture. Heifers reared on a concentrate-only diet before weaning eat less forage after weaning compared with calves reared on a forage plus concentrate before weaning (Khan et al., 2012), likely due to differences in abilities to ingest, accommodate, and digest forage. Miller-Cushon et al. (2013) reported that exposure to a ration containing finely ground forage can increase feed sorting when calves are later fed a ration containing coarsely chopped forage. The nature of solid feed (e.g., provision of forage, feed particle size, and feeding method) provided to calves early in life can affect foraging ability, forage intake, feed sorting, and feeding behavior after weaning.

Individually reared calves may be reluctant to accept forages. Food neophobia refers to avoidance and reluctance to taste unfamiliar foods and is well known in ruminants (Chapple and Lynch, 1986). Costa et al. (2014) found that rearing calves in social groups helps to reduce food neophobia. Furthermore, early socialization during the milk-feeding phase improves solid feed consumption (including forage intake) and helps transition calves to new social and feeding environments (de Paula Vieira et al., 2010, 2012). These effects of social housing on feeding behavior are consistent with data indicating that individual housing results in cognitive deficits and heightened responses to novelty (Gaillard et al., 2014; Meagher et al., 2015). Delayed acceptance of new food items can be a welfare and production concern, as dairy cattle are often exposed to new feed types. Individual rearing may reduce the calf's ability to adapt to changes in feed and perhaps other changes in their environment (Costa et al., 2014). A recent study by Costa et al. (2016b) investigated whether being grouped with experienced dairy cows would affect the development of grazing behaviors in naïve animals. This study demonstrated that providing heifers with pasture-experienced social companions when first in-

roduced to pasture promotes a more rapid onset of grazing and helped improve the transition to pasture. Together, these results indicate that individual housing is not ideal in preparing the growing calf for dietary transitions.

Numerous studies (Hibbs et al., 1956; Leibholz, 1975; Hill et al., 2008a,b) have argued that feeding forage (hay or straw) to preweaned dairy heifers reduces starter feed and overall DM consumption. Collectively, these studies suggest that low fermentation rates of fibrous material in the rumen increase gut fill and thus reduce intake of the more energy-dense starter feed. However, others (Kincaid, 1980; Phillips 2004; Suárez et al., 2006a; Castells et al., 2012) reported either an increase in starter feed intake or no effect on DMI with the inclusion of forage. Coverdale et al. (2004) found that inclusion of forage increased total DMI in calves through positive effects on ruminal environment (pH and acid load). Suárez et al. (2006a) substituted concentrate for different roughage (dried hay, silage, straw) in the diets of calves and concluded that substitution of part (30% of total DM) of the concentrate with roughage did not affect DMI. Khan et al. (2011b) demonstrated that provision of chopped hay to calves fed high volumes of milk at an early age promoted solid feed intake and did not affect empty BW gain. Furthermore, early exposure to hay promoted forage and nutrient consumption after weaning, compared with calves receiving no forage (Khan et al., 2012). Montoro et al. (2013) fed a mixed ration containing (on a DM basis) 90% crumb starter concentrate with either 10% coarsely chopped (3 to 4 cm) grass hay or 10% finely ground (2 mm) grass hay, and observed greater feed consumption and feed efficiency in calves fed coarse forage than those fed fine forage. Furthermore, heifers fed a starter feed and hay before weaning consumed more feed, were taller, and had smaller bellies after weaning than calves that had previously received starter feed alone (Khan et al., 2012).

Castells et al. (2012) evaluated inclusion of various forages in the diets of young calves and found that the provision of chopped grass hay or grass silage improved intake and gains without impairing nutrient digestibility and gain-to-feed ratio. The highest intake of starter feed and overall performance was obtained when chopped oat hay, chopped barley straw, or triticale silage was offered ad libitum from 2 wk of age until weaning. These benefits were not observed when calves were fed chopped alfalfa ad libitum along with a pelleted starter feed, perhaps because calves consumed much more forage (14% of total solid DM vs. 4% when fed chopped oats hay; Castells et al., 2012, 2013). Together, these results indicate that forage supplementation can promote total solid feed consumption and true

BW gain in calves, but highly palatable forages (i.e., fresh grass) or low digestible forage (i.e., straw) may depress starter feed intake and BW gain, and increase gut fill.

There have been concerns about the potential confounding effects of gut fill when introducing forages to young calves (i.e., apparent gains could be driven by differences in gut fill). For instance, Stobo et al. (1966) limited starter feed and offered hay at different proportions (from 4 to 61% of total solid feed intake) and reported an increase in gut fill from 24 to 33% of total BW, with increasing amounts of total solid feed. Similarly, Strozinski and Chandler (1971) and Jahn et al. (1970) reported an increase in gut fill from about 7 to 10% and 20 to 24% when feeding 0 to 5% or 60 to 90% inclusion of hay in the diet of calves, respectively. Interestingly (and contrary to what would be expected a priori), provision of chopped oat hay to calves improved rumen passage rate and tended to improve ADG over time, without increasing gut fill (in fact, gut fill was reduced by feeding oat straw) compared with feeding only a pelleted starter feed (Castells et al., 2013). The increased passage rate is largely explained by increased total DMI (about 23% more than the intake observed in calves fed the pelleted starter feed only; Castells et al., 2012, 2013). Providing forage during the milk feeding period may bring additional benefits. For instance, access to forage reduces the frequency of calves licking their buckets and pens, vocalization, the time spent investigating their pen (Phillips, 2004), and stereotypic behaviors (Castells et al., 2012; Terré et al., 2013). Thus, gut fill in calves appears to differ with the type of forage provided and the amount eaten; however, future work addressing the role of dietary forage and fiber sources for young ruminants will help to further understanding of the links between diet composition, passage rate of digesta, gut fill, and performance.

