Chewing behaviour of growing cattle

Tuggbeteende hos växande nötkreatur

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Abstract

Chewing behaviour includes both eating and ruminating activity. Chewing behaviour is of great importance for the feed intake as through the action of chewing (i.e. eating and ruminating) animals mechanically process the forages in small particle sizes and prepare the food for digestion. As cattle grow the chewing behaviour changes along with increasing body weight and chewing efficiency is increased. The aim of this thesis was to review the available scientific literature in order to describe chewing behaviour in growing cattle, as well as the factors that affect this behaviour. The processes of eating and ruminating have different functions with regards to the particle size reduction. Eating prepares the food for swallowing and ruminating reduces the size of the intractable material. The literature that is reviewed in this thesis suggests that chewing behaviour is affected by a number of aspects, such as maturity stage of the forage at the time of harvest, fibre content of the animal feed and feed particle size. In growing cattle changes are observed in chewing duration, most likely due to physiological development (i.e. growth) of the animal. Bite and rumination efficiency increases with age and body weight in cattle. Various methods and techniques are used in determining chewing behaviour of cattle. Information provided in this thesis suggests that these techniques aim to monitor the different frequencies and patterns of jaw movements. Although chewing behaviour of ruminants is well documented in the literature, limited information is available on the aspect of modelling the eating and rumination behaviour of ruminants. In addition, as there are some opposing findings in relation to the duration of chewing time in growing cattle, more research is required to clarify this.

Sammanfattning

Tuggbeteende, inkluderar både att äta och idissla, är mycket viktigt eftersom djur processar fodret mekaniskt när de tuggar. Under nötkreaturens växtperiod förändras tuggbeteendet och tillsammans med en ökande kroppsvikt ökar tuggeffektiviteten. Det finns dock begränsat med information och forskning på ämnet. Syftet med detta arbete är att beskriva tuggbeteende samt att sammanställa tillgänglig forskning om detta beteende hos växande nötkreatur. De båda processerna att äta och idissla har olika funktioner när det gäller att reducera födans partikelstorlek. När djuret äter förbereds födan för att sväljas medan idissling reducerar partikelstorleken hos de mera svårnedbrytbara materialen. Tuggbeteende påverkas av ett antal faktorer, såsom grovfodrets mognadsstadium vid skörd, fiberinnehåll och partikelstorlek. Varierande metoder och tekniker används i studier av tuggbeteende hos nötkreatur. Vanligt är att studera de olika frekvenserna av käkrörelser som utmärker de båda tuggaktiviteterna. Begränsad information finns dock vad det gäller tiden nötkreatur spenderar att äta och idissla för att skatta modeller av tuggaktivitet. Hos växande nötkreatur förändras tiden de tuggar sin föda, troligen till följd av djurets fysiologiska utveckling. Effektiviteten hos tuggandet och idisslandet ökar med nötkreaturens ålder och kroppsvikt. Det behöver dock forskas mer om tuggbeteende hos växande nötkreatur, även för att klargöra oklarheter gällande tiden som föda tuggas.

Introduction

Chewing activity includes both eating and ruminating activity. The action of chewing, together with the characteristics of the forage, has a great impact upon intake and utilisation of roughage in ruminants. Ruminants are, due to their physiologic construction of their digestive tract and the microbial fermentation in the rumen, well adapted to digest and utilise roughages. The slow process of rumination and fermentation may be prolonged if the digestible components are not small enough to be extracted in the rumen. If these processes would be prolonged, i.e. the forage would be kept longer in the rumen, the throughput and thereby the daily intake, would be reduced. This directly correlates to the animal's production and performance (McDonald et al., 2002).

Chewing behaviour, including both eating and ruminating behaviour, is of great importance for food utilisation as animals mechanically process the forages in small particle sizes by the action of chewing. These particles should be able to pass through from the reticulo-rumen into abomasums and the intestinal tract (Ulyatt et al., 1986; McLeod & Minson, 1988). It is important for the fibre degradation to take place in the rumen and not in the large intestine. This is due to the formation of the important volatile fatty acids which take place in the rumen (Sjaastad et al., 2003).

Many characteristics of forage have been identified as affecting the intake in ruminants. Some of these are the content of neutral-detergent fibre (NDF) and lignification of forage, both also affects the digestion rate. Lignin has high resistance to chemical degradation, which means that lignified forage is inaccessible to the enzymes normally digesting carbohydrates (Akin, 1986; Sjaastad et al., 2003). Because of the difficulties in digesting lignified and high fibrous roughages animals often show prolonged chewing activity, which means that their chewing behaviour depends considerably both on the type and the content of the fibrous parts of the plants (Akin, 1986; McDonald et al.,2002). Mature forages tend to be richer in lignin and NDF than earlier harvested forages. Maturity stage of roughage therefore appears to be of importance for chewing behaviour (Fahey & Berger, 1988; McDonald et al., 2002). In general there is a lot of information available on how forage characteristics affect feeding behaviour in dairy and beef cattle, but also in other ruminant species. However, less information is available on how the proportion and type of forage, e.g. hay or maize silage, in the diet affects the chewing behaviour in growing cattle.

