University of Alberta

Alternate-Day Feeding and Rotating of Feeds in the Diet of Beef Cattle

By

Sonja Nicole Lemm ©

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ALTERNATE-DAY FEEDING AND ROTATING OF FEEDS IN THE DIET OF BEEF CATTLE submitted by Sonja Nicole Lemm in partial fulfillment of the requirements for the degree of Master of Science in Animal Science.

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Abstract

An incomplete 5 x 5 Latin Square with three steers (554 ± 10 kg) was conducted to determine if voluntary intake of straw, weight of reticulorumen contents, forage degradability, and rumen ammonia and volatile fatty acid concentrations are affected through changes in dietary feeding patterns. Dietary treatments consisted of 1) hay ad libitum, 2) hay at maintenance level with straw ad libitum daily, 3) hay fed at twice maintenance on alternate days with straw ad libitum at all times, 4) hay and straw rotated in the diet each day, and 5) hay fed for two days rotated with straw for the next two days. Straw intake was increased when hay was not fed every day. Cattle did not eat to constant rumen dry matter fill.Although hay intake was numerically increase above normal ad libitum intake following a day when only straw was fed, the increase was not statistically significant. Ruminal ammonia concentrations were not sufficient to support fiber digestion on the second day of straw feeding. It was concluded that feeding regimens in which hay is fed only every second day have potential, feeding only straw for 2 consecutive days is not recommended.

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CHAPTER 1

Introduction

Alberta is home to approximately 5.3 million cattle, raised on 36,000 farms, of which 35% are beef cows (Statistics Canada 1996). Winter feeding of cows is the single most important cost in cow-calf production, averaging 30% of average production costs in 1994 and accounting for $34.40-$37.53 per 100 pounds of calf weaned (Kaliel et al. 1995). Reduction of winter feed costs thus could potentially have a very positive economic impact upon cow-calf producers as the margin of profitability is quite small. The majority of cows are over-wintered on conserved feed to meet their nutrient requirements for maintenance and reproduction. These observations suggest that it would be very worthwhile to examine alternative feeding methods which, through changes of behavioral or physiological factors, may result in an increase in the voluntary intake of straw throughout the wintering period. Cow winter feeding strategies often rely on incorporating by-products feeds such as straw and chaff into the diets or allowing the cows to consume some of these products when they are used as bedding. It is recommended that cows receive some high quality feed such as hay, silage or grain each day when straw-based diets are fed (NRC 1996).

One of the major problems in the utilization of straw in ruminant diets is that voluntary consumption is quite low, averaging 1.4% of body weight in an experiment reported by Mathison et al. (1981). It was formerly believed that rumen fill is the only factor involved in intake control when low quality feeds such as straw are fed and therefore physical characteristics of feed was assumed to be the primary factor regulating voluntary intake. This concept has, however, been challenged. It is now recognized that the voluntary intake of animals fed the same feed can vary widely depending upon the physiological status of the animal, behavior factors, and environmental conditions which implies that the animal has considerable control over intake (Mathison et al. 1995). The importance of palatability factors in affecting intake is perhaps best demonstrated by the classical experiment of Greenhalgh and Reid (1971) who found that straw consumption was increased two-fold when cattle ate hay and had an equal amount of straw put into the rumen through a fistula rather than when they ate straw and had an equal amount of hay put into the fistula. Similarly, Villalba and Provenza (1997) concluded that nutrient feedback from the gut should be viewed as an important factor affecting feed preferences in ruminants.

Another problem with straw is its low digestibility , which means that supplemental feed must be provided. In the ruminant animal, interactions can occur when different feeds are fed together and these associative effects- a reduction in digestibilty of mixed diiets that may occur at high levels of intake and may either increase or decrease the efficiency of feed use (Van Soest 1982). Positive results are to be expected if the supplemental feeds supply limiting essential nutrients. In contrast, in some instances provision of high quality nutrients can reduce both the population of cellulolytic microorganisms in the rumen as well as their production of the cellulase enzyme (Van Soest 1982). It is therefore impossible to know whether intermittent provision of supplemental feed will enhance or reduce ruminal and whole tract digestibility in an animal fed straw-based diets.

Little or no attention has been paid to alternate day feeding of hay or grain portion of the diet when straw is continuously available ad libitum even though such a feeding system would decrease labor and equipment costs and maintain the health of the animals. Hand et al. (1995) calculated that if an alternate day feeding regime was implemented for pregnant cattle it would be possible to save $30 per animal in decreased overwintering costs. This would lead to an increase in the profitability of the beef industry as a whole and an increased income to individual producers; potential savings to cow calf producers could be in the neighborhood of 2.3 million dollars annually in Alberta alone. Skip-a-day feeding, where no feed is fed one day, is used in the hog and poultry industry. In the poultry industry this technique is used to limit pullet energy intake during the critical growing period to decrease the incidence of metabolic disease (Robinson et al. 1992), decrease growth rate and associated health problems (Robinson et al. 1992; Goerzen et al. 1996), and reduce the incidence of ascitites (Arce et al. 1992). The hog industry restricts feed intake in gilts during prepubertal development (Booth et al. 1996) and sows during pregnancy (Wojcik and Widenski 1991) through skip-a-day feeding techniques.

There is very little information on alternate-day feeding of high quality feeds to cattle. The prevailing concept has been that ruminants need to be fed the same ration each day to maintain stable conditions within the rumen. Previous research, however, does not always support this concept. McIlvain and Shoop (1963) studied the effects of daily versus every third day feeding of protein supplements to beef steers on winter range and there was no indication of differences in liveweight gains compared to animals fed supplements daily. In contrast with the situation with alternate-day feeding, there is considerable information on the effects of feeding cattle more than once daily. Increasing feeding frequency has been commonly used in feedlot beef and dairy production where high production demands are placed on the animal. The animal's interest in feed is increased if animals are fed several times a day thereby increasing the amount that the animal will consume (Robinson 1989). In addition, animal efficiency may also increase because a more constant rumen environment is maintained. Nocek (1992) stated that the stabilization of the rumen environment, which occurs with more frequent feeding, should enhance fiber digestibility, maintain stabilized production of microbial end products and maximize microbial yield. Increasing feeding frequency to more than once daily is, however, labor intensive and such high input feeding methods are generally reserved for high production animals where high intakes are required.

Another potential alternative feeding system is a rotating system where one feed is fed one day and another the next on a continual rotating basis. Two-day rotations could also be used. We are unaware of any research that has examined such a system, however it may have something to offer. Specifically, since more good quality feed (e.g. hay) would be given on the days when it was fed, it would help alleviate the problem of boss cows keeping more timid ones away from good quality feed which often occurs when limited amounts of hay are fed on a daily basis. The rotational feeding system may have beneficial (or detrimental) effects on digestion because of associative effects within the rumen or on intake of straw because of changes in animal behavior.

On the basis of the above discussion, it is clear that substantial savings could be achieved if alternate-day feeding and possibly rotational feeding could be practiced by the cow-calf producer. There is, however, essentially no information concerning the effect that such practices would have on the utilization of straw-based diets. In addition, examination of alternate-day feeding and rotating feeds in the diet will provide additional, and much needed, basic information on ruminant digestion and metabolism. Almost all intensive research on ruminant nutrition in the past has been conducted with animals that have received each feed in the diet at least once daily.

1.1 Objectives

There are a number of hypotheses for this experiment. The first is that providing hay less frequently than once daily can increase overall voluntary consumption of straw diets. As well, the challenge was to determine whether ruminal capacity could be affected to allow higher than ad libitum intakes of hay and straw when the feedstuffs are alternated on a two-day basis. The specific objectives were to compare the following treatments: 1) feeding hay ad libitum daily, 2) feeding hay at the maintenance feeding level with straw available continuously and free-choice, 3) feeding hay ad libitum every second day with straw available ad libitum at all times, 4) rotating hay and straw in the diet on a daily rotation basis, and 5) rotating hay and straw in the diet by feeding hay for 2 consecutive days followed by straw for 2 consecutive days.

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CHAPTER 2

Literature Review

2.1 Cereal Straw in Diets of Wintering Beef Cows

Crop residues from cereal grain production represents a tremendous potential feed source in North America. In measurements made by Narasimhalu et al. (1998), the amount of straw produced in the USA averaged 44 to 48% of the weight of the total barley crop produced. In the United States over 90 million tons of crop residue was available after cereal harvest (USDA 1984); this volume, along with proper supplementation, is enough to feed 17.5 million brood cows for a 5 month period (Males 1987).

Straw can constitute a major portion of a maintenance diet for cows over winter (Ball 1971). Research is continually demonstrating that relatively high levels of low quality forages can be used in maintenance animal diets. Kay et al. (1968) reported body weight changes for cows of -0.19 to –0.29 kg/d during the final five months before calving in two consecutive winters as a result of the daily consumption of 7.4 to 7.5 kg of long barley straw and 2 kg of barley grain. The animals did lose weight however, no other health problems were noted nor were there any calving difficulties encountered. In the first year of the trial, birth weights were lower than average in the second year birth weights averaged 34 kg and were 4 kg heavier than the previous year. The cows had regained their winter weight loss by the time they were re-bred 10 weeks after calving and no rebreeding problems were encountered.

Ball et al. (1971) conducted a study in which a set of cows beginning as heifers were used in a series of trials completed in 3 consecutive years. During the wintering period from the first of November to the last week in April, the cows were fed diets containing 76-82% barley straw. The energy and protein supplements used varied from year to year but the diets were similar in terms of metabolizable energy. Barley and urea were the major supplements used. There was very little difference in performance among diets with weight losses averaging 55 kg during the 175 to 180 day winter feeding period, which included the calving period. The weight loss was more than recovered during the summer grazing season resulting in an additional gain of 45 to 50 kg annually. The exception was found in the first year when the heifers only regained the weight they had lost over the winter.

In Saskatchewan, Johnson (1972) reported cases of abomasal impaction when diets containing a large percentage oat straw were fed and daily straw intake rose to 1.5% of the animal's weight. Provision of additional grain or hay alleviated the problem. Milk production, weight gain and backfat change were not different in lactating beef cows fed diets based upon grain and straw in comparison with hay. Animals fed straw, however, required 13 days longer to conceive.

In Alberta, Weisenburger and Mathison (1977) reported that daily gain averaged 0.28 kg d^{-1} when pregnant wintering beef cows were fed diets containing an average of 86% pelleted, chopped or ground barley straw along with concentrate. In a subsequent trial, Mathison et al. (1981) reported that abomasal impactions and acute hypomagnesemia occurred in wintering beef cows fed diets containing 94% barley straw. Males (1982) could not detect any difference in days to first estrus or postpartum interval to conception when diets containing 100% alfalfa hay were compared with those containing 33, 67 or 75% wheat straw. These diets were fed to dry pregnant beef cows in the winter to meet 80% of energy requirements. Cows gained weight prior to calving while on these diets but post-calving winter weight losses ranged from 6 to 56 kg. Males and Gaskins (1982) fed diets containing 35 to 77% straw with concentrate and determined that heifers fed ammoniated straw consumed from 65 to 90% more straw than those fed untreated straw. Bartle et al. (1984) successfully fed prepartum-diets containing 75% wheat straw.

Hand et al. (1996) demonstrated that incorporating straw into maintenance diets had little or no effect on the weight gains or losses for mature pregnant cows. However, there were significant weight losses in the heifers being fed straw in maintenance diets since these animals have higher nutrient requirements for maintenance and growth.

Cereal crop residues are low in protein and high in neutral detergent fiber (NDF), and are unable to sustain animals without adequate supplementation. The supply of energy and nutrients from straw to the animal is also dependent upon the amount consumed. The voluntary intake of straw is limited by the capacity of the reticulo-rumen and by the rate of disappearance of digesta from this organ (Campling et al. 1962). The rate of disappearance of digesta depends on the volume of feed in the ruminoreticulum, the composition of feed, and the particle size of the feed. Because of the importance of intake and digestibility in the utilization of straw, physiological and plant factors influencing these factors are discussed in the next sections. Protein supplementation is also discussed below in relation to its effect on intake and digestion. Supplementation with minerals and vitamins is also important but a discussion of these factors is outside the scope of this review.

2.2. Factors Influencing Voluntary Intake of Straw-Based Diets

One of the main limitations to straw-based diets is the low voluntary consumption of straw by cattle. If intake could be increased, less supplemental feed would be required. Also, there are economic advantages if the voluntary intake of supplemental high quality forages could be increased enough so that daily feeding is not required. To properly evaluate each of these limitations to alternate-day or rotating feeding systems, an understanding of control of feed intake in ruminant animals is required as well as a that of specific information on straw-based diets.

2.2.1 Animal Factors Affecting Intake

2.2.1.1 Rumen Fill

Voluntary intake of straw is very low (see Section 2.1.1). A prevailing concept in ruminant nutrition is that the intake of low quality forages is limited by the amount of material that the animal can hold in its digestive tract. There is a high amount of rumen fill when a slowly fermenting feed with a high content of structural carbohydrates is included in the diet which leads to a restriction in DM intake (Aitchison et al. 1986; National Research Council, 1987; Ketelaars and Tolkamp 1992). Physical restrictions in intake because of gut fill have thus been assumed to be a major cause of the low intake of straw. The exact mechanism by which fill influences intake is not clear (Aitchison et al. 1986). McDonald et al. (1988) points out that there is a threshold of rumen distention which the animals will attempt to achieve and not exceed even if their energy requirements have not been satisfied. In contrast Ketelaars and Tolkamp (1992) point out that actual feed intake does not depend only on the filling effect of a feed but also the tolerance of the animal to a certain rumen fill and that this tolerance may increase with the energy needs of the animal.

The importance of fill in influencing intake has been examined by removing/adding material to the rumen. Numerous experiments have been carried out to investigate how feed intake changes amount of contents in the ruminoreticulum. Transfer of ruminal contents from a donor animal (Campling and Balch 1961; Carr and Jacobson 1967), intraruminal additions of feed (Greenhalgh and Reid 1971), or removal of digesta from the rumen (Campling and Balch 1961; Carr and Jacobson 1967) have all resulted in some compensation in feed intake. Large additions of indigestible materials to the rumen show an immediate response through a decrease of intake. Campling and Balch (1961) found a linear relationship between animal intake and the removal of digesta from the rumen while the animal was eating; compensation though intake was found to be more complete when digesta was removed soon after a meal than when it was removed some hours later when the digesta is primarily indigestible.

Anil et al. (1993) found that forage intake decreased by 40% when balloons containing 15 L of water were placed in the rumen; whereas a decrease of 50% was noted when 20 L of water was inserted when a silage-based diet was fed. In contrast, Johnson and Combs (1992) found that additions of 23 L water filled bladders to the rumen did not depress intake which lead them to conclude that bulk was not the factor limiting intake for a diet containing 25% concentrates.

2.2.1.2 Clearance of Undigested Particles

Ingested feed can be cleared from the rumen either by microbial degradation and subsequent absorption of fermentation products or by passage to the lower gut. With diets containing a high proportion of roughage, voluntary intake may be limited by both capacity of the ruminoreticulum and the rate of clearance of digesta from this area (Hyer et al. 1991). Bosch et al. (1991) states that rumen clearance capacity is partly determined by rumen fill which depends on rumen volume. Several factors such as feed intake, chemical and physical nature of the diet, microbial degradation, physiological state, pregnancy, frequency of feeding, and time of day may influence rumen volume and motility and thereby change passage rates and outflow of rumen constituents (Faichney 1984; Owens and Goetsch 1986; Bosch and Bruining 1995).

Grovum and Williams (1977), Owens and Goetsch (1986) and Holden et al. (1994) indicate that as DM intake increases, ruminal liquid volume, DM percentage in ruminal contents, and particle passage rate increase. This is supported by Balch and Campling (1965) and Faichney (1984) who suggest that increases in feed intake usually result in faster rates of passage of solutes and particulate matter through the rumen and whole gastrointestinal tract. Decreasing the level of intake from 99% to 50% of maintenance lengthened the mean retention time by 12 to 27 hours in the study of Luginbuhl et al. (1994). Okine and Mathison, (1991b) observed a linear relationship between feeding level (1.0, 1.3, 1.5, 1.7 x maintenance) and ruminal and total tract particulate passage rate in nonlactating dairy cows. However, an increase from a low level of feed intake has not consistently increased particle passage rate (Okine and Mathison 1991b), due to compensatory increases in rumen volume (Van Soest 1982; Owens and Goetsch 1986). The effect of intake on ruminal particulate passage rate decreased as the volume and DM content of the ruminoreticulum increased in studies of Luginbuhl et al. (1994). With higher feed intake, rates of liquid passage were 1.8 and 1.96 times faster for sheep on medium and high concentrate diets compared to sheep on low concentrate diets; comparable figures for cattle were 1.69 and 1.81 compared to low concentrate diets (Colucci et al. 1990). Feed type and chemical composition of a diet can also cause differences in passage rates.

Van Soest (1967, 1982) concluded that when ruminal volume is maximal and intake continues to rise the animal compensates by allowing larger particles to pass through the reticulo-omasal orifice. Thus as feed intake increases the extent of both ruminal and total tract digestion decreases (Owens and Goetsch 1986).

Goetsch and Galyean (1983) demonstrated that there was no difference in passage rate when the feeding frequency of steers fed a 75% concentrate diet was increased from two to eight times daily. This is supported by Robinson and Sniffen (1985) who reported no difference in passage rates when comparing dairy cows fed once or four times daily. In contrast, Ruckebusch (1991) stated that frequency of feeding has a marked effect on amount of digesta flowing from the abomasum and that feeding three times daily versus once daily increased digesta flow by 30%.

2.2.1.3 *Palatability*

Feed intake is reduced when more mature forages are fed due to reduced palatability, toxic secondary characteristics, and limiting nutrients (Galyean and Goetsch 1993). Campling and Lean (1983) have suggested that the flavor of a food is an important factor affecting its voluntary intake. Conrad (1966) and Ketelaars and Tolkamp (1992) indicate that oral sensations affect the level of voluntary feed intake and that the animal exploits these as a source of information to discriminate between nutritious and less nutritious or even toxic feeds rather than just to enjoy a more palatable meal. However, it has often been concluded that, when choice is available, palatability is of minor importance in affecting intake (Campling et al. 1962; Conrad 1966).

Behavioral and electrophysiolgical studies have demonstrated that animals can distinguish between salty, sweet, bitter, and acid solutions (Campling and Lean 1983). In the study by Grovum and Chapman (1988), the effects of feed additives on palatability was clearly discernible if additives were incorporated with feed rather than with water. It was concluded that the controls of the intake of water might operate differently from those of feed intake controls. These authors also noted that there are reductions in intake when foodstuffs containing added urea are fed to ruminants, which may be the result of either bitter taste or a post-ingestive effect including an increase in rumen and plasma ammonia levels. Villalba et al. (1997) has concluded that nutrient feedback from the gut should be viewed as an important factor affecting feed preferences in ruminants. Palatability influences have therefore previously been considered to be of minor importance in the majority of low intensity production systems since a choice is not offered.

2.2.1.4 Physiological Factors

The physiological control of voluntary intake achieves an approximate match between intake and energy expenditure, resulting in an increase in body weight of growing animals and a fairly constant adult body weight for maintenance animals. The basic urge to consume feed is the tendency of the animal to realize a genetically determined maximum capacity for growth and milk production, at the maximum rate at which tissue can utilize nutrients (Ketelaars and Tolkamp 1992). The food supplied to the animal will determine if this basic urge can be met. However, although it is often said animals control their feed intake based on energy requirements (Bosch et al. 1991), there are no sensors strictly for energy whereas there are receptors for distention, osmolarity, concentration of solutes, and temperature (Forbes and Barrio 1992). Animals do, however, monitor blood leptin concentrations which are related to the amount of fat in their bodies (Hossner 1998) and which is inversely related to voluntary consumption.

Physiological factors play a key role in determining voluntary intake. It is essential to understand the interrelationships of these factors since, although it is not possible to change physiological state of the animal, it may be possible to use alternative feeding practices to take advantage of the changing needs and requirements of the animal. The physiological aspects that are beyond the short-term control of the animal, which will be discussed below, include frame size, degree of fatness caused by previous plane of nutrition (body fat), animal breed, sex, and lactation.

2.2.1.4.1 Body fat Feed intake is not controlled by actual body condition rather it is controlled by the metabolites; glucose, insulin, triglycerol; produced through either breakdown of feed or adipose tissue. Current research on monogastric animals has shown that the influence of body fat on food intake is primarily through circulating glucose and triglycerol levels (Louis 1991). There is evidence that glucose plays a secondary role in feed intake regulation in ruminants and circulating triglycerol act similarly in the two types of animals. Insulin has been found to stimulate lipid synthesis in adipose tissue in ruminant animals by increasing the uptake of glucose and acetate and promoting fatty acid synthesis (Vernon 1986). Forbes (1984) stipulates that adipose tissue becomes less sensitive to the lipogenic effects of insulin as the cells become replete with fat. Other research conducted by Hossner (1998) determined that leptin, which is primarily produced in adipose tissue, is now known to be a key regulator of appetite and energy metabolism. The National Research Council (1996) has reported that body condition and percentage of body fat may play a role in controlling feed intake. Studies conducted by Fox et al. (1988) suggested that dry matter intake (DMI) decreases 2.7% for each 1% increase in body fat over the range of 21.3 to 35.1% body fat.

2.2.1.4.2 Breed According to Chewning et al. (1990) there are significant differences in average feed intake based on breed. They measured intake differences ranging up to

25% in Charolais, Hereford, Simmental and Beefmaster breeds. Schmidt and Schonmuth (1995) measured numerical but non-statistical difference in DMI between Holsteins, Black Pied, Friesians and Jersey animals. Hicks et al. (1990) state that Holstein steers consume 8-15% more feed than do beef steers and suggested that this might be because of a higher maintenance energy demand. According to information found in the Nutrient Requirements of Beef Cattle (NRC 1996), Holsteins have intakes and energy requirements up to 8 and 20% higher, respectively, than beef breeds.

2.2.1.4.3 Sex The National Research Council (1996) states that sex (steer vs heifer) appears to have a limited effect on feed intake. Schwarz et al. (1992) postulated that there are significant differences in intake based on sex although body weight also plays a large role. Anderson et al. (1988) found that bulls ate more feed daily than steers but the DM intake per unit of metabolic body weight was not different between groups. A difference of 13-15% in basal metabolism was observed when steers and bulls were compared in a study by Garrett (1980).

2.1.4.4 Lactation The nutrient requirements for lactation are up to five times higher than those of maintenance or non-lactating animals (Bertoni et al. 1995). In response to these increased energy demands, lactating animals increase intake by 35 to 50% compared with that of non-lactating animals of the same body weight fed the same diet (Agricultural Research Council 1980). As an example, Holden et al. (1994) found that intake of alfalfa hay was increased by 60% when cows were lactating.

The higher intake during lactation is associated with an increase in gut contents and a decrease in digesta retention times resulting in a decrease in digestibility

(Ketelaars and Tolkamp 1992). Due to the high demand for nutrients and the increased transport of blood metabolites to the mammary gland, the physical limitation of the gut may play a greater role in regulating the voluntary intake of the lactating animal. The animal appears to compensate for this however in hypertrophy of the ruminoreticulum; not only does the volume of digesta increase up to 40% compared to late pregnancy and to that of non-lactating control animals (Remond et al 1993), but both weight and the capacity for water increase (Tulloh 1966). The ability of the lactating ruminant to accept a greater degree of abdominal fill than that of the non-lactating animal may be related to more rapid rates of utilization of metabolites and consequent reduction in chemoreceptors which supply the negative feedback information (Forbes 1984; Bertoni et al. 1995). Also, higher requirements may induce a lactating animal to accept a higher rumen fill or a more rapid digesta turnover and this would allow a higher intake (Ketelaars and Tolkamp 1992).