IMPLICATIONS

Under conventional milk feeding systems, calves are provided restricted amounts of milk and weaned onto textured or pelleted starter feeds offered ad libitum until a few weeks after weaning. The high grain intake supplies rapidly fermentable carbohydrates that yield propionate and butyrate and initiate rumen papillae differentiation. Introducing forage during the preweaning period has long been discouraged, as forage is less energy dense and thought to displace concentrate intake and shift rumen fermentation in favor of acetate, potentially delaying rumen papillae differentiation. However, grain-based starter feeds prompt the production of VFA, build lactic acid, and reduce the rumen pH in young calves, promoting conditions that result in

decreased blood flow to the rumen wall and reduced rumen motility, which combined can cause hyperkeratosis and parakeratosis of ruminal epithelium. The provision of high-starch and low-fiber starter feeds to young calves may also delay the development of rumination.

The results of recent research suggest that providing access to forage does not necessarily reduce starter feed intake or impede BW gain. Rather, inclusion of dietary forage may help by maintaining a higher rumen pH by promoting rumination and salivary secretion. Understanding the salivary gland development and role of dietary forage in buffering the rumen of calves are important areas for future research. Furthermore, we speculate that the period when calves transition from liquid to solid feed provides a window for microbial programming to manipulate the rumen microbiome. It is important to note that both the physical form of starter diets and their chemical composition can affect development in calves. Further research is required to identify an optimal balance between physically effective fiber and readily degradable carbohydrates in calf diets to support development of healthy gut and rumen, rumination behavior, and growth in young milk calves.

Intensive feeding programs, feeding relatively large quantities of milk (e.g., 20% of BW or ~8 L/d for Holstein calves), and gradual weaning can improve feed efficiency, reduce incidence of disease, provide greater opportunity to express natural behaviors, and potentially improve future lactation performance (Khan et al., 2011a; Soberon et al., 2012; Soberon and Van Amburgh, 2013). However, Bach (2012) suggested that it is likely the total nutrient supply (from both milk and solid feed), rather than total amount of milk offered, that explains the improvements in milk yield at adulthood. Thus, with increasing interest in feeding high volumes of milk early in life, it is important to reexamine the role of different types of solid feed, including forage and concentrates, on the microbial, metabolic, and physical development of the gastrointestinal tract. Almost all studies to date on the effects of forage on rumen development have been carried out on calves fed restricted amounts of milk; more work is required to develop solid feed management programs for calves provided higher quantities of milk before weaning. Furthermore, the economic and welfare effects of different feeding practices, and the long-term consequence on animal productivity and the environment should be considered when devising feeding recommendation for sustainable dairy production.

ACKNOWLEDGMENTS

We thank the many members of the University of British Columbia Animal Welfare Program for numer-

ous helpful discussions on this topic. M. A. G. von Keyserlingk and D. M. Weary are supported by Canada's Natural Sciences and Engineering Research Council (NSERC) Discovery Program and the NSERC Industrial Research Chair Program with industry contributions from the Dairy Farmers of Canada (Ottawa, ON, Canada), British Columbia Dairy Association (Burnaby, BC, Canada), Westgen Endowment Fund (Milner, BC, Canada), Intervet Canada Corporation (Kirkland, QC, Canada), Zoetis (Kirkland, QC, Canada), Novus International Inc. (Oakville, ON, Canada), BC Cattle Industry Development Fund (Kamloops, BC, Canada), Alberta Milk (Edmonton, AB, Canada), Valacta (St. Anne-de-Bellevue, QC, Canada), and CanWest DHI (Guelph, ON, Canada).

REFERENCES

- Abdelgadir, I. E. O., and J. L. Morrill. 1995. Effect of processing sorghum grain on dairy calf performance. *J. Dairy Sci.* 78:2040–2046.
- Abecia, L., E. Ramos-Morales, G. Martínez-Fernandez, A. Arco, A. I. Martín-García, C. J. Newbold, and D. R. Yáñez-Ruiz. 2014. Feeding management in early life influences microbial colonisation and fermentation in the rumen of newborn goat kids. *Anim. Prod. Sci.* 54:1449–1454.
- Addanki, S., J. W. Hibbs, and H. R. Conrad. 1966. High roughage system for raising calves based on the early development of rumen function. X. Performance of calves fed alfalfa, beet pulp, or soybean flakes as the roughage in complete pelleted rations. *J. Dairy Sci.* 49:976–981.
- Akayezu, J. M., J. G. Linn, D. E. Otterby, W. P. Hansen, and D. G. Johnson. 1994. Evaluation of calf starters containing different amounts of crude protein for growth of Holstein calves. *J. Dairy Sci.* 77:1882–1889.
- Allen, M. S. 1997. Relationship between fermentation acid production in the rumen and the requirement for physically effective fiber. *J. Dairy Sci.* 80:1447–1462.
- Anderson, K. L., T. G. Nagaraja, J. L. Morrill, T. B. Avery, S. J. Galitzer, and J. E. Boyer. 1987. Ruminant microbial development in conventionally or early-weaned calves. *J. Anim. Sci.* 64:1215–1226.
- Anderson, M. J., M. Khojloo, and J. L. Walters. 1982. Effect of feeding whole cottonseed on intake, body weight and reticulo-rumen development of young Holstein calves. *J. Dairy Sci.* 65:764–772.
- Araujo, G., M. Terré, and A. Bach. 2014. Interaction between milk allowance and fat content of the starter feed on performance of Holstein calves. *J. Dairy Sci.* 97:6511–6518.
- Asai, T. 1973. Developmental processes of reticulo-rumen motility in calves. *Nihon Juigaku Zasshi* 35:239–252.
- Bach, A. 2012. Ruminant Nutrition Symposium: Optimizing performance of the offspring: Nourishing and managing the dam and postnatal calf for optimal lactation, reproduction, and immunity. *J. Anim. Sci.* 90:1835–1845.
- Bach, A., J. Ahedo, and A. Ferrer. 2010. Optimizing weaning strategies of dairy replacement calves. *J. Dairy Sci.* 93:413–419.
- Bach, A., A. Giménez, J. L. Juaristi, and J. Ahedo. 2007. Effects of physical form of a starter for dairy replacement calves on feed intake and performance. *J. Dairy Sci.* 90:3028–3033.
- Baldwin, R. L. VI, K. R. McLeod, J. L. Klotz, and R. N. Heitmann. 2004. Rumen development, intestinal growth and hepatic metabolism in the pre- and post-weaning ruminant. *J. Dairy Sci.* 87(E Suppl.):E55–E65.
- Bateman, H. G. II, T. M. Hill, J. M. Aldrich, and R. L. Schlotterbeck. 2009. Effects of corn processing, particle size, and diet form on performance of calves in bedded pens. *J. Dairy Sci.* 92:782–789.
- Beharka, A. A., T. G. Nagaraja, J. L. Morrill, G. A. Kennedy, and R. D. Klemm. 1998. Effects of form of the diet on anatomical,

