



Forage intake and milk production of rangeland beef cows with varying degrees of crossbred influence
by Matthew Wayne Wagner

A thesis submitted in partial fulfillment of the requirements of the degree Cf Master of Science in
Range Science

Montana State University

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Abstract:

A study was conducted during the summer seasons of 1983 and 1984 to estimate the forage consumption of free-ranging beef cows differing in milk production potential. Six lactating cows from Hereford (HH) and 75% Simmental-25% Hereford (3S1H) breeds were used in 1983. In 1984, 3 additional breed types were evaluated: 25% Simmental-75% Hereford (1S3H), 50% Simmental-50% Hereford (SH), and 50% Angus-50% Hereford (AH). Fecal output was estimated during June, July and August each year using the chromic oxide dilution technique. Correction factors were derived by comparing estimated fecal output values to actual measurements using fecal bags. Monthly forage collections for IVOMD determinations were obtained using 4 to 6 esophageal-fistulated cows. Breed groups did not differ significantly in body weight ($P > .10$) in either year. No significant difference in average mean intake expressed as a percentage of body weight/day (%BW/d) were found between the breeds in 1983. In 1984, significant breed group differences were detected ($P < .07$). Average mean intakes for the 1S3H, HH, AH, BH, and 3S1 H were 2.2, 2.3, 2.5, 2.6, and 2.8% BW/d respectively. Milk production accounted for about 60% of the variation in intake between breeds groups, but body size and body condition differences within breeds influenced intake as well. Preliminary efficiency data showed that 3S1H produced an average of 0.98 kg milk per kg OM intake while HH produced 0.77 kg milk.

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I once told a stranger that I was majoring in Range Science. He responded by asking me if I was specializing in the gas or electric kind. Such is the obscurity of the science, one that solicits logical explanations from dynamic, interrelated situations. Understanding that complexity is a life long challenge, and I wish to thank those that helped me begin the journey.

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TABLE OF CONTENTS

	Page
LIST OF TABLES.....	vi
ABSTRACT.....	viii
INTRODUCTION.....	1
LITERATURE REVIEW.....	3
Introduction.....	3
Factors Influencing Forage Intake by Grazing Ruminants.....	3
Physical Limitations.....	6
Physiological Stage.....	8
Forage Factors.....	14
Environmental Factors.....	18
Productive Efficiency of Free-Ranging Cows Varying in Biological Potential.....	21
Previous Intake Estimates Using Chromic Oxide.....	24
MATERIALS AND METHODS.....	25
RESULTS.....	28
Intake Differences Among Breeds - 1983 Trial.....	28
1984 Trial.....	28
Milk Production.....	30
Body Measurements.....	30
Forage Digestibility.....	32
Comparison of Fecal Output Estimates Using the Chromic Oxide and Total Collection Methods.....	33
DISCUSSION.....	34
Factors Affecting Intake Differences Within and Between Breeds.....	34
Forage Digestibility and Intake.....	37
Preliminary Efficiency Evaluations.....	40
SUMMARY.....	42
LITERATURE CITED.....	44
APPENDIX.....	52

LIST OF TABLES

Table		Page
1	1983 Daily forage intake for lactating cows.....	29
2	1984 Daily forage intake for five cow breeds.....	29
3	1984 Average daily milk production for five cow breeds...	31
4	Body weight and weight:height ratios for breeds used in 1983 and 1984.....	31
5	Monthly forage IVOMD for two years.....	33
6	Average daily intake for two breeds over both field seasons.....	37
<u>Appendix Tables</u>		
7	Intake values for various breeds of grazing cows using chromic oxide method for fecal output.....	53
8	Least squares analysis of variance of organic matter intake 1983.....	54
9	Least squares analysis of variance of body weight 1983...	54
10	Least squares analysis of variance of organic matter intake 1984.....	55
11	Least squares analysis of variance of milk production 1984.....	56
12	Least squares analysis of variance of body weight and weight:height ratio 1984.....	56
13	Comparison of OMD between selected samples of extrusa using two drying methods.....	57
14	1983 Fecal output estimates for dry cows using total collection and chromic oxide techniques.....	58
15	Least squares analysis of variance of organic matter intake for HH and 3S1H breeds 1983 and 1984.....	59
16	Intake differences and efficiency evaluations for breeds used in 1984.....	60

LIST OF TABLES - Continued

Table	Page
17 . Least squares analysis of variance of <u>in vitro</u> organic matter digestibility.....	61

ABSTRACT

A study was conducted during the summer seasons of 1983 and 1984 to estimate the forage consumption of free-ranging beef cows differing in milk production potential. Six lactating cows from Hereford (HH) and 75% Simmental-25% Hereford (3S1H) breeds were used in 1983. In 1984, 3 additional breed types were evaluated: 25% Simmental-75% Hereford (1S3H), 50% Simmental-50% Hereford (SH), and 50% Angus-50% Hereford (AH). Fecal output was estimated during June, July and August each year using the chromic oxide dilution technique. Correction factors were derived by comparing estimated fecal output values to actual measurements using fecal bags. Monthly forage collections for IVOMD determinations were obtained using 4 to 6 esophageal-fistulated cows. Breed groups did not differ significantly in body weight ($P > .10$) in either year. No significant difference in average mean intake expressed as a percentage of body weight/day (%BW/d) were found between the breeds in 1983. In 1984, significant breed group differences were detected ($P < .07$). Average mean intakes for the 1S3H, HH, AH, SH, and 3S1H were 2.2, 2.3, 2.5, 2.6, and 2.8% BW/d respectively. Milk production accounted for about 60% of the variation in intake between breeds groups, but body size and body condition differences within breeds influenced intake as well. Preliminary efficiency data showed that 3S1H produced an average of 0.98 kg milk per kg OM intake while HH produced 0.77 kg milk.

