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Review

Why are dairy cows not able to cope with the subacute ruminal acidosis?

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Abstract

One of the largest challenges for the dairy industry is to provide cows with a diet which is highly energetic but does not negatively affect their rumens' functions. In highly productive dairy cows, feeding diets rich in readily fermentable carbohydrates provides energy precursors needed for maximum milk production, but simultaneously decreases ruminal pH, leading to a widespread prevalence of subacute ruminal acidosis. Maximizing milk production without triggering rumen acidosis still challenges dairy farmers, who try to prevent prolonged bouts of low ruminal pH mainly by proper nutrition and management practices. The animals try to avoid overeating fermentable feeds, as it causes negative consequences by disturbing digestive processes. The results of several experiments show that ruminants, including sheep and beef cattle, are able to modify some aspects of feeding behaviour in order to adjust nutrient intake to their needs and simultaneously prevent physiological disturbances. Particularly, such changes (e.g., increased preference for fibrous feeds, reduced intake of concentrates) were observed in animals, which were trying to prevent the excessive drop of rumen fluid pH. Thanks to a specific mechanism called "the postingestive feedback", animals should be able to work out such a balance in intake, so they do not suffer either from hunger or from negative effects of over-ingesting the fermentable carbohydrates. This way, an acidosis should not be a frequent problem in ruminants. However, prolonged periods of excessively decreased rumen pH are still a concern in dairy cows. It raises a question, why the regulation of feed intake by postingestive feedback does not help to maintain stable rumen environment in dairy cows?

Key words: feeding behaviour, postingestive feedback, acidosis, dairy cows, rumen

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Introduction

One of the largest challenges for the dairy industry is to create a feeding ration, which provides energy precursors needed for maximum milk production but does not trigger subacute ruminal acidosis (SARA). SARA has detrimental effects on animal's health and leads to decreased milk production (Krause and Oetzel 2006). Therefore, it causes substantial economical losses, being the most important nutritional disease of dairy cattle (Enemark 2008).

But why are dairy cows not able to cope with subacute ruminal acidosis on their own? The ruminants have a postingestive feedback mechanism which links their food preferences with changes in rumen environment; therefore it should help them to actively influence the composition of ingested feed (Provenza 1995). They are able to modify their feeding behaviour as a function of the consequences – positive or negative, they experience after feed ingestion, as has been confirmed by many studies on sheep or beef cattle. Even a separate access to different feeds (including concentrates) did not contribute to development of acidosis in fattening cattle (Moya et al. 2010). Also dairy cows, when in the state of SARA, are able to change their food preferences towards feeds which could help counteract the excessive drop of rumen fluid pH. The aim of this review is to find an answer, what makes dairy cows so different from other ruminants that, despite the existence of postingestive feedback mechanism, they frequently experience long periods of SARA.

Ruminal acidosis – causes and consequences

The ruminal acidosis can be generally divided into two types – acute or subacute acidosis, which share similar aetiology but are different diseases (Krause and Oetzel 2006). Subacute ruminal acidosis, also known as chronic or sub-clinical rumen acidosis, is characterized by repeated bouts of lowered rumen pH. These bouts of moderately depressed pH (about 5.5-5.0) usually last from several minutes to several hours (Beauchemin and Yang 2005). The pH threshold values for SARA are a matter in dispute (Duffield et al. 2004, Gozho 2005, Jouany 2006). However, desirable rumen pH is certainly above 6.0, as pH below that value reduces the growth of fibrolitic bacteria (Shi and Weimer 2002).

There are several factors which are considered to predispose dairy cattle to SARA. Main nutritional factors include the amount of organic matter fermented in the rumen, the rate and the extent of starch digestion in the rumen, the content of neutral deter-

gent fibre (NDF) in the diet and particle size of the feedstuffs (Stone 2004, Zebeli et al. 2012). Management and environmental factors include heat stress, overcrowding and competition at the feed bunk, feeding forage components separately, inconsistent feed delivery, restricted feeding and inadequate adaptation to highly fermentable diets (Krause and Oetzel 2006).

