NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

THE UNIVERSITY OF ALBERTA

Relationships between chewing activity and voluntary intake, passage rate constants and digestibility in steers

by

Darren D. MacLeod

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

ANIMAL NUTRITION

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

Spring, 1990

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

ISBN 0-315-60181-7

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Darren D. MacLeod

TITLE OF THESIS Relationships between chewing activity and voluntary intake, passage rate constants and digestibility in steers

DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED SPRING 1990

(SIGNED) Darren MacLeod

PERMANENT ADDRESS:

S.S. 1 Site 5-54

Cranbrook, British Columbia

V1C 4H4

DATED November 22 1989

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Relationships between chewing activity and voluntary intake, passage rate constants and digestibility in steers submitted by Darren D. MacLeod in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in ANIMAL SCIENCE.

G. Mathison
Supervisor

L. Ozimek

J. Kennelly

R. Christopherson

Date November 22, 1989

ABSTRACT

The relationships between chewing during eating and ruminating and voluntary intake, passage rates of particles and fluid through the total digestive tract and apparent organic matter digestibility (OMD) were determined using six alfalfa hays harvested at three moisture levels using 12 steers (292-458 kg) in experiment 1. Similar measurements were made using eight steers (292-458 kg) and four barley-grain:hay diets (33/67 and 90/10 ratios containing either rolled or whole grain) in experiment 2.

In experiment 1 OMD of the six hays ranged from 62 to 69% ($P<0.05$) at low intake (67 g dry matter (DM) $kg^{-0.75}d^{-1}$) and from 63 to 68% at high intakes (100 g DM $kg^{-0.75}d^{-1}$). The rate (chews min^{-1}) at which the animals ruminated increased from 43.3 to 47.4 to 51.0 chews min^{-1} as intake increased from low to high to voluntary intake (115 g DM $kg^{-0.75}d^{-1}$) feeding levels. Eating chews min^{-1} decreased ($P<0.05$) from 66.5 to 60.5 to 58.0 chews min^{-1} for the corresponding intakes. Total rumination chews d^{-1} were higher ($P<0.05$) at the high (20,300) and voluntary (21,400) intake feeding levels then at the low feeding level (15,100). No consistent relationships were found between chewing activity and individual animals for OM digestibility or passage rates within a feed at either the low or high feeding level. Particulate passage rates (PPRC) were similar ($P>0.05$) for all hays at both the low and high feeding levels and ranged from 2.77 to 3.16% h^{-1} and 2.96 to 3.29% h^{-1}, respectively.

In experiment 2 steers fed diets containing 33% whole barley/67% hay (33 W), 90% whole barley/10% hay (90 W), 33% rolled barley/67% hay (33 R) and 90% rolled barley/10% hay (90 R) consumed 55, 42, 54 and 39 g DM $kg^{-0.75}d^{-1}$ at a low feeding level; 96, 82, 90 and 73 g DM $kg^{-0.75}d^{-1}$ at a high feeding level and 116, 110, 116 and 92 g $kg^{-0.75}d^{-1}$ at a voluntary intake feeding level. Daily ruminating chews across all intakes were higher ($P<0.05$) for steers fed the 33 W (16,104) and 33 R (16,141) diets than for steers fed 90 W (11,300) and 90 R (9,400) diets.

It is concluded that both eating and ruminating chews increase with increasing intake and so does the time spent chewing. However, chewing activity does not appear to explain differences in particulate or fluid passage rates or organic matter digestibility between animals given the same feed at the same level of intake.

ACKNOWLEDGEMENTS

I would like to sincerely thank my graduate supervisor Dr. G.W. Mathison for his guidance and encouragement. Dr. R.J. Christopherson is also thanked for assuming the role of interim supervisor.

Mrs. Joanne Walker, Mr. Steve Melnyk, Mr. Julien Daniel and Mr. Tracey Stallard are thanked for their professional and personal support. Mrs. Kay Olsen and Mrs. Pat Marceau are thanked for the countless number of samples processed.

Mrs. Irena Vlach is acknowledged for her long hours of data manipulation and for programming the chew monitoring device. Brian Kerrigan is thanked for his technical assistance in setting up my project.

Mr. Ray Weingardt and Mr. Gavin Godby played an important role in the statistical analysis of the data and are therefore thanked.

The financial support of Farming for the Future and Mrs. Harry J. Hardgrave made this project possible and is therefore gratefully acknowledged.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

1.0 GENERAL INTRODUCTION

The productivity of ruminant animals fed forage based diets is largely dependent on the voluntary intake of the animal and digestibility of the forage (Van Soest 1982). It is commonly accepted that the retention time of material in the reticulorumen and thus rate of passage from the reticulorumen are important factors involved in the control of intake and digestibility of diets fed to ruminants (Colucci et al. 1982; Welch 1982).

Ingestive mastication and rumination are important mechanisms for reducing the particulate size of plant material (Welch 1986). Particle size reduction results in increasd surface area available for microbial attachment and allows passage of particles through the reticulo-omasal orifice (Ulyatt 1986). Chewing during eating and ruminating thereby aids in the relief of rumen fill and thus has a modulating effect on intake (Welch and Hooper 1988). However, despite the evident importance of chewing very few studies were found in the literature which attempt to relate voluntary intake directly with chewing activity.

In at least some circumstances the digestibility of feeds is decreased when passage rates increase (Colucci et al. 1982; Welch 1982). It thus could be predicted that increased chewing activity would result in decreased diet digestibility, although there is also evidence that increased chewing activity may result in increased rates of colonization of plant material by rumen microorganisms (Cheng et al. 1980) and thus increased rates of digestion of plant

material (Poppi et al. 1981b). Again, however, no studies were found in which differences in chewing activity between animals were related directly to variations in digestibility between animals.

Chewing activity may also influence other parameters of ruminant metabolism either directly or indirectly. For example, methane production might be increased by increased chewing if increased reticulorumen digestibility resulted from chewing whereas decreases in methane production would occur if increased chewing activity resulted in faster rates of passage from the forestomach. The heat production of animals is increasd during eating (Osuji et al. 1975). There is no information in the literature however, concerning the effect of chewing activity on methane production and only indirect (i.e. chewing is only part of the processes of eating) measurement concerning the relationship between chewing and heat production.

The two experiments described in this paper were thus undertaken to obtain information on the relationships between chewing activity and voluntary intake, organic matter digestibility, and passage rates in steers.

2.0 LITERATURE REVIEW

2.1 Chewing during eating

2.1.1 Behavioral aspects

Ruminants spend up to 12 h a day eating when they are on pasture, the majority of which occurs during two main meals, after dawn and before twilight (Dulphy et al. 1980). Wet weather conditions modify grazing patterns as the animals are less prone to long periods of inactivity and therefore the major meals are not clearly delineated (Ruckebusch and Bueno 1978).

Confined animals fed forage based diets spend approximately 2 to 7 h eating daily and start their largest meals after receiving feed, even if there is feed remaining from the previous day (Wilson and Flynn 1974; Dulphy et al. 1980). Confined animals may also modify their eating habits if subjected to heat stress; feedlot steers experiencing heat stress ate when it was cooler regardless of the feeding time (Ray and Roubicek 1971).

Frequency of chewing during eating is reportedly 125 to 150 chews min^{-1} for sheep and 70 to 80 chews min^{-1} in cattle (Gill et al. 1966; Ulyatt et al. 1986). However, these reported chewing rates can be misleading as the animals were monitored immediately after the initial feeding at which time they would be eating consistently and enthusiastically. If measured over the total eating period in the day it is unlikely the average chewing rate

would be this high. Luginbuhl et al. (1989) recognized this problem and measured the first 40 min of randomly chosen meals only. Using this procedure they also found the chewing rate to be approximately 70 min^{-1}. It remains to be established how monitoring the animals continuously for 24 h periods will influence estimates of chewing rate.

2.1.2 Mechanical damage to plant material

2.1.2.1 Particle size reduction: Chewing during eating reduces large forage particles in size to a point where they can be formed into a bolus and swallowed. Chewing also reduces a fraction of the ingested feed to a size where it could possibly escape from the rumen without further size reduction (Gill et al. 1966). Reid et al. (1979), using esophageal fistulated sheep, reported that ingestive mastication reduced the percentage of chaffed lucerne hay particles larger than 1.18 mm from 97% to 48%. In contrast, McLeod and Minson (1988) found that cattle eating perennial ryegrass reduced the 5014 g of large particles eaten in the stem fraction to 3759 g after mastication, thus large particle reduction was 25%. The particles of the leaf fraction of the perennial ryegrass larger than 1.18 mm were reduced from 5464 g to 3605 g after mastication or, alternatively 36%. The difference in large particle reduction between the two studies cited could possibly be explained by the high tensile strength of perennial ryegrass leaves and animal species differences (Mcleod and Minson 1988).

In a comparison of species, Poppi et al. (1981) noted that sheep reduced 22.4% of ingested dry matter to less than 1.18 mm, whereas cattle had 18.2% of particles eaten reduced below 1.18 mm. This indicates a more thorough chewing by sheep. There can also be consistent differences between animals of the same species with regard to their ability to chew a particular diet (Ulyatt et al. 1982).

Pond et al. (1984) demonstrated the considerable effect that feeding hay versus grazing the same forage had on the percentage of particles reduced below 1.0 mm during eating. Fifty-two percent of grazed coastal bermudagrass was reduced to particles with a size less than 1.0 mm by chewing during eating while grazing. Conversely, the percentage of coastal bermudagrass hay particles reduced below 1.0 mm was only 15.5% when hay was fed.

Luginbuhl et al. (1989) examined the influence of intake level on the effectiveness of particle size reduction by ingestion and found that the proportion of particles retained on a 4.0 mm screen decreased linearly as the feed level rose whereas the proportion of particles retained on 2.0, 1.0 and 0.25 mm seives increased linearly. This led to the conclusion that chewing effectiveness was greater at higher intakes because the animals ingested the feed more slowly and therefore the thoroughness of chewing was greater (Luginbuhl et al. 1989).

2.1.2.2 Release of intracellular constituents: A further consequence of mastication is the release of soluble intracellular

constituents into the rumen liquor where they are rapidly fermented by rumen microbes (Doyle 1967). The soluble nitrogen release attributed to chewing was determined to be 60% by Reid et al. (1962) and 31 to 59% by Bryant (1964). Bryant (1964) also measured the soluble carbohydrate release and found it to range between 22 and 86% The proportion of soluble constituents released from fresh herbages during eating was determined by collecting boluses at the cardia and then chemical analysis of the juice extract, it was assumed that that all cellular constituents evident were released by chewing.

Ulyatt et al. (1982) compared three fresh herbages and one hay and determined that during eating the release of soluble cellular constituents was markedly higher in fresh herbages as opposed to hay. The results were obtained by measuring the fermentation rates in mL gas g^{-1} organic matter of collected feed boluses over 300 min. The range of gas production varied from 60 to 126 mL gas for lucerne chaff and fresh sweet clover respectively. The fermentation rates of the bolus juice alone were also determined and found to range between 129 and 206 mL gas g^{-1} organic matter over the 300 min period, which supports the concept that intracellular constituents are emptied into the rumen liquor.

Initial studies on the release of soluble nutrients from masticated feed were undertaken because of a supposed link between plant soluble proteins and the stable foam produced in the rumen of bloat-prone animals. However, Bryant (1964) could not find a clear relationship between animals that chewed more effectively (ie.

caused more damage to plant cell walls and therefore a greater release of soluble nitrogenous compounds) and their susceptibility to bloat.

2.2 Chewing during rumination

2.2.1 Behaviorial aspects

Rumination is the process by which previously ingested feed material is regurgitated, remasticated, reinsalivated and reswallowed. The ruminating bouts of both cattle and sheep number between 10 and 20 daily with a majority of the bouts occurring at night (Dulphy et al. 1980). Sheep spend approximately 3 to 10 h a day ruminating depending on the type and feeding level of the diet (Gordon 1968). Cattle are less selective than sheep in choosing forage types while grazing and in choosing specific segments when stall-fed (ie. stems versus leaves) and therefore tend to ruminate more under many circumstances (Dulphy et al. 1980). However, the maximum time spent ruminating by cattle is approximately the same as sheep (Welch 1982). Kennedy (1985) found that cattle fed 11.6 kg of bromegrass ruminated 9.78 h daily.

Chewing during rumination is characterized by a slower more deliberate chewing, and a more rhythmical pattern than chewing during eating (Welch and Hooper 1988). The rate of chewing during rumination has been reported for sheep to be as low as 73 chews min^{-1} and as high as 100 chews min^{-1} (Gordon 1968). Cattle chew

during rumination at rates varying from 40 to 60 chews min^{-1} (Dulphy et al. 1980; Ulyatt et al. 1986).

The drive to ruminate is extremely strong as was amply illustrated by Welch (1982). Steers were muzzled for 10 h and then allowed to eat for 2 h. After several days the animals chose to ruminate rather than eat during the eating times. During the trial the steers' intake dropped from approximately 10 to 5 kg daily. In a similar trial by Chai et al. (1988), the prevention of rumination also caused a 50% reduction in the feed intake of sheep. In the same study it was also interesting to note that the sheep that were muzzled chewed more during the period allotted for eating than the non-muzzled sheep in an apparent attempt to offset the lack of time for rumination.

2.2.2 Mechanical damage to plant material

Chewing during rumination is an effective way for the animal to reduce the particle size of refractory material in the rumen. Chai et al. (1984) measured the reduction in large particles by chewing during rumination (ie. particles greater than 3.35 mm) as a proportion of the total amount of large particles in the regurgitated bolus and found the reduction ranged from 58 to 75%. Two esophageal fistulated, forage-fed beef steers were used in this trial. Ulyatt (1983), in a trial with sheep, found that the chewing of the regurgitated bolus reduced particles greater than 1.0 mm by 69% when expressed as a proportion of the starting material.