Increase in food intake during lactation often exceeds, in relative terms, the increase in gut capacity. Faichney (1984) concluded that this discrepancy could be accounted for by increased digestibility of food or by faster passage rate. Increase in rumen microbial activity and the activity of animal enzymes due to increased feed intake from paturition to weaning in lactating cows was observed by Weekes (1972). Notwithstanding, it is generally concluded during ration formulation, it is necessary to increase the energy provided to the lactating cow to maintain similar body condition postpartem (NRC 1996).

2.2.2 Diet and Feed Characteristics Affecting Intake and Digestion

2.2.2.1 Forage Quality

Digestion can be broadly defined as the summation of processes by which macromolecules in food are degraded to simpler compounds which are absorbed from the gastrointestinal tract (Merchens, 1988). This process is generally accomplished though fermentation by microbial action and chemical breakdown by way of enzymes of dietary components. Although the ruminant is characterized by microbial fermentation occurring in the forestomach, postruminal digestion is equally as important. A problem with straw-based diets is that the digestibility is relatively low.

As might be expected, there is a relationship between apparent digestibility of the diet and voluntary intake. Intakes of hay and dried grass were directly related to the digestibility of the foods in the whole alimentary tract and in the ruminoreticulum alone and inversely related to the mean retention time of residues in the alimentary tract in studies of Freer and Campling (1963). Hovell et al. (1986) and Costantini et al. (1993) found that there were progressive reductions in the voluntary intake of DM as hay digestibility decreased. Hovell et al. (1986) found that with forages a decrease in digestibility by 25% resulted in a decrease of 37% in intake.

Dulphy and Demarquilly (1980) observed that increased maturity level of forage caused intake to decrease from 103 g kg $^{-0.75}$ body weight (BW) to 80 g kg $^{-0.75}$ BW in dairy heifers. This could lead to a conclusion that with increased maturity the contents of cell wall, and its resistance to breakdown in the ruminoreticulum, largely determine the extent to which the food is eaten by ruminants (Campling and Balch

1961). However, decreased feed intake with increases in forage maturity may be a function of palatability and toxic secondary characteristics in addition to the ability of the forage to supply nutrients (Galyean and Goetsch 1993).

Clearance rate from the reticulo-rumen of undigested particles with their burden of microbes is related to chemical and physical properties of the feed (Kennedy and Doyle 1993). Chemical characteristics such as cell wall concentration and ligninfication affect nutrient digestibility and feed intake (Galyean and Goetsch 1993; Ingvartsen 1994). The intake differences observed between high quality forage diets and low quality forage diets are dependent upon protein and nitrogen levels present in the plant material as well as fiber levels. These feed characteristics can change based on maturity levels as well as chemical changes occurring after harvesting of the material.

Rate of digestion depends on microbial species and activity, rate of attachment, surface area, and rate of hydrolysis, as well as ruminal conditions, feed properties and processing (Owens and Goetsch 1986). Digestibility is expressed as total extent of digestion independent of time. However, within any segment of the digestive tract, digestion is usually calculated as the percentage of the digestible residue which is digested per unit of time or as fractional rate of digestion (Owens and Goetsch 1986). Digestive rate may be dependent upon feeding frequency that may influence intake levels and hence digesta retention times.

Forages generally have a relatively slow rate of digestion due to cell wall and this is associated with decreased voluntary intake (Campling et al. 1962; Kaufmann 1976; Mertens and Ely 1979; Colucci et al. 1990; Bosch et al. 1992; Ketelaars and

Tolkamp 1992; Allen 1996). As cell contents are more rapidly digested, duration of digestion depends on the proportion of cell walls in the forage (Conrad 1966; Dulphy and Demarquilly 1980; Van Bruchem et al. 1991; Bosch et al. 1992). The slow degradation rate of forage only allows a part of its potential digestibility to be achieved during the time that it is retained in the rumen.

Total tract digestion is dependent on a number of feed characteristics as well as the quality of the feed. Both forages and concentrates have specific digestibilities that are influenced by their quality however chemical and physical compounds may alter the rates at which these feeds are broken down.

2.2.2.2 Physical and Chemical Processing of Feed

The most common reason for processing forages is to increase voluntary intake. Other reasons are to decrease the sorting behaviour of animals or to incorporate low and high quality forages together. Processing can affect not only digestibility, but also the rate and site of digestion in the rumen as well as voluntary intake. Excessive processing may be harmful through the shift in digestion sites and rates (Givens et al. 1993). Many methods exist for mechanically or chemically altering the physical nature of roughage and thus influencing intake and digestibility.

The effect of physical form of forage based diets on voluntary intake of ruminants has been studied by Wallace et al. (1961), Knox et al. (1964), Nicholson and Cunningham (1964), Wilkins et al. (1972), Greenhalgh and Reid (1973), Weisenburger et al. (1977), and Weston and Kennedy (1984). The results of these authors are in agreement that, as the particle size of the forage decreases, voluntary intake increases.

This effect appeared to be most pronounced when low quality forages are fed (Minson 1963; Greenhalgh and Reid 1973). Grinding can reduce particle size to the point where the feed particles are small enough to pass the reticulomasal orifice immediately after entering the rumen (Pigden and Heaney 1969). In such cases the particles need only absorb moisture to allow them to sink, thereby shortening the residence time of particles in the rumen; this in turn would be expected to lead to increased voluntary consumption.

Numerous physical processes have been used to improve intake of high fiber, low quality roughage. Grinding, pelleting (Nicholson 1981) and high pressure steam (Satter 1983) have been effective in improving intake. In the study of Dulphy and Demarquilly (1980) cattle fed hay chopped at 2 to 4 cm lengths had a 5 to 10% greater intake than those fed lacerated forage. Marsh (1978) concluded that intake of silage increased with the fineness of chop; however there was little evidence to support an optimum particle size. Voluntary feed intake for sheep was increased from 75 to 98 g DM per kg per day by grinding the feed (Faichney 1984). Results from Weston and Kennedy (1984) indicate that grinding facilitates flow of particles to the reticulum perhaps through decreased raft formation.

The use of pelleted diets instead of ground diets of the same particle size has resulted in variable effects on voluntary intake. Grinding and pelleting of forages result in an increase in voluntary consumption particularly with poor quality forage (Allen 1996). Mertens and Ely (1979) state that pelleting of forage results in less fiber fill and greater maximum dry matter intake if rumen volume is considered limiting. Greenhalgh and Reid (1973) demonstrated that intake of a low quality hay increased by approximately one third when the diets were fed in the pelleted form instead of the chopped form. Weisenburger and Mathison (1977) determined that cows fed pelleted diets containing 86% barley straw voluntarily consumed 13% more than those fed chopped straw. Similarly, Botkins et al. (1957), Cloete and Rossouw (1970) and Beacom et al. (1973) observed increases in intake due to pelleting. However Knox et al. (1964) and Levy et al. (1972) found decreased consumption of pelleted diets relative to ground diets. The process of grinding and pelleting decreases retention time and may decrease the digestibility of high quality forages (Mertens and Ely 1979; Galyean and Goetsch 1993).

Much research has been dedicated to chemical modification of feedstuffs to improve intake and utilization by ruminants. Kerley et al. (1985) found that by treating low quality forage with alkaline peroxide it was possible to significantly increase intake of this forage compared to the untreated control. Ward and Ward (1987) demonstrated that forage intake could be increased by treating low nutritive forage with anhydrous ammonia which is in agreement with the results of Chestnut et al. (1988) who reported an increased intake of urea-treated forage.

It is possible to increase the digestibility of straw through the use of chemical agents such as sodium hydroxide and ammonia or urea. Silva and Orskov (1988) demonstrated that the degradation of untreated straw is improved when it is incubated in the rumen of animal fed alkali treated straw compared to when animals are fed untreated straw. It was suggested that this may be due to more favorable rumen conditions created by the increase in digestible cellulose of the alkali treated straw. Lindberg et al. (1984) demonstrated that sodium hydroxide treatment could increase the fraction of straw which is soluble and can also increase the rate of digestion of the insoluble fractions in the rumen. These factors likely contribute to the observed increased voluntary intake of sodium hydroxide treated straw by sheep (Alawa and Owen 1984) and cattle (Ngambi and Campling 1991).Both in vitro and in vivo digestibilities of straw were increased with NaOH treatment however, animal performance was quite variable and seemed to be related to the amount of straw in the diet. This improved feed intake and increased DM disappearance in vivo is associated with a decrease in ruminal retention time (Coombe et al. 1979). The sodium hydroxide treatment also increases the solubilization of the hemicellulose in the straw without affecting the solubilization of cellulose (Lesoing et al. 1980). Treatments of straw with ammonia has been shown to increase digestibility and intake although the responses are somewhat less than for sodium hydroxide despite the fact that nitrogen content is also increased by ammonia treatment (Givens et al. 1991).

To summarize, responses in intake and digestibility have been observed as a result of physical and chemical processing of forages and straw. However, these feed modification procedures are expensive and are not cost effective in most production systems (Fahey and Berger 1986).

2.2.2.3 Protein supplementation

Nitrogen is required by rumen microorganisms for metabolism and growth (Hungate 1966). In low protein diets additional nitrogen may stimulate higher levels of microbial growth and increase the rate of digestion in the rumen. Increases in digestion and passage rates in turn stimulate increased voluntary intake of low quality roughage (Coombe and Tribe 1963; Pigden and Heaney 1969).

Trials involving sheep have demonstrated the effects of nitrogen supplementation on intake. Voluntary intake of poor hay increased from 510 to 760 g/day when supplemental urea was increased from 0 to 12 g/day in sheep (Pieterse et al. 1966). Jones et al (1973) reported that voluntary intake increased as crude protein was increased from 5 to 20% for wethers although ewe intake did not respond to crude protein levels beyond 10%. Coombe and Tribe (1963) found that urea added to straw and molasses diets increased voluntary intake of the sheep until the animals were in a positive nitrogen balance, beyond which excess nitrogen was excreted in the urine.

Supplementation of straw-based diets has a variable effect on the digestibility of organic matter. Straw intake of steers was not affected by the addition of 75 g of urea and 1.36 kg of barley daily when a diet consisting of about 75% straw was fed (O'Donovan 1968). Similarly, Kay et al. (1968) found little evidence of improvement in intake of barley straw (5 to 7% crude protein) when diets were supplemented with urea. Lyons et al. (1970) found that daily allowances of 1.37 kg of concentrate providing 4.8, 5.8, 7.2, or 9.91% crude protein in the diet of cattle resulted in a 25% increase in intake as crude protein increased to 5.82%. Fishwick et al (1973) demonstrated similar results when oat straw intake increased by 20% when crude protein was increased by 6%. Wintering cows supplemented with protein increased voluntary consumption of brome hay in the study of Clanton and Zimmerman (1965). Saghier and Campling (1991) found that supplementing a straw diet with soybean meal to increase protein content of the diet from 50 to 110g/kg had no effect on straw intake and resulted in no improvement in the digestibility of the diets. Similarly, Fick et al (1995) demonstrated that although protein supplementation increased digestible DM intake and forage DM intake, and tended to increase digestible NDF intake, it did not alter apparent DM or NDF digestibility. This is in contrast to work by Ortigues et al (1989) who demonstrated an improved digestibility of cellulose and xylose by up to 7% when fishmeal was included at levels of 11 and 12% by weight to the diets of steers. This addition of fishmeal also shifted digestion toward the large intestine.

Pre-formed protein as a supplement has been shown to be more effective than nonprotein nitrogen supplements for increasing intake and performance in cattle fed high levels of straw (Weisenburger and Mathison 1977; Church and Santos 1981; Mathison et al. 1981; Males et al. 1982). This improvement in performance with additional protein supplementation does not appear to be to result from the additional N (Pritchard and Males 1982) and is most probably derived from the small levels of amino acids present in the pre-formed proteins. Wallace (1991) suggested that adding pre-formed protein, pre-formed amino acids, or peptides would stimulate the mixed microbial population of the rumen where the supply of amino N is low, as in the case of straw diets. The maintenance of the population is due to the fact that cellulolytic bacteria require small amounts of amino acids and peptides as well as branched chain fatty acids which are growth factors and can be synthesized from amino acids (Wallace 1991).

In summary, it is clear that substantial increases in intake and variable responses in digestibility may occur when supplemental protein sources are included in the diet of ruminant animals which are fed a low protein roughage such as straw.

2.2.2.4 Level of energy supplementation

Total DM intake of wintering cows decreased when the proportion of oat straw in a straw-concentrate diet was increased from 72 to 86% (Mathison 1974). Straw intake, however, remained constant. Andrews et al. (1972) also found that when adequate protein was present in the diet there was no change in the straw intake when the percentage of barley straw fed increased from 62 to 73%. Blair et al. (1974) found a significant decrease in total intake as wheat straw levels were increased from 17.5 to 47.5% in diets for lactating dairy cows. Owens et al. (1969) observed that voluntary intake of lambs was not uniformly depressed with increased dilution of the diet with ground oat husks when these were added up to 60% of the diet. Bines and Davey (1970) demonstrated that there were no significant differences in intake among non-lactating cows as a result of feeding from 20-60% chopped straw in the diet.

Fahmy et al. (1984), supplemented ammonia treated straw with rolled barley at an inclusion rate of 200 g per kg with no effects on straw intake and dry matter degradation. At higher inclusion rates, there was a significant decrease in DM degradation. This corresponds with a decline in rumen pH below 6.2. Mould et al. (1984) demonstrated that digestion of fiber is reduced when pH falls below 6.1, a situation which may occur if large amounts of grain are fed with straw. Beck et al. (1992) found that the intake of ammonia treated straw was increased with supplementation of energy, in the form of sorghum grain, and protein, in the form of soybean meal. These authors also demonstrated an increase in the ruminal liquid dilution rate with energy supplementation.

It would thus appear that intake will be depressed when the level of low quality roughage in the diet is increased. With high roughage diets, the addition of small amounts of concentrate does not appear to affect the daily consumption of straw. The ability of supplements to increase intake and performance is generally due to increases in total intake, moderate changes in digestion and subsequent increase in the input of total digestible nutrients.

2.2.3 Concluding remarks

Interacting physiological and metabolic factors are involved in controlling feed intake and there is no simple switch over from physical control to metabolic regulation at some fixed point (Egan, 1970). Rather than considering a static relation between degree of distention required to inhibit, feeding will depend on the extent to which the other families of abdominal receptors are being stimulated (Mbanya et al. 1993). Stretch receptors found along the rumen wall are sensitive to touch and distention and chemical receptors respond to osmotic load and the VFA present in the digesta. There is potential for integration of signals because receptors may be responsive to more than one stimulus and because one stimulus may be responsible for more than one receptor, thereby increasing the additivity of signals to the animal (Forbes 1996). The integration of signals is the most logical explanation in controlling feed intake and the additivity of the signals may cause differing levels of satiety at different intake levels in ruminant animals.

2.3 Effect of Feeding Frequency on Intake, Ruminal Conditions and Digestibility

2.3.1 Dry matter Intake

2.3.1.1 Feeding More than Once Daily

A review by Gibson in 1981 states that increases in DMI can be achieved by increasing feeding frequency but no reasons are given as to why this phenomenon occurs. The concept of increased intake with increased frequency of feeding is supported by research such as that of Knox and Ward (1961) where DMI increased when the frequency of feeding of long alfalfa and concentrate was increased from 2 to 8 times daily. Clark and Keener (1962) also observed that feed intake was increased when feeding frequency was increased from 4 to 24 times a day.

There are, however, many experimental observations in the literature in which voluntary feed intake did not increase with increased frequency of feeding. Putman et al. (1961) found no significant increase in intake of alfalfa hay by hiefers when frequency was increased from two to ten times a day. Rhodes and Woods (1962) increased the feeding frequency of roughage from 2 to 4 to 6 times daily for fattening lambs and did not find any advantage correlated with increased intake. Campbell et al. (1963) fed a restricted amount of concentrate daily along with hay ad libitum diet either 2 or 6 times daily and found no increase in intake with the more frequent feeding. Charmley et al. (1991) found no difference in alfalfa intake when feeding frequency was increased from 2 to 8 times daily. Similar conclusions were reached by Fletcher et al. (1968) who fed a grain silage mixture 2 and 4 times daily, and by Woods et al. (1962) who fed a complete diet 2 and 6 times daily and found no increase in DMI with increased frequency of feeding. This is in agreement with studies by Renton and Forbes (1974) who fed a restricted concentrate and hay ad libitum diet one, two, and three times daily where no significant increase in intake was observed. Similarly Clark and Keener (1962) found that there was no advantage in feeding at more frequent intervals when growing ruminants are fed. Moreover similar results have been found with dairy cows. French et al. (1990), demonstrated that when dairy animals where fed 60% pelleted concentrate and a 40% chopped alfalfa hay increasing feeding frequency shows no significant difference in intake. Robinson and Sniffen (1985) reported no difference in intake of chopped hay when increasing feeding frequency of dairy cows from 1 to 4 times daily. Braggs et al. (1985) did not find any differences in intake when dairy cattle were fed either 2 or 8 times a day with a silage concentrate diet. Similarly Nocek and Braund (1985) noted that with a total mixed ration (TMR) mean daily DMI was not significantly influenced by increasing feeding frequency from one to four times daily. Macleod et al. (1994) found no difference in intake levels of concentrate fed to dairy cows when feeding frequency was increased from 2 to 6 times daily. Studies by Hunt et al. (1989) and Judkins et al. (1991) are in agreement that no significant increase in intake was observed with increased feeding frequency. Also, Robinson and McQueen (1994) found no significant increase in feed intake when dairy cows were fed concentrate and alfalfa silage 2 compared to 5 times daily.

In summary, it would appear that although in some instances DMI can be increased by increasing the number of times cattle are fed daily, this response does not occur in many situations.

2.3.1.2 Feeding Less than Once Daily

There is very little information on the effect of frequencies of less than once daily and studies which are available are connected with the feeding of supplements. McIlvain and Shoop (1963) did not detect any decrease in liveweight gain when steers on winter range were fed protein supplements every third day rather than daily. Brandyberry et al. (1992) found no difference in intake when supplements were included either every day or on alternate days. Similarly, Beaty et al. (1994) found no difference in supplement intake when feeding daily compared to three times weekly, however there was an increase in straw intake with increasing protein level of the supplements. No differences in intake were observed when cottonseed meal was provided daily, every second day, or every fourth day to cows fed a low quality hay (7.9% protein) in the study of Coleman and Wyatt (1982). However, these authors reported a reduction in DM intake when wheat forage fed every second or fourth day rather than every day was used to supplement a hay-based diet (3.3% crude protein) for cows. Beaty et al. (1994) supplemented wheat straw-based diets with concentrate daily, or three times weekly. Reducing supplementation frequency decreased straw intake by 17%.

2.3.2 Effect of Frequency of Feeding on Rumen Environment and Metabolism

In general, offering the daily feed in smaller portions at more frequent intervals tends to have a stabilizing effect upon rumen fermentation (Kaufmann 1976: Jensen and Wolstrup 1977), however more frequent feeding may increase water consumption and subsequently the rate of ingesta removal from the rumen (Ulyatt et al.

1984), possibly resulting in greater escape of potentially degradable substrates from the rumen. Whether this represents a positive or negative shift in digestive efficiency depends on the potential compensatory digestion in the lower gastrointestinal tract.

2.3.2.1 Fermentation of Feeds

Optimum feed utilization by ruminants is dependent on achieving maximum rumen fermentation and absorption (Hoover and Miller 1992). Continuous or frequent feeding has often been used as a method to decrease rumen diurnal fluctuations and establish steady state conditions of rumen fermentation and nutrient outflow (Goetsch and Galyean 1983). It has been assumed that a steady supply of substrate for fermentation leads to an increased efficiency of microbial feed breakdown and utilization however this concept has not been adequately proven.

Owens and Goetsch (1986) state that with forage diets, fermentation of cellulose and pectin may continue for a period of 25 hours after which very little substrate is available for use. This is in agreement with Leedle et al. (1982) who demonstrated that cellulose and hemicellulose fermentation peaks about 16 hours post-feeding and with some being available for digestion for 24 hours. Protein and nonprotein nitrogen are rapidly hydrolyzed in the rumen with peak ammonia levels reached 1.5 to 4 hours after feeding after which there is a steady decline (Davis and Stallcup 1967). However, since the maximum rate of cellulose digestion may not occur for another 4 to 8 hours or even longer after the peak of protein breakdown (Sutton 1971), ruminal ammonia concentrations may limit the activity of cellulolytic bacteria (Pritchard and Males 1982).

2.3.2.2 Ruminal pH

With roughage diets, slow and gradual enzymatic hydrolysis of fiber sets the pace for fermentation and controls release of easily degraded cell contents. Under these conditions ruminal pH is generally ideal for rumen microflora. Most rumen microbes thrive when pH exceeds 6.5, whereas a low unstable pH limits diversity of microbial population and selects for amylolytic species. Some facultative cellulolytic microbes, which can shift from fiber digestion to fermentation of sugars, will survive at a low rumen pH (Yokoyama and Johnson 1988). Relative to cellulolytic microbes, an amylolytic population is less adaptable to changes in substrate availability. Fiber content in the ration plays a role in ruminal pH, increases in crude fiber level shows a linear relationship with increase in pH (Kaufmann 1976). A depression in digestibility can be avoided if rumen pH is maintained above the level inhibitory to cellulolysis (6.0-6.1) and this may be achieved by providing roughage either in chopped or long form to stimulate rumination and salivation (Mould et al. 1983; Braggs et al. 1986). Fluctuations in pH, which occurs with a sudden change in diet, can be deleterious to ruminal populations and frequent feeding attempts to alleviate this occurrence. Froetschel (1990b) has suggested that a steady supply of nutrients may maintain a more steady pH in the rumen. Kaufmann (1976) suggested that attenuation of ruminal pH by feeding more frequently might be instrumental in increasing ruminal cellulolytic activity and subsequently increasing intake.

Many studies failed to modify rumen pH by varying meal frequency from 1 to 4 (Bath and Rook 1963; Malestein et al. 1981), 6 (Hardie et al. 1985), or 8 times daily (Nocek and Braund 1985). Nocek and Braund (1985) found no difference in daily mean pH when comparing one, two, four, or eight times daily feeding of dairy cattle on a total mixed ration (TMR). The findings of Bunting et al. (1984) reported no significant difference in mean ruminal pH when feeding frequency of a forage diet to wethers was increased from 2 to 16 times daily. Goetsch and Galyean (1983) feeding up to 8 times daily and Robinson and Sniffen (1985) found that there is no significant effect of increasing feeding frequency on mean pH values. Braggs et al. (1986) reported no difference in ruminal pH when increasing feeding frequency from 2 to 8 times daily when the dairy cattle were fed a 60% silage 40% concentrate diet. In 1994, Macleod et al. reported that increasing feeding frequency of concentrates to dairy animals had no effect on ruminal pH. Froetschel and Amos (1991) found no difference in ruminal pH when increasing feeding frequency from 1 to 12 times daily. French and Kennelly (1990) reported that no change in ruminal pH was observed when the frequency of feeding dairy cows was increased from 2 to 12 times daily. Robinson and McQueen (1994) found similar results in that the diurnal patterns of rumen pH were not significantly influenced by protein source or by increasing frequency of feeding from 2 to 5 times daily although pH for cows fed twice daily was numerically lower.