It is widely known that SARA has detrimental effects on animal's health. Ruminal epithelial cells are vulnerable to the chemical damage by acids even during short periods of subacute acidosis, as they are not protected by mucus. Thus, the low ruminal pH can further lead to rumenitis, ruminal parakeratosis and ulceration of the ruminal epithelium (Xu and Ding 2011). Once the ruminal epithelium is inflamed, bacteria may colonize the papillae and enter the bloodstream, causing abscesses in liver, then colonize lungs, heart valves, kidneys or joints (Nordlund et al. 1995, Nocek 1997). The consequences of SARA are reduced fibre digestion, inconsistent feed intake, diarrhoea, decreased milk fat, but also foot problems such as laminitis, subsequent hoof overgrowth and sole abscesses (Nocek 1997, Plaizier et al. 2008, Aschenbach et al. 2011).

There is general agreement that proper diet formulation and good management practices are crucial for SARA prevention (Schwartzkopf-Genswein et al. 2003, Jouany 2006, Greter et al. 2010). Preventing SARA is mainly achieved by limiting the intake of rapidly fermentable carbohydrates, providing adequate ruminal buffering and allowing ruminal adaptation to high grain diets. The most effective strategy to reduce the fermentation rate in the rumen is to increase the proportion of roughage in the diet, because it is eaten much more slowly than grain (Beauchemin and Yang 2005). Moreover, increasing dietary content of physically effective fibre (peNDF) from roughage, stimulates chewing and secretion of saliva, which buffers fermentation acids (Allen 1997, Zebeli et al. 2012).

Intensive cattle production systems tend to minimize the content of roughage in the diet in favour of highly fermentable grain, which easily acidifies rumen environment (Plaizier et al. 2008, Zebeli et al. 2012). The grain is eaten at faster rates and ruminated less than roughages, which leads to reduced secretion of saliva and reduced inflow of salivary buffers to the rumen, predisposing to the acidosis. Therefore, the prevalence of SARA is widespread in dairy herds and, as suggested by Enemark (2008), SARA is the most important nutritional disease of dairy cattle. Because of the nonspecific symptoms, difficulties with diagnosing and decreased milk production, subacute ruminal acidosis can be a huge financial problem for the dairy industry (Krause and Oetzel 2006).

Postingestive feedback in ruminants

Improper nutrition, which does not sufficiently meet all physiological needs of the animals, is obviously the main cause of rumen acidosis in dairy cows. Particularly, ingested feed is too rich in easily fermentable carbohydrates or does not contain sufficient amount of physically effective fibre, leading to decreased ruminal pH. As ruminal pH affects the growth of microbial populations and physiological functions of the rumen, it is a crucial factor for stable functioning of this organ (Nagaraja and Titgemeyer 2007). Therefore, the ruminants should have some mechanisms, linking food preferences with changes in rumen environment, to actively influence the composition of ingested feed. Indeed, many researchers agree that ruminants are able to modify their feeding behaviour as a function of the consequences – positive or negative, they experience after feed ingestion. This mechanism allows the animal to meet its nutritional needs and simultaneously prevents disturbances (such as subacute ruminal acidosis) in digestive processes (Yearsley et al. 2006).

A concept that the animal's body itself is enough wise to meet its physiological needs without causing severe disruptions in digestive processes, was fully explained by Provenza (1995). He implied that ruminants may have some kind of a "nutritional wisdom", which helps them to select feeds that meet their needs and avoid feeds that cause negative consequences. Due to the fact that animals can doubtfully taste or smell nutrients or toxins in feeds directly, another mechanism must be involved in food preferences instead. Therefore, the hypothesis of recognizing effects of feed ingestion was proposed (Provenza 1995). This mechanism – behaviour by consequences – assures that individuals should be able to cover their nutritional requirements and simultaneously prevent unwanted consequences of feed digestion.