INTRODUCTION

To effectively manage rangelands for optimum livestock production, it is necessary to have knowledge of the forage consumption by the grazing animal. Van Dyne (1960) estimated the yearly dry matter intake from data summarizing 31 studies of grazing cattle to be about 1.8% body weight/day (%BW/d). With the increased use of heavier mature weight, high milk-producing breeds of cattle, there may be a need to adjust stocking rates based on forage consumption estimates.

When abundant, good quality forage is available, the voluntary intake of grazing ruminants is influenced by energy demand (Arnold, 1970). The energy balance of an animal is determined by the difference between energy input (feed) and the energy expended for maintenance, milk production, reproduction and activity (Braumgardt, 1970). Because of the bulky and fibrous nature of most range forages, the physical limitation of intake due to gut fill usually occurs before energy satiety (Campling, 1970). The point where physical distention of the rumen limits intake and metabolic signals begin to dominate is believed to be when forage digestibility is approximately 62 - 70% (Conrad et al., 1964; McClymont, 1967; Montgomery and Braumgardt, 1965), however this range may vary with body size and stage of production (Conrad et al., 1964). If physical conditions limit intake on low quality forages, then rumen capacity, fermentation and passage rate of forage would determine the amount of feed an animal could ingest. While it is true that the main determinant of rumen capacity is the size of the animal (Nutt et al., 1980; Van

Soest 1982), changes in ruminal volume are not necessarily equal to changes in body weight. Bines (1971) stated that intake is broadly related to the liveweight of the animal, which is also related to the size of the abdominal cavity. Ruminal hypertrophy has been documented in lactating ewes (Fell et al., 1964) and dairy cows (Smith and Baldwin, 1974; Tulloh, 1966) and may also impact the digestive capacity of ruminants varying in production.

If ruminants consume forages of high digestible energy concentration, then metabolic signals associated with the energy balance of an animal may regulate food intake (Bines, 1971). Under these conditions, breed differences in level of milk production could cause forage intake differences.

Research was initiated in 1981 at the Northern Agricultural Research Center, located near Havre, Montana to determine the relative efficiency of grazed forage consumed by five beef cow breeds. This study was conducted during the summers of 1983 and 1984 to (1) estimate the daily forage organic matter intake of five beef cow breeds differing in milk production potential, and (2) provide information necessary to assess the relative production efficiency of each breed type on native rangelands.

LITERATURE REVIEW

Introduction

When grazing cattle of different genetic potentials for dam and offspring performance are deriving nutrients from the same forage base, the interaction between energetic demand and subsequent productivity may determine their dry matter intake. Metabolic energy demand is a function of several factors including the maintenance requirement of an animal. Maintenance demands may be increased from 40 to 60% (Havstad and Malachek, 1982) for cattle grazing rangeland as compared with confined situations. There are variations in maintenance requirements based on breeds and physiological age as well (NRC, 1984). In order to ultimately identify the productive potential and adaptability of various breeds to a particular grazing environment, it is necessary to estimate their forage consumption. A brief review of the factors influencing the intake of grazing ruminants will help elucidate a complex and interactive system.

Factors Influencing Forage Intake by Grazing Ruminants

There is a vast array of stimuli that affect the foraging behavior of grazing ruminants. In addition, the rangeland environment and its diversity serves to add to the complexity of the animal's nutritional ecology. To explain the impact of the variables driving voluntary forage intake, three criteria must be evaluated. They are: (1) intake regulation inherent to the animal, (2) forage base characteristics, and (3) environmental factors. These influences

combine to form a dynamic model, one in which a change in one element denotes a change somewhere else in the scheme.

Innate regulatory mechanisms are controlled by metabolic balance, physical limitations and the physiological state of the animal.

McClymont (1967) states that the only intrinsic stimulus facilitating phagic behavior in the grazing ruminant is total energy demand. This demand is a summation of the energy required for maintenance, growth, gestation, milk production, exercise and environmental stresses. When short term demand exceeds metabolic energy available to the animal, feeding begins. As energy is supplied beyond the level required, feeding will cease (Blaxter, 1962; Forbes, 1980). This energy balance may be governed by the hypothalamus, which "senses" various feedback signals such as distention stimuli and changes in metabolite concentration. As forage digestibility increases, digestible energy concentration increases, and the regulation of food intake becomes metabolic in nature (Bines, 1971). This level of digestible energy is believed to be at the point where forage digestibility reaches about 62 - 70%. Below this level, physical distention of the rumen limits intake; above it, energy intake becomes the overriding factor inhibiting forage consumption (McClymont, 1957). Conrad et al. (1964) concluded from their results with lactating dairy cows that the point where physical limitations on eating cease and metabolic influences dominate varies with body size and production. Montgomery and Braumgardt (1965a) reported that for dairy heifers consuming rations of increasing dry matter digestibility (DMD), intake decreased as a result of energy satiety. Conrad et al.