Ulyatt (1983) also provides strong evidence that the major role of rumination is to reduce the size of indigestible material in the rumen to a point where it can pass into the omasum and thereby create space for the next meal. His conclusion was based on the observation that the proportion of the rumen dry matter which was ruminated increased from 4% during the first 4 h post-feeding to 96% 20 to 24 h later. Despite the fact that 24 h after feeding the amount of dry matter in the rumen was at it's lowest, the animals drive to ruminate was very strong (Ulyatt 1983). Further evidence illustrating the vital role of rumination can be obtained by calculating the dry matter flow through the rumen. Sheep were fed a total of 1019 g of dry matter daily in hourly increments to approximate a steady state condition (Ulyatt 1986). The amount of dry matter ruminated was determined to be 1957 g, the amount digested in the rumen was 359 g and the amount passed into the omasum was 660 g. These results further support the hypothesis that rumination is the rate limiting step in clearing dry matter from the rumen.

Chewing during rumination also aids microbial digestion by increasing particle surface area in a manner analogous to chewing during eating. However, unlike chewing during eating, rumination is not considered an important mechanism for release of intracellular constituents.

2.3 Importance of chewing

2.3.1 Chewing and passage from the ruminoreticulum

It is a well documented principle that dietary feed residues must be reduced in size to escape from the ruminoreticulum (Balch and Campling 1962; Welch 1967). The time delay imposed on the feed particles allows 60% or more of the organic matter in the rumen to be digested but it also restricts further intake until the indigestible residues can be cleared (Campling et al. 1962; Ulyatt et al. 1986). Uden and Van Soest (1982) demonstrated that the passage of feed particles to the lower gastro-intestinal tract is influenced by particle size to a greater extent in ruminants than non-ruminant herbivores. The functional anatomy of the reticulo-omasal orifice slows the passage of large feed particles while the tube-like gut of the horse or rabbit has no such impediment (Uden and Van Soest 1982). These authors thus corroborated earlier findings by Balch and Campling (1962) that particle size discrimination occurs prior to the omasum.

Feed particles are reduced in size by the process of chewing during eating, chewing during rumination, microbial degradation and rumen contractions (Ulyatt et al. 1986). It was thought until very recently that microbial degradation and detrition (rumen contractions) were of little consequence in regards to their overall effect on particle size reduction (Ulyatt et al. 1986). McLeod and Minson (1988) disagree with this premise and have demonstrated that

17% of particles greater than 1.18 mm in the rumen are reduced in size by microbial degradation and detrition. However calculation of particle size reduction in this study relies heavily on the assumption that the large particle (> 1.18 mm) breakdown by rumination was only 50%. This is considerably lower than the findings of other researchers (Chai et al. 1984).

2.3.1.1 Critical size and escape probability: The fact that dietary residues must be reduced in size to escape the rumen has lead to the theory that there is a critical particle size above which little material can escape the rumen (Pearce 1967; Poppi et al. 1980). This model assumes that there are two pools of dry matter in the rumen. One pool consists of particles that cannot escape the rumen without further reduction and a second is a homogeneous pool in which all particles may escape with equal ease. Critical size for particles passing out of the rumen of sheep and cattle are reportedly between 1.0 and 2.0 mm and 2.0 to 4.0 mm respectively (Thomas and Campling 1977; Bae et al. 1981; Welch 1982; Bae et al. 1983). Welch and Hooper (1988) make the general assumption that very little material above 1 mm can escape the rumen in cattle or sheep, however larger material may escape by an end-on presentation to the reticulo-omasal orifice (Ulyatt et al. 1986).

Faichney (1986) provides an alternate model to describe the particulate flow out of the rumen. The model assumes three particulate dry matter pools, large (> 1.18 mm), medium (< 1.18 mm

but > 0.15 mm) and small (< 0.15 mm). Faichney (1986) designated the particles into three pools with members within each pool having the same probability of rumen escape. Particles in the large pool have a low probability of escape from the rumen until they are reduced in size to that of the medium pool. The author states that the model was designed to simplify the mathematics, but stresses that the dry matter pools are not homogeneous but rather a continuum of sizes, and that as the particle size gets larger the probability of escape becomes smaller.

2.3.1.2 Specific gravity: The fact that 60 to 70% of material in the rumen is normally below the critical size for passage has led researchers to explore other physical characteristics of the ingested feed particles which may influence passage rates (Ulyatt et al. 1986). One such physical parameter is the specific gravity of the individual particles. Particle reduction plays a key role in changing the specific gravity of the particles because as the particles are reduced in size there is a concomitant rise in density and therefore specific gravity (Hooper and Welch 1985).

Campling and Freer (1962) reported that in cattle receiving roughage diets, particles that had a specific gravity of 1.12 passed through the entire digestive tract faster than particles with a higher or lower specific gravity. Welch (1986) introduced 7 cm sections of polypropene ribbon into the rumen of steers and determined that particles of 1.17 to 1.42 specific gravity passed the most rapidly.

Hooper and Welch (1985) demonstrated that feed particles ground in a Wiley mill to a size of 1.0 mm and incubated in water had a specific gravity associated with rapid movement out of the rumen. These particles also increased in specific gravity faster than particles ground to larger sizes (Hooper and Welch 1985b). This augments the critical size theory which states that particles of 1.0 mm or less have the greatest chance of escape from the rumen.

2.3.1.3 Other factors: Smith et al. (1965), Troelsen and Campbell (1968) and Van Soest (1982) demonstrated that fecal particle size was influenced by feeding level and processing, but Bae et al. (1981) and Waghorn et al. (1986) found little difference in fecal particle sizes when the animals were fed at high versus low intake levels. These conflicting arguments do not diminish the importance of particle size reduction within the animal because, even if fecal particle sizes increase with high levels of intake, the probability of escape from the rumen rapidly increases as the particles are reduced in size to less than 1.0 mm (Poppi et al. 1980).

Uden and Van Soest (1982) reported large differences in fecal particle size of large verses small heifers, but Bae et al. (1983) found little difference in fecal particle size in cattle from 261 to 861 kg.

The influence of feed processing on the particle sizes which escape the rumen has yet to be definatively addressed. Van Soest (1982) states that pelleted feeds increased fecal particle size but

Ulyatt et al. (1986) report that pelleting or grinding of the diet had little influence on the particle sizes obtained from the abomasum of sheep.

2.3.2 Chewing and voluntary intake

The productivity of ruminant animals fed forage based diets is largely dependent on voluntary intake (Van Soest 1982). Welch (1986) states, in an approximation of the same concept, that the productivity of ruminant animals is linked to the rate of passage of feed particles through the digestive tract. Chewing during eating and ruminating aids in the relief of rumen fill thus providing space for incoming feed (Welch and Hooper 1988).

The fact that ruminant animals have a limit to the amount of time they spend ruminating each day has led to the concept of rumination efficiency. Rumination efficiency, as defined by Welch and Hooper (1988), is the weight of neutral detergent fibre eaten divided by the rumination time. In contrast Dulphy et al. (1980) define rumination efficiency as the voluntary dry matter intake divided by ruminating time. Another definition, total chewing efficiency, is defined by Deswysen and Ellis (1988) as unitary mastication time (min g^{-1} organic matter $kg^{-0.75}$) which was shown to be closely related to voluntary intake in six beef heifers. Total chewing time has also been demonstrated to be a good indicator of forage quality (Balch 1971).

There are genetic variations in ruminating efficiency both

within and between species of domestic animals (Welch and Hooper 1988). Frish and Vercoe (1969) examined the relationship between eating rate and voluntary intake and found they were significantly correlated. These researchers examined the differences in eating rates of three different breeds and found that the differences in intake rates were associated with live weight and not the breed of the animal.

It is not meant to imply that physical restrictions to feed intake are the only factors governing the intake of forages. Short term control of voluntary intake is also thought to be influenced by volatile fatty acids in the ruminal digesta and ruminal vein or liver (Grovum 1988). Hormones such as insulin, glucagon and gastrin also influence short term forage intake (Grovum 1988).

Genetic variances will have to be further explored and exploited in order to optimize forage use. Grovum (1987) suggests it is reasonable to genetically select animals based on characteristics of passage rate through the digestive tract. Since chewing during eating and ruminating plays a central role in particle size reduction, and therefore the passage rate of particles out of the rumen, it may be prudent to select for efficient chewing animals.

2.3.3 Chewing and digestibility

Chewing during eating causes mechanical damage to the ingested feed particles creating openings through which rumen microorganisms can invade (Cheng et al. 1979). Rumen bacteria can only penetrate

the epidermis of uninjured plant material via the stomata, however, in leaves damaged by chewing the colonization of underlying tissue is relatively rapid (Cheng et al. 1980). Although this might suggest that the chewing during eating was essential for digestion this is not so, as demonstrated by Baily and Balch (1961). These researchers fed two groups of cows; one group was fed by placing the feed directly into the rumen, the other fed normally. It was found that the feed digestibility was the same with both methods.

Poppi et al. (1981b) approached the situation differently and noted that while digestibilty did not change if unchewed hay was placed directly into the rumen in nylon bags the rate of digestion did. The fractional rate of digestion of dry matter for chewed feed was 0.022 h^{-1}, while for unchewed hay it was 0.016 h^{-1}. This is a significant difference in itself, but combined with the fact that the time elapsed before significant digestion occurred was 15.5 h for unchewed hay and 3.1 h for chewed hay, it becomes obvious that chewing during eating plays a vital role in the digestibility parameters of feed.

The digestibility of forages fed to ruminants, aside from the inherent quality of the feed itself, could potentially be indirectly associated with chewing, however there is no data confirming this hypothesis. Chewing facilitates passage of feed particles out of the rumen via the particle size reduction process. Passage rates and digestibility are competitive means for the removal of organic matter from the gastro-intestinal tract and therefore the faster particles pass through the digestive tract the

lower the digestibility will be (Colucci et al. 1982). In a trial using dairy cattle Colucci et al. (1982) found that the correlation between total retention time (rumen retention time plus lower tract retention time plus calculated time for first appearance of the marker in the feces) and gross energy digestibility was 0.81.

Faster passage of feed particles however, does not unequivocally produce a depression in digestibility. Deswysen and Ellis (1988) illustrated that in animals with high voluntary intakes, and therefore high passage rates, the site of digestion shifted away from the rumen towards the cecum and colon but the total digestibility of the feed was altered very little. Okine et al. (1989) demonstrated that digestibility of a long or chopped forage fed at 1.4% of body weight did not decrease significantly when passage rates were artifically increased.

2.3.4 Methane Production

Energy losses in the form of methane production account for 5 to 12% of the ingested digestible energy consumed by ruminants (Van Soest, 1982). Blaxter and Clapperton (1965) showed that as intake increased methane production (kcal methane per 100 kcal feed) decreased. High intakes have been shown to increase passage rates and therefore it is logical to presume that an increase in passage rates will lead to a reduction in methane production per unit of feed. Okine et al. (1989) reported that ruminal particulate passage rate constants accounted for 28% of the variation in methane

production in animals at constant intakes whereas 25% of the variation could be explained by ruminal fluid dilution rates. The relationship between chewing and methane production has yet to be elucidated but it can be speculated that animals that chew more efficiently may have faster passage rates and hence lower production of methane per unit intake of feed.

2.3.5 Heat production

The heat production associated with feed ingestion by ruminant animals has been termed the heat increment of feeding. The physiological origins of this heat production arise from: 1) eating and ruminating 2) microbial fermentation in the gut and 3) metabolic activities in the gut and other tissues (Webster 1980). In this discussion heat production associated with eating and ruminating will only be considered as it is most relevant to the topic.

Young (1966) determined that daily energy expenditure attributable to feeding for sheep fed a lucerne chaff diet ranged between 1.8% and 3.1% of the daily energy expenditure of the animals. The increase in energy expenditure associated with eating was found to range between 5.3 and 12.4 cal min^{-1}. To prove that the increased energy expenditure during eating was caused only by eating and not digestive or metabolic processes the animals were sham fed (i.e. 77% of ingested feed was removed via a eosophageal fistula) and the energy expenditure was not significantly different. Adam et al. (1985) determined the energetic cost of

cattle eating a pelleted concentrate diet to be 0.01 of metabolizable energy (ME) and 0.05 of the ME of a long lucerne hay diet. These researchers also elucidated that the length of the time required to ingest the feed was the factor exerting the most influence on the amount of heat produced during eating. Similarly, Osuji et al. (1975) found increases in heat production during and after fistula feeding to be only 2-8% of the values obtained during eating.

A very small increase in heat production is associated with ruminating even though animals fed poor quality forages ruminate twice as long as they eat (Balch 1971). Osuji et al. (1975) and Webster (1980) report that energy expenditure by rumination is only 10-20% of that of eating per unit time.

2.4 Chew monitoring methodology

There are several systems available to monitor chewing in ruminant animals. The early models consisted of toy balloons placed under one of the straps of a leather halter and connected by pressure tubing to tambours operating pens leaving a continous ink record on chart paper (Balch 1958). Law and Sudweeks (1975) improved this system by converting the air pressure changes caused by jaw movements into an electrical signal. The electrical signal could easily be amplified and transmitted to a recording device located a reasonable distance away from the animal. Kokjer and White (1986) using a similar method of jaw motion detection

developed a telemetry system that would allow chew monitoring as the animals grazed. Strain guages have also been used to measure chewing in small ruminants by converting jaw motion directly into electrical energy (Duranton and Bueno 1982).

The problem with the afore mentioned systems is not the method of jaw motion detection but the method of data storage and retrieval. The interpretation of vast lengths of chart paper was tedious, error prone work. To avoid this problem, Murphy and Jaster (1984), attached an electrical transducer to a flexible nose band and recorded the jaw movements with a microcomputer. Luginbuhl et al. (1987) expanded on Murphy and Jaster's idea and devised a program in BASIC to automatically separate chews during eating and ruminating with the use of a microcomputer. The originality of this system was the direct transformation of individual jaw movements into binary notation. In this system data collection is interupted every hour for 6 sec and it takes approximately 10 to 12 min to remove 12 h of data from the computer (Luginbuhl et al. 1987). Monitoring one animal for 24 h results in one floppy disk full of data (Luginbuhl et al. 1987).