The mechanism, which connects feeding behaviour with the after-effects of feed ingestion, may be explained by the postingestive feedback concept (Yearsley et al. 2006). The feed, which provides chemicals required by an animal at a certain point in space and time, will be more preferred than other feeds. In contrast, if a feed contains compounds which cause negative effects to the organism or the ones which are not needed in that particular point (e.g., excess of nutrients), the preference for the feed will decrease (Villalba et al. 2010b). On this basis, ruminants preferentially ingest feeds high in nutrients (Villalba and Provenza 1997) and low in toxins (Provenza et al. 1990), but they avoid specific nutrients when needs are met (Villalba and Provenza

1999), and eat toxins when they provide desirable medicinal (e.g., antiparasitic) effects (Villalba et al. 2010a). Thus, the process of food selection can be interpreted as the constant search for chemicals which restore homeostasis (Villalba and Provenza 2007). Such pattern can be observed in animals eating grain. The production of organic acids from starch digestion causes malaise, therefore the intake declines. Nonetheless, this negative feedback is followed by the positive feedback (satiety), so as the time passes, the aversion to grain decreases (Provenza 1995). Also, the food preferences are changed and the animal chooses different amounts or different types of feeds to prevent future negative consequences of eating grain.

The concept of postingestive feedback is relatively new and has not been widely accepted in the past or presently (Villalba et al. 2010b). Most of the scientists assume that formulated ration is ideal for an animal, as it covers expected nutritional requirements of the cow (Villalba et al. 2010b). Therefore, the animals should eat to meet, what human considered to be, their needs. Such thinking ignores the fact that each individual is unique and all processes in the organism are dynamic. Thus, animals are not machines (Provenza and Villalba 2006) – their needs may change even during a single day. According to Provenza and Villalba (2006), the feedback provides detailed information about the states of all the cells in the organism through nerves to the central nervous system, therefore it should affect behaviour on the basis of the most current needs.

Feeding behaviour changes in response to the disturbances in the rumen

Evidences from the experimental studies on sheep confirm that they are capable of choosing different compounds of forage to attenuate lowered rumen pH. Feeding grain too frequently or in excess decreased sheep preference for grain, which may be the effect of ruminal pH drop (Phy and Provenza 1998a). Interestingly, sheep increased their intake of sodium bicarbonate and lasalocid, which attenuated the aversion to grain. Sodium bicarbonate buffers hydrogen ions of organic acids, whereas lasalocid reduces populations of specific lactic acid-producing bacteria. It was suggested, that these supplements in the diet provided relief from adverse effects of low rumen pH (Phy and Provenza 1998a,b), however, the conclusions could not be drawn as pH was not measured.

An important role of the rumen environment in food selection was also confirmed in an interesting

study by Cooper et al. (1995). Experimental treatments included ruminal infusion of HCl, NaOH or NaCl of different concentrations and osmolalities. Clear tendencies were observed for the treatment administered to have an effect on feed intake during four hours of the infusion and two hours after it had ended. Although not statistically significant, the feed intake was depressed for the treatments of highest concentration within each treatment type (HCl, NaOH or NaCl). Moreover, in response to increasing treatment osmolality, the intake of high energy density feed declined significantly during the infusion period. It was proposed, that this decline could have been caused by the rapidly fermented compounds of high energy density feed, which entailed plummeting pH and rising osmolality. The sheep may have been able to associate this feed with unfavourable changes in rumen environment (Milewski et al. 2012), such as low pH and high osmolality, and altered their feeding behaviour in response to these consequences (Cooper et al. 1995).

Results of numerous experimental studies confirm that also cattle modify several aspects of feeding behaviour to prevent physiological disturbances, such as low ruminal pH. Fattening calves offered free-choice of different feeds, including easily fermentable grain, did not develop acidosis (Atwood et al. 2001). Moreover, all animals in the study were able to ingest proper amounts of nutrients and maintain rumen pH in physiological limits, but no two animals chose the same amounts of different ingredients. During the first week of the trial, cattle that selected their own diets ate more than animals fed the total mixed ration (TMR), apparently because they had a possibility to try different feeds with various flavours and nutrient contents. However, during the rest of the trial animals offered a choice tended to eat less than animals offered the TMR. Interestingly, the rate of body weight gain did not differ between these two groups. During the experiment no individual routinely selected the same feeds and none consumed a diet similar to nutritionally balanced TMR (Atwood et al. 2001). All these results highlighted the pronounced role of individual variability in food choice.