In growing cattle differences and changes in chewing behaviour can be observed from the time of weaning, as well as later when they increase in size. Shortly after weaning in very young animals the differences and changes are greater and more irregular due to very limited ruminating ability (Welch & Hooper, 1988). The changes are not only physiological but also behavioural as they start eating less forage in relation to their bodyweight (Bae et al., 1983; Forbes, 2007). In general there is a relation between body weight of cattle and total chewing time per kg ingested DM. Heavier and bigger animals are more efficient in chewing. As animals grow bigger and reach maturity eating and ruminating activity per kg DM intake decreases, which suggest that animals become more efficient in chewing as they grow (Bae et al., 1983).

Daily intake and feed utilisation is of immense significance in growing cattle as it can affect animal welfare, but also their productivity and thus, production economy. Knowledge on the relationships between feed intake behaviour and feed characteristics can be used for increased animal productivity (Forbes, 2007). Chewing behaviour is therefore a subject of great interest, as it is directly related to intake and feed utilisation of growing ruminants.

The aim of this thesis is multifaceted. First, to review available research regarding chewing behaviour (i.e. eating and ruminating behaviour) in growing cattle. Secondly, to describe chewing behaviour based on the current literature, as well as factors affecting this behaviour, with special focus on the effect of the diet and the fibre content. Thirdly, to describe selected methods and techniques, common for studying the chewing behaviour. Finally, to review available studies on predicting and modelling of chewing behaviour. The current study is part of a research project that takes place at SLU in Skara and aims to investigate the effects of maturity stage of whole-crop maize silage on feed intake, chewing behaviour and performance of growing bulls.

Chewing behaviour: eating and ruminating

Chewing behaviour involves the processes of eating and ruminating. These two processes have different functions in relation to particle size reduction. When the animal is eating, it prepares the food for swallowing by breaking down plant tissues for the latter microbial digestion, releases soluble components and limits the energy needed to break the particles down (Boudon et al., 2002). During eating the animal mixes the food particles with saliva and eliminates some of the air that is held inside. Through this process the particle density is increased (Church, 1988). During rumination, the primary function of chewing activity is to reduce the size of the more intractable material, making the cell walls exposed to the microbial digestion (Ulyatt et al., 1986; Phillips, 2002). Chewing activity during rumination also contributes to the sorting of the food particles according to their density. During the regurgitation a solution rich in high density particles is immediately re-swallowed and the chewing of the digesta reduces some fermentation gases. One of the key features of chewing activity is to induce salivation, which is necessary for swallowing the food (Church, 1988). Indirectly, chewing activity affects the ruminal pH, due to the buffering function of saliva. This plays a major role in the situation of lactic acidosis. Lactic acidosis occurs when cattle are given a diet rich in concentrates and a lack of fibrous feeds. Highly fibrous feeds increases chewing activity which in return prevents a decrease of rumen pH (Baumont et al., 2006).

Diurnal pattern and regularity of chewing behaviour

Even from 70 years ago it has been documented that grazing takes place mainly during daytime (Atkeson et al., 1942). Cattle spend approximately five to eight hours grazing; the time they spend depends on the quality of the pasture (Johnstone-Wallace & Kennedy, 1944). Usually cattle graze in two major segments; just after sunrise and in the late afternoon until sunset (Hughes & Reid, 1951).

According to Koene (2006), jaw movements allow cattle to get food into bites and to chew it before swallowing. On pasture they collect forage with their tongues and bite it loose, often by pulling together with a short head movement. The forage is being chewed and formed into a bolus before swallowed (Laca & WallisDeVries, 2000). After an inactive period, when the animal has collected enough forage, the rumination starts. The inactive period after the meal varies from a few minutes to over one hour (Koene, 2006). The duration of this period is related inversely to the size of the meal. Larger meals give a higher stimulation for rumination than shorter meals (Baumont et al., 2006). The duration of the rumination can vary from a quite short period, 15-30 minutes, up to longer periods of 2-6 hours. The shorter rumination bouts tend to mainly occur close to the eating period and the longer periods during nighttimes (Welch & Hooper, 1988). Ulyatt et al. (1986) and Ruckebush (1988) however claims that rumination in cattle lasts between five to nine hours, never exceeding ten hours. Calves spend approximately five hours ruminating per day (Ruckebush, 1988). Rumination occurs in 12-18 periods per day and in regular succession of a cycle with short breaks of four to eight seconds. During the breaks the chewed bolus are re-swallowed and the next bolus is repeated through the process again (Ruckebush, 1988; Baumont et al., 2006). Growing heifers, fed with corn silage, spend between 51-55 seconds on each bolus according to Deswysen et al. (1987a).