3.0 MATERIALS AND METHODS

3.1 Chew monitoring methodology and measurement

3.1.1 Hardware

A bicycle inner-tube (d. 3.175 cm) was cut to a length of 21 cm and glued over a brass insert. The insert consisted of two circular end pieces (d. 3.5 cm) connected by a 15 cm long hollow brass tube which had two small holes (d. 0.1 cm) in the middle. One end of the brass tube was sealed and at the other end a shrader valve was welded on to allow inflation of the inner-tube (Plate 3.1). There was a small (d. 0.5 cm; l. 2.5 cm) section of metal tubing attached through the brass end piece, adjacent to the shrader valve, to provide a connection for flexible tubing which was attached to a pressure transducer. The brass insert and inner-tubing were held inside a section of rigid plastic pipe (d. 3.6 cm; l. 18 cm). The middle top half of the pipe (2 cm opening) was removed so upon inflation the inner-tube would expand beyond the confines of the pipe and rest comfortably under the jaw of the animal. A section of grooved plastic (w. 6 cm; l. 13 cm) was glued to each end of the plastic pipe at right angles and attached to the halter to keep the sensing device from rotating during eating. The entire pneumatic device was fastened, via threaded ends on the hollow brass tube, to a modified halter that could be easily adjusted to accomodate varying animal sizes and shapes.

Flexible tubing (i.d. 0.3175 cm; o.d. 0.9525cm; l. 180 cm)

connected the sensing device to a pressure transducer (Honeywell Inc., Toronto Ont.). The voltage output from the transducer was processed by a signal conditioner board (locally fabricated) containing a differential circuit which resulted in a voltage output only being obtained when the pressure was changed in the tubing attached to the pressure transducer. A 5-V DC power supply (Hammond Ltd., Quelph Ont.) was applied to the circuit containing the pressure transducer and signal board. The output from the system thus consisted of negative voltages associated with the animal closing its mouth and positive voltages associated with opening the mouth. The voltage output from the system ranged from -5 to +5 volts.

The conditioner board was connected to the computer by a Exp-16 multiplexer board (Metrabyte Inc., Taunton Mass.) mounted adjacent to the computer. The analog to digital converter consisted of a Metrabyte Dash-16 A/D (Metrabyte Inc., Taunton Mass.) card internal to the computer. The microcomputer was an Apco-XT (Apco Inc., Vancouver B.C.) equipped with a, Hercules monochrome monitor, standard keyboard, 640 K memory, 20 meg hard disk drive and two 5.25 inch floppy drives. The system could accomodate four animals at one time.

3.1.2 Software

A multipurpose menu-driven software package, Labtech Notebook Ver. 4.01 (Labtechnologies Inc., Boston Mass.) was chosen for data acquisition. This package had two advantages: 1) no programming

language is required and 2) after the parameters are set the program could be automated using a DOS Ver. 3.3 (IBM Inc., Toronto Ont.) batch file.

Data was sampled continuously for 24 h at 6 Hz. The demarcation point between jaw movements and background noise was established at 0.2 V. Incoming voltages less than -0.2 were assigned a value of +1 and all other readings were assigned a value of 0 by the software. Negative voltage readings were chosen over positive readings to determine chews because the negative voltage readings had larger voltage values on average. Blocks of +1 values, separated by 0 values, were considered to be a single chew. The Labtech notebook was designed to calculate the number of chews min^{-1} from the six voltage inputs collected each second. When the buffer filled, data was written to a hard disk. Data for 1 d from four animals could be stored on one 360K floppy disk.

3.1.3 Verification of system

The accuracy of the system was tested by two methods. The first method consisted of repeated manual squeezing of the pneumatic device with comparisons being made between the number of chews min^{-1} displayed on the computer screen and the number of times the tube was squeezed. The second method of verification involved actually counting the number of chews made by the animal and comparing this with the computer display. Data from both tests were then analysed using paired t-tests (Steel and Torrie, 1980).

3.1.4 Experimental chewing measurements

In experiment 1 and 2 the animals were monitored for two consecutive 24 h periods at voluntary, high intake (approximately twice maintenance) and low intake (approximately maintenance) levels of intake for each designated feed. Data was averaged these 2 d. Chewing measurements were made when the animals were in the metabolic crates. Measurements were taken concurrently with digestibility measurements, except at voluntary intake levels when urine and fecal samples were not collected.

Ruminating and eating chews were separated manually on the basis of three criteria: 1) number of chews per min (eating chews min^{-1} were normally higher 65-80, while ruminating chews min^{-1} were between 40-60); 2) rumination chews min^{-1} within a bout of rumination formed a more consistent pattern than the eating chews; and 3) the time of feeding.

Due to technical difficulties the chew monitoring system was only in operation for periods 2 and 3 of experiments 1 and 2. When the system was operational the inflatable inner-tubes would periodically lose pressure therefore, the number of observations was less than initially projected.

3.2 Feedstuffs

3.2.1 Experiment 1

Six first cut alfalfa hays (Medicago sativa L.) (Table 3.1) were harvested at Lacombe Alberta in cooperation with V. Baron,

Agriculture Canada commencing on the 25th of June 1987. Baling was initiated when the moisture content of the bales averaged 251, 185 and 137 g kg^{-1}. These three moisture levels were designated as High, Medium and Low. Within each moisture level half of the 32 round bales were treated at the time of baling with a neutralized propionate preservative having a propionic acid equivalent of 680 g kg^{-1} and a pH of 6.2. These feeds are designated as treated while untreated bales are identified as control. The preservative was applied to the hay at 1.25% (wt wt^{-1}). The bales were stored on posts in a covered shed at the Agriculture Canada Research Station, Lacombe, Alberta before they were moved to the Ruminant Feed Evaluation Unit and fed (Mathison et al. 1984).

3.2.2 Experiment 2

Barley (Hordeum vulgare L.) grain either whole or rolled was fed in combination with a alfalfa-grass hay (Table 3.2). The grain to hay ratios were either 33% barley grain plus supplement with 67% standard hay (33/67),or 90% barley grain plus supplement with 10% hay (90/10). The standard hay was comprised of 25% smooth bromegrass (Bromas inermis L.), 25% fescue (Festuca rubra L.), 35% alfalfa (Medicago sativa L.), and 15% timothy (Phleum pratense L.). The supplement fed to animals receiving the 33/67 diet consisted of 47% barley, 40% canola (Brassica napus L.) meal and 13% minerals and vitamins (Table 3.2). Supplement fed to animals receiving the 90/10 diet contained 41.5% barley, 35% canola and 10.4% minerals and vitamins.

3.3 Apparent digestibility, passage rates and voluntary intake

3.3.1 Experiment 1

Data was gathered in the Ruminant Feed Evaluation Unit (Mathison et al. 1984). Twelve growing Hereford steers ranging in weight from a minimum of 292 kg at the begining of the trial to a maximum of 458 kg at the end of the trial were used. Feed evaluation occurred over a period of 7 months (June 1988 to December 1988). Equal portions of the ration were fed to the animals at 8:00 and 16:00 h after the hay had been ground through a 7.62 cm screen in a tub-grinder (Model 390, Sperry New Holland, New Holland, Pennsylvania).

Animals were randomly assigned into two groups with each animal within a group receiving a different hay in each of the three experimental periods. Due to the limited number of metabolic chambers and crates available, steers moved through the system in groups of four with each group of animals being separated by 3 days. The animals were initially fed a standard alfalfa-grass hay diet for 7 d. The test feeds were then introduced and voluntary intake measurements were made over the last 7 d of the 17 d ad libitum period. Following the voluntary intake measurements, the animals in one group received a diet at a feeding level of approximately twice maintenance whereas the other group was fed at approximately maintenance. Digestibility measurements were made for 8 d following a 10 d adaptation period for both groups. Measurements of respired gasses and oxygen consumptions by animals were made concurrently with digestibility measurements over a 48 h

period at the start of the digestibility period and for an additional 48 h period at the end of the total collection period by methods outlined by Okine et al. (1989). Intake levels were then exchanged for the groups and the process was repeated. The steers were then reallocated to different hays and the measurements were repeated in the two remaining periods.

Fluid and particulate passage rates were measured at the same time as the fecal collections were made for the digestibility measurements. Steers were dosed on the day of the first fecal collection prior to the 8:00 feeding. Cobalt-ethylenediamine tetraacetic acid (Co-EDTA) was used as the liquid marker and prepared as per Uden et al. (1980). The dosage was 5 g of cobalt, (alternatively 37.5 g of Co-EDTA) dissolved in 1 litre of water and flushed down a Rheinhard oral tube (von Keyserlingk and Mathison 1989). The dosing apparatus was flushed with fresh water to remove any Co-EDTA residues and this too was flushed into the animal. Small quantities of rumen digesta were occasionally regurgitated during tubing.

Particulate passage rates were determined by feeding the animals 3 g Cr (100 g mordanted fibre) prepared in accordance with the procedure of Uden et al. (1980). Representative samples from each feed in the same physical form as that fed to the animals was mordanted. Immediately after the Co-EDTA dosing the animals were fed the chromium-mordanted fibre mixed with a small quantity of the test feed. The mordanted fibre was readily consumed within 15 min of being offered to the animals.

Total collection of fecal samples were made every 24 h and the samples collected at 60, 84 108, 132, 156 and 180 h post dosing were used for marker determination. The feces were mixed thoroughly before sampling and the assumption was made that one defecation occurred at the midpoint of each collection period (Faichney 1980). Samples for marker analysis were dried at 60°C for 7 d which resulted in dry matter contents all above 95%. The samples were then ground using coffee grinders.

Passage rates of fluid and particulate matter through the digestive tract were calculated as the rate of decline in the natural logarithm of marker concentration in the fecal dry matter. Six observations over time were used for calculating the fluid and particulate passage rates within each animal. R^2 values ranged from 0.91 to 0.99 and 0.81 to 0.99 for particle and fluid passage rates, respectively.

3.3.2 Experiment 2

Measurements were made at the Ruminant Feed Evaluation unit (Mathison et al. 1984). Eight growing steers with a minimum weight of 295 kg at the start of the trial and a maximum weight of 458 kg at the end of the trial were used. The animals were randomly assigned into two groups with each animal in each group receiving either whole or rolled barley in 33/67 or 90/10 concentrate-hay diets. Animals fed the 33/67 mixture received 700 g of supplement at the 8:00 feeding at high intake and 350 g of supplement at low intake level. The animals receiving the 90/10 mixture received 800

g of supplement at high intake and 400 g at low intake levels. The amount of supplement fed was considered when calculating the amount of barley grain to be fed daily to each animal to maintain the desired concentrate:hay ratio. Evaluation of all four diets occurred simultaneously, analogous to Experiment 1.

The particulate and fluid passage rates were also determined with the same procedures employed in Experiment 1. Mordanted material consisted of representative samples of the hay fed to animals.

3.4 Chemical analysis

3.4.1 Experiment 1 and 2

Dry matter determinations for all samples consisted of drying 1 g of ground sample at 110°C until a constant weight was reached. Acid detergent fibre, neutral detergent fibre and lignin were analysed as per the procedure of Goering and Van Soest (1970). Crude protein determinations were done using the Kjeldahl procedure (Association of Official Analytical Chemists (AOAC) 1980; procedure #2.057). Calcium and total ash were analysed by AOAC methods (AOAC 1980; procedures 7.097 and 7.009 respectively). Colorimetry (Technicon Autoanalyser II 1978) was used for phosphorous determinations while acid detergent insoluble nitrogen (ADIN) was analysed by the method of Goering et al. (1972).

Fecal samples were prepared for chromium analysis in a similar manner to that used by Okine et al. (1989) by weighing 0.5 g of the sample into a 50 mL Erlynmeyer flask. Thirty mL of 4 N HNO_3 was

added and the solution was allowed to sit for 4 h at room temperature. The flasks were then heated at 75°C for 12 h and then the gross weight recorded so the precise amount of solution could be calculated. The solution was then filtered through Whatman 54 filter paper (Whatman International Ltd. Maidstone, England). The supernatant was diluted (1:10 vol/vol) with 4 N HNO_3 when necessary and the absorption of Cr was determined using an acteylene flame with a Perkin Elmer spectrometer (model 400 Perkin-Elmer Corporation Norwalk, CT).

Cobalt determinations were done by first ashing 0.5 g of the fecal material at 500°C for not less than 12 h (Okine et al. 1989). After the samples had cooled 5 mL of 4 N HCl was added and the solution allowed to sit at room temperature for 30 min. Fifteen mL of deionized water was added and the solution was thoroughly mixed before being centrifuged at 1000 x g for 15 min. The supernatant was removed with a pasteur pipette and dilutions (1:10 vol/vol) with 4 N HCl were made when needed. The absorption of Co was determined by atomic absorption spectroscopy.

3.5 Statistical analysis

The experimental design for experiment 1 was an incomplete randomized block. The effects of periods (n=3), sequence i.e. the order in which the levels of intake were fed (n=2), and feeds (n=6) were considered in the analysis of variance procedure. Feeding levels were analysed both separately and together (n=2). Where appropriate the Student-Newman-Keuls mutlitple range test was used

to compare means.

Simple linear regressions, coefficients of determination (R^2) and standard errors of estimates were calculated according to procedures outline by Steele and Torrie (1980). Scatter diagrams were plotted for all regressions to examine the possibility that curvilinear relationships may have existed; none were found.

In experiment 2, the statistical design and analysis paralled that of experiment 1 except for feeds (n=4).

4.0 RESULTS

4.1 Chew monitoring apparatus verification

The chewing apparatus was verified by comparing computer recorded chews with manual manipulation of the system. The system was monitored throughout the seven month trial period (23 individual tests; 67 total minutes of observation). As can be seen in Table 4.1, the manual and computer recorded results were virtually identical e.g. total chews for the two methods were 2815 and 2816, respectively. The standard error was 2.86 for both the observed and computer recorded data.

Figure 1 illustrates the chews min^{-1} results obtained with this system. Chewing during eating ranged from approximately 25 to 80 chews min^{-1} while the range for rumination chews was between 56 to 58 chews min^{-1}. When animals were monitored using a stop watch and the chews were counted, the computer data was 0.5% higher than the number of chews in the steers ($P<0.05$).

4.2 Experiment 1

4.2.1 Hay dry matter composition

The low, medium and high moisture level alfalfa and their dry matter compositions are listed in Table 3.1. Treatment with propionate preservative did not affect the crude protein percent but the low moisture hay had an average of 0.5% less crude protein than

medium or high moisture hay. Low moisture hay tended to have the lowest fibre and lignin content whereas high moisture hay tended to contain more acid detergent insoluble nitrogen (ADIN). There were no significant differences in the ash, calcium or phosphorous concentrations in the hays.