(1964) found that with high-roughage rations between 67 and 80% DMD, intake decreased with increasing digestibility. In contrast, intakes were lower for cows consuming rations below 60% DMD due to gut fill (Montgomery and Baumgardt, 1965b).

The major suspected chemical feedback signals regulating energy intake by ruminants include volatile fatty acid (VFA) concentration, rumen pH, and hormonal secretion. Among the products of digestion, proprionate plays a similar role in controlling the food intake of ruminants much as glucose is thought to do in monogastric animals, by acting as an index of the rate of absorption of all VFA's (Forbes, 1980). Proprionate is sensed by the portal vein and concentration signals are transferred via the vagas nerve to the hypothalamus. Ruminal acetate concentration has been found to play a central role in controlling meal size on range forages in particular (Waldo, 1969). It has been suggested that there are receptors sensitive to acetate on the lumen side of the rumen (Baile and Forbes, 1974).

Baile and Forbes (1974) state that there is no evidence that growth hormone (GH) is a feedback signal for energy balance under normal conditions, but Forbes (1980) reported that a low insulin:GH ratio stimulates lipolysis and might be expected to occur around the time of meal initiation. He suggested a link between a deficit of energy - yielding metabolites (correlated by an increased secretion of GH) and the onset of feeding. Estrogens are believed to depress intake during estrus and in late pregnancy (Baile and Forbes, 1974), but whether this is an indirect or central action on the satiety center is not known. Balch and Campling (1962) stressed that the

changes in food intake associated with hormone balance may be related to changes in induced metabolism.

There are two ways that adipose tissue contributes to the homeostatic balance of energy in the ruminant. First, the rate at which adipose tissue can synthesize triglycerides seems to be limited. As this limit is approached, receptors sensitive to excess energy will tend to depress intake. Secondly, it has been proposed that "leakage" of fatty acids from adipose cells is positively related to their size. The fatter the animal the stronger the feedback signal on energy availability (Forbes, 1980).

The rapid fermentation of immature forages may produce sufficient acid to cause a drop in rumen pH which delays cellulolytic digestion of forage cell walls, thus depressing intake (Van Soest, 1982). In Jones' (1972) review of the chemical control of feed intake, it was determined that a drop in pH facilitates the absorption of VFA across the rumen epithelium, allowing the activation point of the receptor signal to be accomplished with lower intakes. Baile and Forbes (1974) stated that feed intake is likely depressed when rumen fluid pH falls below 5.5 because of the resulting rumen stasis.

Physical Limitations

Physical bulk of less digestible forages and capacity of the ruminant gastrointestinal tract are dominant factors limiting forage intake by ruminants (Ellis, 1978). Physical regulation of food intake involves stretch receptors in the rumen wall, but the nature and precise location of these is not yet known (Bines, 1971). While it is

true that the main determinant of rumen capacity is the size of the animal, changes in ruminal volume are not necessarily equal to changes in body weight. Intake is broadly related to the live weight of the animal and is determined by the size of the abdominal cavity (Bines, 1971) and by the rate of disappearance of digesta from the reticulorumen. The rate of disappearance depends on the rate of breakdown in the reticulorumen by microbial and mechanical processes (Campling, 1970).

Nutt et al. (1980) found no relationship between rumen capacity and DM digestibility of fescue - legume and fescue pastures although other researchers found that as rumen volume increased, forage DM digestibility increased (Purser and Moir, 1966). Nutt et al. (1980) found that structurally large cows had larger rumen capacities and greater intakes than structurally small cows. As a percentage of body weight however, rumen capacity was not related to structural size reflecting differences in body composition of the cows examined. Milk yield was also non-related to rumen capacity. One way of relating intake to cows of different sizes is to express body size in terms of metabolic body weight (MBW). Metabolic body weight describes surface area and therefore maintenance requirements (Kothmann, 1978). The feed requirement for maintenance becomes proportional to the animal's MBW when intake is regulated by chemostatic mechanisms. It is questionable whether any single expression of live weight can be adopted for animals of all ages and live weights. The relationship between intake and body size changes markedly at weights lower than

400 lbs since the rumen develops more rapidly than the overall development of the body (Holmes et al., 1961).

The amount of body fat also has an effect on abdominal space in the ruminant. When rumen capacity was expressed in proportion to body weight, fatter cows had significantly smaller rumen capacities than did thinner cows (Nutt et al., 1980). Inverse relations between weight of internal fat and weight of gut contents were reported by Balch and Campling (1962). Bines (1971) states that extensive deposition of fat within the abdominal cavity apparently reduces digestive capacity and therefore roughage intake. He concluded that since fat cows did not eat enough hay to maintain weight, and thin cows ate enough of the same hay to gain weight, the existence of a physical regulator appears likely.