In contrast with these results, a study conducted by Nocek (1992) with lactating dairy cows fed high concentrate diets indicated that feeding strategy affected ruminal pH but that diurnal variations caused by combinations of feed were more pronounced with those associated with feeding frequency. At restricted intake levels, some stabilization of diurnal pH variations was observed by Charmley et al. (1991) when feeding frequency was increased.

Beaty et al. (1994) concluded that ruminal pH remained lower in cattle receiving daily supplementation compared to cattle supplemented 3 times weekly. Hunt et al. (1989) concluded that no differences in pH were observed when steers were supplemented every 12, 24, or 48 hours.

2.3.2.3. Rumen Ammonia Concentrations

Ammonia plays an important role in the nutrition of ruminant animals. Microorganisms require ammonia from protein or nonprotein nitrogen along with energy from carbohydrates and to grow and produce microbial protein for subsequent digestion by the ruminant. Microbial protein may provide 50 to 90% of the animal's total daily protein requirement (NRC 1996). Fluctuations in rumen ammonia concentrations thus may cause decreased digestibility of feeds by limiting microbial activity.

Goetsch and Galyean (1983) demonstrated that there was no significant difference in ruminal ammonia levels when feeding frequency was increased from 2 to 8 times daily when steers were fed a concentrate diet at an above maintenance level of intake. Braggs et al. (1986) reported that mean ammonia levels were not significantly different when a diet with a 60:40 concentrate:forage ratio was fed either two or eight times daily. Robinson and Sniffen (1985) found no differences in ammonia levels when increasing feeding frequency from one to four times daily with dairy cows. In contrast, Bunting et al. (1987) stated that ruminal ammonia levels decreased with increased feeding frequency from 2 to 16 times daily when good quality forage was offered. Similarly, Ulyatt et al. (1984) found lower mean ruminal ammonia levels in sheep fed alfalfa hay 24 times versus once daily. These experiments are in opposition to those of Jensen and Wolstrup (1977) who reported marked increases in rumen ammonia levels with increasing the frequency of feeding from two to twelve times daily when concentrate was fed, and to those of Froetschel et al. (1990) who reported a 23% increase in rumen ammonia concentrations when the frequency of feeding Jersey steers was increased from 1 to 12 times daily. Similarly, Pritchard and Males (1982) reported increased ruminal ammonia levels when feeding a protein supplement twice compared to once daily however which was accredited to a more constant concentration of ammonia throughout the sampling period. Yang and Varga (1989) reported more stable ammonia concentrations when feeding frequency was increased from once a day to 4 times daily when feeding dairy cows concentrates. When diets are feed ad libitum, Charmley et al. (1991) found that increasing feeding frequency from 2 to 8 times daily had no effect on rumen ammonia concentrations whereas when feeding level was restricted, greater feeding frequency increased the minimum ammonia concentrations and reduced the maximum values compared with the low frequency

The effect of providing supplements daily has been compared with providing them less frequently. Beaty et al. (1994) reported that ruminal ammonia levels of steers supplemented 3 time weekly declined throughout the supplemented days whereas the daily supplemented steers displayed a peak ruminal ammonia levels 4 hours post feeding. These authors concluded that the manner in which the protein interacted with the frequency of feeding and time functions indicate that steers were able to sustain a somewhat elevated ammonia value on days when they were not supplemented and this would be expected to aid their ability to sustain fiber digestion.

2.3.2.4 Rumen Volatile Fatty Acid Concentrations and Proportions

The major energy yielding substrates from the ruminant digestible tract are the short chain volatile fatty acids (VFA) acetic, propionic, and butyric. With forage diets, VFA provide 50-85% of the metabolizable energy used by the ruminant animal (Church 1988). With roughage diets, fiber barriers limit carbohydrate availability so that the rate of volatile fatty acid (VFA) production is relatively slow. This combined with a constant rate of absorption, results in lower concentrations of VFA in the rumen when low quality forages are fed. Since volatile fatty acids are major products of fermentation in the rumen they are prime candidates for feedback control signals to control voluntary intake (Azahan and Forbes 1992). By decreasing the passage rate of material from the rumen it is possible to increase the time that material remains in the rumen for microbial breakdown and hence production of VFA. Microbial growth and function however is inhibited as the VFA levels increase in the rumen. However, according to Yokoyama and Johnson (1988) capacity for absorption of VFA is 6 to 8 times the maintenance energy requirements of ruminants and therefore absorption is not a limiting step in their removal from the rumen.

The majority of the current literature suggests that feeding frequency does not have a major effect on ruminal VFA concentrations. Owens and Goetsch (1986) state that despite wide swings in microbial population and differences in feed intake, ruminal VFA proportions are remarkably stable, although there are fluctuations in molar concentrations that are pH dependent. Increased feeding frequency did not result in a significant change in average total volatile fatty acid content of the rumen fluid or in the relative amounts of acetic, propionic, butyric, and valeric acids in studies of Braggs et al. (1986). Similarly, Goetsch and Galyean (1983) found no differences in total VFA concentration when frequency of feeding was changed, however there was a difference observed in the individual VFA concentrations; acetate and butyrate molar proportions were higher for twice daily fed animals and propionate was higher for 8 times daily fed animals. Bunting et al. (1985) found that there were no differences in individual ruminal or total ruminal VFA production when feeding frequency was increased from 2 to 16 times daily for wethers consuming a forage diet. Increased feeding frequency of concentrates from 2 to 6 times daily had no effect on the total ruminal VFA concentration or molar proportions of VFA in the study of Macleod et al. (1994).

There have, however, been reports of changes in ruminal VFA concentrations in more frequently fed animals. Thus Ruiz (1989) reported that VFA concentrations were lower in more frequently fed animals, probably as a result of less fermentable mass entering the rumen at any one meal. Also there was an increase in passage rate in this experiment which again would have tended to lower VFA concentrations in the frequently fed cattle. This is contrasted by the work of Knox and Ward (1961) who found significant increases in total VFA production and individual concentrations when a diet consisting of alfalfa hay and concentrates was fed eight times daily compared with twice daily. Froetschel (1990) also observed an increase in total VFA (21%) when comparing animals fed 12 times rather than once daily.

There is only a limited amount of research in which daily feeding of supplements has been compared with less than daily feeding. Hunt et al. (1989) found no differences in total VFA concentrations when comparing 12, 24, and 48 hour provision of supplements. Total volatile fatty acid concentrations were not affected by diet when crude protein sources were fed at 48h and 96h intervals in the study of Collins (1992).

2.3.2.5 Effect on Microorganisms

Digestion of substrate is dependent upon bacterial, protozoal and fungal populations. To maintain an optimal microbial population it is considered desirable that substrate is consistently available for growth and development. When feed is supplied more frequently the ruminal environment is maintained through repeated fermentation in which end products are constantly removed (Owens and Goetsch 1986). Yokoyama and Johnson (1988) state that increasing frequency of feeding reduces variation in both protozoal and bacterial populations by providing a constant supply of substrate. A change in diet can invoke a transition period for the microbial populations and those which best accommodate the dietary change will continue to survive and proliferate. Adaptation may take an extended period of time if the change is from a high fiber diet to one with a large amount of readily fermentable carbohydrates.

The rumen microbial population may be influenced indirectly by changes in the rumen environment. Rumen bacteria do show marked difference in sensitivity to pH, redox potential, and osmolarity and this may influence how the bacteria compete against each other (Church 1988). Protozoal numbers and type are also influenced by pH and passage rate and can be responsible for bacterial shifts indirectly since protozoa consume bacteria. Froetschel and Amos (1991) reported that feed intake levels and frequency of feeding affected microbial species and cellular composition. Similarly. Clark and Keener (1962) state that a change from a once or twice daily feeding routine to feeding several times daily altered rumen microbial population and/or changed the ratio of end products of fermentation for at least a few weeks. In contrast, Robinson and Sniffen (1985) reported that the ruminal bacterial composition was not affected by frequency of feeding when multiparous dairy cows where fed a high forage diet up to four times daily. Also, Leedle et al. 1982) reported that even when high forage diets were fed once daily bacterial populations were stable enough so that digestibility was equivalent to that in more frequently fed animals.

Rumen protozoal populations are affected by feeding frequency. Froetschel et al. (1990) reported that increasing the feeding frequency of a concentrate diet from once to twelve times daily increased protozoal numbers from 2.18×10^6 to 3.51×10^6 per milliliter of rumen fluid. This was thought to occur because of a continual supply of substrate and a higher ruminal pH (Froetschel 1990b). The observation that protozoal numbers are increased with increased frequency of feeding tends to agree with the results of Hungate (1966) when ruminants were fed concentrate and of Braggs et al. (1986) when dairy cattle where fed a silage-concentrate mix. Even as a higher ruminal pH is beneficial for protozoa, their presence also tends to keep the pH high (Braggs et al. 1986) which will result in an efficiency of growth for all microorganisms (Yokoyama and Johnson 1988).

2.3.3 Digestibility

2.3.3.1 Ruminal Digestion

Frequency of feeding plays an important role in the ruminal parameters that may influence the digestion occurring in the rumen. Robinson and Sniffen (1985) state that increased feeding frequency will lead to less fluctuation in ruminal characteristics and this may theoretically increase efficiency of nutrient digestion in the rumen.

Ulyatt et al. (1984) concluded that neither the extent nor primary sites of digestion of cell wall components were significantly affected by increasing the feeding frequency from 1 to 24 times daily in sheep fed alfalfa hay. Feeding frequency of tall fescue hay to wethers did not affect NDF digestibility occurring in the rumen but values tended to be lower for feeding frequencies lower than twice daily compared to 4, 8, and 16 times daily (Bunting et al. 1987). In multiparous Holstein cows fed a diet of chopped hay and concentrates, Robinson and Sniffen (1985) found that feeding frequency had little influence on forestomach digestion DM, organic matter (OM), neutral detergent fiber (NDF), cellulose, or lignin when feeding frequency was increased from 1 to 4 times daily. Froetschel et al. (1990) demonstrated that ruminal digestion of OM, crude protein (CP), acid detergent fiber (ADF), NDF, and starch was unchanged when feeding frequency of a silage: concentrate diet was increased from 1 to 12 times daily. Similarly McGuire et al. (1966) reported no differences in the digestibility of dry matter, crude fiber, or gross energy when increasing frequency of feeding from 1 to 6 times daily for steers fed a complete pelleted ration. As well, Robinson and Sniffen (1985) demonstrated that there was no difference in dry matter digestibility when feeding frequency of a complete ration was increased from 1 to 4 times daily. Nocek (1992) noted that an increase in frequency of feeding has no effect on rumen DM digestion when cows were fed a forage:concentrate diet once or twice daily.

In contrast with the above results, McGuire et al. (1966) noted that increasing the frequency of feeding of yearling steers receiving a complete pelleted ration from 1 to 6 times daily significantly decreased crude protein digestibility. This is contrary to the reports of Rhodes and Woods (1962) who found no significant difference in protein digestibility by increasing the frequency of feeding for lambs from two to four to six times daily when a hay:concentrate was diet.

2.3.3.2 Post Ruminal Digestion

No differences in post ruminal digestion of dry matter, organic matter or neutral detergent fiber were observed in dairy cows fed chopped hay once or four times daily (Robinson and Sniffen 1985). As well no significant differences were observed for post ruminal digestibility for NDF, ADF, and hemicellulose on tall fescue hay diets when the frequency of feeding wethers was increased from two to sixteen times daily (Bunting et al. 1987). Rhodes and Woods (1962) found no difference in post-ruminal digestion of DM, and OM when the frequency of feeding was increased from two to four to six times daily for fattening lambs. Nocek (1992) determined that there was no difference in postruminal digestion of a forage:concentrate diet when feeding frequency of once daily was compared to twice daily. Robinson and Sniffen (1985) reported that when increasing the feeding frequency from once to four times daily there was no difference in apparent digestibility in the intestinal tract.

2.3.3.3 Whole Tract Digestion

Whole tract digestion is based on the combination of pre- and post-ruminal digestibilities. It is generally assumed that there is no effect of feeding frequency on ruminal or post-ruminal digestion there will be none on whole tract digestion but it is possible that even if the differences in ruminal digestion and post-ruminal digestion are not significant, the summation of these differences may be significant.

Despite effects of feeding frequency on rumen metabolite concentration, there was no effect on whole tract digestibility, rate of passage from and rate of digestion in the rumen (Charmley et al. 1991). Bunting et al. (1987) demonstrated that the apparent total tract digestibility of dry matter, organic matter and cell wall constituents were not affected by feeding frequency in lambs fed Kentucky tall fescue either 2 or 16 times daily. Similarly no difference in DM, OM, NDF, cellulose, lignin, and hemicellulose digestibility was noted when increasing the frequency of feeding cows a complete ration from one to four times daily (Robinson and Sniffen 1985). Ruiz et al. (1989) experimented with eight ram lambs fed either once or eight times daily, and reported that there was no difference in total tract digestibility of DM, OM, NDF, or ADF between the experimental groups. This agrees with the results of Ulyatt et al. (1984) and Satter and Baumgardt (1962) who could not detect any effect of frequency of feeding on digestibility of alfalfa hay. Renton and Forbes (1974) concluded that when comparing frequency of feeding of once, twice, and three times daily a concentrate to a basal hay diet, there was no apparent difference in digestion of DM, OM, or crude protein. However it is in disagreement with earlier work by Ruiz and Mowat (1987) who detected differences in digestibility of DM and OM when feeding frequency was increased from once to four times daily when feed intake was limited to 90% of voluntary DMI.

When cattle fed straw ad libitum and supplemental concentrate once daily were compared with those in which supplemental concentrate was provided only three times per week, both DM and NDF digestibilities were increased with the less frequent supplementation regimen in the study of Beaty et al. (1994).

2.3.4 Concluding Remarks

It is difficult to determine the effects of frequency of feeding on the rumen environment and metabolism, as the research does not agree on many aspects. Numerous studies suggest that it is difficult to modify rumen pH and rumen ammonia levels on the basis of changing the frequency of feeding, which has an effect on the microbial population present in the rumen and the fermentation characteristics that are carried along with it. Similarly, the lack of effect of increasing frequency of feed on the ruminal VFA is well documented by authors using diets forages, grains, and the two in combination. Digestibility of the dietary components also failed to respond consistently to changes in frequency of feeding. The lack of change in the digestion of diets is demonstrated throughout the system, both ruminally and post-ruminally as well as in the total tract digestibility of the diet. This information lends itself to the conclusion that an increase in frequency of feeding within a single day does not have a large repeatable effect on the rumen environment or the digestibility within this environment. However there is little information concerning the effects of rotational feeding of high forage diets on the microflora and concentrations of metabolites within the rumen.

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CHAPTER 3

Effects of Alternate-Day Hay Feeding and Rotating Hay and Straw in the Diet on Dry Matter Intake and Weight of Rumen Contents

3.1 Introduction

According to 1999 Cow Calf audit, 25% of Alberta cattle producers are currently balancing rations for their beef herd which is an increase of 17% in the last ten years (AAFRD, 1999). Many cattlemen are supplementing their straw-based diets for beef cows by feeding hay or silage every second day rather than daily in the winter. Such a feeding system reduces labor and equipment costs. Also, since more good quality feed is given on the days when it is fed, this feeding practice helps alleviate the problem of boss cows keeping more timid ones away from good quality feed; a problem which often occurs when limited amounts of hay are fed on a daily basis. This type of feeding practice may have beneficial or detrimental effects on digestion because of associative effects within the rumen or on intake of straw because of changes in animal behavior.

There is limited research information on the effects of feeding cattle less than once daily, particularly in the Canadian winter. McIlvain and Shoop (1963) studied the effects of daily versus every third day feeding of protein supplements to beef steers on winter range and found no indication of reduced liveweight gains in comparison with animals fed supplements daily. Cole (1999) suggested that a feeding system in which there was an oscillating dietary protein intake might increase nitrogen recycling, improve quality of protein entering the small intestine, and increase the metabolic use of absorbed amino acids thereby decreasing the amount of nitrogen required in the diet.

In contrast, Nocek (1992) pointed out that the stabilization of the rumen environment with more frequent feeding should enhance fiber digestibility, maintain stabilized production of microbial end products and maximize microbial yield. In support of the latter concept, Beaty et al. (1994) observed that voluntary intake of wheat straw was reduced by 17% when concentrates were supplemented three times weekly rather than when they were provided daily. Dry matter (DM) digestibility was, however, increased when concentrates were provided less frequently.

One of the major problems in the utilization of straw in ruminant diets is that voluntary consumption is quite low, i.e. 1.4% of body weight in an experiment reported by Mathison et al. (1981). It was formerly believed that rumen fill is the main factor involved in intake control when low quality feeds such as straw are fed and therefore the physical characteristics of feed is the primary factor regulating voluntary intake (Blaxter et al. 1961; Conrad 1966; NRC 1987). This concept has, however, been challenged. It is now recognized that the voluntary intake of animals fed the same feed can vary widely depending upon the physiological status of the animal, behavior factors, and environmental conditions which implies that ruminant animals have considerable control over intake (Mathison et al. 1995). There is limited information concerning the effect of infrequent feeding of hay on interrelationships between voluntary DM intake and rumen fill.

Villalba et al. (1999) determined that there were changes in preference for flavored wheat straw depending upon the time at which starch was infused intraruminally. It is of interest to ascertain if cattle have the ability to modify their intake behavior in response to different timing of feeding. A specific question is whether cattle will increase their intake of hay above normal on days after those on which it is not previously available and in anticipation that it will not be available again the next day.

The hypotheses for this experiment were that overall voluntary consumption of straw by cattle fed hay-straw diets can be increased by providing hay less frequently than once daily, that rumen fill is not the primary factor limiting straw intake when straw-based diets are fed, and that cattle have the ability to increase daily hay intake above their normal ad libitum consumption level when hay and straw are provided on alternate days or rotated in the diet.

3.2 Materials and Methods

3.2.1 Animals and Feed

Five crossbred steers (454±10kg) were used in an incomplete 5x5 Latin square design experiment conducted at the Laird McElroy Environmental and Metabolic Centre, University of Alberta, Edmonotn, Alberta, Canada. At least 90 d before the experiment was initiated steers were fitted with a 10-cm i.d. soft ruminal cannula (Bar Diamond, Parma, ID), using aseptic techniques and local anesthetic (2% lidocaine). After complete recovery from surgery (minimum 6 wks after first surgery) each steer was fitted with a Komarek-type "T" cannula in the proximal duodenum 3 to 5 cm distal to the pylorus (Okine and Mathison 1991) using aseptic techniques with the animal under general anesthetic (acepromazine malate, 11 $\mu g\ kg^{-1}$ body weight; thiopentone sodium, 10 $mg\ kg^{-1}$ body weight; halothane, 2 to 3% in oxygen). Antibiotic therapy after surgery was procaine penicillin G (300,000 IU mL^{-1}; 2 mL 100 kg^{-1} body weight intramuscularly). Steers were maintained indoors in individual 3m x 3m pens with continuous lighting and an ambient temperature of 20 to 22 °C throughout the experiment. All animals in this experiment were cared for in accordance with the guidelines of the Canadian Council of Animal Care (1993) and under the advice of the Faculty of Agriculture Forestry and Home Economics Animal Policy and Welfare Committee.

Dietary treatments were as follows 1) alfalfa (*Medicago sativa*) hay ad libitum, 2) hay fed at maintenance + barley (*Hordeum vulgare*) straw ad libitum, 3) hay available twice maintenance on alternate days + straw ad libitum, 4) rotation of hay ad libitum on day 1, straw ad libitum on day 2, and 5) rotation of hay ad libitum on days 1 and 2, straw ad libitum on days 3 and 4. These treatments are summarized in Table 3.1. The hay contained 12.3% crude protein and 41.4% neutral detergent fiber. Corresponding values for straw were 8.2% and 64.5% which indicates that the straw was of exceptional quality as the average values for barley straw in Alberta are 5.0% for crude protein and 72% for NDF (AAFRD 1994). Forages were chopped to approximately 6 cm through a tub grinder (model 390, Sperry, New Holland, PA). Trace mineralized salt and water were available on a free-choice basis. Animals were weighed before and after each experimental period and maintenance intake was calculated based on these weights according to the relationship $NE_m=0.077kg^{0.75}$ and average feed energy concentrations (NRC 1996).

Each period lasted for 40 days. There was a 4 d adaptation period to the diet before voluntary intake measurements began on day 5. Rumen sample collections and marker administration (results not reported here) were conducted durings days 11-20, calorimetry during days 21-30 (data not reported), and rumen evacuations and nylon bag digestibility durings days 31-40. Feed was offered at 0800h and refusals were removed and weighed prior to feeding the next day.

Following voluntary consumption measurements ruminoreticular digesta was manually evacuated on 2 consecutive days at either 0900 or 1800 h using the procedures outlined by Robinson et al. (1987) with the exception that contents were not covered with carbon dioxide. The animals were left for a minimum of 2 days and then the ruminoreticular contents were evacuated on another 2 consecutive days. For steers assigned to the 2-day hay-straw rotation diets contents of the ruminoreticulum were evacuated for 8 consecutive days during each period.

The DM content of feed samples was determined by drying at 100°C in a forced air oven to a constant weight. Dry matter content of rumen samples was measured by drying rumen contents at 80 ^{0}C until constant weight was achieved. Crude protein was determined using a nitrogen analyzer (LECO, model FP-428, St. Joseph, MI). Acid detergent fiber (ADF) was determined by procedure #973.18 of the Association of Official Analytical Chemists (1997) and neutral detergent fiber (NDF) according to the procedure of Van Soest et al. (1991) without amylase or sodium sulfite.

3.2.2 Statistics

Two animals were lost from the experiment, one at the end of the first period and one during the course of the second period, thus feeding treatments (n=5), periods (n=5), and animals (n=3) were used as the main sources of variation in the experiment.

Mean feed intakes and ruminoreticular contents over the period as well as mean intakes on the days when either hay or straw were given were analyzed over time (days 5-12, 13-20 and 21-28 after the new dietary treatments were introduced) using the repeated measures component of the GLM procedure of SAS (SAS Institute. Inc. 1988). Treatments were compared within time or diet using the analysis of variance procedures of SAS (SAS Institute Inc. 1988). Comparisons were also made between days on which hay or straw were fed. Means were separated using Student-Newman-Keul's test (SAS Institute. Inc 1988). Pearson correlation coefficients were calculated between intake and fill in the ruminoreticulum using SAS (SAS Institute. Inc. 1988).

3.3 Results

Two steers died which substantially restricted the statistical power of the experiment. Autopsies were conducted on both animals: one death was unrelated to the experiment and the other was due to formation of polyps in the duodenum surrounding the cannula. To prevent this problem from reoccurring a slightly smaller plug for the cannula was used in the remaining steers to reduce the amount of negative pressure in the cannula when the plug was removed.

The steers maintained body weight while consuming hay and straw at the levels reported in this experiment.