4.2.2 Voluntary intake, passage rates and apparent digestibilities

Treatment and moisture level of the hays did not influence ($P>0.05$) voluntary dry matter intakes, which ranged from 109.5 to 118.5 g $kg^{-0.75}$ d^{-1} (Table 4.2).

The apparent digestibilities of the hays are given in Table 3.2. Hays baled at the high moisture level had the lowest ($P<0.05$) digestibility of organic matter and crude protein at both feeding levels (Table 4.2). No differences were observed between the digestibility of protein and organic matter in control versus treated hay for low and medium hays at the high feeding level but at the low feeding level, low and medium hay was more ($P<0.05$) digestible. The apparent digestibilities of acid detergent fibre, neutral detergent fibre and hemicellulose did not differ ($P<0.05$) between hays at either feeding level. Mean values for both feeding levels are given in Appendix A.

Particulate passage rate constants (PPRC) were not influenced ($P>0.05$) by hay and ranged from a low of 2.77 % h^{-1} for the low moisture control hay to a high of 3.31 % h^{-1} for the medium control hay (Table 4.3). At the high intake level PPRC ranged from

2.96 % h^{-1} to 3.31 % h^{-1} for low treated hay and medium control hay, respectively. There was a significant difference ($P<0.05$) in the passage rates between the low and high intakes, with the latter being higher (3.0 % h^{-1} vs 3.1 % h^{-1}, respectively).

Fluid passage rate constants (FPRC), Table 4.3, paralled the observations made with PPRC, i.e. there were no differences between hays within feeding levels but there was a significant difference ($P<0.05$) between low and high intakes. In this case, however, steers at the low feeding level had faster ($P<0.05$) passage rates than those at a high feeding level, 3.9 % h^{-1} and 3.4 % h^{-1}, respectively.

4.2.3 Chewing and voluntary intake, passage rates and organic matter digestibility

There were no significant ($P>0.05$) feed effects on chewing rates during rumination thus values for individual hays are not shown. However, chewing increases ($P<0.05$) from 43.3 to 51.0 chews min^{-1} (Table 4.4) occurred as intake increased from 67 to 115 g DM $kg^{-0.75}{}_d{}^{-1}$ (Table 4.4). Increased intakes had the opposite effect on chewing during eating; steers at voluntary intake had the lowest number of chews min^{-1} (58) while steers at low intake had the highest (66.5) eating chews min^{-1}.

Ruminating chews per bout ranged from 1575 to 1035 ($P<0.05$) for voluntary and low intakes, respectively (Table 4.4). The number of eating chews per bout was lower ($P<0.05$) at the high intake levels (i.e. voluntary and high intakes) than at low intake.

The time spent chewing per bout during rumination and eating (Table 4.4) paralled the number of chews per bout (i.e. a higher number of chews were observed in bouts of longer duration).

Ruminating chews d^{-1} (15067) at the low feeding level were less ($P<0.05$) than ruminating chews d^{-1} at high and voluntary intakes which were 20283 to 21405, respectively (Table 4.4). Eating chews d^{-1} increased significantly ($P<0.05$) with intake level (12156, 17367 and 21628 for the low, high and voluntary levels of intake, respectively). Time spent chewing was a reflection of the total number of chews per day.

No significant relationships were found between chewing activity and voluntary intake within a feed (Table 4.5). In most cases however, there was a negative relationship between chews d^{-1} and voluntary intake.

The relationships between chewing activity and PPRC within feeds and feeding levels are examined in Table 4.6. In two of the six treatments at low intake (low and medium moisture control) daily rumination chews were positively related to ($P<0.05$) PPRC. The only significant relationship (negative) at the high level of intake was for the medium moisture control (eating chews d^{-1}) and PPRC passage rates. There was no significant relationship between total chews per day and PPRC in steers fed at the high level.

The relationship between PPRC and OMD is given in Table 4.7. There were no significant coefficients of regression ($P<0.05$) using PPRC as the independent variable and OMD as the dependent variable.

Similarly, there also does not appear to be any pattern of effects across feed for the relationship between OMD and PPRC.

In Table 4.8 the coefficients of regression for chewing and OMD at maintenance intake are shown. The only significant relationships were negative and involved eating and total chews d^{-1} for the high treated hay fed at the high intake. It is of interest that in all comparisons at the high intake level a negative relationship was observed between organic matter digestibility and eating chews d^{-1}. Similarly for total chews d^{-1}, five of six gave a negative relationship at the high intake level.

4.3 Experiment 2

4.3.1 Dry matter composition of four concentrate/hay diets

The chemical compositions of the hay, barley and supplement used in this experiment are given in Table 3.2. It should be noted that the supplement for the 33/67 and 90/10 diets were not the same which explains their different composition.

4.3.2 Voluntary intake, passage rate constants and apparent digestibilities

Voluntary dry matter intakes for the diets containing whole and rolled barley were 116.0 and 115.5 g $kg^{-0.75}$ d^{-1} for steers fed the 33/67 diet and 109.7 and 92.1 g $kg^{-0.75}$ d^{-1} for steers fed the corresponding grains in the 90/10 diets (Table 4.9). Voluntary intake for the 90/10 rolled barley diet was significantly ($P<0.05$)

lower than for the other three other diets.

Organic matter digestibility ranged from a high of 83.4% for the rolled 90/10 diet to 66.7% for the 33/67 whole barley diet at the low intake level (Table 4.9). This trend was upheld at the high feeding level with the difference in OMD between the aforementioned feeds being 19.1%.

The digestible energy (DE) Mcal kg^{-1} was lower ($P<0.05$) by 11.4 and 13.8% for the 90/10 whole barley as opposed to the rolled 90/10 barley mixture at the low and high intake, respectively (Table 4.9). The same general trends held true with the 33/67 barley diets except the differences were less pronounced.

The PPRC of the whole and rolled barley with the 33/67 diet ranged from 2.87 to 2.95% at the high intake level and 2.39 to 2.79% at the low intake level (Table 4.10). The differences in PPRC when the 90/10 ratio were fed were similiar to that observed for the 33/67 diet (e.g. 1.69 vs 1.55% at low intake and 1.92 vs 1.96% at high intake). No differences were observed in FPRC between steers fed whole or rolled barley at either the high or low feeding level.

4.3.3 Chewing versus particulate passage rate constants and organic matter digestibility

Ruminating chews d^{-1} for the 33/67 rolled and whole barley rations were 35.8% higher ($P<0.05$) than the 90/10 mixtures (Table 4.11). Eating chews d^{-1} ranged from 8569 chews d^{-1} for 90/10 rolled barley to 14389 chews d^{-1} for the 33/67 whole barley diet but did not differ ($P>0.05$) between diets because of the large

standard error (1918). Time spent chewing was a reflection of chewing activity.

In Table 4.12, chewing is related to PPRC at low and high feed intake. Significant observations ($P<0.05$) involved eating chews d^{-1} when the animals were consuming a 33/67 whole barley-hay diet at low level intake (positive relationship) and for the 90/10 rolled barley-hay diet at high intake (eating and total chews d^{-1} were negatively related to passage rates).

There were no significant relationships between PPRC and OMD (Table 4.13).

A significant simple linear relationship did not exist between chewing activity and OMD with two exceptions; ruminating chews d^{-1} versus OMD for the 33/67 concentrate-hay diet containing rolled barley at low intake ($P=0.02$) and eating chews d^{-1} for the 90/10 conentrate-hay diet containing rolled barley ($P=0.05$) at the high intake (Table 4.14).

5.0 Discussion

5.1 Chew monitoring apparatus

There are jaw movement sensing devices currently in use that are interfaced to microcomputers (Murphy and Jaster 1984; Luginbuhl et al. 1987). This system, however, is the only one to our knowldge which interfaced a pneumatic device to a microcomputer. The recording device is extremely accurate (Table 4.1) with only a 1 chew difference (2815, 2816) between the manual squeezing and the computer recorded results. Observations of the animals chewing and the recorded results were also extremely close (13681, 13749), although significantly different ($P<0.05$).

Figure 4.1 illustrates a sample data set acquired by this system. Currently work is in progress to devise a program which will separate ruminating and eating chews automatically. This would eliminate the time needed for manual coding of each minute of data (for each animal) and would remove the possibility of any inconsistencies in the coding process. To date the machine has been operated for approximately 3600 steer h and is still functioning satisfactorily.

5.2 Experiment 1

The effect of the propionate treatment and baling moistures of the six alfalfa hays on the apparent digestibilities of various feed parameters is the topic of another research paper (Baron and Mathison unpublished) and as such will not be discussed here.

5.2.1 Particulate and fluid passage rate constants

Fistulated animals could not be accomodated within the experimental setup at the Ruminant Feed Evaluation unit (Mathison et al. 1989) and therefore passage rate constants were determined for the total gastrointestinal tract. It has been suggested by Aitchison et al. (1986) that obtaining representative samples of the rumen digest may be difficult and that it would be prudent to collect fecal samples where thorough mixing would be easier. The assumption that passage rate constants for the whole digestive tract are similar to those of the ruminoreticulum (Pond et al. 1983) was validated by Okine et al. (1989).

Particulate passage rate constants for the hays at the low and high levels of intake ranged from 2.77 to 3.16 % h^{-1} and 2.96 to 3.29 % h^{-1} respectively (Table 4.3). These results resemble closely the findings of von Keyserlingk and Mathison (1989) who found PPRC of 2.8 to 3.5 % h^{-1} and 3.1 to 3.6 % h^{-1} for a similar type of forage at low and high intake levels. Okine et al. (1989) reported PPRC at a slightly lower rate of 2.1 % h^{-1} for animals receiving 66.7 g $kg^{-0.75}d^{-1}$ of a 50:50 mixture of bromegrass and alfalfa hay.

It is generally acknowledged that as intake increases there is a concomitant rise in PPRC (Grovum 1984; Van Soest 1982). This concept is confirmed by our results which show a higher rate of particulate passage for animals at high intake as opposed to low intake. Conversely Ulyatt et al. (1984) reported that increases in intake from maintenance to 1.5 maintenance resulted in increased g

d^{-1} passage rates but not PPRC.

Fluid passage rate constants (FPRC) were higher than PPRC at both feeding levels (Table 4.3). Intake level had a significant effect on FPRC with the low level of intake having a higher rate of passage than the high level of intake. This contradicts the findings of Bull et al. (1979) but agrees with von Keyserlingk and Mathison (1989) who determined that FPRC were unaffected by intake level. This effect may have been due to excessive water consumption at the low intake level.

5.2.2 Chewing activity, voluntary intake and particulate passage rate constants

Chewing rates have been shown to be influenced by the level of feed intake in cattle and sheep (Bae et al. 1979; Bae et al. 1981). These results are corroborated by Table 4.4 in which rumination chewing rates increased from 43.3 chew min^{-1} to 51.0 chew min^{-1} for low and voluntary intakes respectively. Rumination times in cattle usually have an upper limit of 10 h d^{-1} (Welch 1982) and it has therefore been suggested by Bae et al. (1981) that in order to circumvent this time limitation cattle will increase rumination chewing rates as intake increases.

Gill et al. (1966) reported that the chewing rates for cattle fed 5 kg DM d^{-1} of a timothy hay were between 72-74 chews min^{-1}. Similarly, Luginbuhl et al. (1989) measured an average of 70 chews min^{-1} during eating when cattle were monitored for the first 40 min after feeding. In Table 4.4 eating chews min^{-1} range

from 66.5 (low intake) to 58.0 (high intake). This discrepancy suggests that cattle do not eat with the same amount of vigor at higher intake levels. However, no other experimental evidence was found to confirm this observation.

Rumination chews d^{-1} and total time spent ruminating at the voluntary intake level were 21405 chew d^{-1} and 432 min d^{-1}, respectively (Table 4.4). These results are somewhat lower than the values obtained by Kennedy (1985), who reported ruminating chews d^{-1} as 27000 and time spent chewing during rumination as 471 min d^{-1}. This data was obtained using a chopped alfalfa hay but only two animals were used. McLeod and Smith (1989) reported rumination chews d^{-1} of 26000 and time spent ruminating of 425 min d^{-1} when animals were fed alfalfa stems ad libitum. Excellent quality alfalfa was used in our study which would have reduced rumination activity.

Chewing activity during ingestion has not been as thoroughly investigated as ruminating activity due to the supposed link between rumination and clearance of indigestible feed residues from the rumen (Ulyatt 1983). Although there is a paucity of data reporting the time spent eating (e.g 370-380 min d^{-1} Deswysen et al. 1987; Deswysen and Ehrlein 1981) the total number of eating chews per day in a day has not been reported to our knowledge.

Chewing activity per bout shows that the length (23.7 min per bout at low intake to 31.0 min per bout at voluntary intake) and the number of rumination chews (1035 chews $bout^{-1}$ at a low intake to

1575 chews $bout^{-1}$ at voluntary intake) in a bout increase dramatically as intake levels rose. Eating activity was influenced in an opposite direction. Eating chews per bout varied from 4027 at low intake to 2373 at high intake and were associated with a concomitant decrease in time spent eating per bout. Norgaard (1989) employed a slightly different definition of a bout (7 min of chewing activity followed by at least 7 min of non-activity equalled 1 bout) and reported an average ruminating bout length of 20 min for lactating cows fed diets high in concentrates ad libitum .

The rate at which large particles are reduced to a size small enough to escape the rumen is thought to be a major factor regulating the voluntary intake of forages (Freer et al. 1962). Since feed particles are mainly reduced in size during eating and ruminating (Ulyatt 1983) it was prudent to examine the relationship between rumination chews d^{-1}, eating chews d^{-1} and total chews d^{-1} and voluntary intake (Table 4.5). Relationships between chewing activity and voluntary intake were nonsignificant ($P>0.05$). McLeod and Smith (1989) concluded that the time spent ruminating d^{-1} and total rumination chews d^{-1} did not influence the voluntary intake of forages. These authors, however did find a correlation between eating rate (g min^{-1}) and voluntary intake ($r=0.89$; $P<0.01$). The correlation between eating rate and voluntary intake in the aforementioned study was pursued to examine differences between feeds whereas the purpose of our research was to examine the importance of chewing on voluntary feed intake in animals fed the same feed.