- microbial, and fermentative development of the rumen of neonatal calves. *J. Dairy Sci.* 81:1946–1955.
- Bergman, E. N. 1990. Energy contributions of volatile fatty acids from the gastrointestinal tract in various species. *Physiol. Rev.* 70:567–590.
- Block, E., and P. R. Shellenberger. 1980. Woodpulp fines or corn silage as roughages in complete rations or a pelleted complete ration for young dairy replacements from birth through 18 weeks of age. *J. Dairy Sci.* 63:2060–2070.
- Brownlee, A. 1956. The development of rumen papillae in cattle fed on different diets. *Br. Vet. J.* 112:369–375.
- Bull, L. S., L. J. Bush, J. D. Friend, B. Harris Jr., and E. W. Jones. 1965. Incidence of ruminal parakeratosis in calves fed different rations and its relation to volatile fatty acid absorption. *J. Dairy Sci.* 48:1459–1466.
- Bunting, L. D., T. A. Tarifa, B. T. Crochet, J. M. Fernandez, C. L. Depew, and J. C. Lovejoy. 2000. Effects of dietary inclusion of chromium propionate and calcium propionate on glucose disposal and gastrointestinal development in dairy calves. *J. Dairy Sci.* 83:2491–2498.
- Calsamiglia, S., P. W. Cardozo, A. Ferret, and A. Bach. 2008. Changes in rumen microbial fermentation are due to a combined effect of type of diet and pH. *J. Anim. Sci.* 86:702–711.
- Carter, R. R., and W. L. Grovum. 1990. A review of the physiological significance of hypertonic body fluids on feed intake and ruminal function: Salivation, motility and microbes. *J. Anim. Sci.* 68:2811–2832.
- Castells, L., A. Bach, G. Araujo, C. Montoro, and M. Terré. 2012. Effect of different forage sources on performance and feeding behavior of Holstein calves. *J. Dairy Sci.* 95:286–293.
- Castells, L., A. Bach, A. Aris, and M. Terré. 2013. Effects of forage provision to young calves on rumen fermentation and development of the gastrointestinal tract. *J. Dairy Sci.* 96:5226–5236.
- Chapple, R. S., and J. J. Lynch. 1986. Behavioural factors modifying acceptance of supplementary foods by sheep. *Res. Dev. Agric.* 3:113–120.
- Chen, Y., G. B. Penner, M. Li, and L. L. Guan. 2011. Changes in bacterial diversity associated with epithelial tissue in the beef cow rumen during the transition to a high-grain diet. *Appl. Environ. Microbiol.* 77:5770–5781.
- Cline, J. H., T. V. Hershberger, and O. G. Bentley. 1958. Utilization and/or synthesis of valeric acid during the digestion of glucose, starch and cellulose by rumen micro-organisms in vitro. *J. Anim. Sci.* 17:284–292.
- Connor, E. E., R. L. Baldwin, C. Li, R. W. Li, and H. Chung. 2013. Gene expression in bovine rumen epithelium during weaning identifies molecular regulators of rumen development and growth. *Funct. Integr. Genomics* 13:133–142.
- Connor, E. E., R. L. Baldwin, M. P. Walker, S. E. Ellis, C. Li, S. Kahl, H. Chung, and R. W. Li. 2014. Transcriptional regulators transforming growth factor β 1 and estrogen-related receptor- α identified as putative mediators of calf rumen epithelial tissue development and function during weaning. *J. Dairy Sci.* 97:4193–4207.
- Conrad, H. R., and J. W. Hibbs. 1956. A high roughage system for raising calves based on the early development of rumen function. VII. Utilization of grass silage, pasture, and pelleted alfalfa meal. *J. Dairy Sci.* 39:1170–1179.
- Costa, J. H. C., N. A. Adderley, D. M. Weary, and M. A. G. von Keyserlingk. 2016a. Understanding sorting behavior motivation in young dairy calves. *J. Dairy Sci.* <http://dx.doi.org/10.3168/jds.2015-10052>.
- Costa, J. H. C., W. G. Costa, D. M. Weary, L. C. P. Machado Filho, and M. A. G. von Keyserlingk. 2016b. Dairy heifers benefit from having an older experienced cow present when learning how to graze. *J. Dairy Sci.* 99:562–568. <http://dx.doi.org/10.3168/jds.2015-9387>.
- Costa, J. H. C., R. R. Daros, M. A. G. von Keyserlingk, and D. M. Weary. 2014. Complex social housing reduces food neophobia in dairy calves. *J. Dairy Sci.* 97:7804–7810.
- Costa, J. H. C., R. K. Meagher, M. A. G. von Keyserlingk, and D. M. Weary. 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. *J. Dairy Sci.* 98:6381–6386.
- Coverdale, J. A., H. D. Tyler, J. D. Quigley III, and J. A. Brumm. 2004. Effect of various levels of forage and form of diet on rumen development and growth in calves. *J. Dairy Sci.* 87:2554–2562.
- de Paula Vieira, A., M. A. G. von Keyserlingk, and D. M. Weary. 2010. Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. *J. Dairy Sci.* 93:3079–3085.
- de Paula Vieira, A., M. A. G. von Keyserlingk, and D. M. Weary. 2012. Presence of an older weaned companion influences feeding behavior and improves performance of dairy calves before and after weaning from milk. *J. Dairy Sci.* 95:3218–3224.
- Doppenberg, J., and D. L. Palmquist. 1991. Effect of dietary fat level on feed intake, growth, plasma metabolites and hormones of calves fed dry or liquid diets. *Livest. Prod. Sci.* 29:151–166.
- Drackley, J. K. 2008. Calf nutrition from birth to breeding. *Vet. Clin. North Am. Food Anim. Pract.* 24:55–86.
- Eadie, J. M. 1962. Interrelationships between certain rumen ciliate protozoa. *J. Gen. Microbiol.* 29:579–588.
- Flatt, W. P., R. G. Warner, and J. K. Loosli. 1958. Influence of purified materials on the development of the ruminant stomach. *J. Dairy Sci.* 41:1593–1600.
- Fonty, G., P. Gouet, J. P. Jouany, and J. Senaud. 1983. Ecological factors determining establishment of cellulolytic bacteria and protozoa in the rumens of meroxenic lambs. *J. Gen. Microbiol.* 129:213–223.
- Fonty, G., P. Gouet, and J. M. Nebout. 1989. Development of the cellulolytic microflora in the rumen of lambs transferred into sterile isolators a few days after birth. *Can. J. Microbiol.* 35:416–422.
- Fonty, G., P. Gouet, H. Ratefiarivelo, and J. P. Jouany. 1988. Establishment of *Bacteroides succinogenes* and measurement of the main digestive parameters in the rumen of gnotoxenic lambs. *Can. J. Microbiol.* 34:938–946.
- Franklin, S. T., D. M. Amaral-Philips, J. A. Jackson, and A. A. Campbell. 2003. Health and performance of Holstein calves that suckled or were hand-fed colostrum and were fed one of three physical forms of starter. *J. Dairy Sci.* 86:2145–2153.
- Franzolin, R., and B. A. Dehority. 1996. Effect of prolonged high concentrate feeding on ruminal protozoa concentrations. *J. Anim. Sci.* 74:2803–2809.
- Gaillard, C., R. K. Meagher, M. A. G. von Keyserlingk, and D. M. Weary. 2014. Social housing improves dairy calves' performance in two cognitive tests. *PLoS ONE* 9:e90205.
- Galfi, P., S. Neogrady, and T. Sakata. 1991. Effects of volatile fatty acids on the epithelial cell proliferation of the digestive tract and its hormonal mediation. Pages 49–59 in *Physiological Aspects of Digestion and Metabolism in Ruminants: Proceedings of the Seventh International Symposium on Ruminant Physiology*. T. Tsuda, Y. Sasaki, and R. Kawashima, ed. Academic Press Inc., San Diego, CA.
- Górka, P., Z. M. Kowalski, P. Pietrzak, A. Kotunia, W. Jagusiak, J. J. Holst, P. Guilloteau, and R. Zabielski. 2011. Effect of method of delivery of sodium butyrate on rumen development in newborn calves. *J. Dairy Sci.* 94:5578–5588.
- Gozho, G. N., D. O. Krause, and J. C. Plaizier. 2006. Rumen lipopolysaccharide and inflammation during grain adaptation and subacute ruminal acidosis in steers. *J. Dairy Sci.* 89:4404–4413.
- Graham, C., I. Gatherer, I. Haslam, M. Glanville, and N. L. Simmons. 2007. Expression and localization of monocarboxylate transporters and sodium/proton exchangers in bovine rumen epithelium. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 292:R997–R1007.
- Greenwood, R. H., J. L. Morrill, E. C. Titgemeyer, and G. A. Kennedy. 1997. A new method of measuring diet abrasion and its effect on the development of the forestomach. *J. Dairy Sci.* 80:2534–2541.
- Hall, M. B., T. D. Nennich, P. H. Doane, and G. E. Brink. 2015. Total volatile fatty acid concentrations are unreliable estimators of treatment effects on ruminal fermentation in vivo. *J. Dairy Sci.* 98:3988–3999.