Physiological Stage

Another major determinant of the forage intake of grazing ruminants is the physiological condition of the animal. Lactation, pregnancy and growth contribute to increase energy demands and subsequent need for additional feed intake. Lactation is an energetic cost demanding three times the maintenance requirement in high producing dairy cows (Baile and Forbes, 1974). Journet and Remond (1976) observed that the DM intake of roughages increased by 2 kg/d during the first eight weeks of lactation and did not depend greatly on the level of roughage intake before calving. Johnson et al. (1966) noticed that Holstein cows increased their DM hay intake 50% during the first one-third of lactation, peaking by the 17th week. Intake

differences averaging about 50% were observed between dry and lactating twin Jersey crossbred cattle, although peak gross energy intake was not obtained during peak milk yield, but 15 weeks later. This time lag may represent a period for repletion of body reserves used in early lactation (Hutton, 1963). In contrast, Forbes (1971) stated that food intake reaches a peak about the sixth week of lactation. He suggests that the expulsions of the fetus immediately gives ample room for rumen expansion, so the time lag is most likely not dependant on an increase in digestive capacity.

An interesting adaptation to the energy demands of lactation is an increased digestive capacity due to hypertrophy of the reticulorumen and intestines. An adaptation of this kind would enable a lactating cow to maintain a greater intake without changing the rate of passage or the digestibility of the diet (Tulloh, 1966). The first report concerning hypertrophy described the histological, chemical and physical changes occurring in the alimentary canal of lactating rats (Fell et al., 1963). They observed that the parietal cells in the stomach of lactating animals became hypertrophied, and by the 16th day of lactation, the total nitrogen content of the stomach, small intestine and caecum had increased an average of 65% over that of the controls. In addition, the average weight of the stomach was 50% greater than that of non-lactating rats. But the most striking feature of the hypertrophy was an increase in the height and thickness of the intestinal villi. It was suggested that the results were due to an adaptive response of the intestinal mucosa to the increased

energy demands of lactation rather than the direct effect of physical distention due to increased food intake.

A similar study performed by Fell et al. (1964) showed many of the same results in lactating ewes. There was a definite enlargement of the alimentary canal indicated by weight, total nitrogen gains and histological comparisons to non-lactating controls. Hypertrophy of ruminal mucosa has also been confirmed by Fell et al. (1972) and Weekes (1971). Weight increases were found to occur in the ruminal mucosa, abomasum and small intestine of lactating cows fed a ration of approximately 70% dry matter digestibility (DMD). Weekes (1971) found that in conjunction with increasing rumen mucosal weight, enzyme activities and in vitro lactate production per rumen also increased. It was thought that this could increase the supply of substrate for gluconeogenesis during lactation. An associated study (Moon and Cambell, 1973) revealed that hypertrophic changes in the rumen wall were combined with an increase in the size of individual papilli and a regression of a hyperkeratotic condition. Peak rumen weight was reached at about 20 days of lactation, when the lambs were weaned. It was concluded that hypertrophy of the ruminal mucosa is due partially to increased cell division. Peak values of DNA and RNA occurred approximately at the time when cell division was greatest. RNA was used as an index to protein synthesis and may reflect growth processes in the cell.

Smith and Baldwin (1974) used mature dairy cows to determine the effects of pregnancy and lactation on the weights of gastrointestinal tract organs and tissues. They state that although organ weight is a

function of body weight, relative changes in organ weights are not equivalent to relative changes in body weight. Log-Log regression analysis was used to allow comparisons of tissues and organs between non-lactating and lactating cattle on a common body weight basis. Weights of the gastrointestinal organs for non-lactating and lactating cows were 3.75 and 4.85% of total body weight respectively, representing a 30% increase with lactation. The authors suggest that this increase coupled with increases in the weights of the liver, heart and mammary tissues during lactation may account for an estimated 10% increase in maintenance energy requirements for lactating cows. Tulloh (1966) reported increases in the length of the small intestine, the internal circumference of the lumina in the small and large intestine, and the weights of the main parts of the alimentary tract of lactating versus non-lactating twin dairy cattle. Water-filled capacities of the reticulo-rumen were 29% greater for the lactating twins as well. He suggests that these changes take place slowly and may be associated with metabolism of abdominal fat.

The observations reported give evidence to suggest the notion of organ hypertrophy during lactation. What is not clear is the casual relationship between intake and hypertrophy. Fell et al. (1963) offers three possible causes of hypertrophy. The first is thought to be "work hypertrophy" as a result of prolonged distention associated with an increase in food consumption. Secondly, there may be hormonal stimulation of the gut wall brought about by lactogenic hormones, lactation itself or by suckling. Hypertrophy could also be a functional adaptation not directly due to increased intake, but to the

increased demands made on the body during lactation. It is possible that food intake is closely involved in the epithelial hyperplasia associated with lactation. The most likely mechanisms appear to be direct stimulation of epithelial cell metabolism during VFA absorption and metabolism (Fell and Weekes, 1975).