The frequency of chewing is more regular and less intense when cattle ruminate than when they eat (Welch & Hooper, 1988; Phillips, 2002).

Growing cattle eat about 10-14 meals per day (Bae et al., 1983; Mialon et al., 2008), with each meal lasting approximately ten to twenty minutes (Chase et al. 1976; Mialon et al., 2008). Meal bouts appear to last in total between two and four hours per day (Mialon et al., 2008). Cattle with lower nutrient requirements are eating fewer as well as shorter meals (Phillips, 2002). It has been questioned whether cattle eat in the form of meals, when grazing. The argument against the meal-eating form is that ruminants usually graze continuously for long periods during a day. Ruminants appear to generally have a slow grazing rate, making it more difficult to distinguish a meal-pattern. It has also been suggested that meals can be distinguished when the feed is more easily grassed and the eating rate is faster than the utilization time (Forbes, 2007).

Cattle try to maintain the intake rate by higher bite frequency and decreased time per bite. The effort for maintaining the intake rate is more intense when the height and density of the grass changes, as the bite mass will in turn change as well (Hall, 2002; Phillips 2002). Due to the technique of wrapping the tongue before pulling to grasp, cattle are limited to plants higher than one cm (Hall 2002). Despite the preference for longer grasses cattle can graze shorter grasses, but then with a higher bite rate up to 70 bites per minute, in order to maintain the intake rate (Dumont et al., 1995). As bite size increase the same jaw movement is used for both grasping and chewing the forages (Laca et al., 1994). When cattle are fed indoors the bites from the feeding trough tend to be less frequent but larger, when compared to foraging on pasture. This change is due to the fact that animals do not have to search, nor gather, their forage (Baumont et al. 2006). Therefore, the eating time decreases about 30-50% when animals are fed indoors compared to the time they spend grazing outdoors (Faverdin et al., 1995). Mainly are studies performed indoors referred to in the continued study, if not it is clearly stated.

Related chewing behaviour and activities

Different feeding-related activities are seen more frequently in connection with oral stereotypies, such as licking and sniffing of the feeding trough. The connection between stereotypies and such feeding related activities are a signal for frustrated feeding behaviour (Forbes, 2007). Frustrated feeding behaviour occurs for instance when forage is removed from the diet, which compromises the welfare of the animals (Faleiro et al., 2010).

In cattle, a number of different chewing related behaviours have been observed, the most common are the selective intake and grazing. Selective behaviour is often related to particle size of forage as cattle usually select in favour of smaller particles. An experiment by Cozzi et al. (2009) confirmed this by selection indexes based on chemical analysis’s of feed. Cattle select for maximum bite weight, together with maximum intake rate. This is observed for instance when they are presented with the choice of dense forage areas with short straw length, and more sparse forage areas with short straw length. Cattle then select against the more sparse areas of forage. When instead offered dense and high areas they select in favour for the dense, high areas and do not prefer short, dense areas (Distel et al., 1995).

Behavioural changes in chewing during growth

Animals grow and increase their body weight considerably from birth until puberty. This high rate of body weight gain is followed by a slowdown before a final stabilisation of the weight at that of maturity. Along with this increasing in size and weight also an increase in organs, tissues and anatomical parts is observed (McDonald et al., 2002). Additional fat deposition, common for bulls, leads to further weight gain, even in mature animals (Bae et al., 1983; Forbes, 2007). Feed intake increases with the growth (Bae et al., 1983), but will not remain at the same proportion of the live weight (Forbes, 2007).

Despite the increased intake there is no greater variation in the time that growing cattle spend for eating and ruminating. The limited changes in chewing time are most likely depending upon an increase and growth of the involved organs, such as the jaws and rumen along with the increased live weight. Increased chewing efficiency is observed in older and mature cattle when compared to three year old steers (Bae et al., 1983). Welch and Hooper (1988) suggest that growing cattle younger than two years old, have limited rumination ability compared with mature cattle. This is because growing cattle cannot ruminate large amounts of cell wall contents. The rumination ability develops after weaning along with an increasing body size as the animals grow (Welch & Hooper, 1988). As a result the time that the animals spend in chewing one kg dry matter (DM) decreases with age and weight. In addition, bites are more efficient in older animals resulting in a better particle size reduction of the ingested feed (Baumont et al., 2006). Maximum chewing and rumination efficiency is reached as cattle are around two years old (Welch & Hooper, 1988).