- Hepola, H. P., L. Hänninen, S. Raussi, P. Pursiainen, A.-M. Aarnikoi-vu, and H. Saloniemi. 2008. Effects of providing water from a bucket or a nipple on the performance and behavior of calves fed ad libitum volumes of acidified milk replacer. *J. Dairy Sci.* 91:1486–1496.
- Hibbs, J. W., H. R. Conrad, W. D. Pouden, and N. Frank. 1956. A high roughage system for raising calves based on early development of rumen function. VI. Influence of hay to grain ratio on calf performance, rumen development, and certain blood changes. *J. Dairy Sci.* 39:171–179.
- Hill, T. M., J. M. Aldrich, R. L. Schlotterbeck, and H. G. Bateman II. 2007. Protein concentrations for starters fed to transported neonatal calves. *Prof. Anim. Sci.* 23:123–134.
- Hill, T. M., H. G. Bateman, J. M. Aldrich, and R. L. Schlotterbeck. 2008a. Effects of the amount of chopped hay or cottonseed hulls in a textured calf starter on young calf performance. *J. Dairy Sci.* 91:2684–2693.
- Hill, T. M., H. G. Bateman, J. M. Aldrich, and R. L. Schlotterbeck. 2008b. Effect of feeding different carbohydrate sources and amounts to young calves. *J. Dairy Sci.* 91:3128–3137.
- Hill, T. M., H. G. Bateman II, J. M. Aldrich, and R. L. Schlotterbeck. 2009. Roughage for diets fed to weaned dairy calves. *Prof. Anim. Sci.* 25:283–288.
- Hinders, R. G., and F. G. Owen. 1965. Relation of ruminal parakeratosis development to volatile fatty acid absorption. *J. Dairy Sci.* 48:1069–1073.
- Hodgson, J. 1971. The development of solid food intake in calves. 5. The relationship between liquid and solid food intake. *Anim. Prod.* 13:593–597.
- Hollon, B. F., R. K. Waugh, G. H. Wise, and F. H. Smith. 1958. Cottonseed meals as the primary protein supplement in concentrate feeds for young calves. *J. Dairy Sci.* 41:286–294.
- Huntington, G. B. 1997. Starch utilization by ruminants: From basics to the bunk. *J. Anim. Sci.* 75:852–867.
- Jahn, E., P. T. Chandler, and C. E. Polan. 1970. Effects of fiber and ratio of starch to sugar on performance of ruminating calves. *J. Dairy Sci.* 53:466–474.
- Jami, E., A. Israel, A. Kotser, and I. Mizarah. 2013. Exploring the bovine rumen bacterial community from birth to adulthood. *ISME J.* 7:1069–1079.
- Jami, E., and I. Mizrahi. 2012. Composition and similarity of bovine rumen microbiota across individual animals. *PLoS ONE* 7:e33306.
- Jasaitis, D. K., J. E. Wohlt, and J. L. Evans. 1987. Influence of feed ion content on buffering capacity of ruminant feedstuffs in vitro. *J. Dairy Sci.* 70:1391–1403.
- Kay, M., B. F. Fell, and R. Boyne. 1969. The relationship between the acidity of the rumen contents and rumenitis in calves fed barley. *Res. Vet. Sci.* 10:181–187.
- Kay, R. N. B. 1960. The rate of flow and composition of various salivary secretions in sheep and calves. *J. Physiol.* 150:515–537.
- Kellaway, R. C., T. Grant, and J. W. Chudleigh. 1973. The effect of roughage and buffers in the diet of early weaned calves. *Aust. J. Exp. Agric. Anim. Husb.* 13:225–228.
- Kertz, A. F., L. R. Prewitt, and J. P. Everett Jr. 1979. An early weaning calf program: Summarization and review. *J. Dairy Sci.* 62:1835–1843.
- Khan, M. A., H. J. Lee, W. S. Lee, H. S. Kim, S. B. Kim, K. S. Ki, S. J. Park, J. K. Ha, and Y. J. Choi. 2007. Starch source evaluation in calf starter: I. Feed consumption, body weight gain, structural growth, and blood metabolites in Holstein calves. *J. Dairy Sci.* 90:5259–5268.
- Khan, M. A., H. J. Lee, W. S. Lee, H. S. Kim, S. B. Kim, S. B. Park, K. S. Baek, J. K. Ha, and Y. J. Choi. 2008. Starch source evaluation in calf starter: II. Rumen parameters, rumen development, nutrient digestibilities, and nitrogen utilization in Holstein calves. *J. Dairy Sci.* 91:1140–1149.
- Khan, M. A., D. M. Weary, and M. A. G. von Keyserlingk. 2011b. Hay intake improves performance and rumen development of calves fed higher quantities of milk. *J. Dairy Sci.* 94:3547–3553.