Chewing during eating and ruminating is thought to influence particulate passage out of the rumen via two mechanisms: 1) particle size reduction (most particles escaping the rumen are less than 1.18 mm in size for both cattle or sheep) (Poppi et al. 1980); and 2) particles with specific gravities between 1.17 and 1.42 have the greatest chance of escape from the rumen and particles smaller than 1 mm in size generally meet this criterion (Welch 1986). Table 4.6 examines the relationships between various chewing activities and PPRC. To our knowledge, this is the first study which attempted to examine the relationship between chewing and PPRC. At the low level of intake four of the six hays illustrated a positive relationship between PPRC and rumination, however only two of these were significant ($P<0.05$). In contrast, at the high feeding level, the relationship between rumination and chewing activity was negative in five of the six comparisons (Table 4.6). Generally, it can be stated that chewing during rumination did not have a consistent influence on PPRC. However, it is of interest that in five of six comparisons at the low intake and in four of six comparisons at the high level, the relationship between total chews and PPRC was positive as might be expected. A study in which a lower quality hay and more animals were used is needed to clarify this relationship.

5.2.3 Particulate passage rate constants, apparent digestibilities and chewing activity

Passage rates and digestibilities are expected to be inversely related (Kennedy and Milligan 1978; Orskov et al. 1988). Orskov et

al. (1988) compared two groups of cows, one group was selected because of inherently high PPRC and the other for low PPRC. They found that animals with lower PPRC had higher organic matter digestibilities at ad libitum intakes. The relationship between PPRC and OMD with different feeds is examined in Table 4.7. Although no significant relationships were noted, the experimental limitations of a high quality feed and too few animals may have prevented the detection of significant relationships. These results mimic those obtained by Okine et al. (1989). These authors artifically increased PPRC from 2.1 to 4.1 % h^{-1} by placing a 24 kg weight in the rumen and could not distinguish any significant depression in OMD. It has been postulated by Hoover (1978) that incomplete digestion in the ruminoreticulum could be compensated for by increased digestion in the lower gastrointestinal tract.

Chewing during eating and ruminating creates openings through which rumen microflora can invade ingested plant material (Cheng et al. 1979). The increased surface area resulting from particle size reduction during chewing creates a greater area per gram of feed for attachment and digestion by rumen microbes (Welch and Hooper 1988). It thus might be predicted that a greater chewing activity would be associated with higher OMD. The effect of rumination chews, eating chews and total chews d^{-1} on OMD was not significant in animals within feeds with the exception of those given treated high moisture hay at the high intake level where a negative relationship was observed (Table 4.8). Again however, experimental limitations may have prevented us from detecting real differences. It is of

interest that in five of six cases at the high feeding level there were indications that increased chewing numerically reduced OMD. This observation, if confirmed with more animals and a lower quality feed, would suggest that the effect of increased passage rates depressing digestibility was of more importance in influencing OMD than any improvemnt brought about by chewing improving microbial digestion.

5.3 Experiment 2

The effect of processing barley on the apparent digestibilities of various feed components is the topic of another project (Mathison and Engstrom, unpublished) and will not be discussed here.

5.3.1 Particulate and fluid passage rate constants

Components of a mixed diet have been shown to have different PPRC (Warner 1981). Campling and Freer (1962) reported that the mean retention time for plastic particles was 60 h when animals were fed hay but increased to 110 h when concentrates were fed. In our study, the PPRC of the Cr mordanted hay (Table 4.10) at both the low and high intakes showed a faster rate of passage for the hay fraction at the 33/67 concentrate-hay ratio than the 90/10 ratio. These differences could arise from the fact that dry matter intake was greater for the hay based mixture (as was noted in experiment 1 - increased intake caused an increase in PPRC).

The FPRC passage rates (Table 4.10) at the low level of intake were faster for the hay based diets than the concentrate diets. These results were not surprising as salivation is limited on high

concentrate diets (Pond et al. 1986).

5.3.2 Chewing activity and particulate passage rate constants

The feeding of pelleted or concentrated diets is known to drastically reduce rumination time (Balch 1958; Van Soest 1982). Lack of tactile or pressure stimulation of the rumen wall by coarse material is thought to cause this decline in rumination (Van Soest 1982). Data in Table 4.11 validates this relatioship since animals given the high concentrate diets (90/10 concentrate-hay ratio) had substantially less rumination chews d^{-1} than those fed the hay based diet (33/67 concentrate-hay ratio). Daily eating chews also tended to be higher for the forage based diets but not significantly so ($P>0.05$). Balch (1971) examined the influence of concentrate in the diet of cows on ruminating and eating time and found increased ruminating time and eating time as the level of roughage increased.

The relationship between chewing activity and PPRC was examined in Table 4.12. Chewing during eating had a positive effect ($P<0.001$) on PPRC at the low level of intake for the whole barley 33/67 grain-hay diet. As this feed was subject to only 3 observations this result is thought to be an experimental artifact and not indicative of a consistent chewing influence on PPRC.

5.3.3 Particulate passage rate constants, organic matter digestibility and chewing activity

In agreement with experiment 1, PPRC and OMD were not related

(Table 4.13). Bines and Davey (1970) in a similar type of trial fed cows diets which had varying percentages of concentrate. They found no differences in PPRC between treatments but differences in OMD were evident. Passage and digestion are competitive means for the removal of digesta from the rumen (Van Soest 1982). It can therefore be proposed that diets used in this study were digested at rapid rates and changes in PPRC were therefore inconsequential.

Chewing activity did not influence OMD in a predictable manner (Table 4.14) as was the case in experiment 1.

6.0 GENERAL DISCUSSION AND CONCLUSION

Research pertaining to the chewing activity in ruminants has concentrated almost exclusively on the particle size reduction of the ingested feed. This is a logical first step but in order to demonstrate pertinence to practical animal production relationships between chewing and the various physiological parameters which influence productivity needed further elucidation. This was the objective of this study.

In experiment 1, as intake increased the animals increased the rate of rumination chews min^{-1} in an apparent effort to process more feed particles within a limited amount of time. This complements the findings of Ulyatt (1983) who suggested that rumination acts as a waste removal system for indigestible feed residues within the rumen. It was also clear from experiment 2 that diets high in concentrates drastically reduce rumination chews d^{-1}.

Chewing during eating and ruminating aids in the relief of rumen fill which is thought to play a role in modifying voluntary intake of forages by ruminants (Welch and Hooper 1988). Chewing activity was therefore examined for a relationship with voluntary intake, however, none was found. The quality of the alfalfa hays was quite good in this study, and possibly for this reason chewing was not a contributory factor in regulating intake. Future research in this area should be restricted to poor quality hays and straws where individual animal capabilities in terms of chewing would be more

apparent.

Particulate passage rates and chewing activity was examined with the knowledge that chewing during eating and ruminating is primarily responsible for the reduction of ingested feed particle size and hence, an increased possibility of escape from the rumen (Poppi 1980). Generally, it can be concluded that chewing activity (chews d^{-1}) had little influence on PPRC in both experiment 1 and 2. As PPRC do not reflect absolute volumes of digesta moving through the alimentary tract, research should concentrate on measuring flows of digesta in terms of mass or volumes and relating this to chewing activity. A further area to address is the effectiveness of chewing (i.e. some animals may possess the ability to reduce particles in size with fewer chews than other animals). This possibility could be studied by sieving fecal samples since material passing through the reticulo-omasal orifice do not undergo further size reduction (Uden and Van Soest 1982).

Particulate passage rate constants were shown to have little influence on OMD in either experiment 1 or 2. These results are in agreement with Okine et al. (1989). It can also be concluded that chewing did not have a noticeable impact on OMD in this study.

Chewing activity when animals were fed moderate to good alfalfa hays (experiment 1) or barley-hay diets (experiment 2) appeared to exert little influence on the parameters affecting productivity.

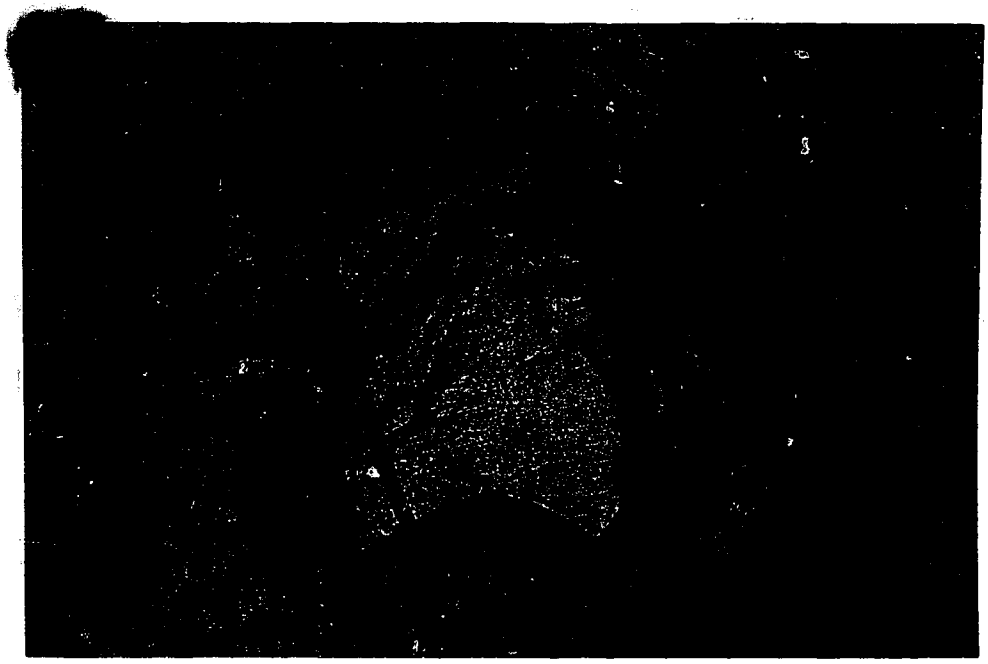

Plate 3.1 Chew monitoring apparatus

Table 3.1. Composition of dry matter in six alfalfa hays

	Low moisture		Medium moisture		High moisture		
	Control	Treated+	Control	Treated+	Control	Treated+	S.E.*
Crude protein (%)	18.6c	19.0bc	19.9a	19.4ab	20.1a	19.6ab	0.19
Acid detergent fibre (%)	30.7c	30.2c	32.3b	31.0c	34.1a	32.4b	0.26
Neutral detergent fibre (%)	38.9cd	38.0d	41.0b	39.7c	44.4a	41.7b	0.45
Nitrate (%)	0.05d	0.07c	0.12a	0.07c	0.09b	0.07c	0.003
Lignin (%)	5.91ab	5.66b	6.38ab	6.24a	6.74a	6.56ab	0.24
ADIN++(%)	0.97bc	0.81d	0.97bc	0.92cd	1.15a	1.08ab	0.04
Ash (%)	10.8	10.2	9.9	9.9	10.6	10.7	0.31
Calcium (%)	1.9	1.9	1.9	1.9	2.0	1.9	0.02
Phosphorous (%)	0.21	0.21	0.21	0.21	0.21	0.21	0.00

+Treated refers to the addition of 1.25% wt wt^{-1} propionate preservative at the time of baling.

*Standard error of the mean is based upon twelve observations per mean.

++Acid detergent insoluble nitrogen.

a-d values in the same row not followed by the same letter differ significantly ($P<0.05$).

Table 3.2. Composition of dry matter in four barley grain-hay diets

	Whole barley		Rolled barley		
	33/67*	90/10*	33/67*	90/10*	S.E.+
Hay					
Crude protein (%)	15.8	15.8	15.8	15.9	0.12
Acid detergent fibre (%)	35.7	35.9	35.9	36.0	0.33
NDF ++ (%)	49.7	49.9	49.9	50.0	0.26
Ash (%)	8.9	9.0	9.0	9.0	0.08
Calcium (%)	1.8	1.8	1.8	1.8	0.02
Phosphorous (%)	0.19	0.18	0.18	0.18	0.004
Barley					
Crude protein (%)	14.1a	14.1a	13.8ab	13.6b	0.11
Acid detergent fibre (%)	7.4c	7.5bc	8.2a	7.8b	0.11
NDF (%) ++	17.6	17.6	18.5	18.4	0.27
Ash (%)	2.8b	2.8b	3.3a	3.3a	0.11
Phosphorous	0.40	0.40	0.40	0.40	0.003
Supplement					
Crude protein (%)	23.0a	19.2b	22.8a	19.6b	0.17
Acid detergent fibre (%)	12.0a	10.9b	12.1a	10.9b	0.10
NDF (%) ++	18.9a	17.5b	18.9a	17.8b	0.30
Ash (%)	10.2b	22.8a	10.1b	22.8a	0.42
Calcium (%)	1.0b	7.1a	1.0b	6.8a	0.12
Phosphorous (%)	1.06	1.10	1.04	0.65	0.23

*Ration of barley to hay.
+Standard error of the mean is based upon twelve observations per mean.
++Neutral detergent fibre.
a-c values in the same row not followed by the same letter differ significantly ($P<0.05$).