3.3.1 Feed intake

3.3.1.1 Mean Daily Voluntary Consumption

Hay consumption was lower (P = 0.05) when hay was fed at maintenance than with all other diets when it was available (Table 3.2), with overall consumption being 12.0, 7.3, 12.8, 14.1 and 12.3 kg d^{-1} for diets in which hay was fed ad libitum, at maintenance, on alternate days, in the daily hay-straw rotation, and the 2 d hay-straw, rotation, respectively. There was also a tendency (P = 0.07) for hay intake to change with time, averaging 11.9, 11.5, and 11.6 kg d^{-1} during d 5-12, 13-20, and 21-28, respectively. In particular, hay intake when the 2 d hay-straw rotational diet was fed dropped by 11% from the first to the last period and there was some weighback when hay was fed at maintenance during days 13-20. When the 2 d hay-straw rotation diet was given no differences (P = 0.13) could be detected in hay intake between the first and second day of feeding hay (Table 3.3), even though intake was numerically 13% less on the second day.

When the steers were given straw in the 2-day hay-straw rotational diet they consumed more (P = 0.04) than they did when hay was fed at maintenance or on alternate days (Table 3.2), with overall consumption being 0, 0.87, 1.36, 2.29 and 3.78 kg d^{-1} for diets in which hay was fed ad libitum, at maintenance, on alternate days, in the daily hay-straw rotation, and the 2 d hay-straw, rotation, respectively. Straw intake did not change over time, although a numerical drop in straw intake of 0.75 kg d^{-1} in the 21-28 day period in comparison to earlier times when the 2 d hay-straw rotation was fed. When the 2 d hay-straw rotation diet was given no differences (P = 0.21) could be detected in overall straw intake between the first and second day of feeding straw (Table 3.3), even though intake was numerically 16% greater on the second day. Voluntary consumption of straw was however significantly higher 23% (P=0.03) on the second day of straw feeding.

3.3.1.2 Mean Period Consumption

Steers given hay ad libitum consumed more ($P < 0.05$) hay during days 5-12 and 21-28 and overall than steers on any of the other dietary treatments when mean intakes over the period were calculated (Table 3.4). A similar difference was found during days 13-20 but it was not significant. There was a time effect ($P<0.01$) and an interaction ($P=0.02$) of time and dietary treatment on hay intake. One animal fed hay at maintenance did not consume all of the hay offered during days 13-20 and hay consumption decreased with time when steers were fed ad libitum and in the 2-day hay-straw rotation treatment.

Steers fed hay ad libitum, hay at maintenance, hay on alternate days, hay and straw on daily rotational basis, and hay and straw on a 2-day rotational basis consumed diets containing a mean of 0, 11, 17, 14, and 22% straw over the experimental period (Table 3.4). Over the total experimental period more ($P < 0.05$) straw was consumed by steers when the 2-day hay-straw rotational diet was given than was consumed when hay was fed at maintenance and straw was continuously available. During days 13-20 there was also enough statistical power to detect a greater straw intake ($P < 0.05$) in steers fed hay and straw on the two-day rotation basis than in steers assigned to the 1-day hay-straw rotation. No differences in voluntary consumption of straw over time could be detected although with the 2-day hay-straw rotation diet straw intake during days 21-28 was only 76% of the intake during the previous 8 day period.

Overall total DM intake ranged from 7.8 to 8.2 kg d^{-1} when straw was included in the diet (Table 3.4). Although total DM intake was numerically higher when hay was fed ad libitum (12.0 kg d^{-1}), this difference was not significant. Steers changed their voluntary consumption of total DM over time ($P < 0.01$) and there was an interaction between time and dietary treatment ($P = 0.02$). In particular, voluntary consumption was 13% lower ($P=0.03$) during days 21-28 than during days 5-12 in the 2-day hay-straw rotational dietary treatment. Total intake during days 13-20 was also low with the diet in which hay was fed at maintenance because one steer did not consume all of it's hay.

3.3.1.3 Ruminoreticulum Contents

No differences in total weight of ruminoreticulum contents (mean 72.2 kg), water (mean 62.4 kg), DM weight (mean 9.8 kg), or in percentage DM in ruminoreticulum contents (mean 13.5%) were detected when the ruminoreticulum of the steers were evacuated at 0900 h and at 1800 h (Table 3.5). There were also no interactions between time of evacuation and dietary treatments.

Dietary treatment had no influence ($P = 0.32$) on mean total weight of ruminoreticulum contents, over the experimental period (Table 3.5). However the total weight was 31% greater ($P=0.02$) on days when hay was fed on the alternate day hat dietary regimen when ruminoreticular were evacuations at 1800h (Table 3.6). Similarly, there were no differences between dietary regimens for the amount of water in the ruminoreticulum (Tables 3.5) and there was 29% more ($P=0.02$) water in the rumen when hay was fed in the alternate day hay feeding regimen (Table 3.6).

The least ($P = 0.05$) amount of DM (mean 8.8 kg) was found in the ruminoreticulum of steers fed straw ad libitum and hay on an alternate day basis (Table 3.5). No differences were detected between DM in the ruminoreticulum between other dietary treatments. We were unable to detect a difference in DM in the ruminoreticulum on days in which hay was fed and days in which it was not fed when hay was fed on alternate days or when it was rotated daily with straw in the diet (Table 3.7). However with the 2-day hay-straw rotational diet overall ruminoreticular total DM content was 20 and 64% higher ($P<0.1$) on the first and second day of hay feeding than on the first and second day of straw feeding, respectively (Table 3.7).

The highest percentage DM in the ruminoreticulum was observed when hay was fed continuously at the maintenance feeding level ($P < 0.05$) and the lowest was found when hay was fed on alternate days (Table 3.5). Differences between hay and straw feeding days were observed only for the 2-day hay-straw rotational diet when the highest ($P < 0.05$) mean percentage DM in ruminoreticular contents was observed when hay was fed and the lowest was observed on the second day of straw feeding (Table 3.7).

3.3.2 Relationships Between Voluntary Intake and Weight of Ruminoreticulum Contents

Correlation coefficients between voluntary consumption of steers and weights of their ruminoreticular contents are given in Table 3.8.

Total DM and percentage of DM in ruminoreticular contents were positively correlated ($P < 0.05$) with voluntary consumption of hay when the ruminoreticulum was evacuated at 0900 h on the day on which intake was measured. No relationships were, however, detected between total weight or amount of water in the ruminoreticulum and hay intake at this time. At 1800 h weight of total material, water, and DM in the rumen, but not percentage DM, was positively related to hay intake. Consumption of straw was not correlated with amount of ruminoreticular contents at 0900 h or at 1800h (Table 3.8). Correlation coefficients between consumption of total DM by the steers and weight of ruminoreticular contents mirrored those with hay alone at both times of evacuation with the exception that there also tended (P=0.1) to be a positive relationship between total DM intake and percentage DM in ruminoreticular contents at 1800 h.

No significant correlations were observed between weight of material in the ruminoreticulum and intakes on the previous day nor were correlation coefficients markedly improved when data from days when only hay or straw were fed were compared.

3.4 Discussion

3.4.1 Relationship Between Ruminoreticular Fill and Voluntary Consumption

The mean ruminoreticular contents for the diets were equivalent to 15.9% of animal body weight and the mean percentage DM in ruminoreticular contents was 13.5%. These parameters are slightly higher than those obtained by Teeter and Owens (1983) who found that total contents of the ruminoreticulum were 13.2, 12.2 and 10.1% of body weight when prairie hay, alfalfa hay, and concentrates were fed to steers in amounts equivalent to approximately 1.6% of body weight. Corresponding values for the percent DM in ruminal contents were 11.4, 11.7 and 12.2%. Okine et al. (1993) obtained slightly higher amounts in steers fed diets containing straw ad libitum; weight of total ruminoreticular contents increased from 13.6 to 15.7% of body weight as the percentage of straw in a barley straw-alfalfa hay diet increased from 0 to 100%. Percentage DM in forestomach contents correspondingly decreased from 15.3 to 11.7%.

If, as generally believed, rumen fill is the primary determinant of voluntary intake (Blaxter et al. 1961; Campling and Balch 1961; Conrad 1966; NRC 1987) it would be predicted that the amount of DM in the ruminoreticular contents would be similar across dietary regimens. In contrast, differences were detected, with the greatest weight of DM occurring on days when hay was fed in the 2-day hay-straw rotational diet and the least weight on days when straw was fed with this diet and when only straw was fed on the alternate day basis (Table 3.7). Differences in fiber concentrations in the ruminoreticulum were too small to influence this relationship: NDF contents in ruminal DM were 69.4, 71.2, 72.1, 73.4, and 74.3% for diets in which hay was fed ad libitum, at maintenance, on alternate days, in the 1 day rotational hay-straw diet, and the 2-day rotational-straw diet, respectively. Corresponding values for ADF were 51.8, 51.6, 52.5, 54.3, and 53.8%.

The increase in ruminal contents with DM intakes observed in this study (Table 3.8) is consistent with the summary provided by Owens and Goetsch (1986). Hannah et al. (1991) also noted that increased intakes of low quality dormant range forage were positively related with weight of ruminoreticulum contents and suggested that factors other than rumen distention were more important than this factor in controlling intake in steers consuming low-quality roughages. Shaver et al. (1988) reported that weight of ruminal contents increased with the digestibility of the diet. Stafford et al. (1996) found that protein supplementation increased intake and hence the amount of material in the ruminoreticulum when measured after feeding, but there was a reduction in weight of ruminoreticular contents with increasing dietary protein when measured before feeding, possibly because of an increased rate of passage from the forestomach when dietary protein concentrations were increased. In contrast, Okine et al. (1993) detected no difference in weight of ruminoreticular contents when steers were fed diets containing from 33 to 100% barley straw with the remainder of the diet being hay. Contents weighed less, however, when 100% hay was fed. In general, then, these results concur with other literature observations and lend support to arguments of Ketelaars and Tolkamp (1992) and Mathison et al. (1995) that ruminant animals do not necessarily maintain a constant weight of DM in the rumen, particularly when low quality forages are fed. It is therefore clear that the effect of physical characteristics of feeds on rumen fill is not the main factor regulating intake under at least some circumstances. This supports our original hypothesis.

3.4.2 Voluntary Consumption of Straw-based Diets

One of the hypotheses for this experiment was that voluntary intake of straw over the feeding period could be increased if hay was fed only on alternate days or was rotated with straw in the diet. This hypothesis was confirmed since steers assigned to the alternate day hay feeding, 1-day hay-straw rotational, and 2-day hay-straw rotational feeding regimens consumed 56, 32 and 111%, respectively. more ($P < 0.05$) straw than those fed hay at maintenance with straw continuously available.

Voluntary straw consumption over the experimental period averaged 0, 0.19, 0.30, 0.25 and 0.40% of body weight daily for steers fed hay ad libitum, hay at maintenance, hay on an alternate-day basis, hay and straw rotated in the diet, and hay and straw rotated in the diet every 2 days, respectively (Table 3.4). Corresponding values for straw consumption on only the days for which straw was fed averaged 0, 0.19, 0.30, 0.50 and 0.83 % of body weight. These intakes are lower than the maximum voluntary consumption possible when straw-based diets are supplemented with either hay or concentrates. Okine et al. (1993) measured voluntary straw consumptions equivalent to 0.6, 1.1 and 1.5% of body weight when straw was included in diets containing 33, 67 and 100% straw with the remainder of the diet being alfalfa hay. The mean daily intake in the study of Mathison et al. (1981) was 1.4% of body weight when concentrates were used to supplement straw-based diet. Johnson (1972) in Saskatchewan reported straw intakes above 1.5% of the animal's weight, with intake increasing above this level, impaction of the stomach occured. Rode et al. (1997) reported voluntary intakes of untreated barley straw of 0.32% of body weight which is similar to the intakes noted here. Although results from this experiment demonstrated that although voluntary consumption of straw can be increased when different feeding methods are used, voluntary straw intakes were less than would be desirable in a high-straw diet for wintering cows where the percentage of straw in an all-forage diet might approach 50%.

It is well documented that intake of low quality forages can be increased by protein supplementation (Hannah et al. 1991). The possibility that a protein deficiency occurred when steers were fed for 2 consecutive days on straw alone may be the cause of reducing straw consumption with time and the numerically lower total DM intakes in the 2-day hay-straw rotational diet deserves comment. In this regard, the mean percentages of protein in the diets consumed by the steers were 12.3, 11.9, 11.6, 11.7, and 11.4% for steers hay ad libitum, hay at maintenance, hay on an alternate-day basis, hay and straw on a daily rotational basis, and hay and straw on a 2-day rotational basis, respectively. Dietary protein intakes would therefore have been adequate on days in which hay was fed. Moreover, scientific literature indicates that provision of protein supplements less frequently than on a daily basis has no adverse effect on animal performance in many circumstances when low quality forages are fed (Melton et al. 1960; McIlvain and Shoop 1962; Coleman and Wyatt 1982; Brandyberry et al. 1992; Collins and Pritchard 1992). With high concentrate diets, Cole (1999) even suggested that a feeding system in which there was an oscillating dietary protein intake might increase nitrogen recycling, improve quality of protein entering the small intestine, and increase the metabolic use of absorbed amino acids thereby decreasing the amount of nitrogen required in the diet. Therefore, in this study it is unlikely that protein limitations were the reason for the decrease in straw consumption over time for the 2-day hay straw treatment or the fact that intakes were numerically the lowest for this treatment. Reduced frequency of concentrate supplementation has, however, had a measurable negative effect on animal performance when low quality forages are fed in some studies (Kartchner and Adams 1982; Beaty et al. 1994). Information presented on concentrations of ruminal metabolites in the companion paper will be useful in addressing this issue in more detail.

It is our opinion that behavioral factors, possibly mediated through nutrient supply to that animal, were responsible the low voluntary consumption of straw. Support for this suggestion comes from the lack of relationship of ruminoreticular fill with DM consumption in this experiment. There is evidence in the literaturethat timing of feed supply can influence feeding behavior. Villalba and Provenza (1997) concluded that nutrient feedback from the gut should be viewed as an important factor affecting feed preferences in ruminants. In a later study (Villalba et al. 1999) determined that changes in preference for flavored wheat straw in a starch-supplemented diet depended upon the time at which starch was infused intraruminally. The importance of behavioral factors in affecting intake is also demonstrated by the classical experiment of Greenhalgh and Reid (1971). These researchers reported that straw consumption was increased two-fold when cattle ate hay voluntarily and had an equal amount of straw put into the rumen through a fistula rather than when they ate straw and an equal amount of hay put into the fistula. Our study, in which straw intakes could be changed by changing feeding regimens, confirms that steers will modify their eating habits in response to the changing cycle of nutrient supply or sensory characteristics of the feeds.

Total DM consumption by steers of diets in which hay was fed on alternate days or rotated in the diet either daily or every second day were markedly similar (7.8 to 8.2 kg d^{-1}). Although this would suggest that these feeding regimens would be equally effective, caution may be warranted with the 2-day hay-straw rational diet.

Hay intake was numerically the least with this diet during all periods. Additionally, there was a 13% reduction in DM intake with increasing length of time the steers were on the diet. Moreover variability of straw intake, as evidenced by standard errors, became greater as the feeding period progressed. This increase in data variability was attributable solely to an increased variation when steers were fed the 2-day rotational hay-straw diet; one animal maintained a relatively high intake throughout the 28-d straw feeding period whereas the other two animals decreased intake with time. These factors suggest that the 2-day hay-straw rotational diet might not be as effective for wintering cattle in the long term as would either the alternate day feeding of hay or the daily rotating of hay and straw in the diet.

3.4.3 Maximal Voluntary Consumption of Hay

Steers fed hay on either an alternate day or on a rotating basis consumed statistically similar amounts of hay as steers fed hay ad libitum on those days on which hay was fed (Table 3.2). However, in all cases consumptions were numerically higher when the steers were fed the hay in alternating or rotating hay diets. Moreover, when the steers were fed the 2-day hay-straw diet, intakes on the first day of hay feeding were 7% higher then on steers in which hay was provided ad libitum and 13% higher then heir intake on the second day of straw feeding (Tables 3.2 and 3.3). This suggests that an experiment with more statistical power might demonstrate an increased intake in cattle not fed hay the previous day.

We are unaware of experiments with ruminants in which the effect of either anticipation of a reduced feed supply or compensation for a reduced feed supply on feed intake has been determined. Variable results have been obtained with monogastric animals. Starved rats there may be a hyperphagic response upon refeeding (Turk 1988) or there may be none (Hill et al. 1984). Dulloo (1997) has reported that there is a hyperphagic response in man after starvation. De Castro (1997) was able to demonstrate that in humans the amount previously ingested has a negative effect on food ingested the next day but a larger effect on the second day. Any effect of feed intake differences disappeared by the fourth day.

In conclusion, although this experimental data did not statistically support the hypothesis that steers would consume more hay after a day in which none was provided than they would if hay was always continuously available, nevertheless our data numerically supported this concept and this would be consistent with some of the literature with monogastric animals.

3.5 Conclusions and Implications

Voluntary consumption of straw was increased both on any one day and over the experimental period when feeding systems in which hay was rotated in the diet with straw were compared with a feeding system in which hay and straw were continuously available. However straw intakes achieved when hay was fed at the maintenance feeding level, included in the diet on alternate days, or rotated with straw in the diet did not approach intakes from other experiments where straw and hay have been fed in fixed proportions. When hay and straw were rotated in the diet steers did not statistically increase voluntary consumption of hay on the days on which hay was available above ad normal libitum intake. However, such hyperphagic responses have been observed in monogastric animals and, because of missing animals, our experiment would only have had enough statistical power to detect very major differences in intake. The amount of dry matter in the ruminoreticulum was positively related to dry matter intake. Behavioral attributes, whether mediated through nutrient supply or in some other manner, may play a more important role in influencing voluntary consumption of low quality forage than rumen fill.

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Table 3.1 Summary of experimental treatments

	Controls		Alternate hay	Rotate hay and straw	
	Ad libitum hay	Hay Maintenance Straw	Hay-Straw	Hay, Straw	Hay, Hay, Straw, Straw
Day 1	Hay ad libitum	Hay maintenance straw ad libitum	Hay ad libitum, straw ad libitum	Hay ad libitum	Hay ad libitum
Day 2	Hay ad libitum	Hay maintenance straw ad libitum	Straw ad libitum	Straw ad libitum	Hay ad libitum
Day 3	Hay ad libitum	Hay maintenance straw ad libitum	Hay ad libitum, straw ad libitum	Hay ad libitum	Straw ad libitum
Day 4	Hay ad libitum	Hay maintenance straw ad libitum	Straw ad libitum	Straw ad libitum	Straw ad libitum

Table 3.2. Mean daily intakes of hay and straw dry matter on days in which these feeds were fed

Days	Hay ad libitum	Hay M Straw[Z]	Alternate: Hay-Straw	Rotate hay and straw: Hay, Straw	Rotate hay and straw: Hay, Hay, Straw Straw	SE[Y]	Probability	Repeated measures: SE[X] treatment	Repeated measures: Probability of treatment	Repeated measures: Probability of time	Repeated measures: Probability of Treatment x time
Dry matter intake (kg d^{-1})											
Hay											
Days 5-12	12.5	7.5	12.9	13.7	12.6	0.79	0.06	0.787	0.05	0.07	0.13
Days 13-20	11.6ab	6.3b	12.5ab	14.6a	12.5ab	0.91	0.05				
Days 21-28	11.8	8.0	13.0	14.1	11.2	0.78	0.06				
Overall	12.0a	7.3b	12.8a	14.1a	12.3a	0.65	0.04				
Straw											
Days 5-12	0.0c	1.17b	1.30b	2.39b	4.10a	0.209	<0.01	0.807	0.04	0.85	0.26
Days 13-20	0.0b	0.57b	1.47b	2.24b	4.01a	0.343	0.03				
Days 21-28	0.0	0.88	1.30	2.24	3.26	0.532	0.16				
Overall	0b	0.87b	1.36b	2.29ab	3.78a	0.34	0.04				
Dry matter intake (g kg$^{-0.75}$)											
Hay											
Days 5-12	112	66	115	121	111	7.7	0.07	7.51	0.06	0.11	0.13
Days 13-20	103	55	111	128	111	8.4	0.06				
Days 21-28	105	70	115	124	100	7.4	0.07				
Overall	108ab	64b	114ab	124a	109ab	7.3	0.05				
Straw											
Days 5-12	0.0c	10.1c	11.4c	21.0b	36.3a	2.00	<0.01	3.17	0.04	0.86	0.26
Days 13-20	0.0b	5.0b	13.1b	19.7b	35.5a	3.15	0.03				
Days 21-28	0.0	7.7	11.6	19.7	28.9	4.82	0.17				
Overall	0b	7.6b	12.0b	20.1ab	33.5a	3.17	0.04				

[Z] Hay fed at maintenance feeding level and straw ad libitum.
[Y] Pooled standard error is based upon three animals per mean.
[X] Pooled standard error is based upon three measured times for three animals.
[a-c] Means in the same row not followed by the same letter differ ($P<0.05$).

Table 3.3. Mean daily intakes with 2-day hay-straw rotational feeding system

	Day of new feed				Repeated measures			
	First	Second	SE[Z]	Probability	SE[Y] treatment	Probability of treatment	Probability of time	Probability of treatment x time
					Dry matter intake (kg d^{-1})			
Hay								
Days 5-12	13.4	11.9	0.56	0.20	0.49	0.13	0.02	0.53
Days 13-20	13.4	11.8	0.49	0.14				
Days 21-28	12.3	10.2	0.58	0.12				
Straw								
Days 5-12	3.68b	4.52a	0.11	0.03	0.22	0.21	0.14	0.51
Days 13-20	3.59	4.39	0.60	0.45				
Days 21-28	3.24	3.28	0.13	0.83				
					Dry matter intake (g $kg^{-0.75}$)			
Hay								
Days 5-12	118.0	104.8	4.92	0.20	4.37	0.13	0.02	0.53
Days 13-20	118.0	103.5	4.31	0.14				
Days 21-28	109.1	89.9	5.24	0.12				
Straw								
Days 5-12	32.6b	40.0a	0.43	0.03	1.93	0.21	0.14	0.51
Days 13-20	31.7	38.9	5.37	0.44				
Days 21-28	28.7	29.0	1.14	0.84				

[Z] Pooled standard error is based upon three animals per mean.

[Y] Pooled standard error is based upon nine three observations for three animals.

[a,b] Means in the same row not followed by the same letter differ ($P<0.05$).