- Khan, M. A., D. M. Weary, and M. A. G. von Keyserlingk. 2011a. Invited Review: Effects of milk ration on solid feed intake, weaning and performance in dairy heifers. *J. Dairy Sci.* 94:1071–1081.
- Khan, M. A., D. M. Weary, D. M. Veira, and M. A. G. von Keyserlingk. 2012. Postweaning performance of heifers provided hay during the milk feeding period. *J. Dairy Sci.* 95:3970–3976.
- Kincaid, R. L. 1980. Alternative methods of feeding alfalfa to calves. *J. Dairy Sci.* 63:91–94.
- Knott, K. K., P. S. Barboza, and R. T. Bowyer. 2005. Postnatal development and organ maturation in *Rangifer tarandus* and *Ovibos moschatus*. *J. Mammal.* 86:121–130.
- Kosiorowska, A., L. Puggaard, M. S. Hedemann, J. Sehested, S. K. Jensen, N. B. Kristensen, P. Kuropka, K. Marycz, and M. Vestergaard. 2011. Gastrointestinal development of dairy calves fed low- or high-starch concentrate at two milk allowances. *Animal* 5:211–219.
- Krause, K. M., and G. R. Oetzel. 2006. Understanding and preventing subacute ruminal acidosis in dairy herds: A review. *Anim. Feed Sci. Technol.* 126:215–236.
- Kristensen, N. B., J. Sehested, S. K. Jensen, and M. Vestergaard. 2007. Effect of milk allowance on concentrate intake, ruminal environment, and ruminal development in milk-fed Holstein calves. *J. Dairy Sci.* 90:4346–4355.
- Laarman, A. H., and M. Oba. 2011. Short communication: Effect of calf starter on rumen pH of Holstein dairy calves at weaning. *J. Dairy Sci.* 94:5661–5664.
- Laarman, A. H., A. L. Ruiz-Sanchez, T. Sugino, L. L. Guan, and M. Oba. 2012. Effects of feeding a calf starter on molecular adaptations in the ruminal epithelium and liver of Holstein dairy calves. *J. Dairy Sci.* 95:2585–2594.
- Leibholz, J. 1975. Ground roughage in the diet of the early-weaned calf. *Anim. Prod.* 20:93–100.
- Lesmeister, K. E., and A. J. Heinrichs. 2004. Effects of corn processing on growth characteristics, rumen development, and rumen parameters in neonatal dairy calves. *J. Dairy Sci.* 87:3439–3450.
- Lesmeister, K. E., and A. J. Heinrichs. 2005. Effects of adding extra molasses to a texturized calf starter on rumen development, growth characteristics, and blood parameters in neonatal dairy calves. *J. Dairy Sci.* 88:411–418.
- Li, M., M. Zhou, E. Adamowicz, J. A. Basarab, and L. L. Guan. 2012b. Characterization of bovine ruminal epithelial bacterial communities using 16S rRNA sequencing, PCR-DGGE and qRT-PCR analysis. *Vet. Microbiol.* 155:72–80.
- Li, R. W., E. E. Connor, C. Li, R. L. Baldwin VI, and M. E. Sparks. 2012a. Characterization of the rumen microbiota of pre-ruminant calves using metagenomic tools. *Environ. Microbiol.* 14:129–139.
- Maiga, H. A., D. J. Schingoethe, F. C. Ludens, W. L. Tucker, and D. P. Casper. 1994. Response of calves to diets that varied in amounts of ruminally degradable carbohydrate and protein. *J. Dairy Sci.* 77:278–283.
- Malmuthuge, N., J. P. Griebel, and L. L. Guan. 2014. Taxonomic identification of commensal bacteria associated with the mucosa and digesta throughout the gastrointestinal tract of pre-weaned calves. *Appl. Environ. Microbiol.* 80:2021–2028.
- Margerison, J. K., T. R. Preston, and C. J. C. Phillips. 2002. Restricted suckling of tropical dairy cows by their own calf or other cows' calves. *J. Anim. Sci.* 80:1663–1670.
- McBurney, M. I., P. J. Van Soest, and L. E. Chase. 1983. Cation exchange capacity and buffering capacity of neutral detergent fibers. *J. Sci. Food Agric.* 34:910–916.
- McGavin, M. D., and J. L. Morrill. 1976. Dissection technique for examination of the bovine ruminoreticulum. *J. Anim. Sci.* 42:535–538.
- Meagher, R. K., R. R. Daros, J. H. C. Costa, M. A. G. von Keyserlingk, M. Hotzel, and D. M. Weary. 2015. Effects of degree and timing of social housing on reversal learning and response to novel objects in dairy calves. *PLoS ONE* 10:e0132828.
- Mertens, D. R. 1997. Creating a system for meeting the fiber requirements of dairy cows. *J. Dairy Sci.* 80:1463–1481.