Level of milk production as it affects voluntary intake has been difficult to determine for the grazing cow. Correlation coefficients between milk yield and digestible organic matter intake have been as high as .45 (Curran and Holmes, 1970) but are generally lower (Bines, 1976). Johnson et al. (1966) found that the two variables were interdependent, to the extent that the coefficient of correlation between them approached 0.6. The relationship is confused as to which is the casual mechanism. If the energy requirements for lactation are met, then milk production would determine the amount of forage needed. When intake is restricted by physical factors however, milk yield will more likely depend on the amount of metabolizable energy the animal can derive from the feed (Baile and Forbes, 1974). Jones et al. (1965) estimated summer digestible organic matter intake to be about 2.3% of body weight for high milk production (38 lbs fat-corrected milk (FCM)/d) and 2.1% for low milk producing (28 lbs FCM/d) Ayrshire cattle. Mean live body weights did not differ between yield level groups. Field (1966) found no relationship between milk production and dry matter intake as milk yield of lactating dairy cows dropped markedly from May to October. These results may have been masked by herbage availability and low live weight changes. Milk production has been shown to depend on the amount of digestible energy a cow

consumes. Diets containing 0 to 25% roughage contain similar amounts of digestible energy. As roughage increases to 50 or 75%, intake but not milk yield may become depressed. At 100% roughage, digestible energy intake becomes low enough to depress milk yield of dairy cows. The cows examined produced between 12 and 20 kg/d milk and liveweight changes were generally negative for all rations (Nelson et al., 1968 as cited by Bines, 1976).

Pregnancy has been shown to have a positive effect on intake in the early stages but a negative effect later on. Compression of the digestive tract due to fetal growth is a major influence on intake during pregnancy (Bines, 1971; Campling, 1966; Forbes, 1971). As the volume of the uterus plus abdominal fat increases, the volume of rumen contents decreases as does the voluntary intake of roughage (Forbes, 1971). This is especially evident during the last five weeks before parturition. In order to compensate for this decline in intake, the animal is apparently able to increase the rate of passage of food as pregnancy advances (Bines, 1971). Intake depression may also be related to metabolic changes that occur with pregnancy (Campling, 1966). Oestrogen depresses food intake and there is a progressive increase in oestrogen secretion during the second half of pregnancy in ruminants (Forbes, 1971).

It is generally accepted that the cow does not reach mature physical size until six or seven years of age (Bines, 1976). During this time, under most conditions, the energy cost of a unit weight gain will be between 1.2 and 8.0 mcal/kg of fat-free body weight (NRC, 1984). Assuming that range forages provide approximately 5 mcal/kg of

DM (Havstad, 1984) a continuously growing cow would need between .25 and 1.6 kg of forage just to satisfy her growth requirement. Voluntary intake increases as the animal achieves mature weight but not in direct proportion to the increases in body weight. For example Forbes (1971) showed that cattle weighing 225 kg consumed 5.6 kg of dry matter whereas the same cattle at 425 kg consumed 7.2 kg, an increase of 28% versus a body weight increase of 89%. Intake increases when the energy needs for growth are higher, about 1 kg DM for cows between the first and second lactation over the additional intake due to increase in body weight (Journet and Remond, 1976). In mature animals of the same breeding, changes in body weight and visual rating of body condition has been shown to have little relationship to intake differences (Johnson et al., 1966). Arnold (1970) as cited by Allison (1985) stated that intake is related to body condition, but the individual variation of grazing animals makes liveweight changes a poor index of intake even when accounting for differences in productivity.

Forage Factors

Grazing ruminants exhibit distinct selectivity when presented with an array of forage choices (McClymont, 1967). Rangelands typically produce diverse vegetation, not all of which is preferred by domestic herbivores. In order to describe how grazing strategy affects intake, it is necessary to identify those characteristics of forage that influence preference. There is no evidence that high palatability per se affects total daily food intake, but

unpalatability can certainly reduce it (McClymont, 1967). The animal can recognize plants by senses of sight, touch, taste and smell, although there is no relationship between odor and palatability (Van Dyne et al., 1980). Plant selection depends on the quantity and quality of forage species, and will change with season and utilization the species. Among those factors associated with the quality of forage and hence its digestibility, are the amount of fiber and green leaf material. Grazing animals select green in preference to dry material (Arnold, 1964). The selected material usually is higher in nitrogen and lower in fiber, signifying that chemical composition may be associated with physical characteristics of selected plant parts (Arnold, 1964). Many studies have depicted a relationship between intake and digestibility. In one study, digestibility was influenced by forage nitrogen, soluble carbohydrate content, available dry matter and time of year (Arnold, 1970). Van Soest (1965) concluded that the interrelationships among intake, digestibility and chemical composition are highly plant oriented. He reported a positive association between maturity and voluntary intake of tall fescue, possibly because of some unpalatable toxic substance present in the young plant. The only consistent effect for all forages was found to be the total fibrous fraction or cell wall constituents which is inversely related to digestibility (Van Soest, 1982). As this fraction increases, voluntary intake declines. The point at which this fiber mass becomes limiting occurs when cell walls make up 50 to 60% of the forage dry matter (Van Soest, 1965). On high quality forages there is some evidence of satiety before rumen fill

from the fact that intake of cell walls is lower. Osbourn (1974) as cited by Van Soest (1982) suggested that intake of high quality immature forages is limited because of the high soluble carbohydrate content which may cause a drop in rumen pH. Thin cell walls of immature forages are not only more digestible, but are more likely to collapse upon rumination (Van Soest, 1982). Corbett et al. (1963) found DOM intake of dairy cows to fall by 20% as digestibility fell from 80 to 68% during the growing season. Holloway et al. (1979) showed that the intake of lactating beef cows fell by 1.3 kg DM/d as forage DMD dropped from about 61% to 58%. Crude protein content is highly related to the palatability of range forages. The critical level of protein is commonly in the range of 4 to 6%. Values below this level may limit digestion (Streeter et al., 1974). Several chemical constituents such as lignin and tanins are generally associated with low palatability, but high proportions of fats and ether extract are correlated with high palatability. It may be that a combination of chemical compounds rather than the individual constituents affect palatability (Van Dyne et al. 1980).