Very similar results were obtained in a recent study on crossbred beef cattle, where heifers had a separate access to different feeds (barley grain, corn silage, distillers grain). The heifers did not develop acidosis even though they had an unlimited access to highly fermentable feeds, like barley grain. Ruminal pH and volatile fatty acids profiles were not different among cattle fed free-choice diets or the TMR (Moya et al. 2010).

Relation between rumen pH and feeding behaviour in dairy cattle

Several experiments proved that dairy cows, when in the state of ruminal acidosis, are able to change their food preferences towards feeds which could help counteract the excessive drop of rumen fluid pH. An experiment by Keunen et al. (2002) showed a strong change of food preferences of dairy cows in the state of subacute acidosis. When cows were given a choice between alfalfa hay and alfalfa pellets, they chose the hay more willingly when in the state of acidosis. The change of food preferences could help attenuate the rumen acidosis, since long particles increase rumination time and salivary secretion.

Lactating dairy cows usually sort feeds for the smaller particles (like grain and concentrates), but against the longer forage particles, NDF and peNDF. For cows fed low forage diets, such sorting behaviour additionally increases the intake of grain and decreases the intake of roughages, which may significantly contribute to the occurrence of ruminal acidosis (Leonardi and Armentano 2003, DeVries et al. 2007). The experiments show that cows induced with subacute acidosis tend to prefer forage particles which are long and high in NDF, to stimulate rumination and salivation (Beauchemin and Yang 2005, Yang and Beauchemin 2006). These observations are entirely opposite to the normal behaviour of cows – sorting for short and against long particles. DeVries et al. (2008) also observed an altered sorting behaviour of dairy cows in response to repeated acidosis challenges, induced by offering cows the meals of grain. Severe acidosis was associated with increased sorting for the longer and against the shorter particles, likely to attenuate the effects of low ruminal pH. Furthermore, the observations from the same experiment showed that the cows in the state of acidosis manifested more aversion to grain with each challenge (Dohme et al. 2008). Over-eating the concentrates caused some kind of discomfort which must have stimulate the cows to change their behaviour.

Why the mechanism regulating feed intake does not sufficiently prevent subacute ruminal acidosis in dairy cows?

Above examples clearly indicate that dairy cows, like other ruminants, are able to change their feeding behaviour in response to changes in rumen environment, particularly towards feeds which could help them attenuate the acidosis. This indicates that the mechanism of postingestive feedback is present also in dairy cows and the behavioural response may be in-

duced by the lowered rumen pH. Nevertheless, the acidosis is widespread among dairy cows. What more, in some cases their behaviour (e.g., sorting) contribute to further lowering the rumen pH (DeVries et al. 2008). The selection for increased milk yield has always favoured animals that eat more, prefer forages with higher energy content and are able to select them when offered a choice (Fisher 2002). Therefore, the strong preference for energy-rich feeds is not surprising in cows. It is strange, however, that in dairy cows this preference is not effectively counteracted by the negative consequences of over-ingesting such feeds. It may be concluded then, that the regulating mechanism is apparently not able to either effectively prevent SARA or to help cows recover from it.

Two alternative explanations of this phenomenon have been formulated (explicitly or implicitly) in the literature. Both of them have been founded on the evidence that energy requirements of dairy cows are exceptionally high, in comparison to other domesticated ruminants, so to cover their needs dairy cows have to ingest big quantities of energy-rich feeds. Therefore, the feeding rations are rich in easily fermentable carbohydrates and poor in physically effective fibre, predisposing cows to SARA (Zebeli et al. 2012).