- Miller-Cushon, E. K., and T. J. DeVries. 2011. Effect of early feed type exposure on diet-selection behaviour of dairy calves. *J. Dairy Sci.* 94:342–350.
- Miller-Cushon, E. K., C. Montoro, A. Bach, and T. J. DeVries. 2013. Effect of early exposure to mixed rations differing in forage particle size on feed sorting of dairy calves. *J. Dairy Sci.* 96:3257–3264.
- Minato, H., M. Otsuka, S. Shirasaka, H. Itabashi, and M. Mitsumori. 1992. Colonization of microorganisms in the rumen of young calves. *J. Gen. Appl. Microbiol.* 38:447–456.
- Mirza, S. N., and F. D. Provenza. 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. *Appl. Anim. Behav. Sci.* 28:255–263.
- Mirza, S. N., and F. D. Provenza. 1994. Socially induced food avoidance in lambs: Direct or indirect maternal influence? *J. Anim. Sci.* 72:899–902.
- Montoro, C., and A. Bach. 2012. Voluntary selection of starter feed ingredients offered separately to nursing calves. *Livest. Sci.* 149:62–69.
- Montoro, C., E. K. Miller-Cushon, T. J. DeVries, and A. Bach. 2013. Effect of physical form of forage on performance, feeding behavior, and digestibility of Holstein calves. *J. Dairy Sci.* 96:1117–1124.
- Morrisse, J. P., D. Huonnic, J. P. Cotte, and A. Martrenchar. 2000. The effect of four fibrous feed supplementations on different welfare traits in veal calves. *Anim. Feed Sci. Technol.* 84:129–136.
- Naeem, A., J. K. Drackley, J. Stamey, and J. J. Looor. 2012. Role of metabolic and cellular proliferation genes in ruminal development in response to enhanced plane of nutrition in neonatal Holstein calves. *J. Dairy Sci.* 95:1807–1820.
- Nocek, J. E., C. W. Heald, and C. E. Polan. 1984. Influence of ration physical form and nitrogen availability on ruminal morphology of growing bull calves. *J. Dairy Sci.* 67:334–343.
- NRC. 2001. *Nutrient Requirements of Dairy Cattle*. 7th rev. ed. National Academy Press, Washington, DC.
- Owen, F. G., and L. L. Larson. 1986. Effect of probiotic and starter preparation on calf performance. *Coop. Ext. Ser. Univ. Nebr.* 1986:36–37.
- Penner, G. B., and M. Oba. 2009. Increasing dietary sugar concentration may improve dry matter intake, ruminal fermentation, and productivity of dairy cows in the postpartum phase of the transition period. *J. Dairy Sci.* 92:3341–3353.
- Penner, G. B., M. A. Steele, J. R. Aschenbach, and B. W. McBride. 2011. Molecular adaptation of ruminal epithelia to highly fermentable diets. *J. Anim. Sci.* 89:1108–1119.
- Petri, R. M., R. J. Forster, W. Yang, J. J. McKinnon, and T. A. McAllister. 2012. Characterization of rumen bacterial diversity and fermentation parameters in concentrate fed cattle with and without forage. *J. Appl. Microbiol.* 112:1152–1162.
- Petri, R. M., T. Schwaiger, G. B. Penner, K. A. Beauchemin, and R. J. Forster. 2013. Characterization of the core rumen microbiome in cattle during transition from forage to concentrate as well as during and after an acidotic challenge. *PLoS ONE* 8:e83424.
- Phillips, C. J. C. 2004. The effects of forage provision and group size on the behavior of calves. *J. Dairy Sci.* 87:1380–1388.
- Porter, J. C., R. G. Warner, and A. F. Kertz. 2007. Effect of fiber level and physical form of starter on growth and development of dairy calves fed no forage. *Prof. Anim. Sci.* 23:395–400.
- Pounden, W. D., and J. W. Hibbs. 1949. Rumen inoculations in young calves. *J. Am. Vet. Med. Assoc.* 114:33–35.
- Quigley, J. D. III, T. M. Steen, and S. I. Boehms. 1992. Postprandial changes of selected blood and ruminal metabolites in ruminating calves fed diets with or without hay. *J. Dairy Sci.* 75:228–235.
- Sander, E. G., H. N. Warner, H. N. Harrison, and J. K. Loosli. 1959. The stimulatory effect of sodium butyrate and sodium propionate on the development of rumen mucosa in the young calf. *J. Dairy Sci.* 42:1600–1605.
- Schadt, I., J. D. Ferguson, G. Azzaro, R. Petriglieri, M. Caccamo, P. Van Soest, and G. Licitra. 2012. How do dairy cows chew?—Particle size analysis of selected feeds with different particle length distributions and of respective ingested bolus particles. *J. Dairy Sci.* 95:4707–4720.