Quality of plant material is also determined by the degree of use or availability of preferred vegetation. Pieper et al. (1959) as cited by Kartchner and Cambell (1979) stated that intake decreases with heavy grazing as does the digestibility of the nutrients consumed. Protein, gross energy, ether extract and phosphorous tend to decrease as well. The grazing bovine moves in a horizontal plane but selects forage in a vertical plane, choosing leaf in preference to stem (Arnold, 1964). Availability includes yield as well as the

physical presentation of feed. The presence of spines, plant morphology and excessive dead growth may inhibit accessibility to otherwise preferred forage. A study conducted by Arnold (1964) showed that diets between two groups of sheep at different stocking rates were similar in quality and composition, yet intake was significantly less for sheep at the lower stocking rate due to an impenetrable pasture structure and the inability of the sheep to graze properly. Intake depression due to decreased forage availability has been shown by other researchers as well (Alden and Whittaker, 1970; Arnold, 1970). There is little consistency as to the lower limit of adequate herbage. Hodgson and Wilkinson (1967) as cited by Arnold (1970) found that intake of cows, heifers and calves was unaffected when availability was reduced from 8,000 to 2,000 kg/hectare. Nastis (1979) found that only 143 kg DM/hectare was necessary for the optimum intake of heifers, while Handl and Rittenhouse (1972) as cited by Havstad et al. (1983) described a decline in intake when forage availability was less than 176 kg/hectare. Havstad (1981) estimated the intake of heifers to be 1.3% BW throughout a forage supply of 880 kg DM/hectare to 284 kg DM/hectare. Under bulk limiting conditions, where digestibility energy content is less than 2.7 kcal/g DM, the quantity of forage available to heifers may not affect voluntary daily intake (Havstad et al., 1983). Other factors such as decline in the quality of available forage or grazing fatigue may be responsible for reduction in the voluntary intake of these animals.

Availability may be more closely related to plant height rather than yield which may account for the lack of agreement in the

literature between intake and herbage availability. In a study conducted with lambs and yearling sheep, intake increased rapidly with increasing tiller length up to 15 cm. Thereafter, there was little change in intake as tiller length increased (Allden and Whittaker, 1970). As forage becomes scarce, increased grazing time is needed to maintain the same intake level on pastures of low forage availability. Intake per hour decreases as grazing time increases, because lower intake per bite is not fully compensated by increasing bite per minute (Arnold, 1964).

Environmental Factors

Besides the more apparent components creating the food intake model in grazing ruminants, there are other stimuli surrounding the animal which inhibit or enhance its foraging mode. Social interaction and environmental temperature are especially important for animals exposed to a variety of living conditions. Besides the instinctive behavior exhibited by young animals, McClymont (1967) discusses four learning processes that determine selectivity and consequently forage intake. The first is allelomimetic or mimicing behavior most often displayed as imitation of the dam. Sheep diets of dams and their daughters differed less than unrelated sheep as dam/daughter groups tend to occupy the same home range and hence graze the same plant communities. It therefore appears that the numerous groups that comprise a flock of sheep do not occupy the same nutritional environment (Hunter and Milner, 1963). Secondly, habit or preference due to previous experience has an effect on selectivity when animals

are presented with a diverse forage resource. Arnold and Maller (1977) as cited by Arnold and Dudzinski (1978) stated that intake of sheep inexperienced on pasture may be lower by 50% than that of experienced sheep. A third learned response to grazing is an avoidance of plants producing a negative response such as intoxication. The chances of an animal learning from such an effect are reduced when the cumulative damage is slow acting and when a large selection of plants is available. Lastly, habituation can cause an animal to reduce selectivity when repeated or continued exposure to a particular food promotes addiction (Arnold and Maller, 1977). Habituation can be accelerated by a nutrient deficiency or from a positive palatability reaction. The fact that grazing ruminants learn from previous experiences lends evidence to a hedaphagic rather than a euphagic foraging strategy.

Grazing ruminants interact socially with others, mutually causing changes in grazing time and distribution. It is conceivable that psychic stress induced by high stocking rates with low forage availability may reduce intake of animals low in the social order (McClymont, 1967). Sheep have shown a grazing hierarchy in which the weaker ewes are forced to disperse to the poorer patches of vegetation (Hunter and Milner, 1963). Social interaction plays an important but variable role in affecting grazing time. Tribe (1950) reported that supplemented sheep grazed longer when mixed with unsupplemented sheep, an effect regarded as social facilitation. Holder (1962) also noted a social inhibition effect on mixed unsupplemented sheep, causing them to reduce grazing time.