Table 3.4. Mean period intake of hay and straw dry matter

	Hay ad libitum	Hay M-Straw[Z]	Alternate Hay-Straw	Rotate hay and straw: Hay, Straw	Rotate hay and straw: Hay, Hay, Straw, Straw	SE[Y]	Probability	Repeated measures: SE[X] Treatment	Repeated measures: Probability of treatment	Repeated measures: Probability of time	Repeated measures: Probability of Treatment x time
Dry matter intake (kg d^{-1})											
Hay											
Days 5-12	12.5a	7.5b	6.5b	6.9b	6.3b	0.45	0.04	0.912	0.04	<0.01	0.02
Days 13-20	11.6	6.3	6.3	7.3	5.8	0.55	0.08				
Days 21-28	11.8a	8.0b	6.5b	7.0b	5.6b	0.42	0.03				
Overall	12.0a	7.3b	6.4b	7.1b	6.4b	0.40	0.04				
Straw											
Days 5-12	0.0c	1.17b	1.30b	1.19b	2.05a	0.055	<0.01	0.100	0.01	0.99	0.11
Days 13-20	0.0c	0.57bc	1.47ab	1.12b	2.14a	0.155	0.02				
Days 21-28	0.0	0.88	1.30	1.12	1.63	0.215	0.11				
Overall	0b	0.87b	1.36a	1.15a	1.84a	0.089	<0.01				
Total											
Days 5-12	12.5	8.6	7.8	8.1	8.4	0.51	0.18	0.438	0.14	0.01	0.02
Days 13-20	11.6	6.9	7.7	8.4	7.9	0.41	0.16				
Days 21-28	11.8	8.9	7.8	8.2	7.3	0.48	0.09				
Overall	12.0	8.1	7.8	8.2	8.2	0.40	0.17				
Dry matter (g $kg^{-0.75}$)											
Hay											
Days 5-12	112a	66b	58b	60b	56b	4.18	0.04	4.12	0.04	<0.01	0.02
Days 13-20	103	55	56	64	51	4.75	0.07				
Days 21-28	106a	70b	58b	62b	50b	3.79	0.03				
Overall	107a	64b	57b	62b	56b	3.60	0.04				
Straw											
Days 5-12	0.0c	10.1b	11.4b	10.5b	18.1a	0.480	<0.01	0.952	0.01	0.98	0.11
Days 13-20	0.0c	5.0bc	13.1ab	9.9b	18.9a	1.430	0.02				
Days 21-28	0.0	7.7	11.6	9.9	14.4	1.952	0.12				
Overall	0b	7.6a	12.0a	10.1a	16.1a	0.87	<0.01				
Total											
Days 5-12	111	76	69	71	74	4.64	0.18	4.022	0.14	0.01	0.02
Days 13-20	103	60	69	74	70	3.48	0.12				
Days 21-28	105	78	69	72	64	4.57	0.10				
Overall	107	71	69	72	72	3.68	0.16				

[Z]Hay fed at maintenance feeding level and straw ad libitum.
[Y]Pooled standard error of the mean is based upon three animals per mean.
[X]Pooled standard error of the mean is based upon three measurements for three animals.
[a-c] Means in the same row not followed by the same letter differ (P<0.05).

Table 3.5. Effect of dietary treatment and evacuation time on weight of ruminoreticular contents

			Alternate	Rotate hay and straw				Repeated measures			
Days	Hay ad libitum	Hay M - Straw[Z]	Hay-Straw	Hay, Straw	Hay, Hay, Straw, Straw	SE[Y]	Probability	SE[X] treatment	Probability of treatment	Probability of time	Probability of Treatment x time
Total weight (kg)											
0900 h	73.8	68.9	70.0	72.4	71.9	2.57	0.51	1.54	0.32	0.52	0.93
1800h	75.3	72.0	72.6	71.5	73.5	3.59	0.69				
Overall	74.6	70.4	71.3	71.9	72.9	1.88	0.32				
Water (kg)											
0900 h	64.4	58.2	61.4	62.3	62.0	2.33	0.62	1.40	0.47	0.54	0.93
1800 h	64.7	61.8	63.7	61.6	63.4	3.36	0.81				
Overall	64.6	60.0	62.6	62.0	62.7	1.71	0.47				
Dry matter (kg)											
0900 h	9.4	10.7	8.6	10.1	10.0	0.41	0.08	0.16	0.01	0.66	0.61
1800 h	10.6	10.2	9.0	9.8	10.1	0.46	0.06				
Overall	10.0a	10.4a	8.8b	9.9a	10.0a	0.19	0.01				
Dry matter (%)											
0900 h	12.6b	15.3a	12.2b	13.7ab	13.7ab	0.35	0.01	0.18	0.01	0.92	0.56
1800 h	14.1	14.2	12.2	13.3	13.5	0.65	0.11				
Overall	13.4b	14.8a	12.2c	13.5b	13.6b	0.22	0.01				

[Z] Hay fed at maintenance feeding level and straw ad libitum.
[Y] Pooled standard error of the mean is based upon three animals per mean.
[X] Pooled standard error of the mean is based upon three measurements for three animals.
[a-c] Means in the same row not followed by the same letter differ ($P<0.05$)

Table 3.6. Effect of hay vs. straw feeding days on total weight and water in ruminoreticular contents

Time	Hay days		Straw days				Repeated measures			
	First	Second	First	Second	SE^Z	Probability	SE^Y treatment	Probability of treatment	Probability of time	Probability of treatment x time
						Total weight (kg)				
Hay on alternate days										
0900 h	71.6		68.4		5.49	0.72	5.1	0.16	0.42	0.09
1800 h	82.5a		62.8b		1.85	0.02				
Overall	77.0		65.6		3.68	0.16				
Hay, straw rotation										
0900 h	70.6		74.2		5.76	0.70	4.36	0.72	0.91	0.90
1800 h	70.7		72.2		8.14	0.91				
Overall	70.7		73.2		4.29	0.72				
Hay, hay, straw, straw rotation										
0900 h	75.8	77.3	68.0	66.7	4.64	0.34	4.46	0.20	0.41	0.71
1800 h	79.0	81.0	68.7	65.2	4.94	0.16				
Overall	77.4	79.1	68.3	66.0	4.46	0.20				
						Water (kg)				
Hay on alternate days										
0900 h	62.5		60.2		4.64	0.76	3.10	0.17	0.44	0.10
1800 h	71.6a		55.7b		1.66	0.02				
Overall	67.1		58.0		3.07	0.17				
Hay, straw rotation										
0900 h	61.0		63.6		5.18	0.75	2.99	0.83	0.93	0.83
1800 h	61.9		61.4		5.68	0.95				
Overall	61.5		62.5		2.99	0.83				
Hay, hay, straw, straw rotation										
0900 h	63.9	65.5	58.8	59.6	4.17	0.64	4.22	0.40	0.42	0.54
1800 h	68.6	68.5	59.1	57.4	4.88	0.31				
Overall	66.3	67.0	59.0	58.5	4.22	0.40				

[Z]Standard error is based upon three animals per mean.
[Y]Starndard error is based upon two measurements for three animals.
[a,b]Means in the same row not followed by the same letter differ ($P<0.05$).

Table 3.7. Effect of hay vs. straw feeding days on dry matter in ruminoreticular contents

	Hay days		Straw days				Repeated measures			
Time	First	Second	First	Second	SE[Z]	Probability	SE[Y] treatment	Probability of treatment	Probability of time	Probability of treatment x time
						Dry matter (kg)				
Hay on alternate days										
0900 h	9.0		8.1		1.15	0.62	0.93	0.21	0.33	0.04
1800 h	10.9		7.0		0.72	0.06				
Overall	9.9		7.6		0.93	0.21				
Hay, straw rotation										
0900 h	9.6		10.6		1.02	0.56	1.58	0.57	0.86	0.75
1800 h	8.8		10.8		2.45	0.62				
Overall	9.2		10.7		1.58	0.57				
Hay, hay, straw, straw rotation										
0900 h	11.9	11.8	9.1	7.1	1.13	0.06	0.47	<0.01	0.91	0.73
1800 h	10.5b	12.4a	9.5bc	7.8c	0.54	<0.01				
Overall	11.2a	12.1a	9.3b	7.4c	0.47	<0.01				
						% Dry matter				
Hay on alternate days										
0900 h	12.4		12.0		1.13	0.82	0.64	0.51	0.80	0.04
1800 h	13.2		11.3		0.94	0.30				
Overall	12.8		11.6		1.03	0.52				
Hay, straw rotation										
0900 h	13.4		14.1		1.02	0.66	1.29	0.52	0.47	0.28
1800 h	12.3		14.4		1.57	0.45				
Overall	12.8		14.2		1.28	0.52				
Hay, hay, straw, straw rotation										
0900 h	15.7	15.5	13.3	10.1	1.46	0.10	0.62	<0.01	0.88	0.63
1800 h	13.3	15.5	13.6	11.6	0.93	0.12				
Overall	14.5a	15.5a	13.4a	10.9b	0.62	0.01				

[Z]Standard error is based upon three animals per mean.
[Y]Starndard error is based upon two measurement for three animals.
[a,b]Means in the same row not followed by the same letter differ ($P<0.05$).

Table 3.8. Correlation coefficients among intake and rumen contents[z]

	Intake (kg d^{-1})			Rumen contents (kg)			
	Hay	Straw	Dry matter	Total (kg)	Water (kg)	Dry matter (kg)	Dry matter (%)
				Rumen evacuation at 0900 h			
Intake (kg d^{-1})							
Hay	1						
	(<0.01)[y]						
Straw	-0.70	1					
	(<0.01)	(<0.01)					
Total dry matter	0.96	-0.47	1				
	(<0.01)	(<0.01)	(<0.01)				
Rumen contents (kg)							
Total wt (kg)	0.24	-0.13	0.25	1			
	(0.16)	(0.44)	(0.15)	(<0.01)			
Water (kg)	0.10	-0.06	0.09	0.95	1		
	(0.58)	(0.71)	(0.59)	(<0.01)	(<0.01)		
DM (kg)	0.48	-0.23	0.51	0.46	0.15	1	
	(<0.01)	(0.17)	(<0.01)	(<0.01)	(0.37)	(<0.01)	
Dry matter (%)	0.37	-0.10	0.42	0.33	0.06	0.87	1
	(0.03)	(0.55)	(0.01)	(0.05)	(0.72)	(<0.01)	(<0.01)
				Rumen evacuation at 1800 h			
Intake (kg d^{-1})							
Hay	1						
	(<0.01)						
Straw	-0.74	1					
	(<0.01)	(<0.01)					
Total dry matter	0.97	-0.54	1				
	(<0.01)	(<0.01)	(<0.01)				
Rumen contents (kg)							
Total wt (kg)	0.60	-0.24	0.65	1			
	(<0.01)	(0.15)	(<0.01)	(<0.01)			
Water (kg)	0.49	-0.21	0.53	0.95	1		
	(<0.01)	(0.22)	(<0.01)	(<0.01)	(<0.01)		
DM (kg)	0.56	-0.20	0.62	0.54	0.27	1	
	(<0.01)	(0.24)	(<0.01)	(<0.01)	(0.11)	(<0.01)	
Dry matter (%)	0.24	-0.05	0.28	0.32	0.08	0.78	1
	(0.16)	(0.79)	(0.10)	(0.06)	(0.62)	(<0.01)	(<0.01)

[z]Correlation coefficiencts are based upon 36 observations.
[y] Values in brackets are probabilities.

CHAPTER 4

4.0 Effects of Changing Rumen Environment on In Situ Forage Digestibility

4.1 Introduction

Straw, which is a low quality forage, is commonly used in diets of beef cows in Western Canada. One of the major problems with straw is that it has a relatively low digestibility, which means that supplemental feed must be provided. Little attention has been paid in previous research with straw based-diets to alternate-day feeding of the hay or grain portion of the diet when straw is continuously available ad libitum or rotating hay with straw in the diet even though such feeding systems would decrease labor and equipment costs.

McIlvain and Shoop (1963) studied the effects of daily versus every third day feeding of protein supplements to beef steers on winter range and found no indication of a change in liveweight gains compared to animals fed supplements daily. Similarly, Melton et al. (1960), Coleman and Wyatt (1982), and Collins and Pritchard (1992) indicated that feeding protein supplements less than once daily had no adverse effect on animal performance. Hand (1996), however, conducted a preliminary on farm study with an alternate day feeding strategy in which hay was fed every second day and noted that although mature animals maintained weight, young cows and heifers did not as growth and maintenance may be limited by dry matter intake (NRC 1996). We are unaware of any research in which hay and straw have been fed on different days by rotating their inclusion in the diet.

The feed and feeding schedule determines the physio-chemical conditions of the rumen as well as the nutrients available to the microorganisms (Tatman et al. 1991). Digestive interactions can occur in the ruminant animal when different feeds are fed together and these associative effects may either increase or decrease the efficiency of feed use (Van Soest 1982). Positive results within the rumen and animal are expected if supplemental feeds supply limiting essential nutrients. In contrast, provision of high quality feeds containing high levels of starch can reduce the population of cellulolytic microorganisms in the rumen as well as their production of the cellulase enzyme (Yokoyama and Johnson 1988). It is therefore probable that manipulation of ruminal environmental conditions by changing feeding patterns will influence ruminal conditions and digestibility of a straw-based diet.

The hypothesis for this experiment was that in situ degradability of forages in the rumen of cattle can be increased when high quality feeds such as hay are fed with straw on an alternate-day basis or when hay and straw are rotated in the diet in comparison with hay when hay is provided daily. Ruminal degradability of hay and straw dry matter (DM) as well as ruminal pH, volatile fatty acids, and ammonia concentrations were measured to assess this hypothesis.

4.2 Materials and Methods

4.2.1 Animals and Feed

Five crossbred steers (454±10kg) were used in an incomplete 5x5 Latin square design experiment conducted at the Laird McElroy Environmental and Metabolic

Centre. These steers were fitted with a 10-cm i.d. soft ruminal cannula (Bar Diamond, Parma, ID) at least 90 days before the experiment as described in Chapter 3. The animals were cared for in accordance with the guidelines of the Canadian Council of Animal Care (1993) under the auspices of the Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare committee.

Dietary treatments were as follows 1) alfalfa (*Medicago sativa*) hay ad libitum, 2) hay fed daily at maintenance with barley straw (*Hordeum vulgare*) continuously available, 3) hay fed at twice maintenance every second day with straw continuously available, 4) hay and straw rotated in the diet on a daily basis, and 5) hay and straw rotated in the diet on a 2-day rotation basis. The hay contained 12.3% protein and 41.4% neutral detergent fiber. Corresponding values for straw were 8.2% and 64.5% which indicates the straw was of exceptional quality. Each period lasted for 40 days. There was 7 d of adaptation to the new diets between periods. Feeds were offered at 0800 h and refusals were removed and weighed prior to feeding the next day. Forages were chopped to approximately 6 cm through a tub grinder (model 390, Sperry, New Holland, PA). Animals were weighed before and after each experimental period and maintenance intake was calculated based on these weights according to the relationship $NE=0.077w^{0.75}$ (NRC 1996). A trace mineralized salt lick and water were available free choice.

Each period lasted for 40 days. There was a 4 d adaptation period to the diet before voluntary intake measurements began on day 5. The treatment period contained intake measurements, day 1 to 10, rumen metabolite collection and markers, day 11-

20, calorimetry on days 21-30, and rumen evacuations and nylon bag digestibility for days 31-40.

4.2.2 In Situ Degradability in Nylon Bags

The degradability of dry matter in hay and straw under different ruminal conditions was determined by means of nylon bag incubations conducted from d-16 through d-23 of the 40 d period. Forage samples were placed in the rumen of each animal at the morning feeding for 8 consecutive days and incubated for 0, 24 or 48 h.

Samples for the in situ incubation were ground (Thomas Mill Model 4, Philadelphia USA) through a 2 mm screen and placed in 5 cm x 10 cm nylon bags with a pore size of 50 μm (Ankrom, New York USA). Two to three grams of feed were placed into the bags that were then sealed with a plastic tie. A total of 12 bags (three bags per forage per time of incubation) were prepared and suspended in the rumen in a polyester mesh bag which was weighted with a sand-filled bottle (de Boer et al. 1987). Samples were introduced in reverse sequence; the 48-h bags were placed in the rumen first followed by the 24-h bags. Upon removal from the rumen, bags were frozen at -10 °C until they were thawed and washed simultaneously in a conventional washing machine. The bags were then dried at 60°C to constant weight and weighed to determine percent loss of dry matter (DM). Zero hour bags were used to correct for the soluble fraction in the digestibility calculations so that insoluble DM degradabilities could be reported.

4.2.3 Ruminal pH, Ammonia, and Volatile Fatty Acids

Rumen samples were taken every 3 h starting at 0000 h and ending at 2100 h to determine the effect of feeding regimen on the concentration of fermentation products in the rumen. The pH was measured immediately upon sampling with a pH meter (Expandomatics SS2, Beckman Instruments, California). Rumen samples were then prepared for VFA analysis by adding 1 mL of 25% phosphoric acid to 4 mL of rumen fluid prior to freezing at -5 °C. Prior to analysis, samples were thawed, centrifuged, and 1 mL was placed in a 1.5 mL glass sample tube and combined with 0.2 mL of isocaproic acid (internal standard) and sealed until analyzed. The internal standard solution was prepared by adding 0.3343 mg isocaproic acid to 100 mL distilled water in a volumetric flask.

The VFA concentrations were then determined by gas-liquid chromatography (Varian Model 3600, Sunnyvale, Ca) with a 30 m stable wax DA glass capillary column using helium saturated with formic acid as a carrier gas.

4.2.4 Statistical Analysis

The experimental design for the in situ procedure was originally a 5 x 5 Latin square design with five animals and five feeding strategies. Because of the loss of two animals from the experiment (see Chapter 3) the effects of feeding strategy (n=5), period (n=5), and animal (n=3) on mean in situ degradability were considered separately for each forage type incubated (hay or straw) and time (24 or 48 h) using the GLM procedure of SAS (SAS Institute Inc. 1988). These main effects, as well as time of incubation, were analyzed by the repeated measures analysis of the GLM procedure of SAS (SAS Institute 1988) to determine an overall effect of treatment and time of incubation on ruminal degradability within a forage species. The effect of adding bags to the rumen on days when hay or straw was fed was examined by a simple analysis of variance within each dietary treatment and time. Mean rumen pH and metabolite concentrations over the 4 d period were analyzed similarly within each time of measurement. In addition, ruminal pH and metabolite concentrations were compared for days on which hay or straw were fed within each time period. Also, within each dietary regimen, the effect of sampling time (n=8) and hay vs. straw feeding (n=2) were analyzed by the repeated measures analysis of the GLM procedure of SAS (SAS Institute, Inc. 1988). Means were separated using Student-Newman-Keul's test (SAS Institute, Inc. 1988).

4.3 Results and Discussion

Two animals had to be removed from the experiment (Chapter 3) which reduced the statistical power of the experiment. Moreover, there were missing samples at some times for a steer given the 1-day hay-straw rotation diet. In spite of these problems, the statistical power of the experiment was enough to detect differences in many instances.

4.3.1 In Situ Degradability of Hay and Straw

The nylon bags contained 20 to 30 mg sample per cm^2 of bag surface. This relatively high weight to surface area ratio was used by 16% of researchers in a summary by Vanzant et al. (1998). Although this is higher than the recommended value of 10 mg cm^{-2}, the effect of weight per surface area is not great when slowly degrading forages such as straw are used (Vanzant et al. 1998). The use of a 2 mm screen for grinding and a 50 micrometer pore size are consistent with recommendations of Vanzant et al. (1998).

Overall degradabilities of hay and straw at 24 and 48 h are shown in Table 4.1. No differences in hay degradability due to dietary regimen could be detected at either 24 h (59 to 66%) or 48 h (67 to 71%). Similarly, straw degradability ranged from 38 to 43% at 24 h and from 51 to 56% at 48 h and was not affected by dietary regimen. Type of forage in the diet has been shown to affect in situ degradation (Van Keuren and Heinemann 1962; Vanzant et al. 1998). Forage degradability is also depressed when animals are fed concentrates rather than roughages Vanzant et al. (1998). The fact that no differences were detected across diets in this experiment may not be surprising, however, since the diets were very similar; the percentage of hay in the diet exceeded 75% in all circumstances (Chapter 3) and the statistical power of this experiment was not great. These results are in agreement with those of Hunt et al. (1989) who found that altering the time between feeding of cottonseed meal supplement from 12, 24 or 48 h had no effect on in situ fiber digestibility.

After 48 h of incubation in the rumen of steers assigned to the alternate-day hay feeding, hay degradability was slightly higher (P=0.04; 71.4 vs. 70.3%; Fig. 4.1) when initially placed in the rumen on straw feeding days then when placed in the rumen on hay feeding days. With the 1-day hay-straw rotational dietary regimen, no differences were attributable to whether the sample bags were first inserted on hay or straw feeding days. In contrast, after 48 h incubation, ruminal degradabilities of straw for the 2-day hay-straw rotation dietary regimen were markedly influenced ($P < 0.01$) by day on which the straw was first put into the rumen. Straw DM degradabilties were 52.7, 58.4, 55.4, and 58.5% for the first hay, second hay, first straw, and second straw feeding days, respectively (Fig. 4.1); straw degradability averaged 8% higher when the straw was first placed in the rumen on the second day of feeding a particular feed type in comparison with when the straw was placed in the rumen on the first day of exposure to the feed. This improvement in digestibility may be associated with the type of bacteria which initially attach to the forage or type of substrates available to the microorganisms over their period of growth. Van Soest (1982) has noted that interactions within the rumen may influence digestibility of feeds.

In conclusion, although these experimental results did not support the hypothesis that changing the feeding pattern could be a means of increasing overall rate and extent of digestion in the rumen, relatively large numerical differences were observed between dietary treatment means as well as significant differences in degradability depending upon whether or not hay was fed on a particular day.

4.3.2 Ruminal ammonia concentrations

Overall ruminal ammonia concentrations tended ($P = 0.1$) to be influenced by diet, with the lowest mean concentration (5.0 mM) occurring with the 2-day hay-straw rotation diet and the highest with the diet in which hay was fed at maintenance and straw was continuously available (Table 4.2). Also, at 1500 h mean rumen ammonia concentrations were 30 and 60% higher ($P < 0.05$) for the treatment in which hay was fed at the maintenance feeding level than when it was fed on an alternate basis with straw or included in the 2-day hay-straw rotation diet, respectively. The lower mean ruminal ammonia concentrations which occurred with the 2-day hay-straw rotation dietary regimen was not surprising as less nitrogen was consumed by steers on this dietary regimen; although total feed intakes did not differ between treatments (Chapter 3). This diet contained a mean of 22% straw whereas when hay and straw were provided daily the diet consisted of 11% straw. Lower rumen ammonia concentrations for the alternate-day hay is also consistent with a slightly reduced nitrogen intake because of the nonsignificant reduction in DM intake and the higher percentage straw in this diet than in steers fed hay at the maintenance feeding level and straw daily (17 vs. 11%). However, Pritchard and Males (1982) noted that mean rumen ammonia concentrations were higher in cattle fed straw-based diets when protein supplements were fed twice daily than when they were fed once daily because of a more constant rumen ammonia concentration throughout the day.

Rumen ammonia concentrations reflect rate of its formation as feed protein is degraded and nitrogen is recycled to the rumen as well as rate of loss via absorption or passage and utilization by ruminal microorganisms for protein synthesis. There is contradictory evidence with respect to whether alternating a higher protein feedstuff in the diet can influence nitrogen recycling to the rumen. Liu et al. (1995) observed that changes in total body protein flux and synthesis and degradation occurred essentially immediately when lambs were switched from an adequate to deficient protein diet; these metabolic changes could influence nitrogen recycling to the rumen. Cole (1999), on the basis of a 38% increase in nitrogen retention in lambs, when crude protein levels were oscillated between 10 and 15% every 48 hours, concluded that it might be possible to increase transfer of nitrogen from the large intestine to the rumen by varying the timing of protein feeding. The rational for this suggestion was that nitrogen diffusion into both the large intestine and rumen is positively related to plasma urea nitrogen concentrations and negatively related to ammonia concentrations at the digestive site. Therefore increased recycling of nitrogen to the rumen could occur if there was an excess of ammonia in the large intestine and a deficiency in the rumen. The ultimate effect of varying dietary protein concentrations on ruminal ammonia concentrations would, according to Cole (1999), thus be dependent upon the effect of timing of feeding and the synchrony between the retention time of feed in the digestive tract. Henning et al. (1993) see plasma as a reserve nitrogen pool which may provide for microbial growth during periods of dietary deficiency. Krehbiel et al. (1996) did not detect any difference in nitrogen recycling to the rumen when ewes, fed a low quality forage, were provided with protein supplements at 1, 2 or 3 day intervals.