Similar differences in chewing efficiency as for growing animals are also observed in older animals that differ in body sizes (Bae et al., 1983). A study that compared the chewing efficiency between mature cows of 550 kg and growing bulls weighing 350 kg showed that chewing efficiency increased with both age and body weight. In addition, although bulls had lower feed intake than the cows, they spent more time eating than the cows (Baumont et al., 2006). Apart from age, chewing efficiency is also correlated to animal's metabolic weight. According to Bae et al. (1983) is this because there is a potential for an increased fibre intake in relation to the animals maintenance requirements along with its metabolic body size.

According to Forbes (2007), the meal size increases while the feeding frequency decreases as animals grow. Chase et al. (1976) however, showed in an experiment with growing steers that meal size in those animals was relatively constant per unit body weight, g/meal/kg or g/meal/kg^{0,75}. Eating rate however, was unaffected by larger meals as shown by eating rate levelling off for larger meals and reaching a plateau (Chase et al., 1976). Furthermore, differences have been shown between eating rate of growing steers and mature dairy cows when given diets that differed in ratios of maize grain and hay, according to Nordin and Campling (1976). In the study of Nordin and Campling (1976) growing steers showed higher eating rate than mature cows. In the study was it also observed that growing steers spent more time ruminating, but less time eating each kg DM forage than mature cattle. In total lasted the chewing activity of the young steers double as long as the chewing activity of the mature cattle, per kg DM (Nordin & Campling, 1976).

Except for age and body size of cattle has it been suggested that chewing behaviour can be affected by breed as well. However, these differences are very likely to be connected to the differences in feed intake that is observed between breeds and also to the breed differences in size (Bae et al., 1983; Cozzi et al., 2009). As these differences have been reviewed earlier in this thesis the breed effect will not be further examined herein.

Chewing behaviour, apart from the animal production state (i.e. age, body size), is affected by a number of other aspects such as the maturity stage of the forage (Teller *et al.*, 1993), fibre content of the diet (Welch & Smith, 1974), diseases (Forbes, 2007), environmental temperature (Houpt, 2005), taste and palatability (Landau et al., 2000; Provenza & Willalba, 2006), parasites and viruses (Houpt, 2005) and other parameters. This thesis will focus to those aspects that are directly related to the physiology and fibre content of the feeds and those are described below.

Factors affecting chewing behaviour

The importance of the fibre content, maturity stage at harvest, the particle size of the feed and the proportion of forage included in the diet are frequently described in literature. Those aspects are particularly important as the diet of cattle can be easily controlled and therefore it can affect animal's performance and welfare state (Forbes, 2007).

Diet and its fibre content

Diet composition of different plant species has an impact upon cattle's voluntary feed intake as well as their chewing behaviour. For instance, according to Welch and Hooper (1988), when mature legumes are given to stall-fed cattle, feed-intake will decrease and chewing time will increase, because of the higher fibre content. The phenomenon is less evident in grass legumes. The differences are due to different cell-wall content in the different plants as they mature. Rumination time is closely related to the intake of cell-wall content, both for cattle and sheep (Welch & Hooper, 1988).

Chewing activity is stimulated by the composition of the feeds in a diet (Phillips, 2002). Fibres in the diet, for instance, increase chewing time and saliva production as well as stimulate rumination. Cattle therefore have a great need for sufficient long and fibrous particles in the diet (Welch & Smith, 1974). Because of the importance of enough fibre content of the diet Balch (1971) suggested a definition of the fibrousity of feed based on chewing time per kg DM. More recent suggestions have also become available after the studies of Balch in 1971 (Baumont et al., 2006).

Another important factor affecting chewing behaviour is the physical presentation of the forage in the diet, e.g. the particle size. Cattle tend to for instance select for the shorter particles of the forage in the diet they are presented. Due to the animals preference for shorter feed particles it was observed in a study by Provenza and Villalba (2006) that grinding and chopping can reduce time spent chewing radically, as well as increase intake.

Many examples have been seen of negative relationships between the fibre content of feed and the intake by ruminants, such as a lower intake due to prolonged chewing time. However, variations of fibre digestion rate, as well as the extent of the degradability, are likely to cause variations in forage intake. The variations of intake occur since a rapid digestion releases digestive capacity quickly and allows more food to be accepted. Several types of fibre exist in most of forage types, where lignin is the most common. Lignin is indigestible and its content is therefore inversely related to digestibility, but it has no reliable relationship with voluntary intake (Fahey & Berger, 1988). Cellulose and hemicellulose are degradable by ruminal microorganisms, but the rate of digestion is variable (Forbes, 2007).