Thermostatic control of feed intake was reviewed by Baile and Forbes (1974), and Jones (1972). In order to maintain body heat, animals must eat, but to prevent hyperthermia, eating must cease (Brobeck, 1948 as cited by Balch and Campling, 1962), Jones (1972) stated that thermostatic regulation of feed intake in ruminants is a response to environmental temperature rather than heat generated from metabolism of feed nutrients. There is generally a positive relationship between temperature and intake, but at extremely high temperatures, intake is halted (Van Dyne et al., 1980). Continuous high temperatures depress intake such that zero energy balance cannot be maintained, and above 40° C ruminants of temperate climates do not eat at all (Baile and Forbes, 1974). Increasing the temperature of rumen contents from 38° C to 41.3° C decreased intake by 15% (Baile and Forbes, 1974). In order to maintain intake during hot weather, free-ranging animals will adjust their grazing time by grazing at night or during the coolest part of the day (Arnold and Dudzinski, 1978; McClymont, 1967).

Increases in food intake due to cold stress are necessary to maintain energy balance and body temperature. The greater the heat loss, the greater the increase in intake. The food intake rate of dairy cows increased by about 3 kg as the daily air temperature decreased from 4 to 1° C and continued for at least 24 hours after cold stress (McDonald and Bell, 1958 as cited by Van Dyne et al., 1980). Typical low critical temperatures, below which the animal is unable to maintain body heat, are believed to be between -10 and -20 C for dry, pregnant beef cows. Recent studies have also shown a

depression in the ability of ruminants to digest feed during cold stress, independent of their food intake. Digestibility decreases by about 2 percentage units per 10 C drop in ambient temperature (Young 1980). After shearing, DOM intakes rose by 42-62% in grazing sheep. The increase was explained by an accelerated rate of energy metabolism induced by cold stress (4-27° C) (Wheeler et al., 1963).

The effect of day length on intake is not clearly understood. One study with sheep showed that animals with 16 hours of light per day had 6% higher food intakes than those with 8 hours of light (El-Shahat et al., 1974 as cited by Van Dyne et al., 1980).

Productive Efficiency of Free-Ranging Cows Varying in Biological Potential

Information on the feed efficiency of grazing cows is essentially nonexistent. Considering the difficulty in obtaining reliable determinations of forage intake for rangeland cattle, efforts to make conclusive interpretations of the balance between feed input and productive output are in the primitive stages. Although some of the principles involved in efficiency determinations of stall-fed animals may apply to the grazing animal, many more factors affect the efficiency of feed utilization on the range due to the more varied environment. Confounding the situation further is the energy balance of the animal, determined by its grazing activities and need for thermal regulation. After estimating the forage intake and forage digestibility for free-ranging ruminants, the remaining variation in animal performance will be incorporated in its efficiency (Van Soest, 1982).

In relating phenotype to the efficiency of grazing cows, Holloway and Butts (1983) noted that efficiency of milk production was positively related to level of milk production and negatively related to structural size regardless of pasture quality. Structurally larger cows grazing fescue-legume pastures consumed more forage but produced no more milk than smaller cows. Therefore, they produced milk less efficiently. In addition, larger cows grazing fescue did not increase intake in proportion to their size and were again less efficient producers of milk and calf gain than cows of smaller structural size. The relationship between structural dimension and efficiency for cows grazing fescue was confounded by changes in cow weight and fatness during lactation and calf weaning weight: cow weight ratios. Fatness was not significantly related to milk production for cows grazing either fescue - legume or fescue pastures, but thin cows grazing fescue tended to be more efficient producers of milk than fat cows.

Results from Nutt et al. (1980) show that structurally large cows have larger rumen capacities than small cows. Although cows with large rumen capacities consumed more forage on low quality pastures (DM digestibility of 55%) than cows with smaller rumens, rumen capacity was not related to either milk production or calf weaning weight. These results suggest that cows with large rumen capacities utilize their extra nutrients for functions other than milk production.

In an effort to determine the influence of season on the efficiency of cows varying in frame size and fatness, Holloway and Butts (1984) concluded that much more variation in milk production and

calf growth was noted for cows grazing fescue legume during the spring. Efficiency of conversion of DE above maintenance to milk was again negatively related to frame size for cows grazing both fescue - legume and fescue pastures, but was much more pronounced for cows grazing fescue.

According to Kronberg (1983) lactating Hereford cows grazing summer foothill range consumed .84 kg OM per kg of milk produced during June, 1983, while 3/4 Simmental x 1/4 Hereford cows required 1.12 kg per kg milk. The Herefords weighed an average of 441 kg and yielded approximately 11 kg of milk daily while the 3/4 Simmentals weighed 563 kg and produced about 12 kg per day. The relationship between efficiency of milk yield and body size of dairy cows was thoroughly reviewed by Morris and Wilton (1976). The average correlation between dairy efficiency (milk yield/feed intake) and measures of body size was found to be -0.18 and genetic correlations averaged -0.37. In contrast, overall correlations between dairy efficiency and level of milk yield were 0.81 and genetic correlations were about 0.89. The overall relationship between milk yield and body size was 0.33 within breeds of dairy cattle while genetic correlations averaged 0.14. Holmes (1973) found no nutritional advantage in increased body size for milk production, but an apparent advantage for meat production. Results from Bowden (1981) support a general conclusion that the conversion of energy consumed by a cow and calf to weight of weaned calf during the first lactation does not differ significantly between biological types of cows under the same

management. Other measures of efficiency are outside the context of this literature review although equally important.