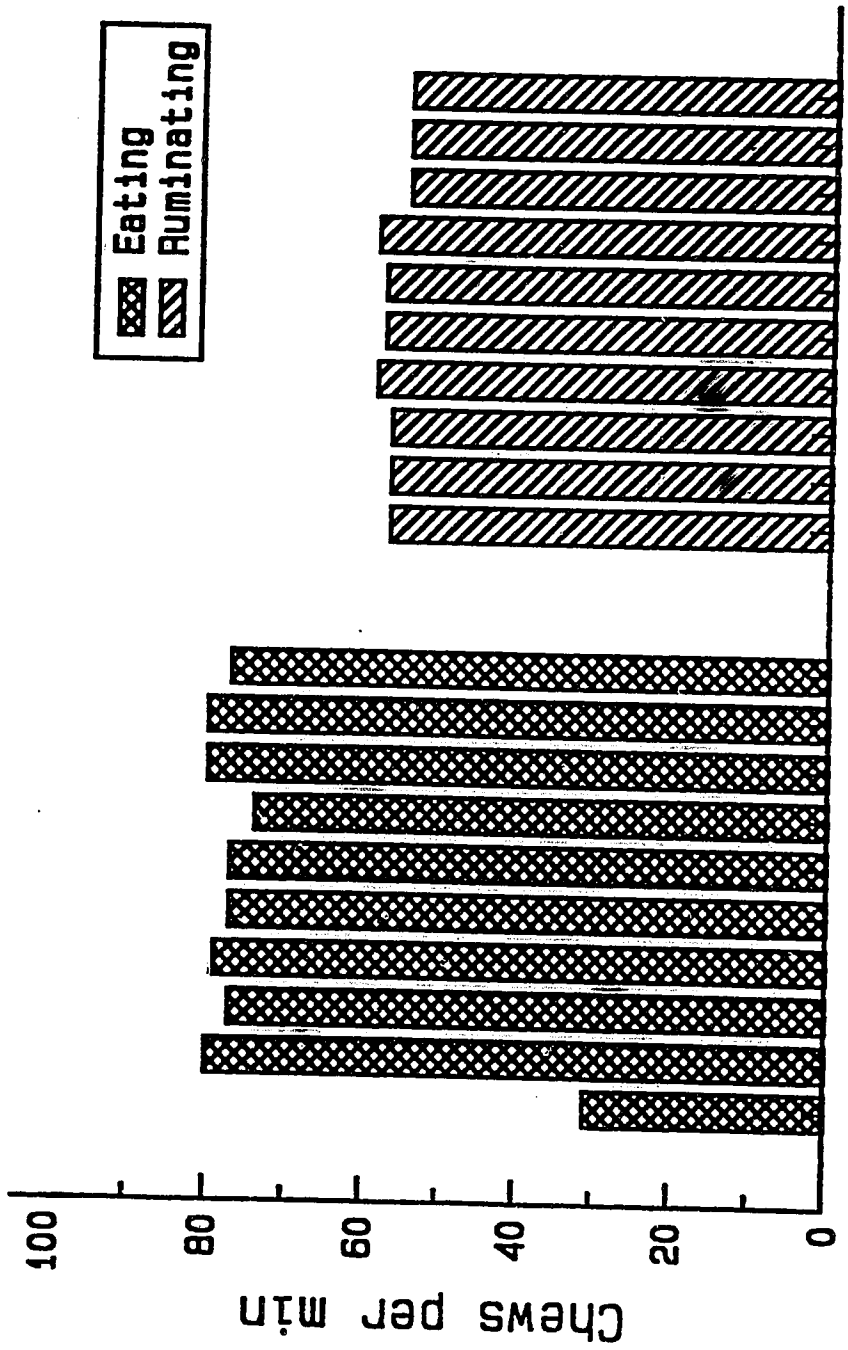

Figure 1.0 A sample data set of the pattern of chewing during eating and ruminating.

Table 4.1. Verification of data acquisition system

	Observed	Computer recorded
Manual Testing		
No. of trials	23	23
No. of observations	67	67
Average chews min^{-1}	42.01	42.03
Total chews recorded	2 815	2 816
SE	2.86	2.86
Animal test		
No. of trials	71	71
No. of observations	213	213
Average chews min^{-1}	64.23	64.55*
Total chews recorded	13 681	13 749
SE	1.12	1.14

*P<0.05

Table 4.2. Apparent digestibilities of dry matter (DM), organic matter (OM), crude protein (CP), acid detergent fibre (ADF), neutral detergent fibre (NDF), hemicellulose and energy (DE) of six alfalfa hays fed at two intake levels

	Low moisture		Medium moisture		High moisture		
	Control	Treated	Control	Treated	Control	Treated	S.E.+
Voluntary intake							
Dry matter intake (g $kg^{-0.75}$ d^{-1})	109.5	117.2	114.8	115.5	111.8	118.5	13.17
Low intake							
Dry matter intake (g $kg^{-0.75}d^{-1}$)	65.2	66.9	67.4	66.8	67.3	66.4	0.39
Apparent digestibility (%)							
DM	67.4a	65.3b	63.3c	65.8b	61.3d	62.5cd	0.43
OM	69.2a	67.4b	65.4c	67.1b	62.4e	63.9d	0.43
CP	76.9a	76.4a	74.0b	75.5ab	69.6c	70.4c	0.56
ADF	53.0	48.3	49.1	50.4	51.5	50.0	1.28
NDF	52.7	47.3	48.9	52.0	54.0	51.3	1.65
Hemicellulose	83.7	80.3	82.8	85.5	85.3	83.3	1.42
Digestible energy (Mcal kg^{-1})	3.01a	2.84ab	2.84ab	3.00a	2.70b	2.80b	0.04
High intake							
Dry matter intake (g $kg^{-0.75}d^{-1}$)	93.0	98.8	96.3	103.6	107.8	103.0	4.16
Apparent digestibility (%)							
DM	66.0	65.1	63.9	66.0	62.1	63.9	0.84
OM	67.6a	67.0a	65.6ab	67.4a	62.7b	63.0b	0.89
CP	75.8a	76.2a	74.5a	75.8a	69.4c	72.3b	0.56
ADF	50.8	47.9	48.7	51.4	51.0	51.7	1.92
NDF	49.2	45.3	50.4	52.1	53.6	52.1	1.94
Hemicellulose	81.0b	80.3b	83.7a	85.0a	86.3a	84.9a	0.79
Digestible energy (Mcal kg^{-1})	2.932	2.838	2.812	2.985	2.762	2.853	0.06

+ Standard error of the mean is based upon six observations per mean.

a-d Values in the same row not followed by the same letter differ significantly ($p<0.05$).

Table 4.3. Particulate and fluid passage rate constants in steers fed six alfalfa hays

	Low moisture		Medium moisture		High moisture		
	Control	Treated	Control	Treated	Control	Treated	S.E.+
Low intake							
Rate of passage (% h^{-1})							
Particulate	2.77	2.79	3.31	2.94	3.07	3.16	0.13
Fluid	4.12	3.62	4.02	3.74	3.86	3.90	0.22
High intake							
Rate of passage (% h^{-1})							
Particulate	2.98	2.96	3.31	3.26	3.16	3.29	0.13
Fluid	3.28	3.50	3.87	3.33	2.99	3.44	0.28

+Standard error of the mean is based upon six observations per mean.

Table 4.4. Chewing activity of steers fed six alfalfa hays at three levels of intake

	Low intake	High intake	Voluntary intake	S.E.+
Chewing rates				
Ruminating chews min^{-1}	43.3c	47.4b	51.0a	0.90
Eating chews min^{-1}	66.5a	60.5b	58.0c	0.84
Per bout*				
Ruminating chews $bout^{-1}$	1035c	1283b	1575a	64.0
Eating chews $bout^{-1}$	4027a	3065b	2373b	312.2
Time spent chewing				
Ruminating min $bout^{-1}$	23.7b	27.0a	31.0a	1.02
Eating min $bout^{-1}$	61a	49	41b	5.54
Chews per day				
Ruminating chews d^{-1}	15067b	20283a	21405a	1087
Eating chews d^{-1}	12156c	17367b	21628a	1203
Total chews	27223c	37650b	43033a	1601
Time spent chewing (min d^{-1})				
Ruminating chews	347b	429a	432a	20.1
Eating chews	185c	285b	371a	18.6
Total chews	532c	714b	803a	24.2

+Standard error of the means is based upon twelve observations per mean.

*Bout refers to any sustained chewing activity greater than seven minutes in duration and separated from other bouts of chewing by at least five minutes of non-activity.

a-b values in the same row not followed by the same letter differ significantly ($P<0.05$).

Table 4.5. Relationship between ruminating, eating and total chews (X) and voluntary intake (Y) in steers fed six alfalfa hays

	R^2+	S.E.	Probability
Low moisture			
Control			
-0.007(Rumination chews d^{-1}) + 130.7	0.02	18.1	0.43
-0.002(Eating chews d^{-1}) + 134.1	0.13	17.1	0.32
-0.001(Total chews d^{-1}) + 130.7	0.07	17.7	0.35
Treated			
0.0001(Rumination chews d^{-1}) + 115.4	0.00	28.1	0.48
-0.002(Eating chews d^{-1}) + 141.1	0.05	27.4	0.38
-0.0002(Total chews d^{-1}) + 122.1	0.00	28.0	0.47
Medium moisture			
Control			
-0.0002(Rumination chews d^{-1}) + 119.9	0.02	6.7	0.44
0.0004(Eating chews d^{-1}) + 112.2	0.06	6.0	0.38
0.0001(Total chews d^{-1}) + 114.6	0.01	6.2	0.46
Treated			
0.003(Rumination chews d^{-1}) + 75.54	0.33	15.8	0.21
-0.003(Eating chews d^{-1}) + 160.4	0.76	9.2	0.06
-0.001(Total chews d^{-1}) + 150.6	0.15	17.6	0.30
High moisture			
Control			
-0.003(Rumination chews d^{-1}) + 149.7	0.54	5.3	0.13
-0.0001(Eating chews d^{-1}) + 113.8	0.00	7.8	0.48
-0.002(Total chews d^{-1}) + 164.1	0.45	5.8	0.16
Treated			
-0.005(Rumination chews d^{-1}) + 182.4	0.51	15.2	0.24
-0.0001(Eating chews d^{-1}) + 121.1	0.01	21.7	0.47
-0.002(Total chews d^{-1}) + 163.8	0.22	19.2	0.34

+Regression relationships are based upon four observations from individual animals per feed.

Table 4.6. The relationship between ruminating chews d^{-1} (X_1), eating chews d^{-1} (X_2), total chews d^{-1} (X_3) and the particulate passage rates (Y) of six alfalfa hays in steers fed at two levels of intake

Low intake	R^2*	S.E.	P+	High intake	R^2*	S.E.	P+
Low moisture				**Low moisture**			
Control				Control			
$0.00006(X_1) + 1.76$	0.85	0.21	0.04	$-0.00014(X_1) + 6.11$	0.81	0.36	0.14
$0.00004(X_2) + 1.93$	0.64	0.32	0.10	$0.00003(X_2) + 2.36$	0.24	0.71	0.33
$0.00003(X_3) + 1.77$	0.79	0.25	0.05	$0.00001(X_3) + 2.73$	0.01	0.82	0.46
Treated				Treated			
$0.00005(X_1) + 1.84$	0.17	0.72	0.30	$-0.00003(X_1) + 3.51$	0.09	1.39	0.40
$0.00014(X_2) - 0.27$	0.51	0.55	0.14	$-0.00007(X_2) + 5.12$	0.21	1.29	0.35
$0.00008(X_3) - 0.48$	0.55	0.53	0.13	$-0.00014(X_3) + 9.00$	0.77	0.69	0.15
Medium moisture				**Medium moisture**			
Control				Control			
$0.00019(X_1) - 0.85$	0.83	0.17	0.04	$-0.00009(X_1) + 5.34$	0.04	1.07	0.40
$-0.00003(X_2) + 3.84$	0.17	0.39	0.30	$-0.0001(X_2) + 4.90$	0.95	0.23	0.01
$0.0000(X_3) + 3.40$	0.00	0.42	0.44	$-0.00009(X_3) + 7.20$	0.98	0.12	0.006
Treated				Treated			
$-0.00003(X_1) + 3.62$	0.80	0.15	0.06	$-0.00003(X_1) + 3.91$	0.91	0.03	0.09
$-0.00002(X_2) + 3.41$	0.30	0.29	0.23	$0.00002(X_2) + 2.84$	0.82	0.05	0.14
$-0.00002(X_3) + 3.89$	0.98	0.05	0.03	$0.00001(X_3) + 2.65$	0.17	0.10	0.36
High moisture				**High moisture**			
Control				Control			
$-0.00001(X_1) + 3.28$	0.01	0.55	0.45	$0.00004(X_1) + 2.13$	0.41	0.35	0.18
$0.00009(X_2) + 1.59$	0.69	0.30	0.08	$0.0000(X_2) + 3.12$	0.00	0.45	0.49
$0.00003(X_3) + 1.90$	0.21	0.49	0.27	$0.00007(X_3) + 0.30$	0.71	0.25	0.08
Treated				Treated			
$0.00005(X_1) + 2.17$	0.38	0.44	0.27	$-0.00014(X_1) + 5.76$	0.44	0.44	0.27
$0.00003(X_2) + 2.53$	0.81	0.24	0.15	$0.00002(X_2) + 2.95$	0.25	0.51	0.33
$0.00002(X_3) + 2.32$	0.68	0.31	0.19	$0.00001(X_3) + 2.92$	0.12	0.55	0.38

*Regression relationship based upon four observations from individual animals per mean except the low intake high moisture feed (treated), high intake level low moisture (control and treated), high intake medium moisture (treated) and high intake medium moisture (treated) which were based on three.

+Probability.

Table 4.7. The relationship between particulate passage rate constants (X_1 low intake and X_2 high intake) and organic matter digestibility (Y) in steers fed six alfalfa hays at low and high intake levels

	R^2*	S.E.	Probability
Low moisture			
Control			
$-3.95(X_1) + 80.12$	0.38	2.21	0.13
$1.17(X_2) + 64.107$	0.14	1.89	0.27
Treated			
$1.28(X_1) + 63.83$	0.29	1.21	0.13
$-1.40(X_2) + 71.32$	0.10	3.15	0.26
Medium moisture			
Control			
$-1.12(X_1) + 69.15$	0.37	0.68	0.09
$0.14(X_2) + 65.12$	0.01	1.18	0.42
Treated			
$-0.06(X_1) + 67.27$	0.00	0.95	0.48
$-2.28(X_2) + 74.87$	0.05	2.49	0.34
High moisture			
Control			
$-0.89(X_1) + 65.02$	0.08	1.29	0.29
$-0.77(X_2) + 65.19$	0.01	2.57	0.42
Treated			
$0.13(X_1) + 63.44$	0.00	1.08	0.45
$-0.43(X_2) + 65.22$	0.01	2.36	0.44

*Regression relationships are based upon six observations from individual animals per feed.