Proportion of different forage types in the diet affecting time spent chewing

A quite large number of experiments have been done on cattle and the effects of different forages, together with different proportions in the diet. Weller and Phipps (1985) performed preference tests where dairy heifers choose a mean ratio of 60 percent corn silage and 40 percent grass silage. The individual preferences however, varied widely from 34 percent to 75 percent in favour for the corn silage. It is often observed that grass silages are eaten in lower quantities than grass hay or maize silage. A great individual variation, similar as for the experiment of Weller and Phipps (1985), were also argued by Forbes (2007).

Galli et al. (2006) performed an experiment in which it was shown that alfalfa hay required less chewing activity then grass hay. The steers chewed less per unit dry matter intake (DMI) when given alfalfa hay then when given grass hay. There were no differences in chewing activity detected between the fresh forages in the experiment. When growing heifers are fed corn and grass silage both Deswysen et al. (1987a,b) and Teller et al. (1989) argues that the rumination time is increased, in comparison to other forages. An increased rumination time is due to higher fibre level in corn and grass silages. The level of fibre was related to the chewing number per bolus, as well as per unit bolus DM and the total daily chewing number. Offered a diet of high fibre content cattle will reduce their intake if rumination already is at its maximum. If rumination activity is not at its maximum they will instead increase the number of rumination chews. This can be achieved by increased time ruminating and rate of rumination chewing (McLeod & Smith, 1989), which also was observed when steers were given different diets with either silage or hay. Steers tended to spend equal amount of time ingesting larger amount silage than hay, but making less eating chews then for hay. Rumination time consequently increased for the bigger amount of silage. Additionally, the number of chews was increased during rumination along with the number of bolus ruminated. Rumination efficiency was unaffected by the choice of diet in this experiment. Conversely it can be summarized that no difference was seen in regard for rumination time, number of chews during rumination and the number of bolus ruminated per kilogram NDF (Luginbuhl et al., 2000).

Maturity stage at harvest

As pasture matures the cell wall content is increased due to increased proportion of stem and a thickening of cell walls. Increasing maturity also leads to a lower dry matter digestibility of plants and increased fibre content (Akin, 1986; Teller et al., 1993). This typical cell wall increase might however, be lost or decreased by a high carbohydrate accumulation in the plant, e.g. in maize (Wilson, 1994).

In an experiment by Teller et al. (1993) with six Friesian heifers it was indicated that younger forage, which was harvested in the early spring and direct cut, i.e. ensiled directly and without additives, was consumed more rapidly than older forage. It is suggested in the same study that intake might be affected by eating rate through limited rumination time, as for stall-fed animals. When animals eat in a slow rate the eating time will consequently increase. Rumination time is also likely to be reduced (Teller et al., 1993). Also with maize silage does maturity affect digestion characteristics (Phipps et al., 2000). Even though DMI increases as the plant is processed, the fibre digestibility decreases. In addition, maize silage harvested at physiological maturity stage was observed to have lower fibre degradability than maize silage harvested at half the milkline (Phipps et al. 2000; Forbes 2007).

Rustas et al. (2009) did not observe differences in eating rate between different maturity stages of whole-crop barley silages. It was argued that this might be due to similar NDF concentrations for the maturity stages in the same study. In addition, were no effects upon chewing time observed. This finding is in correspondence with that of Boudon et al. (2002) which suggests that maturity stage has no effect upon eating behaviour, except a minor increase in total chewing time. De Boever et al. (1993) however, observed in an experiment with mature Holstein-Friesian cows that chewing time decreased per unit ingested feed of maize silage of higher maturity. This was caused by higher grain content in the maize silage, and not the dropped cell wall content (De Boever et al., 1993), which often in other studies has been argued (Akin, 1986). It is suggested in the study by De Boever et al. (1993) that maize fibres not becomes more difficult to digest with increased maturity and thereby causing the observed decrease of chewing time. This is likely to be due to the fact that chewing time per unit NDF was almost constant. Additionally, the content of lignin was inconsistent between the different maturity stages (De Boever et al., 1993), commonly known for being an indigestible cell wall fraction. Limited knowledge is however available about maturity effect in forages, such as maize silage, on chewing activity.

Feed particle size

Particle size of the forage affects chewing time. Long feed particles of forage increases the chewing time compared to chopped forage. Dry matter intake however, increased when the length of corn silage particle length was decreased (Weigand et al., 1993). Jaster and Murphy (1983) also suggests that heifers have a more even rhythm of their total chewing activity when fed longer feed particle, compared to when feed with shorter particles. Heifers that forage smaller hay particles spread their chewing activity more even throughout the whole day, according to Jaster and Murphy (1983).