The first hypothesis is based on the fact that both dairy cows and dairy heifers have strong preference towards feeds rich in easily fermentable carbohydrates. They consume such feeds in high quantities despite depressed rumen pH, even in situations when such behaviour could not be explained by high energy requirements, as shown by DeVries and von Keyserlingk (2009b) or Greter et al. (2010). This could lead to a conclusion that the innate mechanism, regulating food preferences in dairy cattle, may have been (in some way) misshapen. Long selection for milk yield may have led to the situation in which dairy cows feeding behaviour is so focused on ingesting huge amounts of energy, that even if it causes malaise, cows are not able to change their behaviour in a way to avoid subacute acidosis, and (in a certain sense) they have to tolerate it. In consequence, dairy cows and heifers show fixed, strong preference towards feeds rich in energy, despite current energy requirements. In other words, it is an inherited, misshapen regulating mechanism which predisposes dairy cows to acidosis. If so, dairy cows will not be able to choose proper diet, covering their energy requirements and assuring proper rumen pH, even in situation when they have an access to the array of feeds which should allow them to achieve it.

Described point of view is shared by many (probably the most of) dairy cattle nutritionists and practitioners. Dominating feeding practices have also been

founded on the principle that modern dairy cow itself is not able to choose feeds in such a way to cover nutritional needs and to prevent health disturbances. Even though everyday experience seems to justify the hypothesis that feed intake regulation based on post-ingestive feedback is no longer effective in dairy cows, the opinion is not univocally accepted. It is worth to recall the words of Provenza and Villalba (2006), who stated that "It is highly unlikely that several million years of evolution have been erased by a few thousand years of domestication, especially regarding nutritional wisdom. Acquiring nutrients and avoiding toxins is every bit as important as breathing, which has not changed due to domestication, and is similarly influenced by non-cognitive feedback mechanisms". One can argue, that it is also unlikely that few decades of intensive selection in dairy cattle distorted the regulating mechanism which is fundamental for survival of ruminants.

The alternative hypothesis assumes that innate regulating mechanism remained unchanged in dairy cows. It is the environment which does not allow cows to properly manifest their behaviour. In fact, in many cases the environmental conditions created by a man do not let cows regulate their feeding behaviour in a way to simultaneously cover energy requirements and avoid rumen acidosis. Particularly, the range of offered feeds is often not sufficient to cover all requirements, thus lactating dairy cows give preference to energy-rich feeds, as the energy is usually required in the greatest amounts. Due to enormous energy demands dairy cows have to maximize the intake of energy while maintaining the acceptable level of disturbances in rumen environment. Therefore, animals tolerate some level of discomfort, caused by SARA, in order to ingest needed amount of energy-rich feeds. In other words, prolonged periods of decreased rumen pH are a price which dairy cows have to pay in order to ingest the amount of energy needed for high milk production. Such behaviour may be expected on the basis of previously mentioned theory of food preferences in ruminants, as the nutrients required in the greatest amounts should have the most consistent and compelling influence on food selection (Provenza 1995).

If referred hypothesis is right, cows should be more tolerant to acidosis when their energy requirements are high (particularly during period of high milk production) – they would prefer highly energetic but easily fermentable grain, instead of ingesting proper amount of fibre. On the other hand, they would be less tolerant when their needs for energy are lower (like during dry period), so the fibre would be then consumed in quantities sufficiently preventing the decrease of rumen pH.

However, some observations seem to contradict this supposition. For example, dairy cows and dairy heifers show strong preference towards feeds rich in starch (like grain), even during periods of low energy requirements. Dairy heifers offered roughage and concentrate as a choice (grain concentrate and hay in separate feed bins) or as a top-dressed ration (grain concentrate placed on the top of the hay in one feed bin), rapidly consumed very few large meals of grain, whereas the hay was eaten afterwards (DeVries and von Keyserlingk 2009b). Alternatively, providing feed components as the TMR increased the distribution of dry matter intake over the course of the day and reduced the degree of sorting. Greter et al. (2010) also found that dairy heifers fed the top-dressed ration, consumed the concentrate rapidly and competed more for feed. Even though ruminal pH was not measured in the study, it was observed that animals fed the top-dressed ration had looser faecal consistency than animals offered the same diet mixed as the TMR. This may indicate that top-dressed-fed heifers experienced some level of subacute ruminal acidosis (Aschenbach et al. 2011).