When hay was fed on alternate days and straw was continuously available overall ruminal ammonia concentrations only differed numerically between hay and straw feeding days (Fig. 4.2). At 1800h and 2100h, ammonia concentrations were 60 and 82% higher ($P < 0.05$; Fig. 4.2) during days on which no hay was fed than when hay was fed, respectively. Similarly within the 1-day hay-straw rotation regime concentrations were higher ($P<0.05$) at 2100 h on days when no hay was fed (Fig. 4.2). Ruminal ammonia concentrations were the lowest ($P<0.01$) on the second day of straw feeding in the 2 day hay straw rotational feeding regime whereas relatively high rumen ammonia concentrations were observed on the first day of straw feeding (Fig. 4.2). In contrast, Beaty et al. (1994) observed higher ruminal ammonia concentrations at 2400 h on days when supplemental protein was provided with a straw based diet than on days when no protein was provided. This difference may be because in our experiment straw intakes were very low on days when no hay was provided (0.3 and 0.5% of body weight for the alternate hay and 1-day hay-straw rotational feeding regimens, respectively) in comparison with the straw intakes of 1.2 to 1.4% of body weight in the study of Beaty et al. (1994). There may have been insufficient microbial growth in the rumen of our steers to capture the nitrogen which was recycled to the rumen thus rumen ammonia concentrations were increased on the days when no hay was fed. Similarly, this may explain the relatively high concentrations of rumen ammonia in the first day of straw feeding with the 2-day hay-straw rotational feeding regimen. Alternatively, there may have been extensive degradation of microbial protein in the rumen on the first day when no hay was provided and feed intakes were very low. Dijkstra et al. (1998) modeled the recycling of microbial nitrogen within the rumen and concluded that nitrogen recycling within the rumen could range from 35 to 76% of the microbial protein nitrogen synthesized thus degradation of microbial cells can contribute substantially to rumen ammonia concentrations. The observation of Krehbiel et al. (1996) that nitrogen recycling to the rumen was not influenced by day of supplementation would tend to support the latter source for rumen ammonia.

Satter and Slyter (1974) suggested that a minimal ruminal ammonia concentration of 2.9 mM was necessary for optimal fiber digestion in the rumen. Considerably higher estimates of requirements have also appeared (Song and Kennelly 1990). Mean ruminal ammonia concentrations exceeded the level suggested by Satter and Slyter (1974) with all dietary treatments (Table 4.2) which is not surprising since the hay contained 12.3% protein. Ruminal ammonia concentrations also exceeded these minimal requirements at all times even on days when hay was not fed for the hay maintenance, alternate-day hay, and 1-day hay-straw rotation treatments (Fig. 4.2). With the 2-day hay-straw rotational dietary treatment mean ammonia concentrations were 4.9, 7.1, 5.4 and 2.2 mM on day 1 of hay, day 2 of hay, day 1 of straw, and day 2 of straw feeding, respectively ($P < 0.01$; Fig. 4.2). On the second day of straw feeding ruminal ammonia concentrations only exceeded requirements suggested by Satter and Slyter (1974) at 0900 h and 1200 h. It is of interest that rumen ammonia concentrations were lower on the first day of hay feeding than on the first day of straw feeding. Thus, because of changes in nitrogen recycling to the rumen, capture of ammonia by rumen microbes or microbial protein degradation in the rumen, the steers maintained rumen ammonia concentrations for 1 day after a dietary change but no longer.

Relationships between ruminal ammonia concentration and degradability of forage DM are given in Fig. 4.3. All relationships were negative, with data for straw incubated for 48 h reaching significance ($P < 0.05$). This might suggest that degradation was inhibited when rumen ammonia concentrations were high. However as discussed above, ruminal forage degradability may be influenced by the type of microflora which initally colonized the forage or the availability of substrates and ammonia throughout the total period.

4.3.3 Ruminal pH and volatile fatty acid concentrations

Mean ruminal pH over all times and dietary treatments was 6.74 (Table 4.2) and did not differ between treatments ($P = 0.13$). However, differences ($P < 0.05$) due to dietary treatment were detected at 0300 h when the highest pH occurred in the rumen of steers fed hay ad libitum and the lowest in steers assigned to the 1 day hay-rotation treatment. At 2100 h, ruminal pH was highest in steers fed hay on alternating and lowest in the rumen steers fed hay and straw on a 1- or 2-day rotational basis, with steers fed hay ad libitum or hay at maintenance being intermediate ($P < 0.05$). Day on which hay or straw was fed did not affect ruminal pH when hay was fed on alternate days, hay and straw were rotated in the diet on a daily basis, or hay and straw were rotated in the diet every two days either on an overall basis or at any sampling time (Fig. 4.4). There is limited data concerning the effect of alternate-day feeding of a supplement or basal feed on ruminal pH. Hunt et al. (1989) observed no difference in mean ruminal pH when the diet of steers consuming grass hay was supplemented with cottonseed meal every 12, 24 or 48 h. Similarly, Collins and Pritchard (1992) did not detect a difference in ruminal pH when corn stalk-based diets were supplemented with protein at 24 or 48 h intervals. In contrast, Beaty et al. (1994) measured a decrease in mean ruminal pH of approximately 0.2 pH units when cattle were given straw-based diets supplemented with concentrate three times weekly in comparison with daily supplementation with concentrates on those days which supplemental concentrate was provided. Many experiments have examined the effect of increasing the frequency of feeding within a day on ruminal pH. No effect of increased frequency of feeding was observed Goetsch and Galyean (1983) Bunting et al. (1984), Nocek and Braund

(1985), Robinson and Sniffen (1985) and Froetschel and Amos (1991). Robinson and McQueen (1994) measured a lower mean ruminal pH in cattle fed five times daily than in those fed twice daily. Less variation within a day associated with increased frequency of feeding has also been noted by some researchers (Charmley et al. 1991; Nocek 1992) but not by others (Robinson and McQueen 1994).

We were unable to detect any effect of dietary treatment on total volatile fatty acid (VFA) concentrations in ruminal fluid (Table 4.3). Similarly, with the exception of 1200h for steers fed hay on alternate days, no differences were detected within treatments due to hay versus straw feeding (Fig. 4.4). No differences in total VFA concentrations were observed by Hunt et al. (1989) when cottonseed meal was provided every 12, 24 or 48 h. Also, Collins and Pritchard (1992) reported that ruminal VFA concentration was not affected when protein supplements were provided at 24 or 48 h intervals. In contrast, Pritchard and Males (1982) observed a mean 9% increase in VFA concentration in the rumen of steers fed twice daily in comparison with once daily and Froetschel and Amos (1991) reported a 5% increase in VFA concentration in steers fed 12 times daily in comparison to once daily.

Dietary treatment had no effect on the proportion of acetic acid in the total VFA (Table 4.3) but molar percentage was higher ($P = 0.03$) on the second day of straw feeding (77%) than on other days at 1200 h when the 2-day hay-straw rotational diet was fed (71-72%; Fig. 4.4). However, at 1800 h the percentage of acetic acid was lowest ($P = 0.04$) on the second day of straw feeding. These results were generally consistent with those of Hunt et al (1989) and Collins and Pritchard (1992) who reported that reducing the frequency of supplementation to less than once daily had no effect on acetic acid concentrations. The mean molar percentage of acetic acid in total VFA (77%) was very similar to the 78 to 79% reported by Lintzenich et al. (1995) when bluestem forage was supplemented with alfalfa. Increasing feeding frequency within a day has had a variable effect on the molar proportion of acetic acid (Pritchard and Males 1982; Froetschel and Amos 1991).

The mean molar percentage of propionic acid was not influenced by dietary treatment (Table 4.3) although differences were detected between days on which hay was and was not fed within diets. Thus with the alternate-day hay diet, the percentage of propionic acid in ruminal fluid was generally higher on days when hay was fed than when it was not fed (Fig. 4.5), with the difference reaching significance ($P < 0.01$) at 2100 h (15.2 vs. 12.9%). The lowest ($P < 0.01$) proportion of propionic acid overall in ruminal VFA was measured on the first day of straw feeding with the 2-day hay-straw rotational dietary regimen (Fig. 4.5). Hay or straw feeding days had no influence on propionic acid when hay and straw were rotated daily in the diet (Fig. 4.5). In studies of Hunt et al. (1989) and Collins and Pritchard (1992), the amount of propionate was not influenced by feeding protein supplements less often than once daily. Similarly, Pritchard and Males (1982) did not detect a difference in the percentage of propionic acid in ruminal VFA when supplement was provided either once or twice daily with wheat straw-based diets. No differences between days on which hay was fed and days on which hay was not fed were detected when hay and straw were rotated daily in the diet (Fig. 4) although at 1200 h, 1500 h and 2100h there was a tendency ($P < 0.1$) for ratios to be lower on days when hays was fed (Fig. 4.5).

No differences in acetic to propionic acid ratio were detected between dietary treatments (Table 4.3). No differences between day on which hay was fed and days which hay was not fed were detected with the alternate day diet (Fig. 4.5) although at 1200h, 1500h, and 2100h there was a tendancy ($P < 0.1$) for ratios to be lower on days when hay was fed. Within the 2-day hay-straw rotational dietary regimen, overall mean acetic to propionic acid ratios were 4.0, 4.1, 4.5 and 4.2 on the first day of hay, second day of hay, first day of straw, second day of straw feeding, respectively ($P = 0.01$; Fig. 4.5). Acetate to propionate ratios were not noticeably influenced by feeding frequency within a day (Pritchard and Males 1982; Froetschel and Amos 1991) or when protein supplements were provided on alternate days (Hunt et al. 19989; Collins and Pritchard 1992).

Dietary regimen had no influence on molar percentages of butyric, isobutyric, valeric or isovaleric acids in ruminal VFA (Table 4.4). Similarly, there was no overall effect of days on which whether hay was fed or not fed on these VFAs (Fig. 4.5 and 4.6). However at 0300h, with the alternate-day hay dietary regimen, the percentage of butyric and valeric acid concentrations in VFA were 50 and 69% higher ($P < 0.01$) on days when hay was fed on than on days when it was not fed. No differences were detected for these or other VFA within other dietary treatments. Similarly, Hunt et al. (1989) and Collins and Pritchard (1992) did not detect differences in these VFAs when frequency of feeding was less than once daily. Froetschel and Amos (1991) found differences in the proportion of butyrate in ruminal VFA when supplements were provided more frequently than once daily whereas Pritchard and Males (1982) found this effect for isovalerate as well as butyrate.

4.4. Conclusions and Implications

Although numerical differences of 11% existed between diets, we could not prove our hypothesis that rate and extent of degradation of forages in the rumen can be influenced by changing the percentage straw in the diet, feeding hay on alternate days, or rotating hay and straw. There was evidence to support the concept that ruminal degradation changes depending upon whether a feed first enters the rumen on a day on which hay is fed or on a day on which no hay is fed. This might be related to type of microflora which initially colonize the substrate or to variation in substrates available or endproducts formed throughout the period of digestion. Ruminal pH and volatile fatty acid concentrations were not markedly influenced by when hay was fed on alternate days or rotated with straw in the diet. Although ruminal ammonia concentrations were sufficient to support maximal fiber digestion (2.9 mM) when hay was available at least every second day when diets containing up to 17% straw were fed, animals did not maintain rumen ammonia concentrations at an optimal level when a 2-day hay-straw rotation was used. This, and information in Chapter 3, would suggest that feeding programs in which feeds are given further apart than 48 h may not be advisable.

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Table 4.1 Ruminal degradability (%) of insoluble hay and straw dry matter

Time	Hay ad libitum	Hay M-Straw[Z]	Alternate hay-straw	Rotate hay and straw: Hay, straw	Rotate hay and straw: Hay, hay straw, straw	SE[Y]	Probability
Hay dry matter							
24 h	63.8	59.0	66.4	63.3	64.3	1.82	0.58
48 h	68.7	67.4	70.9	68.0	68.6	0.73	0.76
Overall	66.3	63.3	68.6	65.7	66.5	1.12	0.61
Straw dry matter							
24 h	42.4	37.8	41.7	40.7	42.8	1.96	0.34
48 h	53.6	51.4	55.6	54.5	56.2	0.95	0.15
Overall	48.1	44.5	48.7	47.6	49.5	1.33	0.22

[Z]Hay fed daily at the maintenance feeding level with straw available ad libitum.

[Y]Standard error of the mean. There were 36 and 72 observations per mean for each time and for overall, respectively.

Table 4.2 Mean treatment ammonia concentration and ruminal pH

Time	Hay ad libitum	Hay M-Straw[Z]	Alternate hay-straw	Rotate hay and straw: Hay, straw	Rotate hay and straw: Hay, hay straw, straw	SE[Y]	Probability
Ammonia (mM)							
0 h	6.5	6.7	4.8	5.8	4.1	0.27	0.08
3 h	7.1	7.2	5.4	5.3	4.2	0.49	0.06
6 h	7.4	7.6	5.1	5.8	4.3	0.46	0.06
9 h	11.1	10.8	8.1	9.2	6.7	0.90	0.25
12 h	8.5	10.6	8.9	9.3	6.8	0.50	0.11
15 h	7.2ab	8.3a	6.4b	6.9ab	5.2b	0.15	0.05
18 h	7.6	6.6	5.7	7.0	4.7	0.70	0.31
21 h	6.8	5.9	4.7	5.8	4.1	0.41	0.10
Overall	7.8	7.9	6.2	6.9	5.0	0.35	0.10
Ruminal pH							
0 h	6.81	6.73	6.71	6.59	6.72	0.39	0.10
3 h	6.86a	6.76ab	6.83ab	6.62b	6.73ab	0.025	0.05
6 h	6.93	6.80	6.89	6.62	6.79	0.073	0.39
9 h	6.90	6.75	6.91	6.63	6.82	0.033	0.12
12 h	6.81	6.65	6.89	6.65	6.78	0.068	0.91
15 h	6.78	6.61	6.86	6.67	6.72	0.026	0.40
18 h	6.66	6.62	6.76	6.59	6.69	0.073	0.85
21 h	6.70b	6.71b	6.81a	6.56c	6.62c	0.018	0.02
Overall	6.80	6.70	6.83	6.62	6.73	0.027	0.13

[Z]Standard error of the mean. There were 24 and 192 observations per mean for each time and for overall, respectively.

Table 4.3 Mean treatment ruminal volatiole fatty acid concentration and molar percentages of acetate and propionate

Time	Hay ad libitum	Hay M-Straw[Z]	Alternate hay-straw	Rotate hay and straw: Hay, straw	Rotate hay and straw: Hay, hay straw, straw	SE[Y]	Probability
Total volatile fatty acids (mM)							
0 h	58	60	55	64	60	1.4	0.20
3 h	59	61	54	63	60	2.3	0.50
6 h	56	62	55	63	64	2.2	0.17
9 h	54	63	55	66	65	4.5	0.45
12 h	58	57	57	60	63	2.3	0.36
15 h	60	41	56	71	70	8.2	0.68
18 h	59	68	54	61	69	6.9	0.64
21 h	58	63	57	63	68	4.9	0.70
Overall	58	63	56	64	65	2.0	0.64
Acetic acid (Molar percentage of total)							
0 h	78	77	75	72	72	2.1	0.30
3 h	77	80	80	73	74	3.8	0.58
6 h	78	79	76	74	73	3.3	0.67
9 h	76	78	78	70	72	3.6	0.57
12 h	78	75	77	64	73	5.9	0.54
15 h	76	82	78	70	72	2.1	0.58
18 h	79	78	79	69	71	5.8	0.56
21 h	78	72	78	66	72	6.8	0.54
Overall	78	78	78	70	72	1.4	0.51
Propionic acid (Molar percentage of total)							
0 h	14	14	16	17	17	1.0	0.24
3 h	14	13	17	17	17	2.1	0.51
6 h	13	13	15	16	17	1.6	0.60
9 h	15	14	14	19	17	1.9	0.43
12 h	14	16	15	22	17	3.4	0.47
15 h	15	12	14	19	17	3.1	0.39
18 h	14	15	14	19	18	3.1	0.54
21 h	14	18	14	21	17	4.2	0.58
Overall	14	14	14	19	17	0.9	0.45
Acetic to propionic acid ratios							
0 h	6.5	6.8	6.0	4.8	4.3	0.8	0.23
3 h	6.3	7.2	7.6	6.3	4.4	1.5	0.59
6 h	6.7	7.4	6.4	5.9	4.4	1.2	0.52
9 h	6.0	6.6	6.6	3.9	4.2	1.1	0.42
12 h	6.5	5.7	6.0	4.4	4.4	1.6	0.75
15 h	6.1	7.8	6.8	4.0	4.3	0.8	0.57
18 h	6.6	7.2	6.4	3.9	4.2	1.6	0.48
21 h	6.2	6.0	6.8	3.5	4.3	1.6	0.53
Overall	6.3	6.9	6.6	4.6	4.3	0.4	0.47

[Z]Standard error of the mean. There were 24 and 192 observations per mean for each time and for overall, respectively.

Table 4.4. Mean treatment ruminal butyric, isobutyric, valeric and isovaleric acid concentrations

Time	Hay ad libitum	Hay M-Straw[Z]	Alternate hay-straw	Rotate hay and straw: Hay, straw	Rotate hay and straw: Hay, hay straw, straw	SE[Y]	Probability
Butyric acid (Molar percentage of total)							
0 h	5.7	5.4	6.1	6.8	7.1	0.78	0.59
3 h	5.7	5.0	5.1	6.7	6.6	0.95	0.60
6 h	5.5	5.2	6.2	6.0	7.0	1.05	0.77
9 h	5.9	5.0	5.3	6.7	6.6	0.95	0.73
12 h	5.4	5.9	5.2	8.4	6.3	1.53	0.64
15 h	6.0	4.1	5.2	7.0	7.0	0.78	0.67
18 h	5.3	5.3	5.0	7.6	7.4	1.65	0.64
21 h	5.7	6.7	5.2	8.1	7.0	1.74	0.59
Overall	5.6	5.4	5.4	7.2	6.9	0.36	0.64
Isobutyric acid (Molar percentage of total)							
0 h	0.77	0.72	0.68	1.19	1.00	0.17	0.27
3 h	0.82	0.75	0.63	1.16	0.94	0.20	0.48
6 h	0.86	0.77	0.73	1.14	1.03	0.26	0.70
9 h	0.98	0.74	0.64	1.14	1.12	0.23	0.57
12 h	0.80	0.82	0.75	1.29	1.13	0.29	0.67
15 h	0.85	0.49	0.67	0.97	1.07	0.32	0.89
18 h	0.57	0.68	0.66	1.32	1.14	0.33	0.54
21 h	0.64	0.86	0.64	1.48	0.94	0.35	0.46
Overall	0.78	0.74	0.66	1.22	1.04	0.07	0.54
Valeric acid (Molar percentage of total)							
0 h	0.68	0.69	0.74	0.98	0.80	0.10	0.25
3 h	0.87	0.65	0.54	0.91	0.56	0.23	0.81
6 h	0.74	0.74	0.63	0.99	0.72	0.20	0.82
9 h	0.88	0.84	0.66	1.15	0.82	0.22	0.80
12 h	0.84	0.94	0.74	1.31	0.88	0.33	0.79
15 h	0.99	0.48	0.69	0.98	0.98	0.16	0.62
18 h	0.74	0.80	0.52	1.24	0.88	0.40	0.75
21 h	0.79	0.92	0.62	1.08	0.80	0.31	0.74
Overall	0.81	0.78	0.64	1.08	0.81	0.23	0.72
Isovaleric acid (Molar percentage of total)							
0 h	1.24	1.19	1.22	2.06	1.62	0.32	0.31
3 h	1.30	1.26	1.19	1.95	1.43	0.32	0.49
6 h	1.39	1.30	1.40	1.83	1.64	0.35	0.70
9 h	1.61	1.13	1.19	1.88	1.80	0.39	0.62
12 h	1.20	1.22	1.48	2.29	1.82	0.52	0.60
15 h	1.25	0.77	1.10	1.67	1.70	0.49	0.91
18 h	0.91	1.05	1.13	2.19	1.86	0.51	0.53
21 h	1.01	1.21	1.15	2.53	1.47	0.51	0.34
Overall	1.24	1.15	1.23	2.06	1.67	0.12	0.49

[Z]Standard error of the mean. There were 24 and 192 observations per mean for each time and for overall, respectively.

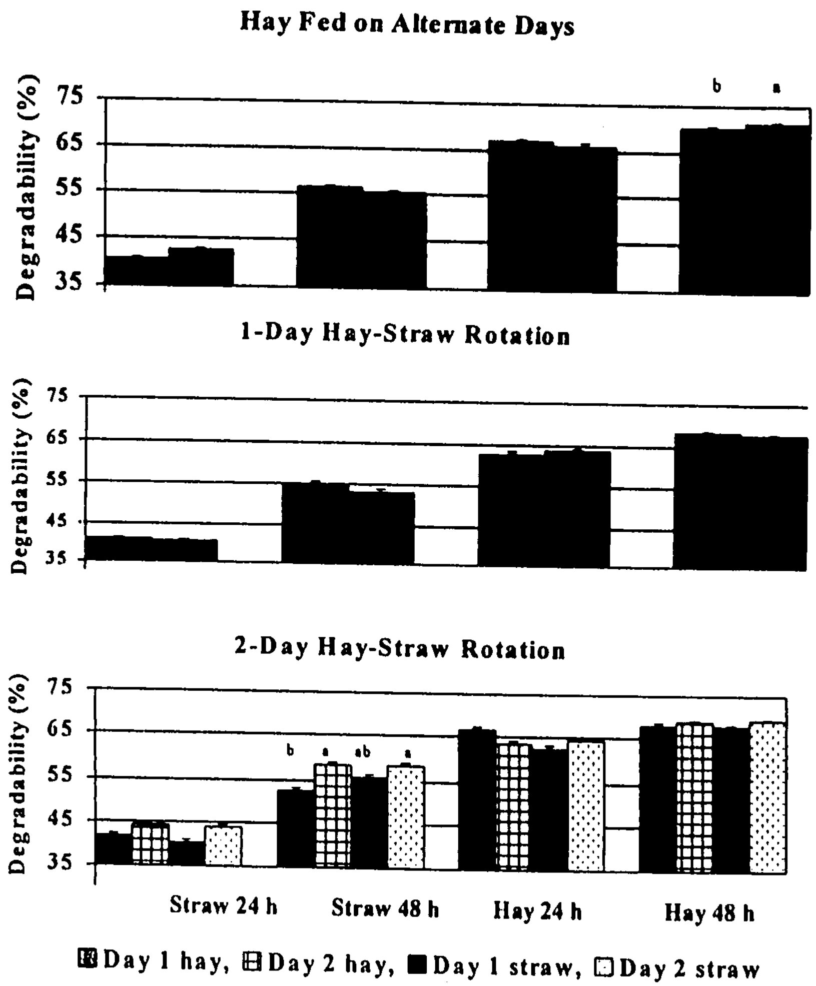

Fig. 4.1 Comparison of day of hay and straw feeding on ruminal degradability (%) of hay and straw incubated for 24 and 48 h. Vertical bars are pooled standard errors. a,b indicate differences ($P < 0.05$) between treatments at specific times. Number of observations per mean were 18, 18 , and 9 for diets in which hay was fed on alternate days, rotated daily in the diet, and rotated in the diet every two days respectively.