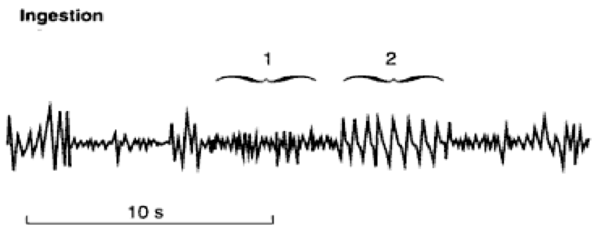
According to Teller et al. (1993), rumination is increased with only 5-7% in heifers that were fed long-chopped silage compared to short-chopped silage. This indicates that a large variation in the intake of silage causes rather small modifications in rumination time, of the DM. The variation in intake depends on physical or chemical treatments which do not affect the dry matter composition, such as wilting and chopping. This agrees well with the fact that rumination is involved in increasing the functional density of feed particles in the rumen by expelling the air and gas pockets (Sjaastad et al., 2003). Higher fibre content in this aspect increases the required rumination time per kilogram DMI, due to the slow hydration, low fermentation rate and high rigidity of the fibres (Teller et al., 1993). The relation between feed particle size and rumination time is furthermore confirmed by the decreased number of boluses processed per minute ruminating as particle size decreases (Jaster & Murphy, 1983). According to McDonald et al. (1991) young beef cattle eat more silage of grass cut at 8 mm at harvest, in comparison with silage cut at 33 mm, the smaller particles were also more digestible.

Luginbuhl et al. (1989) argues in a study with Hereford steers weighing 335-464 kg, that when hay is long-chopped it is being unquestionably more resistant to chewing as well as to the microbial digestion. Steers are expected to adapt and change their chewing behaviour under such conditions, for reducing forage to appropriate particle size for bolus formation. They observed in their study prolonged chewing time when the animals were fed longer forage particles. Chewing during eating, particle size reduction and bolus formation is consequently shorter for smaller feed particles than for longer particles (Luginbuhl et al., 1989).

Methods and techniques commonly used determining chewing behaviour

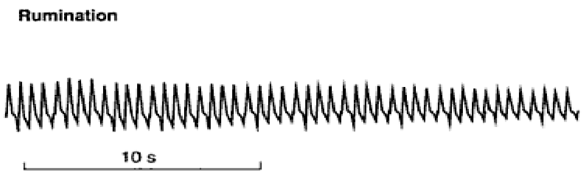
Various methods and techniques are used in determining chewing behaviour of cattle. The animals are often studied and observed during a couple of days up to a week, either in a varying number and length of sessions each day or continuously throughout a few days (Teller et al., 1993; Luginbuhl et al., 2000; Cozzi & Gottardo, 2004; Rustas et al., 2009).

Chewing behaviour is commonly determined and defined through the different frequencies and patterns of jaw movements. Rumination, for instance, is identified by a more consistent frequency of both the jaw movements as well as the time interval in-between the boluses (fig. 1). Eating on the other hand, have more irregular jaw movements. The irregular movements are due to minor interruptions and the alternation between prehension and chewing sequences. Recording of the jaw movements is a useful tool to estimate eating and rumination time, when determining and observing chewing behaviour (Baumont et al., 2006).



Recording at 30 cm/min:
Two types of jaw movements can be distinguished
1) prehension with low amplitude and high frequency
2) mastication with higher amplitude and lower frequency.

Recording at 15 cm/h: Small pauses can be distinguished between the eating bouts



Recording at 30cm/min: Regularity of jaw movements in amplitude and frequency can be observed

Recording at 15cm/h: Successive rumination cycles can be distinguished

Fig. 1 Jaw movement recordings transferred on paper charts (from Baumont in *Nutrition des ruminants domestiques: ingestion et digestion* by Jarrige *et al.,* © INRA Paris 1995).

Direct visual observation

The most traditional and direct technique in determining chewing behaviour is the direct visual observation. This is however difficult and rather laborious. A disadvantage with this kind of observation is that it not allows a detailed and continued monitoring of the jaw movements for several animals simultaneously. As a result a lot of work has been done for developing indoor monitoring systems (Baumont et al., 2006). Most studies performed recently carry out direct visual observation with video recording. By the use of video recording it is possible to observe animals in groups, the individual animal can be recognised and continued monitoring of jaw movements is possible (Forbes, 2007). Another technique developed for indoor monitoring is the use of harness or holders. Holders or harnesses are however not a visual observation, but is often used as an alternative method, and is put around the head of the fixed animal counting the jaw movements together with a sensor (Teller et al., 1989). The results are transferred and recorded on paper charts. The use of paper charts makes it easier to distinguish between eating and ruminating activities (see fig. 1). At the same time are the analysis's of jaw movements on paper charts time consuming and tiresome (Baumont et al., 2006).