Examples like these suggest that dairy cows and heifers show strong preference toward energy rich feeds independently of their current energy requirements and are usually considered as an important argument for the hypothesis of “misshapen regulating mechanism”. However, one can argue that such phenomenon occurs because of other, disregarded factors such as e.g., the lack of previous experience with ingesting large amounts of grain. Dairy heifers must be fed to grow at a high rate, but not become over-conditioned (DeVries 2010). They are typically fed the TMR and have limited access to concentrates thus, dairy heifers have no opportunity to experience the negative consequences of overeating this feed, until they try it for the first time. In contrast, fattening animals are supposed to grow quickly, so they are early accustomed to highly energetic feeds and can associate the consequences of overeating grain early in their lives. The importance of previous experience is confirmed by the observations made by Dohme et al. (2008). They showed that dairy cows quickly associated the negative consequences of decreased rumen pH with over-ingesting grain and tried to avoid them by manifesting aversion to consuming grain. During the experiment, dairy cows were exposed to repeated acidosis challenges, induced by offering cows the meals of four kilograms of ground barley and wheat, after 24 hours of feeding restricted to 50% of *ad libitum* intake (measured during the three previous days). The grain allotment of four kilograms was consumed entirely by all cows during the first challenge, but only 75% and 43% of the cows consumed the

entire allotment during the second and third acidosis challenges, respectively (Dohme et al. 2008). This experiment clearly showed that with gained experience, the cows gradually modified their behaviour. They tried to adjust the intake in a way to avoid unwanted effects of ingesting too much grain. However, in dairy farming the cows usually have a limited access to concentrates, thus they cannot learn about the negative consequences of over-ingesting such feeds.

Another aspect of the environment influencing feeding behaviour is the competition between dairy cows, especially for the feedstuffs which are limited, like the concentrates. The animals learn that such feeds, when available, have to be consumed quickly and in big amounts. The adaptation to increased competition occurs through changes in animals' feeding behaviour, and the direction of these changes may be detrimental to animals' health. To maintain appropriate dry matter intake in situations of high competition, heifers compensate by eating at the faster rates, particularly during periods of peak feeding activity (González et al. 2008, DeVries and von Keyserlingk 2009a). This can be a reason for the earlier mentioned rapid consumption of grain offered separately or as the top-dressed ration (DeVries and von Keyserlingk 2009b, Greter et al. 2010). The competition appears to change also the meal pattern of heifers, as they consume fewer meals per day, which are larger and longer in duration (DeVries and von Keyserlingk 2009a). Given that the severity of within-day ruminal pH drops increases with meal size (Allen 1997), large and long meals may exert a significant impact on rumen fermentation.

In non-competitive conditions dairy heifers can manifest quite different behaviour, as shown by González et al. (2009). In their experiment heifers were subjected to different delays in feed delivery. It was expected that delayed feed delivery would make the animals hungry, so both the eating rate and the size of the first meal would increase. However, feeding behaviour changed towards opposite of expectations. When given the access to feeds after a period of fasting, the heifers reduced the intake of the concentrates in favour of the straw intake, reduced their eating rate and the size of the first meal (González et al. 2009). Apparently, the observed adaptations were aimed at protecting an animal from rapid consumption of large amount of feed and might have helped to maintain stable rumen pH.

Practical implications

Determination, whether dairy cow's postingestive feedback mechanism was misshapen during intensive

selection, or inadequate feeding environment does not allow this mechanism to function properly, would change currently predominating feeding practices. Dohme et al. (2008) suggested that individual variability in feeding behaviour among the cows is one of the reasons why many of them still experience SARA in dairy herds. Individual cows exhibit a great variation in their susceptibility to SARA, even when fed and managed similarly (Beauchemin and Young 2005). Not much is known about what causes this variation, but it is probably related to the combined effects of many aspects of physiology and behaviour, including feeding behaviour (e.g., level of feed intake, eating rate, feed sorting, meal size and frequency). Ignoring this individuality among the cows makes it nearly impossible to completely eliminate the acidosis from high-producing dairy herds (Beauchemin and Young 2005). Therefore, new feeding practices should include this variability in order to solve the problem of SARA.