Table 4.8. The relationship between ruminating chews d^{-1} (X_1), eating chews d^{-1} (X_2), total chews d^{-1} (X_3) and organic matter digestibility (Y, %) in steers fed six alfalfa hays at two levels of intake

Low intake	R^2*	S.E.	P+	High intake	R^2*	S.E.	P+
Low moisture				**Low moisture**			
Control				Control			
$-0.00023(X_1) + 73.22$	0.29	2.8	0.23	$0.00019(X_1) + 64.32$	0.90	0.33	0.09
$-0.00029(X_2) + 75.19$	0.72	1.8	0.08	$-0.00006(X_2) + 69.86$	0.37	0.88	0.29
$-0.00015(X_2) + 74.74$	0.54	2.3	0.13	$-0.00003(X_3) + 70.01$	0.06	1.07	0.42
Treated				Treated			
$0.00006(X_1) + 65.81$	0.05	1.7	0.39	$0.00026(X_1) + 64.11$	0.81	1.66	0.14
$0.00014(X_2) + 63.82$	0.11	1.6	0.33	$-0.00013(X_2) + 71.83$	0.11	3.57	0.39
$0.00008(X_3) + 63.39$	0.14	1.6	0.32	$0.00039(X_3) + 51.09$	0.40	1.17	0.10
Medium moisture				**Medium moisture**			
Control				Control			
$-0.00046(X_1) + 75.34$	0.59	0.8	0.12	$0.00036(X_1) + 57.12$	0.45	0.95	0.16
$0.00005(X_2) + 64.67$	0.04	1.2	0.40	$-0.00008(X_2) + 67.46$	0.50	0.91	0.15
$-0.00002(X_3) + 63.30$	0.02	1.2	0.45	$-0.00006(X_3) + 68.55$	0.30	1.08	0.23
Treated				Treated			
$0.00002(X_1) + 67.01$	0.30	0.4	0.33	$-0.00082(X_1) + 90.98$	0.45	3.45	0.26
$-0.00004(X_2) + 68.08$	0.41	0.4	0.18	$-0.00001(X_2) + 68.26$	0.00	4.67	0.49
$0.0000(X_3) + 67.39$	0.01	0.5	0.46	$-0.00076(X_3) + 104.69$	0.42	3.53	0.27
High moisture				**High moisture**			
Control				Control			
$-0.00014(X_1) + 65.42$	0.40	0.9	0.18	$0.00015(X_1) + 59.90$	0.25	1.72	0.25
$-0.00011(X_2) + 64.38$	0.28	1.0	0.24	$-0.00015(X_2) + 65.63$	0.29	1.67	0.23
$-0.00010(X_3) + 66.15$	0.51	0.8	0.15	$-0.00004(X_3) + 64.84$	0.01	1.98	0.45
Treated				Treated			
$0.0000(X_1) + 64.70$	0.00	0.0	0.50	$-0.00017(X_1) + 67.17$	0.15	1.14	0.37
$0.0000(X_2) + 64.70$	0.00	0.0	0.50	$-0.00009(X_2) + 66.41$	0.99	0.09	0.02
$0.0000(X_3) + 64.70$	0.00	0.0	0.50	$-0.0008(X_3) + 67.57$	0.99	0.12	0.03

*Regression relationships based upon four observations per mean except the low intake high moisture feed (treated), high intake level low moisture (control and treated), high intake medium moisture (treated) and high intake medium moisture (treated) which were based on three.

+Probability.

Table 4.9. Apparent digestibilities of dry matter (DM), organic matter (OM), crude protein (CP), acid detergent fibre (ADF), neutral detergent fibre (NDF), and digestible energy (DE) of four concentrate-hay diets

	Whole barley		Rolled barley		
	33/67*	90/10*	33/67*	90/10*	S.E.+
Voluntary intake					
Dry matter intake (g $kg^{-0.75}$ d^{-1})	116.0a	109.7a	115.5a	92.1b	3.26
Low intake					
Dry matter intake (g $kg^{-0.75}$ d^{-1})	55.3a	41.8b	54.2a	38.7c	0.75
Apparent digestibility (%)					
DM	64.9c	70.8b	68.7b	81.8a	0.87
OM	66.7c	72.3b	70.9b	83.4a	0.85
CP	73.5	69.4	72.8	78.4	2.51
ADF	50.6	47.1	49.8	50.2	2.44
NDF	49.7a	34.9b	53.7a	58.2a	2.00
Digestible energy (Mcal kg^{-1})	2.898c	3.148b	3.087b	3.653a	0.04
High intake					
Dry matter intake (g $kg^{-0.75}$ d^{-1})	96.1a	81.7ab	89.8ab	73.0b	4.1
Apparent digestibility (%)					
DM	63.4c	69.0b	67.2b	78.1a	0.83
OM	65.0c	70.2b	69.2b	80.3a	0.89
CP	69.5b	67.2b	71.6b	75.7a	1.05
ADF	49.7a	46.9a	48.2a	42.3b	1.06
NDF	46.4a	28.9b	50.9a	44.9a	1.79
Digestible energy (Mcal kg^{-1})	2.818c	3.062b	3.008b	3.455a	0.03

*Ratio of barley to hay in the diet.
+Standard error of the mean is based upon six observations per mean.
a-c Values in the same row not followed by the same letter differ significantly ($P<0.05$).

Table 4.10. Particulate and fluid passage rate constants in steers fed four concentrate-hay diets

	Whole barley		Rolled barley		
	33/67*	90/10*	33/67*	90/10*	S.E.+
Low intake					
Rate of passage (% h^{-1})					
Particulate	2.39b	1.69c	2.79a	1.55c	0.11
Fluid	4.53a	3.66ab	4.57a	3.18b	0.27
High intake					
Rate of passage (% h^{-1})					
Particulate	2.87a	1.92b	2.95a	1.96b	0.22
Fluid	3.52	4.01	4.52	3.92	0.33

*Ratio of barley to hay in the diet.
+Standard error of the mean is based upon six observations per mean.
a-c Values in the same row not followed by the same letter differ significantly ($P<0.05$).

Table 4.11. Chewing activity of steers fed rolled barley fed at two different concentrate-hay (means of three intake levels).

	Whole barley		Rolled barley		
	37/67*	90/10*	33/67*	90/10*	S.E.+
Chewing activity					
Ruminating chews d^{-1}	16104a	11254b	16141a	9432b	1328
Eating chews d^{-1}	14389	9806	10538	8569	1918
Total chews d^{-1}	30492a	21060b	26678ab	18000b	2552
Time spent chewing					
Ruminating min d^{-1}	369a	272b	382a	249b	25
Eating min d^{-1}	243	171	180	152	33
Total min d^{-1}	612a	443b	562ab	401b	42

*Ratio of barley to hay.
+Standard error of the mean is based upon eleven observations per mean except whole barley 33/67 grain-hay ratio which is based on nine observations.
a-b Values in the same row not followed by the same letter differ significantly ($P<.05$).

Table 4.12. The relationship between ruminating chews d^{-1} (X_1), eating chews d^{-1} (X_2), total chews d^{-1} (X_3) and particulate passage rate constants (Y) in steers fed four concentrate-hay mixed diets at low and high intakes

Low intake	R^2*	S.E.	P++	High intake	R^2*	S.E.	P++
Whole barley				**Whole barley**			
33/67+				33/67+			
$-0.0001(X_1) + 2.79$	0.09	0.14	0.40		ND		
$0.0067(X_2) - 12.32$	0.99	0.01	0.0003		ND		
$-0.0001(X_3)$ 2.97	0.05	0.15	0.41		ND		
90/10+							
$0.0000(X_1) + 1.86$	0.00	0.29	0.46	$0.00003(X_1) + 1.40$	0.45	0.19	0.26
$-0.00001(X_2) + 2.04$	0.04	0.28	0.40	$0.0000(X_2) + 1.77$	0.00	0.13	0.49
$-0.00004(X_3) + 2.72$	0.05	0.28	0.38	$0.00005(X_3) + 0.65$	0.73	0.14	0.17
Rolled barley				**Rolled barley**			
33/67+				33/67+			
$-0.00027(X_1) + 9.51$	0.41	0.70	0.25	$0.00001(X_1) + 2.97$	0.07	0.45	0.36
$-0.00004(X_2) + 3.67$	0.09	0.88	0.41	$0.0000(X_2) + 3.14$	0.00	0.48	0.48
$-0.00011(X_3) + 7.35$	0.38	0.73	0.29	$0.00001(X_3) + 3.02$	0.03	0.47	0.41
90/10+				90/10+			
$0.00001(X_1) + 1.71$	0.12	0.15	0.38	$0.00004(X_1) + 1.49$	0.31	0.46	0.22
$0.00003(X_2) + 1.58$	0.31	0.13	0.31	$-0.00004(X_2) + 2.45$	0.88	0.19	0.02
$0.00001(X_3) + 1.68$	0.16	0.14	0.37	$-0.00007(X_3) + 3.49$	0.93	0.14	0.01

*Regression relationships based upon four observations except low intake 33/67 and high intake 90/10 which were based on three observations.

++Probability.

+Ratio of barley to hay.

ND=No data available due to technical difficulties.

Table 4.13. The relationship between particulate passage rate constants (X_1 low intake and X_2 high intake) and organic matter digestibility (Y) in steers fed four concentrate-hay mixed diets at low and high intake levels

	R^2*	S.E.	Probability
Whole barley			
33/67+			
$3.89(X_1) + 57.45$	0.51	1.55	0.06
$0.98(X_2) + 65.16$	0.03	3.45	0.36
90/10+			
$6.12(X_1) + 61.8$	0.33	3.97	0.11
$-2.84(X_2) + 75.65$	0.03	5.50	0.36
Rolled barley			
33/67+			
$-1.65(X_1) + 75.47$	0.17	2.09	0.20
$0.85(X_2) + 66.73$	0.05	1.95	0.33
90/10+			
$-2.05(X_1) + 86.61$	0.45	0.96	0.07
$-2.15(X_2) + 84.51$	0.26	1.56	0.15

*Regression relationship based upon six observations.
+Ratio of grain to hay in the diet.

Table 4.14. The relationship between ruminating chews d^{-1} (X_1), eating chews d^{-1} (X_2), total chews d^{-1} (X_3) and organic matter digestibility (Y) in steers fed four concentrate-hay diets at low and high intakes

Low intake	R^2*	S.E.	P++	High intake	R^2*	S.E.	P++
Whole barley				**Whole barley**			
33/67+				33/67+			
$0.0000(X_1) + 68.33$	0.01	0.21	0.47		ND		
$-0.0009(X_2) + 88.34$	0.01	0.17	0.44		ND		
$-0.00001(X_3) + 68.59$	0.02	0.21	0.45		ND		
90/10+				90/10+			
$0.00049(X_1) + 66.59$	0.19	5.34	0.28	$0.00092(X_1) + 55.75$	0.94	1.32	0.07
$-0.00084(X_2) + 80.99$	0.41	4.54	0.17	$-0.00070(X_2) + 76.27$	0.74	2.85	0.16
$-0.00045(X_3) + 82.40$	0.02	5.80	0.48	$-0.00005(X_3) + 68.67$	0.00	5.61	0.48
Rolled barley				**Rolled barley**			
33/67+				33/67+			
$0.00183(X_1) + 27.43$	0.97	0.60	0.02	$0.00012(X_1) + 68.14$	0.31	1.61	0.21
$-0.00029(X_2) + 75.10$	0.18	3.67	0.36	$0.00011(X_2) + 68.68$	0.18	1.76	0.28
$-0.00005(X_3) + 72.87$	0.00	4.03	0.47	$0.00007(X_3) + 68.01$	0.32	1.61	0.22
90/10+				90/10+			
$0.00009(X_1) + 81.50$	0.33	1.10	0.30	$-0.00003(X_1) + 80.99$	0.33	0.34	0.21
$0.00019(X_2) + 81.35$	0.14	1.25	0.37	$0.00003(X_2) + 80.27$	0.80	0.18	0.05
$0.00005(X_3) + 81.40$	0.28	1.14	0.32	$0.00005(X_3) + 79.59$	0.77	0.20	0.06

*Regression relationships are based upon four observations per mean except high intake levels of 33/67 and 90/10 which were based on three.

++Probability.

+Ratio of grain to hay.

ND=No data available due to technical difficulties.

7.0 REFERENCES

Adam, I., Young, B.A., Nicol, A.M. and Degen, A.A. 1984. Energy cost of eating in cattle given diets of different form. Br. Soc. Anim. Prod. 38:53-58.

Aitchison, E.M., Gill, M., Dhanoa, M.S. and Osbourn, D.F. 1986 The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. Brit. J. Nutr. 56:463-476.

Association of Official Analytical Chemists. 1980. Official methods of analysis. 13th ed. AOAC, Washington, D.C.

Bae, D.H., Welch, J.G. and Gilman, B.E. 1983. Mastication and rumination in relation to body size of cattle. J. Dairy Sci. 66:2137-2141.

Bae, D.H., Welch, J.G. and Smith, A.M. 1979. Forage intake and rumination by sheep. J. Anim. Sci. 49:1292-1299.

Bae, D.H., Welch, J.G. and Smith A.M. 1981. Efficiency of mastication in relation to hay intake by cattle. J. Anim. Sci. 52:1371-1375.

Bailey, C.B. and Balch, C.C 1961. The digestion of hay administered to cows through rumen fistulas. Brit. J. Nutr. 15:183-188.

Balch, C.C. 1958. Observations on the act of eating in cattle. Br. J. Nutr. 12:330-345.

Balch, C.C. and Campling, R.C. 1962. Regulation of voluntary food intake in ruminants. Nutr. Abstr. Rev. 32:669-686.

Balch, C.C. 1971. Proposal to use time spent chewing as an index of the extent to which diets for ruminants possess the physical property of fibrousness characteristic of roughages. Br. J. Nutr. 26:383-392.

Bines, J.A. and Davey, A.W.F. 1970. Voluntary intake, digestion, rate of passage, amount of material in the alimentary tract and behavior in cows receiving diets containing straw and concentrates in different proportions. Br. J. Nutr. 24:1013-1028.

Blaxter, K.L. and Clapperton, J.L. 1965. Prediction of the amount of methane produced by ruminants. Br. J. Nutr. 19:511-522.

Bryant, A.M. 1964. The release of plant cell contents and its relation to bloat. Proc. N.Z. Soc. Anim. Prod. 24:57-66.

Bull, A.M. 1964. The release of plant cell contents and its relation to bloat. Proc. N.Z. Soc. Anim. Prod. 24:57-66.

Campling, R.C. and Freer, M. 1962. The effect of specific gravity and size on the mean time of retention of inert particles in the alimentary tract of the cow. Brit. J. Nutr. 16:507-518.

Campling, R.C., Freer, M. and Balch, C.C. 1962. Factors affecting the voluntary intake of feed by cows. Brit. J. Nutr. 16:115-124.