Computerized electric devices

Luginbuhl et al. (1989), Rutter et al. (1997), together with Ungar and Rutter (2006) describes how electronic devices can be used and that they allow an automatic jaw movement recording. Along with the devices has computer software been developed which interpret the movements and events, assisting in reducing data. These kinds of systems are primarily for counting jaw movements, distinguishing between, and estimating the time spent, eating, ruminating and resting. Beauchemin and Buchanan-Smith (1989) on the other hand, describe how a computerized recording and analysis might lead to overestimation of the time spent eating. The reason for the overestimation is the difficulty of distinguishing the actual eating period from other activities, such as licking and self-grooming. The overestimation was compared with the results of visual observations. Baumont et al. (2006) recommends recording the weight of feed troughs together with the computerized recordings. All of the techniques are however not suitable for all animals and species. Holders and harnesses for instance, might not be suitable for bigger animals since they might break them.

Modelling the eating and chewing behaviour

Predicting and modelling the intake of a ruminant is generally difficult as there are interactions between the animal and its diet. In modelling studies different types of mathematical equations and multiple regression analyses are used to account for live weight influence, food quality and energy demand in order to predict intake (Forbes, 2007). Galli et al. (2006) however estimated the DMI in an experiment by using behavioural and acoustic variables, such as the number of chews. Their conclusion was that the duration and intensity of chewing were less useful than acoustic analyses for modelling and predicting DMI. In addition, Nørgaard et al. (2010) described how the feed evaluation system Nordic Feed Evaluation System (NorFor) consists of three sub-models. In the third sub-model the structural value of a diet is calculated based upon chewing time. They argue that this system enables better predictions of diets feeding values, leading to more efficient feed utilisation.

Limited information is nevertheless available in relation to modelling or predicting the eating and ruminating behaviour of ruminants. Such information would help determine chewing behaviour and intake in relation to diseases and other situations when animal welfare is threatened. It is being suggested by Pittroff and Soca (2006) for further research including bite rate, bite mass and chewing time. According to them are such variables necessary for a functional understanding and modelling of chewing behaviour in cattle.

Discussion

The aim of this thesis was to review available research concerning chewing behaviour, i.e. eating and ruminating behaviour, in growing cattle. The chewing behaviour was described according to the available literature as well as the factors that affect this behaviour, mainly focusing on diet characteristics and fibre content. As chewing activity has been more intensively studied with indoor experiments the information in this thesis was derived mainly from indoor studies. However, results from grazing experiments were also included, but to a minor extent due to the limited number of studies performed.

Chewing behaviour of cattle is well documented as there is a great number of studies and information available in the literature. Even 60 or 70 years ago eating behaviour of ruminants attracted the interest of animal scientists. For example Atkeson *et al.* (1942) were among the first to postulate that eating behaviour of cattle is of great importance to agriculture. A lot of work was also performed in the area of chewing behaviour of cattle around late 1970s and onwards. However, despite the fact that chewing behaviour is rather well described there are areas related to it that have not been studied in details, as for example the chewing behaviour of growing or sick animals.

Generally in the reviewed studies, as well as in this study, are eating and ruminating separated and defined through their different jaw movement patterns. The jaw movements of a ruminating animal show a more consistent pattern compared to an animal that is eating. However, differences were found between studies regarding rumination time. This might be due to different definitions of eating and ruminating. Welch and Hooper (1988), for instance, meant that rumination occurs in shorter periods of 15-30 min and longer periods of two and six hours. While Ulyatt et al. (1986) and Ruckebush (1988) were of different opinion claiming rumination to last between five and nine hours. Possible is that they might have overlooked the shorter bouts in-between the meals observed by Welch and Hooper (1988) and included them into eating instead of ruminating activity. As mentioned was a variation of definitions for chewing behaviour noticed, and as a result chewing behaviour was also expressed differently. For instance, some studies expressed chewing behaviour as the time that an animal spends to eat and ruminate (Baumont et al., 2006) one kg DM, while other distinguish between these activities (Nordin & Campling, 1976; Teller et al., 1993). These different approaches made it difficult to compare different study results and that can be confusing.