- Schrama, H. R., B. White, and J. R. Ingalls. 1986. Utilization of whole rape (canola) seed and sunflower seeds as sources of energy and protein in calf starter diets. *Anim. Feed Sci. Technol.* 15:101–112.
- Schwartzkopf-Genswein, K. S., K. A. Beauchemin, D. J. Gibb, D. H. Crews Jr, D. D. Hickman, M. Streeter, and T. A. McAllister. 2003. Impact of bunk management on feeding behavior, ruminal acidosis and performance of feedlot cattle: A review. *J. Anim. Sci.* 81(E. Suppl. 2):E149–E158.
- Shen, Z., H. M. Seyfert, B. Lohrke, F. Schneider, R. Zitnan, A. Chudy, S. Kuhla, H. M. Hammon, J. W. Blum, H. Martens, H. Hagemester, and J. Viogt. 2004. An energy rich diet causes rumen papillae proliferation associated with more IGF type 1 receptors and increased plasma IGF-1 concentrations in young goats. *J. Nutr.* 134:11–17.
- Soberon, F., E. Raffrenato, R. W. Everett, and M. E. Van Amburgh. 2012. Pre-weaning milk replacer intake and effects on long-term productivity of dairy calves. *J. Dairy Sci.* 95:783–793.
- Soberon, F., and M. E. Van Amburgh. 2013. Lactation Biology Symposium: The effect of nutrient intake from milk or milk replacer of preweaned dairy calves on lactation milk yield as adults: A meta-analysis of current data. *J. Anim. Sci.* 91:706–712.
- Stake, P. E., M. J. Owens, and D. J. Schingoethe. 1973. Rapeseed, sunflower, and soybean meal supplementation of calf rations. *J. Dairy Sci.* 56:783–788.
- Stobo, I. J. F., J. H. B. Roy, and H. J. Gaston. 1966. Rumen development in the calf. 1. The effect of diets containing different proportions of concentrates to hay on rumen development. *Br. J. Nutr.* 20:171–188.
- Strozinski, L. L., and P. T. Chandler. 1971. Effects of dietary fiber and acid-detergent lignin on body fill of ruminating calves. *J. Dairy Sci.* 54:1491–1495.
- Suárez, B. J., C. G. Van Reenen, G. Beldman, J. van Delen, J. Dijkstra, and W. J. J. Gerrits. 2006a. Effects of supplementing concentrates differing in carbohydrate composition in veal calf diets: I. Animal performance and rumen fermentation characteristics. *J. Dairy Sci.* 89:4365–4375.
- Suárez, B. J., C. G. Van Reenen, W. J. J. Gerrits, N. Stockhofe, A. M. van Vuuren, and J. Dijkstra. 2006b. Effects of supplementing concentrates differing in carbohydrate composition in veal calf diets: II. Rumen development. *J. Dairy Sci.* 89:4376–4386.
- Suárez, B. J., C. G. Van Reenen, N. Stockhofe, J. Dijkstra, and W. J. J. Gerrits. 2007. Effect of roughage source and roughage to concentrate ratio on animal performance and rumen development in veal calves. *J. Dairy Sci.* 90:2390–2403.
- Suarez-Mena, F. X., T. M. Hill, A. J. Heinrichs, H. G. Bateman, J. M. Aldrich, and R. L. Schlotterbeck. 2011. Effects of including corn distillers dried grains with solubles in dairy calf feeds. *J. Dairy Sci.* 94:3037–3044.
- Sutton, J. D., A. D. McGilliard, and N. L. Jacobson. 1963. Functional development of rumen mucosa. I. Absorptive ability. *J. Dairy Sci.* 46:426–436.
- Svihus, B., A. K. Uhlen, and O. M. Harstad. 2005. Effect of starch granule structure, associated components and processing on nutritive value of cereal starch: A review. *Anim. Feed Sci. Technol.* 122:303–320.
- Swanson, E. W., and J. D. Harris. 1958. Development of rumination in young calf. *J. Dairy Sci.* 41:1768–1776.
- Tamate, H., A. D. McGilliard, N. L. Jacobson, and R. Getty. 1962. Effect of various dietaries on the anatomical development of the stomach in the calf. *J. Dairy Sci.* 45:408–420.
- Tedeschi, L. O., and D. G. Fox. 2009. Predicting milk and forage intake of nursing calves. *J. Anim. Sci.* 87:3380–3391.
- Terré, M., G. Maynou, A. Bach, and M. Gauthier. 2015. Effect of *Saccharomyces cerevisiae* CNCM I-1077 supplementation on performance and rumen microbiota of dairy calves. *Prof. Anim. Sci.* 31:153–158.
- Terré, M., E. Pedrals, A. Dalmau, and A. Bach. 2013. What do pre-weaned and weaned calves need in the diet: A high fiber content or a forage source? *J. Dairy Sci.* 96:5217–5225.
- Terui, H., J. L. Morrill, and J. J. Higgins. 1996. Evaluation of wheat gluten in milk replacer and calf starter. *J. Dairy Sci.* 79:1261–1266.