Studies of nutrition and behaviour usually concentrate on the responses of an “average” animal in a treatment and management recommendations originate from this approach. Current bunk management practices are based on average intakes (Schwartzkopf-Genswein et al. 2003) and TMR diets are formulated for the “average” cow. Unfortunately, this approach ignores the fact that there can be significant differences in the ruminal profiles and feeding behaviour among individuals. Even the half of the animals within a group may differ significantly from the mean in food preferences and nutrient tolerances (Provenza et al. 1996, Villalba and Provenza 1996, Scott and Provenza 1999). Therefore, appropriate nutrition for the average animal may not be accurate for specific individuals. If animals differing from the mean are fed a uniform diet formulated to meet the needs of the average individual, some of them may suffer from the hunger, other from negative consequences of overeating, all of which have the adverse effects on the productivity (Atwood et al. 2001). An alternative for prescribing the averaged ration for all the animals is individualization of feeding which would include current nutritional requirements of the individual. Even though the individual feeding strategy for dairy cows has not been accepted so far mainly due to economic considerations, this issue is worth mentioning because of the above arguments of Dohme et al. (2008).

If the hypothesis of “misshapen feed intake regulation” is right, then the individualization of feeding should be achieved by monitoring physiological state of a cow and providing ration according to this state. A cow itself would not be able to choose feeds according to current energy requirements and always manifest strong preference towards feeds rich in easily fer-

mentable carbohydrates. It would be of a farmer’s interest to provide each cow with a suitable diet, so the farmer should “force” a cow to eat a ration, which is appropriate for the animal. This way, when rumen pH was too low, the cow would get more roughage in the ration, which would prevent the acidosis.

However, if the other hypothesis of the “inappropriate environment” is right, then the individualization of feeding should be achieved by letting cows decide what and how much to eat, as every individual should be able to react appropriately to its own senses and needs. The animals would be able to make a proper use of the postingestive feedback mechanism and compose their own rations according to their physiological demands. However, this would happen only, if they had an opportunity to do so – when they could choose from different feedstuffs with complementary properties (Villalba et al. 2010b). Therefore, the farmer should allow the cow to choose the proper ration itself and only provide the right feeding environment for the animal.

Conclusions

Based on the results of experimental studies published so far, it is presumably impossible to determine if dairy cows are affected by SARA due to misshapen mechanism regulating their food preferences, or due to inappropriate feeding environment. Unfortunately, the methodology in most of these experiments unwittingly neglects the complexity and dynamism of the feed intake regulation. As was emphasized by Provenza and Villalba (2006) all of the interpretations of feeding behaviour should be reconsidered taking into account many factors that influence food selection, but of which we are usually not aware. The authors stated that „An individual animal’s behaviour reflects its evolutionary history (gene-expressed morphology and physiology), its cultural history (experiences of the social and biophysical environments where an individual is conceived, born and reared) and its ongoing interactions with those environments. (...) the behaviour of any organism is determined by connections to a larger historical whole” (Provenza and Villalba 2006).

Past experiences (even as early as in the neonatal life) have life-long influences on diet selection in herbivores by causing neurological, morphological and physiological changes, which affect foraging behaviour (Wiedmeier et al. 2002, Villalba et al. 2010b). However, we seldom notice that, because we do not precisely know or remember the history of an animal. Therefore, most of the studies do not give detailed information about animals’ past history, which could

have a considerable contribution to analysing data. Others ignore the fact that so called “external milieu” significantly affects the proper manifestation of animals’ behaviour (Provenza and Villalba 2006). To be able to fairly and unambiguously resolve the issue of postingestive feedback mechanism in dairy cows, the one should design such an experiment which methodology would eliminate the most of (preferably all) the factors that could in any way affect the functioning of the mechanism. This will be one of the greatest challenges for researchers studying relations between rumen environment and feeding behaviour in dairy cows.

The results of such studies on dairy cows could pave the way for new better feeding practices, allowing animals to meet individual needs and could contribute to solving the problem of SARA in high producing dairy cattle. This will not only enhance health and welfare of cows, but also entail increased profitability of the dairy production.

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