Chai, K., Kennedy, P.M. and Milligan, L.P. 1984. Reduction in particle size during rumination in cattle. Can. J. Anim. Sci. 64 (Supp.):339-340 (Abstr).

Chai, K., Milligan, L.P. and Mathison, G.W. 1988. Effect of muzzling on rumination in sheep. Can. J. Anim. Sci. 68:387-397.

Cheng, K.J., Disdale, D. and Stewart, C.S. 1979. Maceration of clover and grass leaves by Lachnospira multiparus. Appl. Environ. Microbiol. 38:723-729.

Cheng, K.J., Fay, J.P., Howarth, R.E.. and Costerton, J.W. 1980. Sequence of events in the digestion of fresh legume leaves by rumen bacteria. Appl. Environ. Microbiol.

Colucci, P.E., Chase, L.E. and Van Soest, P.S. 1982. Feed intake, apparent digestibility, and rate of particulate passage in dairy cattle. J. Dairy Sci. 65:1445-1456.

Deswysen, A. and Ehrlein, H.J. 1981. Silage intake, rumination and pseudo-rumination activity by radiography and jaw movement recordings. Br. J. Nutr. 46:327-335.

Deswysen, A.G., Ellis, W.C., Pond, K.R., Jenkins, W.L. and Connelly, J. 1987. Effects of [illegible] on voluntary intake, eating and ruminating behavior and ruminal motility in heifers fed corn silage. J. Anim. Sci. 64:827-834.

Deswysen, A.G. and Ellis, W.C. 1988. Site and extent of neutral detergent fiber digestion, efficiency of ruminal digesta flux and fecal output as related to variations in voluntary intake and chewing behavior in heifers. J. Anim. Sci. 66:2678-2686.

Doyle, J.J. 1967. The effect of chewing by sheep on the release of nitrogen and soluble carbohydrate from plant cells. Aust. J. Exper. Agric. 7:318-320.

Dulphy, J.P., Remond, B. and Theriez, M. 1980. Ingestive behavior and related activities in ruminants. Pages 103-122 in: Y. Ruckebusch and P. Thivend, eds. Digestive Physiology and Metabolism in Ruminants. MTP Press, Lancaster.

Duranton, A. And Bueno, L. 1982. Un dispositif simple et fiable d'analyse des mouvements de machoires chez les petits ruminants. Ann. Zootech. 31:489-494.

Faichney, G.J. 1980. The use of markers to measure digesta flow from the stomach of sheep fed once daily. J. Agric. Sci. Camb. 94:313-318.

Faichney, G.J. 1986. The kinetics of particulate matter in the rumen. Pages 173-195 in: L.P. Milligan, W.L. Grovum, and A. Dobson, eds. Control of Digestion and Metabolism in Ruminants. Prentice-Hall, Englewood Cliffs, New Jersey.

Freer, M., Campling, R.C. and Balch, C.C. 1962. Factors affecting the voluntary intake of food by cows.4. The behavior and reticular motility of cows receiving diets of hay, oat straw and oat straw with urea. Br. J. Nutr. 16:279-295.

Frish, J.E. and Vercoe, J.E. 1969. Liveweight gain, food intake, and eating rate in Brahman, Africaneer, and Shorthorn X Hereford cattle. Aust. J. Agric. Res. 20:1189-1195.

Gill, J., Campling, R.C. and Westgarth, D.R. 1966. A study of chewing during eating in the cow. Br. J. Nutr. 20:13-23.

Goering, H.K. and Van Soest, P.J. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Handbook No. 379. ARS-USDA, Washington, D.C.

Goering, H.K., Gordon, C.H., Hemken, R.W., Waldo, D.R., Van Soest, P.J. and Smith, L.W. 1972. Analytical estimates of nitrogen digestibility in heat damaged forages. J. Dairy Sci. 55:1275-1280.

Gordon, J.G. 1968. Rumination and its significance. World Rev. Nutr. Diet. 9:251-273.

Grovum, W.L. 1984. Integration of digestion and digesta kinetics with control of feed intake - a physiological framework for a model of rumen function. In Herbivore nutrition of the subtropics and tropics. (eds F.M.C. Gilchrist and R.I. Mackie), Pretoria, Republic of South Africa.

Grovum, W.L. 1987. A new look at what is controlling feed intake. Pages 1-40 in: F. Owens, D. Gill and K. Lusby eds. Feed Intake by Beef Cattle. Oklahoma State Univ.

Grovum, W.L. 1988. Appetite, Palatability and control of feed intake. Pages 202-216 in: D.C. Church ed. The Ruminant Animal Digestive Physiology and Nutrition. Prentice-Hall, Englewood Cliffs, New Jersey.

Hoover, W.H. 1978. Digestion and absorption in the hindgut of ruminants. J. Anim. Sci. 46:1789-1798.

Hooper, A.P. and Welch, J.G. 1985. Effects of particle size on forage composition on functional specific gravity. J. Dairy Sci. 68:1181-1188.

Kennedy, P.M. 1985. Effect of rumination on reduction of particle size on rumen digesta by cattle. Aust. J. Agric. Res. 36:819-828.

Kennedy, P.M. and Milligan, L.P. 1978. Effects of cold exposure on digestion, microbial synthesis and nitrogen transformation in sheep. Br. J. Nutr. 39:105-115.

Kokjer, K.J. and White, G.R. 1986. A simple telemetry system for monitoring chewing activity of reindeer. J. Wildl. Manage. 4:737-740.

Law, S.E. and Sudweeks, E.M. 1975. Electronic transducer for rumination research. J. Anim. Sci. 41:213-218.

Luginbuhl, J.M., Pond, K.R., Russ, J.C. and Burns, J.C. 1987. A simple electronic device and computer interface system for monitoring chewing behavior of stall-fed ruminant animals. J. Dairy Sci. 70:1307-1312.

Luginbuhl, J.M., Pond, K.R., Burns, J.C. and Russ, J.C. 1989. Effects of ingestive mastication on particle dimensions and weight distribution of coastal bermudagrass hay fed to steers at 4 levels. J. Anim. Sci. 67:538-546.

McLeod, M.N. and Minson, D.J. 1988. Large particle breakdown by cattle eating ryegrass and alfalfa. J. Anim. Sci. 66:992-999.

McLeod, M.N. and Smith, B.R. 1989. Eating and ruminating behaviour in cattle given forages differing in fibre content. Anim. Prod. 48:503-511.

Mathison, G.W., Milligan, L.P. and Weisenburger, R.D. 1984. Ruminant feed evaluation unit. pp 44-47 in 63rd Annual Feeders' Day Report. Department of Animal Science, University of Alberta, Edmonton, Alberta.

Murphy, M.R. and Jaster, E.H. 1984. A computerized sustem for recording and analyzing chewing behavior. J. Dairy Sci. 67 (Suppl. 1):204 (Abstr.).

Norgaard, P. 1989. The influence of physical form of ration on chewing activity and rumen motility in lactating cows. Acta Agric. Scand. 39:198-202.

Okine, E.K., Mathison, G.W. and Hardin, R.T. 1989. Effects of changes in frequency of reticular contractions on fluid and particulate passage rates in cattle. J. Anim. Sci. (In Press).

Osuji, P.O., Gordon, J.G. and Webster, A.J.F. 1975. Energy exchanges associated with eating and rumination in sheep given grass diets of different physical forms. Br. J. Nutr. 34:59-71.

Orskov, E.R., Ojwang, I. and Reid, G.W. 1988. A study of consistency of differences between cows in rumen outflow rate of fibrous particles and other substrates and consequences for digestibility and intake of roughages. Anim. Prod. 47:45-51.

Pearce, G.R. 1967. Changes in particle size in the reticulrumen of sheep. Aust. J. Agric. Res. 18:119-125.

Pond, K.R., Ellis, W.C. and Akin, D.E. 1984. Ingestive mastication and fragmentation of forages. J. Anim. Sci. 58:1567-1574.

Pond, K.R., Luginbuhl, J.M. and Burns, J.C. 1987. Salivation mastication and rumination - Limits to intake by beef cattle. Pages 160-172 in F. Owens, D. Gill and K. Lusby, eds. Feed intake by Beef Cattle. Oklahoma State Univ.

Poppi, D.P., Minson, D.J. and Ternouth, J.H. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of feed in the reticulo-rumen. Aust. J. Agric. Res. 32:109-121.

Poppi, D.P., Norton, B.W., Minson, D.J. and Hendrickson, R.E. 1980. The validity of the critical size theory of particles leaving the rumen. J. Agric. Sci. (Camb.) 94:275-280.

Ray, D.E. and Roubicek, C.B. 1971. Behavior of feedlot cattle during two seasons. J. Anim. Sci. 33:72-76.

Reid, C.S.W., John, A., Ulyatt, M.J. Waghorn, G.C. and Milligan, L.P. 1979. Chewing and the physical breakdown of feed in sheep. Ann. Rech. Vet. 10:205-207.

Reid, C.S.W., Littleton, J.W. and Mangan, J.L. 1962. A method of measuring the effectiveness of chewing in the release of plant cell contents from ingested feed. N.Z. Agric. Res. 5:237-248.

Ruckebusch, Y. and Bueno, L. 1978. An analysis of ingestive behavior and activity of cattle under field conditions. Appl. Anim. Ethol. 4:301-313.

Smith, L.W., Waldo, D.R. and Moore, L.A. 1965. Particle size separation of cell wall constituents. J. Anim. Sci. 24:903-904.

Steel, R.G.D. and Torrie, J.H. 1980. Principles and procedures of statistics - A biochemical approach. McGraw-Hill Book Company.

Thomas, S. and Campling, R.C. 1977. Comparison of some factors affecting digestibility in sheep and cows. J. Br. Grassl. Soc. 32:33-41.

Troelsen, J.E. and Campbell, J.B. 1968. Voluntary consumption of forage by sheep and its relation to the size and shape of particles in the digestive tract. Anim. Prod. 10:289-296.

Uden, P., Colucci, P.E. and Van Soest, P.J. 1980. Investigation of chromium, cerium, and cobalt as markers in digesta. Rate of passage studies. J. Sci. Food Agric. 31:625-632.

Uden, P. and Van Soest, P.J. 1982. The determination of digesta particle size in some herbivores. Anim. Feed. Sci. Technol. 7:35-44.

Ulyatt, M.J. 1983. Plant fibre and regulation of digestion in the ruminant. Pages 103-107 in G. Wallace and L. Bell, eds. Fibre in human and animal nutrition. Royal Soc. N.Z. Wellington N.Z.

Ulyatt, M.J., Dellow, D.W., John, A., Reid, C.S.W. and Waghorn, G.C. 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. Pages 498-515 in L.P. Milligan, W.L. Grovum and A. Dobson, eds. Control of Digestion and Metabolism in Ruminants. Prentice-Hall, Englewood Cliffs, New Jersey.

Ulyatt, M.J., Reid, C.S.W. and Carr, D.H. 1982. Effect of diet on particle size reduction by chewing and subsequent fermentation in the rumen of sheep. Proc. N.Z. Soc. Anim. Prod. 42:159.

Ulyatt, M.J., Waghorn, G.C., John, A., Reid, C.S.W. and Monro, J. 1984. Effect of intake and feeding frequency on feeding behaviour and quantitative aspects of digestion in sheep fed chaffed lucerne hay. J. Agric. Sci. (Camb.) 102:45-657.

Van Soest, P.J. 1982. Nutritional Ecology of the Ruminant. O and B Books Inc., Corvallis, Oreg.

von Keyserlingk, M.A.G. and Mathison, G.W. 1989. Use of the in situ technique and passage rate constants in predicting voluntary intake and apparent digestibility of forages by steers. Can. J. Anim. Sci.:In Press.

Waghorn, G.C., Reid, C.S.W., Ulyatt, M.J. and John, A. 1986. Feed comminution, particle composition and distribution between the four compartments of the stomache in sheep fed chaffed lucerne hay at two feed frequencies and intake levels. J. Agric. Sci. 106:287-296.

Webster, A.J.F. 1980. Energy cost of digestion and metabolism in the gut. Pages 469-484 in Y. Ruckebush and P. Thivend, eds. Digestive Physiology and Metabolism in ruminants. MTP Press, Lancaster.

Welch, J.G. 1967. Appetite control in sheep by indigestible fibers. J. Anim. Sci. 26:844-854.

Welch, J.G. 1982. Rumination, particle size and passage from the rumen. J. Anim. Sci. 54:885-894.

Welch, J.G. 1986. Physical parameters of fiber affecting passage from the rumen. J. Dairy Sci. 69:2750-2754.

Welch, J.G. and Hooper, A.P. 1988. Ingestion of feed and water. Pages 108-116 in W.C. Church ed. The Ruminant Animal: Digestive Physiology and Nutrition. Prentice-Hall, New Jersey.

Wilson, R.K. and Flynn, A.V. 1974. Observations on the eating behavior of individually fed beef cattle offered grass silage and libitum. Irish J. Agric. Res. 13:347-349.

Young, B.A. 1966. Energy expenditure and respiratory activity of sheep during feeding. Aust. J. Agric. Res. 17:355-362.

APPENDIX A

Table 1. The effect of a propionate preservative on the apparent digestibilities of dry matter (DM), crude protein (CP), acid detergent fibre, neutral detergent fibre (NDF), organic matter (OM), hemicellulose and digestible energy.

	Low moisture		Medium moisture		High moisture		
	Control	Treated+	Control	Treated+	Control	Treated+	S.E.++
DM	66.7a	65.2a	63.6b	65.9a	61.7c	63.2b	0.47
CP	76.3a	76.3a	74.2b	75.7ab	69.5d	71.3c	0.47
ADF	51.9	47.8	49.4	50.9	51.3	50.8	1.10
NDF	50.9ab	46.3b	50.1ab	52.0ab	53.8a	51.7ab	1.28
OM	68.4a	67.2ab	65.5b	67.3ab	62.5d	63.8c	0.47
Hemicellulose	82.4ab	80.3b	83.3ab	85.2a	85.8a	84.1ab	0.89
Digestible energy (Mcal kg^{-1})	2.972a	2.838b	2.824b	2.990a	2.732b	2.825b	0.03

+Treated refers to the addition of 1.25% wt wt^{-1} propionate preservative at the time of baling.

++Standard error of the mean is based upon twelve observations per mean.