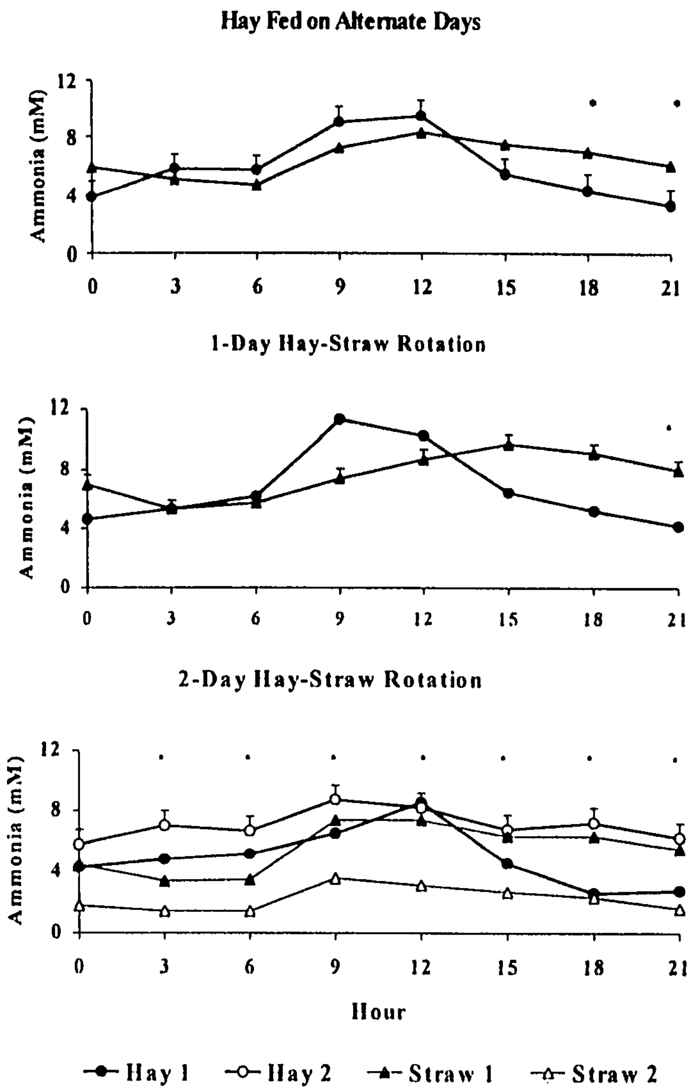

Fig 4.2 Comparison of the effect of day of hay and straw feeding on ruminal ammonia concentrations. Vertical bars are pooled standard errors. * Indicate differences ($P < 0.05$) between dietary treatments at that specific time. There was 12, 12, and 6 observations per mean at each time for diets in which hay was fed on alternate days, rotated daily, and rotated every two days.

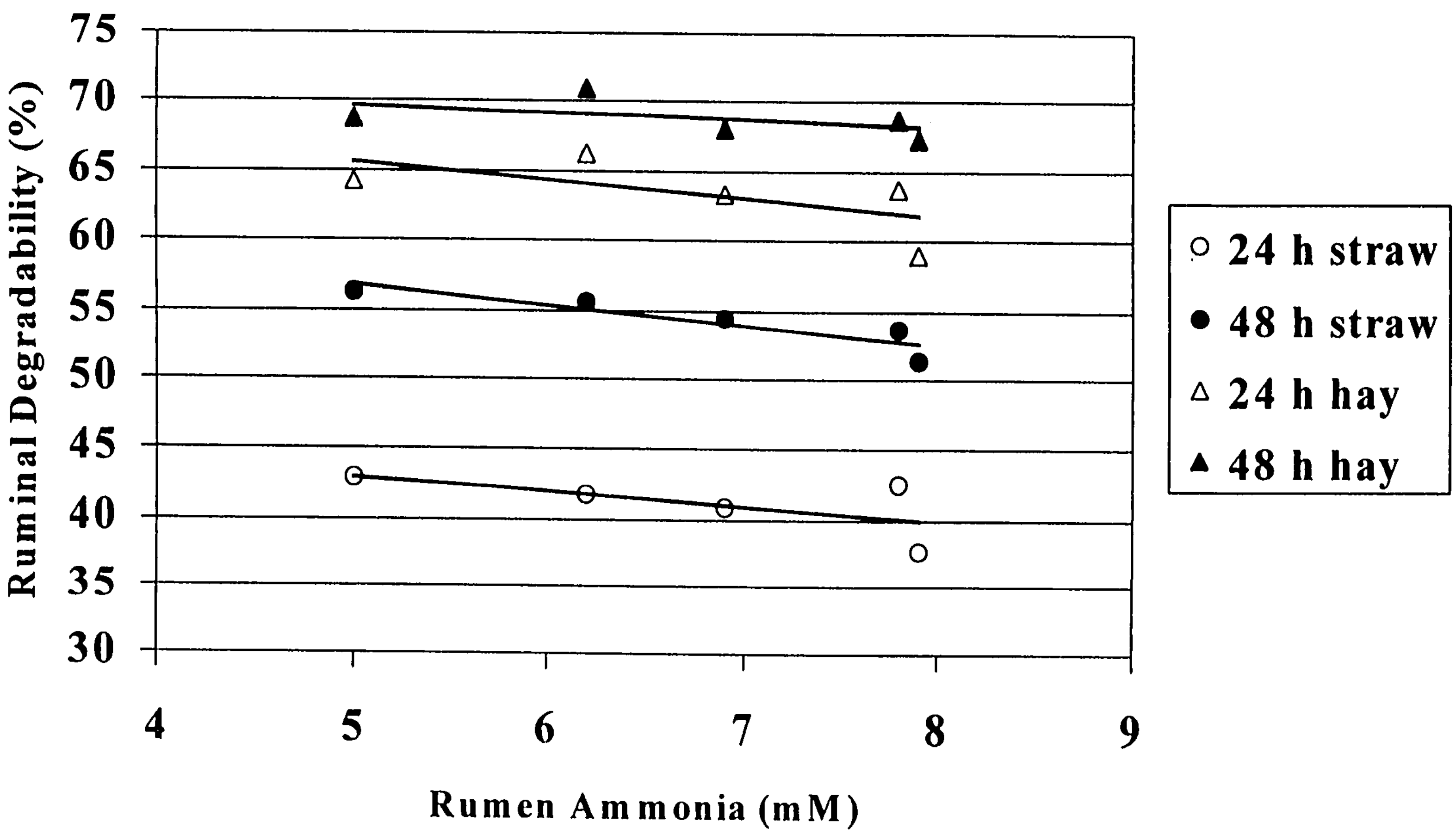

Fig. 4.3 Effect of rumen ammonia concentration on the day the bags were first put into the rumen on ruminal degradability of forage samples after 24 and 48 h of incubation. The relationships for the 24 h straw, 48 h straw, 24 h hay and 48 h hay samples were respectively: Y=47.8-1.00X, R^2=0.36, SE =1.84; Y=63.7-1.39X, R^2=0.79, SE=0.89; Y=72.5-1.36X, R^2=0.36, SE=2.49; Y=71.8-0.45X, R^2=0.17, SE=1.39. There was 12, 12, and 6 observations per mean at each time for diets in which hay was fed on alternate days, rotated daily, and rotated every two days.

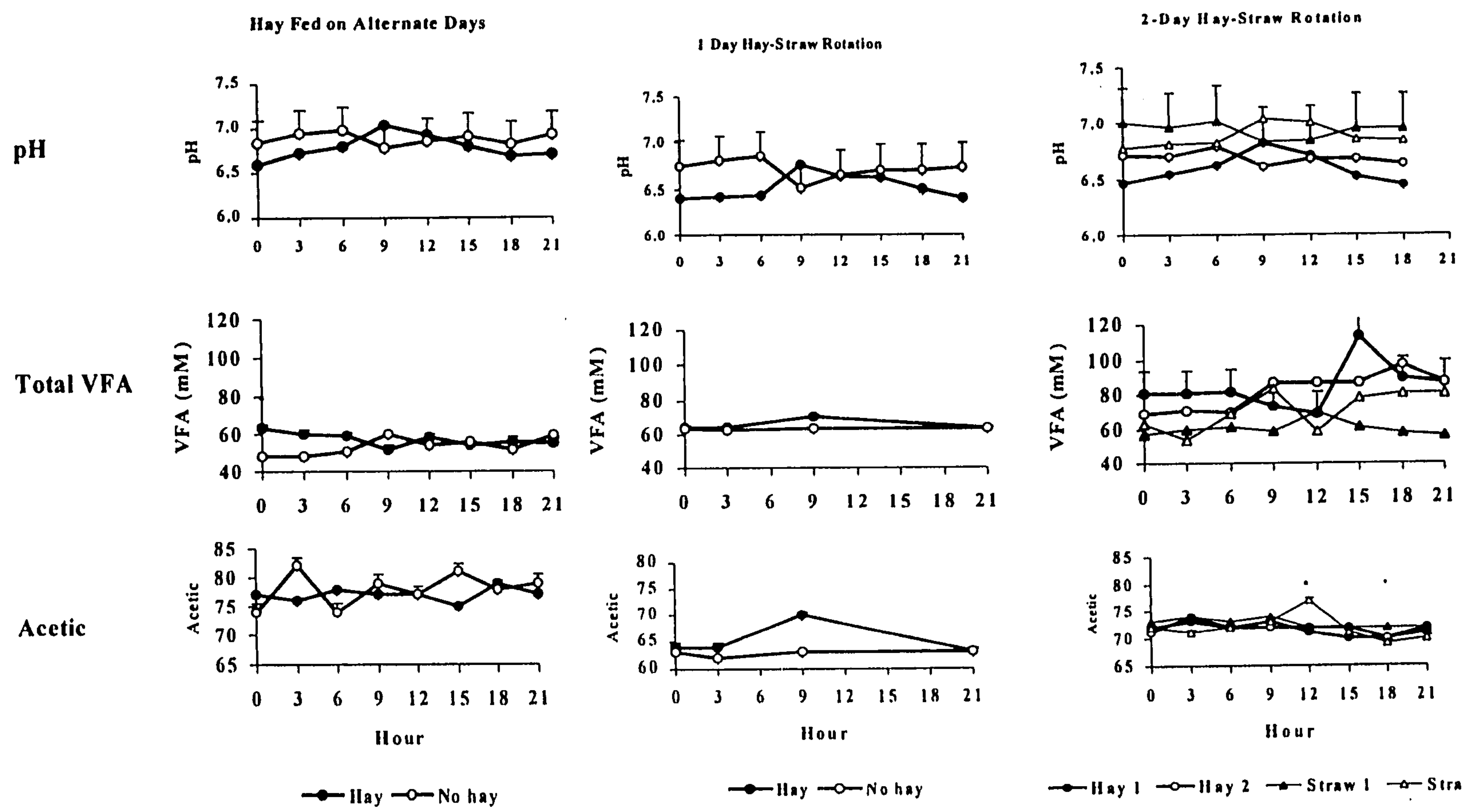

Fig. 4.4 Comparison of the effect of day of hay and straw feeding on ruminal pH, total volatile fatty acid (VFA) concentrations (mM), and molar percentage acetic acid in ruminal volatile fatty acids. Vertical bars are pooled standard errors. * Indicate differences ($P<0.05$) between dietary treatments at that specific time. There was 12, 12, and 6 observations per mean at each time for diets in which hay was fed on alternate days, rotated daily, and rotated every two days.

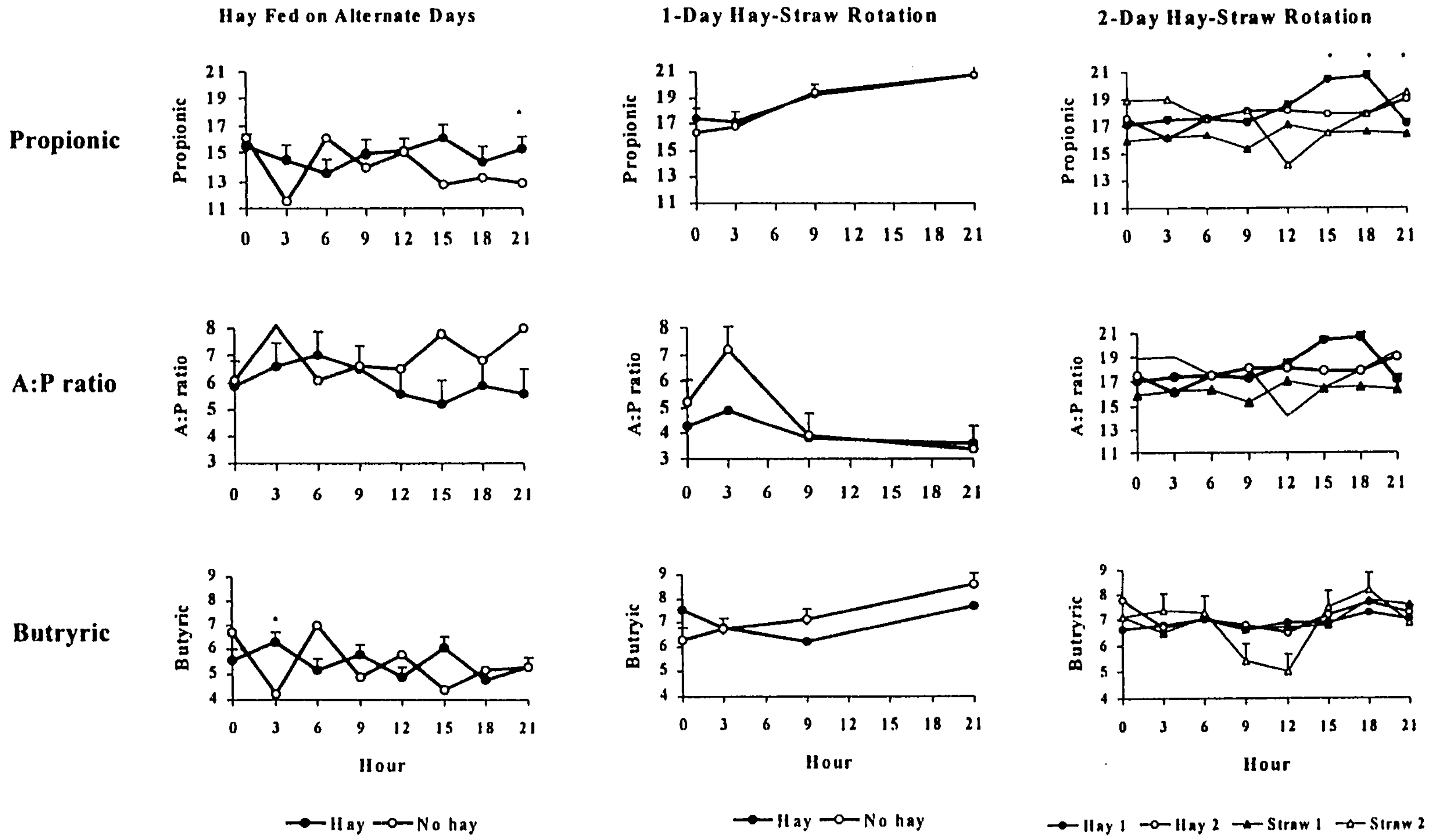

Fig. 4.5 Comparison of the effect of day of hay and straw feeding on molar percentages of propionic and butyrric acids in total ruminal volatile fatty acids and ratio of acetic to propionic acids (A:P ratio). Vertical bars are pooled standard errors. * Indicate differences ($P<0.05$) between dietary treatments at that specific time. There were 12, 12, and 6 observations per mean at each time for the diets in which hay was fed on alternate days, rotated daily, and rotated every two days respectively.

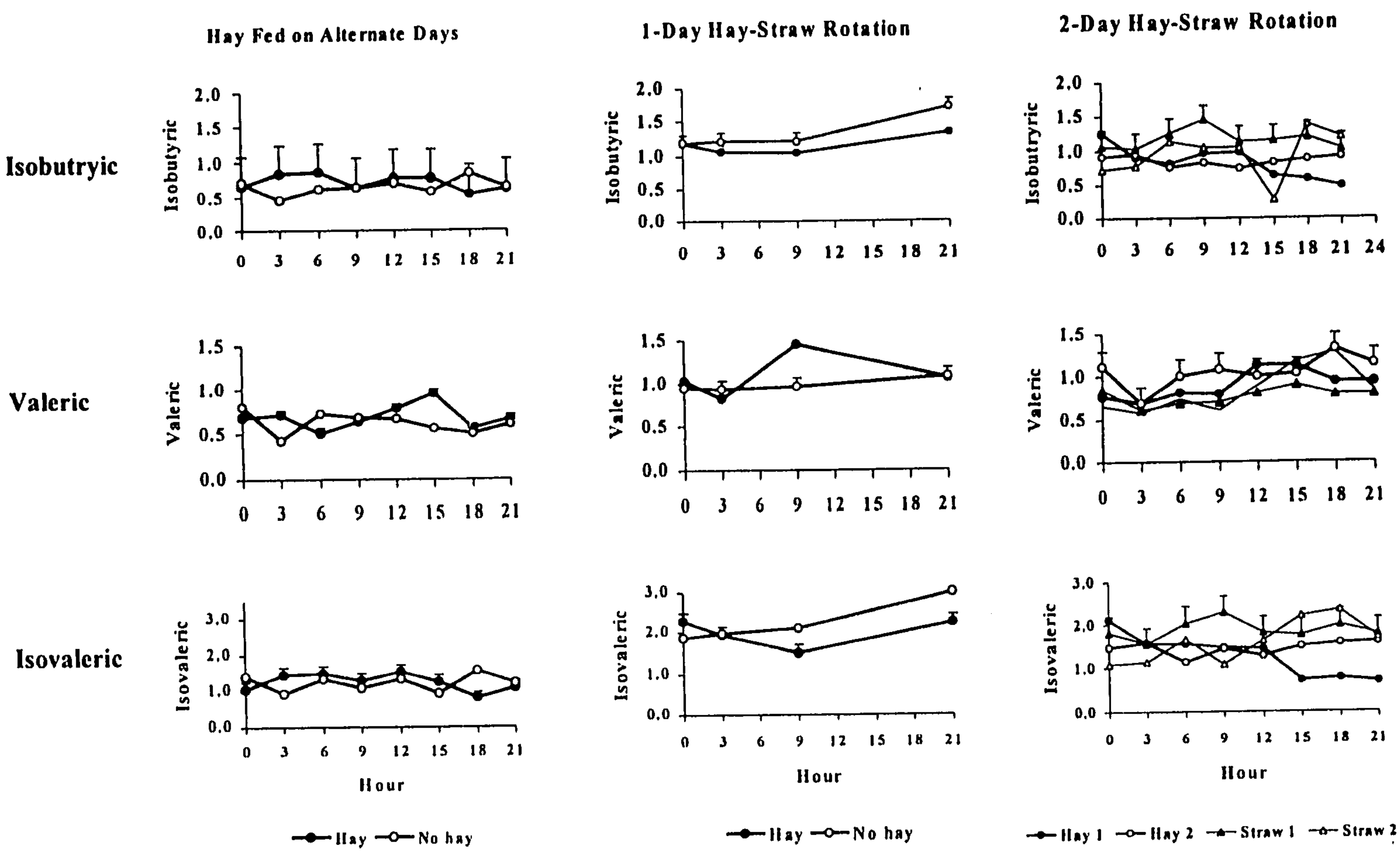

Fig. 4.6 Comparison of the effect of day of hay and straw feeding on molar percentages of isobutyric, valeric and isovaleric acids in total ruminal volatile fatty acids. Vertical bars are pooled standard errors. * Indicate differences (P<0.05) between dietary treatments at that specific time. There were 12, 12, and 6 observations per mean at each time for the diets in which hay was fed on alternate days, rotated daily, and rotated every two days respectively.

CHAPTER 5

5.0. General Conclusions and Discussion

There are a number of reasons for alternative feeding strategies to be used on farm including reduced costs of feeding, reduced labor costs, decreased competition for restricted feeds, increased low quality forage utilization, and increased productivity. The objectives of this animal study were to evaluate the potential constraints that would occur under a similar production system, including voluntary intake levels, ruminal changes, and fluctuations in ruminal digestibility.

The diets that were compared in this study were those similar to diets currently in use on farms in Alberta. Dietary treatments consisted of 1) hay fed ad libitum, 2) hay fed at the maintenance feeding level along with straw ad libitum daily, 3) hay fed twice maintenance levels on alternate days with straw ad libitum at all times, 4) hay and straw rotated in the diet each day, and 5) hay fed for two consecutive days rotated with straw which was fed for the next two consecutive days.

In Chapter 3 it was demonstrated that voluntary consumption of straw averaged 0, 0.19, 0.30, 0.25 and 0.40% of body weight for steers fed hay ad libitum, hay at maintenance, hay on alternate days, hay in a 1-day rotation and hay in a 2-day rotation, respectively ($P < 0.01$). The maximum straw intake achieved by the steers was 0.83% on the second day of straw feeding with the 2-day hay-straw rotational dietary regimen. This data thus confirmed the hypothesis that it is possible to increase straw intake by changing the time at which it is provided in the diet. However straw intake was substantially lower than the values reported by Okine et al. (1993), Mathison et al. (1981), and Johnson (1972). There are a number of reasons that this may have occurred; steers were fed indoors which may have been an important factor and differences in straw protein quality cannot be ruled out. In addition, animal behavior may be important since steers were aware of the dietary treatment of other steers on test. Although the voluntary intake of hay on the day following 2 days of straw was not significantly increased above the ad libitum levels of the other diets, hay intake was 13% higher than in the diet in which hay was fed ad libitum. The lowered level of statistical power of our experiment due to missing animals may have been sufficient to have caused a type II error ad the lack of significance of this difference. There are no other reports with ruminants which deal with intake levels following a day when only low quality feed was available.

Data in Chapter 3 also demonstrated that at 1800 h the mean amount of dry matter in the ruminoreticulum was reduced when steers were fed hay on alternate days with straw available free choice. Moreover with the 2-day hay-straw rotational diet, the amount of dry matter was substantially reduced on days when straw was fed. Hay and dry matter intake were thus positively correlated with the weight of dry matter in the rumen. In general, then, the results of this experiment support suggestions by Mathison et al (1995) and Ketelaars and Tolkamp (1992) that ruminant animals do not necessarily maintain a constant weight of dry matter in the rumen, particularly when low quality forages are fed.

Data in Chapter 4 demonstrated that there were no difference in the ruminal degradability of hay or straw related to the dietary feeding regimen at either 24 or 48 hours. The lack of significant difference is not unexpected, as the makeup of the diets was very similar; the percentage of hay in the diets exceeded 75% under all circumstances. These results are supported by the findings of Hunt et al (1989) that found that altering time between feeding of cottonseed meal had no effect on in situ forage digestibility. However, in our study, hay was slightly more degradable when placed in the rumen on straw feeding days in the alternate day feeding regimen. Also, when animals were fed on the 2-day hay-straw rotation diet, straw dry matter degradabilities were 52.7, 58.4, 55.4, and 58.5% for the first hay, second hay, first straw, and second straw feeding days, respectively ($P < 0.01$). Straw degradability thus averaged 8% higher when the straw was first placed in the rumen on the second day of feeding a particular feed type in comparison with when the straw was placed in the rumen on the first day of exposure to the feed. This study thus demonstrated that although ruminal environment does influence forage degradability, differences will not be large enough to have a major impact on animal performance if hay is fed on alternate days or rotated with straw in the diet.