Despite different approaches and study results were an increasing bite- and rumination efficiency during growth in cattle identified, but due to physiological development, does this only lead to limited changes in chewing time of growing cattle (Bae et al., 1983; Welch & Hooper, 1988). Baumont et al. (2006) also argued that the total chewing time per kg DM decreases with age and weight of growing cattle, due to their increased bite efficiency. Interesting is that Baumont et al. (2006) described that younger and lighter bulls, in comparison with older and heavier cows, show longer eating time, and not ruminating time. It would have been expected that rumination time was longer and eating time instead shorter due to the lower rumination ability of younger cattle. Longer eating time and shorter ruminating time was also observed in the study by Nordin and Campling (1976). Their study regarded the effect roughage in steers. Whether there might be a gender difference part of the differences is not considered by Baumont et al. (2006).

The fibre content of the diet is also an important factor that affects the chewing behaviour considerably of ruminants and no greater differences were found in the literature describing the affects of fibre. It has been suggested throughout the literature that fibre content in the diet increases chewing time, reduces intake and stimulates rumination (Balch 1971, Fahey and Berger 1988, Forbes 2007). With regards to the forage proportion in the diet it seems that there is a great individual variance between animals (Weller and Phipps, 1985; Forbes 2007). Increased proportion of maize and grass silage in diets of growing cattle resulted in increased rumination time, when compared to diets of lower proportions of the silages (Deswysen et al., 1987a, b; Teller et al., 1989). Interestingly, this tendency shows that cattle preferred maize silage which causes prolonged chewing time and thereby a limited total feed intake.

The effect of maturity stage of forage on chewing behaviour of ruminants has also been investigated thoroughly. For instance, both Akin (1986) and Teller et al. (1993) showed a connection between maturity stage and prolonged chewing time, showing that the connection is increased cell wall and fibre content along the increased maturity of forage. Interestingly Wilson (1994) suggested that cell wall content can be decreased if high carbohydrate accumulation occurs in the plant. Rustas et al. (2009) have found in an experiment with steers that total chewing time, including both eating and ruminating, was very little affected by the maturity stage of the forage in the diet, but this is likely due to similar NDF concentrations between the maturity stages of the forages in their study. De Boever et al. (1993) observed a decreased chewing time in animals fed mature maize silage, due to higher grain content and shifting lignin content. Even though a connection between maturity stage of forage and chewing behaviour is well-known information is inconsistent and there are room for more studies.

Particle size is well-known to have an effect upon chewing behaviour. Weigand et al. (1993) observed that there is a relationship between particle size and chewing time as longer particles caused longer chewing time and resulted in reduced intake. These observations are supported by for instance Jaster and Murphy (1983) together with Luginbuhl et al. (1989). Jaster and Murphy (1983) also observed differences in chewing activity when longer and shorter particles were included in diet of cattle.

Chewing behaviour is commonly studied by measuring the frequency of jaw movements. According to Baumont et al. (2006) is the method often argued to be a more objective method and the actions of eating and ruminating are easily defined and distinguished. The interpretation of the results is however argued to be time consuming and some details of the behaviour might be overlooked, if it is used as the only observation technique. Video recording seems therefore to be the most appropriate method when studying chewing behaviour of indoor animals. An advantage with this method is that it allows studying of additional behaviours as well and social interactions. The method also allows multiple animals to be studied at the same time, a continued watching and the possibility to go back for any obscurity to be made clear (Forbes, 2007). The method however implies considerable effort in watching the videos and is time consuming. A good method to record chewing behaviour is also that of holders or harnesses that register jaw movements but it is regarded to be expensive and not appropriate for big animals such as growing cattle (Nørgaard, 2011 personal communication).

Modelling of chewing behaviour was shown to be a rather undiscovered area as very limited information is available. In contrast with the adequate modelling studies available to describe feed intake in animals, there are limited modelling studies available in describing or predicting chewing behaviour in farm animals. Such studies would enhance our knowledge and would enable us to predict through changes in chewing behaviour, such as reduced ruminating time, whether animals suffer from certain diseases (e.g. lameness or infections).

Conclusions

Behavioural changes occur in growing cattle, most likely due to the physiological development of the animals. Observed changes in chewing behaviour include chewing time, increased bite efficiency and rumination efficiency. Factors that affect chewing behaviour of ruminants are also related to the physiology, maturity, particle size, fibre content and proportion of the herbage in the diet of animals. Impact of maturity stage at harvest depends on the level of cell wall and fibre content. In general, chewing behaviour of cattle as well as factors affecting it is well described in the literature. With regards to the growing cattle there is prospective for future work in order to clarify some of the inconsistence about the chewing time. Future studies in modelling and describing the chewing behaviour of ruminants are also required in an attempt to predict intake with more accuracy.

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