- USDA. 2009. Dairy 2007, Part IV: Reference of Dairy Cattle Health and Management Practices. USDA, National Animal Health Monitoring System, Fort Collins, CO.
- van Ackeren, C., H. Steingaß, K. Hartung, R. Funk, and W. Drochner. 2009. Effect of roughage level in a total mixed ration on feed intake, ruminal fermentation patterns and chewing activity of early-weaned calves with ad libitum access to grass hay. *Anim. Feed Sci. Technol.* 153:48–59.
- Vázquez-Añón, M., A. J. Heinrichs, J. M. Aldrich, and G. A. Varga. 1993. Postweaning age effects on rumen fermentation end-products and digesta kinetics in calves weaned at 5 weeks of age. *J. Dairy Sci.* 76:2742–2748.
- Weimer, P. J., D. M. Stevenson, H. C. Mantovani, and S. L. C. Man. 2010. Host specificity of the ruminal bacterial community in the dairy cow following near-total exchange of ruminal contents. *J. Dairy Sci.* 93:5902–5912.
- Williams, P. E. V., R. J. Fallon, G. M. Innes, and P. Garthwaite. 1987. Effect on food intake, rumen development and live weight of calves of replacing barley with sugar beet-citrus pulp in a starter diet. *Anim. Prod.* 44:65–73.
- Williams, P. E. V., and A. J. Frost. 1992. Feeding the young ruminant. Pages 109–118 in *Neonatal Survival and Growth*. Occasional Publ. No. 15. M. Varley, P. E. V. Williams, and T. L. J. Lawrence, ed. Br. Soc. Anim. Prod., Edinburgh, UK.
- Wood, K. M., S. I. Palmer, M. A. Steele, J. A. Metcalf, and G. B. Penner. 2015. The influence of age and weaning on permeability of the gastrointestinal tract in Holstein bull calves. *J. Dairy Sci.* <http://dx.doi.org/10.3168/jds.2015-9393>.
- Wright, I. A., and A. J. F. Russel. 1987. The effect of sward height on beef cow performance and the relationship between calf milk and herbage intakes. *Anim. Prod.* 44:363–370.
- Yáñez-Ruiz, D. R., L. Abecia, and C. J. Newbold. 2015. Manipulating rumen microbiome and fermentation through interventions during early life: A review. *Front. Microbiol.* 6:1133 <http://dx.doi.org/10.3389/fmicb.2015.01133>.
- Yáñez-Ruiz, D. R., B. Macías, E. Pinloche, and C. J. Newbold. 2010. The persistence of bacterial and methanogenic archaeal communities residing in the rumen of young lambs. *FEMS Microbiol. Ecol.* 72:272–278.
- Yang, W. Z., and K. A. Beauchemin. 2006. Effects of physically effective fiber on chewing activity and rumen pH of dairy cows fed diets based on barley silage. *J. Dairy Sci.* 89:217–228.
- Zebeli, Q., J. R. Aschenbach, M. Tafaj, J. Boguhn, B. N. Ametaj, and W. Drochner. 2012. Invited review: Role of physically effective fiber and estimation of dietary fiber adequacy in high-producing dairy cattle. *J. Dairy Sci.* 95:1041–1056.
- Žitnan, R., J. Voigt, U. Schonhosen, J. Wegner, M. Kokardova, H. Hagemester, M. Levkut, S. Kuhla, and A. Sommer. 1998. Influence of dietary concentrate to forage ratio on the development of rumen mucosa in calves. *Arch. Tierernähr.* 51:279–291.