Overall ruminal ammonia concentrations tended to be influenced by diet, with the lowest mean concentration occurring with the 2-day hay-straw rotation diet and the highest with the diet in which hay was fed at maintenance and straw was continuously available. This result is consistent with that of Pritchard and Males (1982) who noted that mean rumen ammonia concentrations were higher in cattle fed straw-based diets when protein supplements were fed twice daily than when fed once daily. However, some of the numeric differences in rumen ammonia concentrations were also explainable by differences protein intake. Of most interest was the observation that, although rumen ammonia concentrations could be maintained for one day of straw feeding, concentrations dropped markedly when straw was fed for two consecutive days. We did not determine whether this result was obtained because of differences in nitrogen recycling to the rumen (Cole 1999), breakdown of microbial nitrogen within the rumen (Dijkstra et al. 1998), or microbial capture of rumen ammonia. Mean ruminal pH was 6.74 and did not differ between dietary treatments. Similarly, no dietary effects were detected for total volatile fatty acid (VFA) concentration. These results are supported by work done by Hunt et al. (1989) and Collins and Pritchard (1992), both who found no effect of alternating supplementation on total VFA. In contrast, Pritchard and Males (1982) and Froetschel and Amos (1991) reported increases in VFA concentration in steers when increasing frequency of supplementation. Dietary treatment had no effect on the mean proportion of acetic and propionic acid present in the rumen fluid nor was there any effect on butyric, isobutyric, valeric or isovaleric acids in ruminal fluid. Differences were, however, noted between days when hay was fed and days when hay was not fed.

Overall, these results demonstrated that voluntary intake and ruminal parameters are not changed substantially when hay is fed on alternate days with straw continuously available or rotated on a daily basis with straw in comparison to when hay is fed at maintenance and straw is continuously available. This confirms that there is potential for cattlemen to use these feeding strategies for maintaining cows in the wintering period in Alberta. However, our data would suggest that it is not advisable to feed only straw for 2 consecutive days since intake may be adversely affected as the cattle will not be able to maintain adequate rumen ammonia concentrations in the rumen.

Alternate-day or rotating feeding strategies could be a practical method of reducing feeding equipment costs, redistributing labor requirements, and reducing competition for high quality restricted feeds. The potential to use alternate day feeding strategies to reduce costs has been explored by Okine (1999). Okine (1999) reported that alternate day feeding required 15.6% less labor than traditional feeding. These differences in labor resulted in a $3.35 per cow savings over the 78 day experimental period (Okine 1999). In their study athere was a savings of 6.72 hours in the use of labor and equipment over the winter in comparison with traditional everyday feeding. This information has been used in conjunction with provincial data collected in Alberta and Saskatchewan and the resultspresented in Table 5.2. According to this data and information on beef cow numbers in Alberta, on farm savings of 9.6 to 16.8 million dollars in labor and equipment costs could be realized annuallyif an alternate day feeding strategy was adopted by cattle producers in Alberta. Cost of the feed itself would probably not change substantially with the every other day feeding of hay or silage unless there was a reduction in wastage. Even so, this level of ssavings is sufficient to encourage beef producers to look at new feeding strategies such as those examined in this thesis and by Hand et al.(1995) and Okine (19999).

In conclusion, since profit margins are so low in cow-calf operations, and because our results concerning the effect of feeding regimes on the digestive physiology of cattle did not detect any major problems, more experiments with alternate day hay feeding or 1 day hay straw rotation in which performance of cattle is monitored are warranted. The ultimate test of a system in which a higher quality feed is fed only every second day along with straw is how the feeding practice influences weight and condition changes, reproductive performance, health, longevity, and animal welfare. Preliminary data on these aspects of alternative feeding systems loo very favorable (Okine et al. 2000).

5.1. References

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Table 5.1. Comparison of every-day and alternate-day feeding of cows (from Okine 1999)

Item	Every-day feeding	Alternate-day feeding
Labor requirements (min per cow for 78 d)	74.6	60.8
Time associated with each activity (%)		
Feeding silage and straw	60.1	51.0
Removing manure	33.3	40.9
Bedding	6.6	8.1

Table 5.2. Cost of winter feeding in Alberta and Saskatchewan

Item	Alberta	Saskatchewan
Labor per cow (h yr^{-1})[Z]	11.3	6.2
Labor for feeding[Y]	3.6	1.9
Yearly savings from alternate day feeding[X]		
Percent	27	27
Hours per cow	0.91	0.51
Dollars per cow	9.10	5.10

[Z]Alberta and Saskatchewan data obtained from Kaliel et al. (1995) and McNinch et al. (1998), respectively.
[Y]Based upon an average of 32% of total labor required for feeding (Kaliel 2000).
[X]Based upon a savings of 27% in total feed and equipment costs associated with alternate-day feeding (Hand et al. 1995) and costs of labor of $10 per hour (Kaliel et al. 1995).

APPENDIX

Tabular Data for Within Diet Comparisons in Chapter 4

Table A.1. Ruminal degradability (%) of insoluble dry matter and the effect of placing bags in the rumen on days when hay or straw was fed

	Hay days		Straw days			
Incubation time	First	Second	First	Second	SE[z]	Probability
			Hay incubated			
Hay on alternate days						
24 h	66.9		66.0		0.44	0.43
48 h	70.3b		71.4a		0.27	0.04
Hay, straw rotation diet						
24 h	62.8		63.8		0.46	0.21
48 h	68.4		67.5		0.32	0.13
Hay, hay, straw, straw rotation						
24 h	66.7	63.5	62.6	64.3	0.72	0.29
48 h	68.1	69.0	68.0	69.3	0.39	0.32
			Straw incubated			
Hay on alternate days						
24 h	40.7		42.7		0.43	0.17
48 h	56.1		55.2		0.44	0.57
Hay, straw rotation						
24 h	40.8		40.7		0.44	0.90
48 h	55.1		53.4		0.51	0.18
Hay, hay, straw, straw rotation						
24 h	41.8	44.2	41.5	43.9	0.67	0.39
48 h	52.7b	58.4a	55.4ab	58.5a	0.59	<0.01

[z]Standard error of the mean is based upon 18 samples per mean when hay was fed on alternate days and rotated daily with straw and 9 samples per mean for the 2 day hay-straw rotation diet.

[Ab]Means in the same row not followed by the same letter differ ($P<0.05$).

Table A.2. Effect of days on which hay or straw was fed on ruminal pH and ammonia concencentration when hay was fed on alternate days and straw was continuously available

Time	Hay fed	Straw fed	SE[z]	Probability	Repeated measures			
					SE treatment	Probability of feeding day	Probability of time	Probability of time x day
pH								
0 h	6.60	6.83	0.28	0.62	0.26	0.72	0.86	0.72
3 h	6.72	6.94	0.30	0.65				
6 h	6.80	6.99	0.23	0.62				
9 h	7.04	6.78	0.05	0.37				
12 h	6.92	6.85	0.21	0.37				
15 h	6.80	6.91	0.13	0.62				
18 h	6.69	6.82	0.27	0.76				
21 h	6.70	6.92	0.27	0.62				
Ammonia (mM)								
0 h	3.8	5.8	0.64	0.17	1.07	0.42	0.01	0.25
3 h	5.7	5.0	0.36	0.38				
6 h	5.6	4.6	0.92	0.53				
9 h	9.0	7.2	1.89	0.58				
12 h	9.5	8.3	1.67	0.65				
15 h	5.4	7.5	1.43	0.39				
18 h	4.3b	6.9a	0.39	0.04				
21 h	3.3b	6.0a	0.31	0.02				

[z]Standard error is based upon 12 samples per mean.

Table A.3. Effect of days on which hay or straw was fed on ruminal total volatile fatty acids, acetic acid, propionic acid, and acetic to propionic ratio when hay was fed on alternate days and straw was continuously available

Time	Hay fed	Straw fed	SE[z]	Probability	Repeated measures			
					SE treatment	Probability of feeding day	Probability of time	Probability of time x day
Total volatile fatty acid concentration (mM)								
0 h	63a	48b	1.89	0.03	2.16	0.20	0.99	0.07
3 h	60	48	5.33	0.27				
6 h	59	51	4.40	0.31				
9 h	52	60	2.59	0.15				
12 h	58	54	4.86	0.60				
15 h	54	56	3.58	0.71				
18 h	56	52	1.71	0.26				
21 h	55	59	2.64	0.43				
Acetic acid (Molar percentage of total)								
0 h	77	74	3.71	0.69	1.47	0.46	0.58	0.23
3 h	76b	82a	0.70	0.02				
6 h	78	74	3.45	0.53				
9 h	77	79	1.88	0.32				
12 h	77	77	1.05	0.87				
15 h	75	81	1.53	0.11				
18 h	79	78	1.23	0.48				
21 h	77	79	0.57	0.11				
Propionic acid (Molar percentage of total)								
0	15.4	16.1	2.79	0.88	1.00	0.38	0.75	0.58
3	14.5	11.5	1.74	0.17				
6	13.6	16.1	2.86	0.60				
9	14.9	14.0	1.40	0.71				
12	15.1	15.0	0.93	0.90				
15	16.1	12.8	0.80	0.10				
18	14.4	13.3	0.53	0.29				
21	15.2a	12.9b	0.16	<0.01				
Ratio of acetic to propionic acids								
0 h	5.9	6.1	0.86	0.89	0.90	0.34	0.62	0.24
3 h	6.6	8.1	1.14	0.45				
6 h	7.0	6.1	1.43	0.69				
9 h	6.5	6.6	0.82	0.97				
12 h	5.6	6.5	0.18	0.07				
15 h	5.2	7.8	0.65	0.10				
18 h	5.9	6.8	0.50	0.33				
21 h	5.6	8.0	0.54	0.09				

[z]Standard error is based upon 12 samples per mean.

Table A.4. Effect of days on which hay or straw was fed on ruminal butyric, isobutyric, valeric acid, and isovaleric, acids when hay was fed on alternate days and straw was continuously available

Time	Hay fed	Straw fed	SE[z]	Probability	Repeated measures			
					SE treatment	Probability of feeding day	Probability of time	Probability of time x day
Butyric acid (Molar percentages of total)								
0 h	5.6	6.7	0.82	0.42	0.41	0.87	0.52	0.07
3 h	6.3a	4.2b	0.06	<0.01				
6 h	5.2	7.0	1.27	0.40				
9 h	5.8	4.9	0.34	0.20				
12 h	4.9	5.8	0.53	0.39				
15 h	6.1	4.4	0.64	0.20				
18 h	4.8	5.2	0.19	0.22				
21 h	5.3	5.3	0.62	0.99				
Isobutyric acid (Molar percentage of total)								
0 h	0.66	0.71	0.13	0.80	0.09	0.51	0.97	0.34
3 h	0.82	0.46	0.14	0.22				
6 h	0.85	0.62	0.21	0.53				
9 h	0.64	0.64	0.13	0.99				
12 h	0.76	0.71	0.08	0.68				
15 h	0.77	0.57	0.09	0.27				
18 h	0.54	0.83	0.15	0.29				
21 h	0.62	0.64	0.05	0.87				
Valeric acid (Molar percentage of total)								
0	0.68	0.80	0.13	0.56	0.05	0.28	0.23	0.10
3	0.71a	0.42b	0.02	<0.01				
6	0.50	0.73	0.13	0.34				
9	0.64	0.68	0.05	0.67				
12	0.79	0.67	0.04	0.16				
15	0.96	0.56	0.15	0.20				
18	0.55	0.49	0.02	0.18				
21	0.66	0.61	0.12	0.84				
Isovaleric acid (Molar percentage of total)								
0 h	1.04	1.40	0.36	0.55	0.19	0.93	0.97	0.69
3 h	1.44	0.93	0.35	0.41				
6 h	1.48	1.34	0.54	0.86				
9 h	1.27	1.07	0.38	0.74				
12 h	1.52	1.31	0.35	0.72				
15 h	1.25	0.92	0.20	0.37				
18 h	0.80	1.57	0.39	0.30				
21 h	1.08	1.20	0.04	0.18				

[z]Standard error is based upon 12 samples per mean.

Table A.5. Effect of day of day on which hay and straw was fed on ruminal pH, total volatile fatty acid concentrations and acetic to propionic acid ratio when hay and straw were rotated in the diet each day

Time	Hay fed	Straw fed	SE[Z]	Probability	Repeated measures			
					SE treatment	Probability of feeding day	Probability of time	Probability of time x day
PH								
0 h	6.40	6.75	0.30	0.49	0.27	0.50	0.99	0.53
3 h	6.42	6.80	0.29	0.45				
6 h	6.44	6.85	0.28	0.41				
9 h	6.76	6.51	0.16	0.39				
12 h	6.64	6.65	0.24	0.91				
15 h	6.62	6.70	0.10	0.64				
18 h	6.49	6.70	0.23	0.59				
21 h	6.40	6.72	0.29	0.52				
Ammonia (mM)								
0 h	4.6	7.0	1.41	0.36	0.65	0.09	0.03	0.07
3 h	5.3	5.3	1.57	0.98				
6 h	6.2	5.7	1.33	0.83				
9 h	11.3	7.4	1.26	0.16				
12 h	10.3	8.7	1.41	0.51				
15 h	6.4	9.7	0.73	0.09				
18 h	5.2	9.1	0.91	0.09				
21 h	4.1b	8.0a	0.59	0.04				
Total volatile fatty acids (mM)								
0 h	64	63	1.1	0.81	0.68	0.10	0.56	0.50
3 h	64	62	1.9	0.39				
9 h	70	63	4.1	0.33				
21 h	63	63	1.1	0.73				
Acetic acid (Molar percentage of total)								
0 h	71	73	3.1	0.60	1.41	0.94	0.05	0.65
3 h	72	72	0.9	0.95				
9 h	71	69	1.2	0.49				
21 h	67	65	2.4	0.62				
Propionic acid (Molar percentage of total)								
0 h	17.4	16.4	2.1	0.76	0.80	0.78	0.07	0.97
3 h	17.1	16.8	0.6	0.74				
9 h	19.2	19.4	1.1	0.92				
21 h	20.7	20.7	1.2	0.98				
Acetic to propionic acid ratio								
0 h	4.3	5.2	0.95	0.61	0.88	0.55	0.12	0.58
3 h	4.9	7.2	1.96	0.49				
9 h	3.8	3.9	0.23	0.68				
21 h	3.6	3.4	0.32	0.72				

[Z]Standard error is based upon 12 samples per mean.

Table A.6. Effect of day on which hay and straw was fed on ruminal butyric, isobutyric, valeric, isovaleric, and ammonia concentrations when hay and straw were rotated in the diet each day

Time	Hay fed	Straw fed	SE[Z]	Probability	Repeated measures			
					SE treatment	Probability of feeding day	Probability of time	Probability of time x day
Butyric acid (Molar percentage of total)								
0 h	7.5	6.3	1.03	0.49	0.46	0.85	0.12	0.32
3 h	6.8	6.7	0.44	0.95				
9 h	6.2	7.1	0.25	0.13				
21 h	7.7	8.6	0.58	0.40				
Isobutyric acid (Molar percentage of total)								
0 h	1.19	1.18	0.07	0.98	0.12	0.18	0.14	0.70
3 h	1.06	1.21	0.20	0.63				
9 h	1.04	1.20	0.09	0.33				
21 h	1.32	1.72	0.21	0.32				
Valeric acid (Molar percentage of total)								
0 h	1.03	0.95	0.25	0.85	0.09	0.41	0.31	0.35
3 h	0.83	0.94	0.10	0.51				
9 h	1.45	0.97	0.14	0.14				
21 h	1.07	1.08	0.04	0.89				
Isovaleric acid (Molar percentage of total)								
0 h	2.29	1.87	0.16	0.21	0.21	0.43	0.15	0.31
3 h	1.93	1.98	0.35	0.93				
9 h	1.49	2.12	0.16	0.11				
21 h	2.24	2.99	0.50	0.40				

[Z]Standard error is based upon 12 samples per mean.

Table A.7. Effect of day on which hay and straw was fed on ruminal pH, ammonia, total volatile fatty acid concentrations and percentages of acetic and propionic acid in steers fed the 2-day hay-straw rotation diet

	Hay days		Straw days				Repeated measures			
Time	First	Second	First	Second	SE[z]	P	SE days	Probability of day	Probability of hour	Probability of dayxhour
pH										
0 h	6.46	6.71	7.00	6.77	0.14	0.15	0.31	0.23	0.20	0.03
3 h	6.54	6.70	6.96	6.81	0.12	0.19				
6 h	6.62	6.78	7.02	6.82	0.14	0.35				
9 h	6.82	6.61	6.83	7.04	0.13	0.24				
12 h	6.71	6.67	6.84	7.00	0.12	0.28				
15 h	6.52	6.67	6.95	6.85	0.15	0.28				
18 h	6.44	6.63	6.95	6.84	0.13	0.12				
Ammonia (mM)										
0 h	4.3	5.8	4.4	1.8	0.97	0.11	0.97	<0.01	<0.01	0.02
3 h	4.8ab	7.0a	3.4bc	1.4c	0.71	<0.01				
6 h	5.2ab	6.7a	3.5b	1.4c	0.54	<0.01				
9 h	6.5ab	8.7a	7.1ab	3.6b	0.86	0.03				
12 h	8.5a	8.2a	7.1a	3.1b	0.67	<0.01				
15 h	4.5ab	6.8a	6.3a	2.7b	0.58	<0.01				
18 h	2.6b	7.2a	6.3a	2.3b	0.59	<0.01				
21 h	2.8b	6.2a	5.5a	1.6c	0.33	<0.01				
Total volatile fatty acids (mM)										
0 h	81	69	57	63	3.5	0.27	12.6	0.69	0.36	0.38
3 h	81	71	60	54	3.6	0.20				
6 h	82	70	61	69	3.5	0.34				
9 h	73	87	59	83	3.4	0.23				
12 h	69	87	70	59	6.4	0.40				
15 h	113	87	61	78	13.0	0.57				
18 h	89	97	58	81	11.0	0.66				
21 h	87	87	56	81	10.5	0.69				
Acetic acid (Molar percentage of total)										
0 h	72	71	73	72	0.9	0.84	0.41	0.10	0.09	0.40
3 h	73	74	74	71	0.9	0.30				
6 h	72	72	73	72	1.2	0.84				
9 h	73	72	74	73	1.3	0.87				
12 h	71b	72b	72b	77a	0.5	0.03				
15 h	70	72	72	71	1.0	0.67				
18 h	70ab	70ab	72a	69b	0.3	0.04				
21 h	71	72	72	70	1.2	0.58				
Propionic acid (Molar percentage of total)										
0 h	17.1	17.5	15.9	18.9	0.49	0.19	0.26	<0.01	0.54	0.08
3 h	17.4	16.1	16.2	19.0	0.86	0.37				
6 h	17.5	17.5	16.3	17.5	0.41	0.33				
9 h	17.3	18.1	15.3	18.1	1.04	0.46				
12 h	18.5	18.1	17.1	14.1	0.78	0.25				
15 h	20.4a	17.9b	16.5b	16.5b	0.36	0.04				
18 h	20.7a	17.9b	16.6b	17.9b	0.33	0.03				
21 h	17.2b	19.0a	16.4b	19.5a	0.33	0.02				

[z]Standard error is based upon 6 samples per mean.

Table A.8. Effect of day on which hay and straw was fed on ruminal butyric, isobutyric, valeric and isovaleric acids in steers fed the 2-day hay-straw rotation diet

Time	Hay days		Straw days		SE[Z]	P	Repeated measures			
	First	Second	First	Second			SE days	Probability of day	Probability of hour	Probability of dayxhour
Ratio of acetic to propionic acid										
0 h	4.3	4.1	4.5	3.8	0.12	0.24	0.09	0.01	0.34	0.06
3 h	4.2	4.6	4.6	3.7	0.25	0.35				
6 h	4.2	4.1	4.6	4.2	0.19	0.54				
9 h	4.2	4.0	4.8	4.1	0.29	0.50				
12 h	3.9	4.0	4.3	5.5	0.22	0.12				
15 h	3.5	4.0	4.4	4.4	0.09	0.06				
18 h	3.4	3.9	4.4	3.9	0.10	0.06				
21 h	3.7b	4.2ab	4.5a	3.8b	0.08	0.02				
Butyric acid (Molar percentage of total)										
0 h	6.6	7.8	7.1	7.1	0.67	0.76	0.65	0.73	0.17	0.85
3 h	6.8	6.7	6.5	7.4	0.32	0.31				
6 h	7.0	7.0	7.1	7.3	0.13	0.12				
9 h	6.6	6.8	6.6	5.4	0.47	0.41				
12 h	6.9	6.5	6.7	5.0	0.73	0.59				
15 h	6.9	7.2	6.8	7.5	0.84	0.90				
18 h	7.3	7.7	7.8	8.2	0.35	0.41				
21 h	7.0	7.3	7.6	6.9	0.60	0.88				
Isobutyric acid (Molar percentage of total)										
0 h	1.24	0.92	1.07	0.73	0.13	0.49	0.21	0.50	0.82	0.84
3 h	0.90	0.94	1.03	0.77	0.24	0.94				
6 h	0.81	0.76	1.25	1.13	0.24	0.66				
9 h	0.97	0.82	1.44	1.05	0.12	0.21				
12 h	0.99	0.74	1.13	1.05	0.09	0.37				
15 h	0.63	0.82	1.16	0.28	0.06	0.22				
18 h	0.58	0.88	1.21	1.38	0.13	0.36				
21 h	0.48	0.91	1.03	1.21	0.29	0.76				
Valeric acid (Molar percentage of total)										
0 h	0.77	1.11	0.84	0.65	0.17	0.62	0.18	0.53	0.01	0.72
3 h	0.69	0.69	0.61	0.57	0.02	0.22				
6 h	0.81	1.01	0.68	0.74	0.13	0.77				
9 h	0.79	1.09	0.71	0.60	0.08	0.19				
12 h	1.13	1.01	0.81	0.90	0.19	0.94				
15 h	1.13	1.04	0.91	1.18	0.18	0.79				
18 h	0.94	1.32	0.80	1.30	0.10	0.13				
21 h	0.94	1.15	0.79	0.84	0.11	0.58				
Isovaleric acid (Molar percentage of total)										
0 h	2.10	1.45	1.80	1.07	0.24	0.40	0.38	0.37	0.94	0.53
3 h	1.54	1.58	1.55	1.14	0.38	0.95				
6 h	1.53	1.13	2.04	1.64	0.42	0.61				
9 h	1.46	1.42	2.29	1.08	0.25	0.15				
12 h	1.42	1.28	1.80	1.62	0.09	0.22				
15 h	0.71	1.49	1.77	2.21	0.16	0.12				
18 h	0.77	1.58	2.00	2.36	0.28	0.27				
21 h	0.68	1.60	1.79	1.70	0.56	0.76				

[Z]Standard error is based upon 6 samples per mean.