Previous Intake Estimates Using Chromic Oxide

When the diet selected by different groups of grazing animals is assumed to be of the same digestibility, errors in comparing relative intakes are created from inaccuracies in estimating fecal output (Langlands, 1975). Although there are many methods of determining fecal output in range nutrition, the use of chromium sesquioxide (CR_2O_3) as an external indicator is considered to be the most satisfactory (Langlands, 1975).

The use of CR_2O_3 has certain limitations, but these have been thoroughly identified by various researchers (Raleigh et al., 1980; Kotb and Luckey, 1972; Langlands, 1975). Once these parameters are defined and the technique is administered accordingly, reliable estimates of fecal output and subsequently forage intake can be obtained. Appendix table 7 is an assemblage of intake estimates and their corresponding digestibility values for various breeds of cows using the chromic oxide technique.

MATERIALS AND METHODS

The study site was located about 50 km south of Havre, Montana in the Bear Paw Mountains. The pasture was 81 ha in size with slopes up to 40%. Elevation averaged 1300 m with annual precipitation ranging from 45.7 to 50.8 cm. Upland areas were dominated by rough fescue (Festuca scabrella), Idaho fescue (Festuca idahoensis), and bluebunch wheatgrass (Agropyron spicatum) with an open ponderosa pine (Pinus ponderosa) overstory. Kentucky bluegrass (Poa pratensis) dominated the lowland vegetation. The area is classified in the Forest-Grassland complex of the western glaciated plains, and is typical of foothill rangeland in north central Montana (USDA-SCS 1976).

The cows used in the study were randomly selected as 6 or 7 year olds from the Havre Research Station herd. All cows were randomly artificially inseminated to either Charlois or Tarentaise bulls. In 1983, 6 dry and 6 lactating cows from straightbred Hereford (HH) and 75% Simmental-50% Hereford (3S1H) breeds were used. In 1984, 3 additional breeds groups were examined, including 25% Simmental-75% Hereford (1S3H), 50% Simmental-50% Hereford (SH), and 50% Angus-50% Hereford (AH). Six lactating cows in each breed were used for a total of 30 head. To estimate daily forage organic matter intake (OMI) the following equation was used: $OMI = \text{daily fecal output (OMB)} / (1 - IVOMD \text{ of the diet})$. Fecal output for each cow was estimated during June, July and August each year using the chromic oxide (Cr_2O_3) dilution technique. Total fecal collections from dry cows equipped with fecal bags were also conducted during the 1983 trial to derive a correction factor for the differences between actual fecal output and predicted

fecal output using Cr_2O_3 . Fecal collection bags and feces-urine flaps as described by Kartchner and Rittenhouse (1979) were placed on the cows for 4 consecutive days each month and bags were changed every 12 hours. Collected fecal material was weighed then subsampled. Subsamples were frozen for dry matter and organic matter analysis at a later date. Beginning 5 days prior to fecal collections, and continuing throughout the collection period, cows were dosed at approximately 1800 h with a 10 g Cr_2O_3 powder bolus. At the same time, rectal grab samples were taken from each cow and frozen. To determine chromium content, grab samples were thawed, dried at 40 C, ground through a 2 mm screen, and prepared for atomic absorption spectrophotometry according to Williams et al. (1962). All fecal samples were analysed for dry matter and organic matter following AOAC (1970) procedures. Daily fecal dry matter (DM) output was estimated using the equation: fecal DM output/d = (10 g Cr_2O_3 fed/d / % Cr_2O_3 in dry fecal sample) x 100.

Forage samples for determination of in vitro digestibility were obtained over a 3-day period each month using 6 esophageally fistulated cows. Extrusa was immediately frozen, then later freeze-dried prior to laboratory analysis. Organic matter digestibility (OMD) was determined using the Barnes modification of the Tilley and Terry in vitro technique (Harris, 1970). Rumen fluid was obtained from a rumen-cannulated cow on an ad libitum grass hay diet that was 55% digestible (IVOMD). This hay was used as the standard in the in vitro trials to correct IVOMD values for extrusa samples.

To express intake as a percent of body weight, all cows were weighed after a 12-hr shrink period prior to fecal collections each month. Hip heights were measured during the final weighing to derive height: weight ratios (ht:wt) as an indication of body condition.

Milk production for all cows used in 1984 was estimated using the weigh-suckle-weigh technique following fecal collections each month.

The data were analysed as a split-plot design. Least squares analysis of variance was conducted using Statistical Analysis System's (SAS) General Linear Model procedure to determine breed differences in intake, milk production, body weight, and wt:ht ratio. The independent variables included in each model of the above factors were: breed, month, a breed X month interaction, sex of calf, sire breed of calf, and calf age. Least squares mean separation was performed using the Least Significant Difference (LSD) procedure.

RESULTS

Intake Differences Among Breeds - 1983 Trial

Monthly least squares mean intakes, expressed as a percentage of body weight per day (% BW/d) for lactating 3S1H and HH cows are given in table 1. No significant differences were found between the breeds when averaged over the summer, or within a month. Monthly values decreased throughout the study period, but dropped significantly only in August compared to June and July. Body weight was not significant in explaining the variation in intake when added as a covariate, and no statistical differences in body weight were detected between the breeds ($P > .10$) (Table 4). Milk production data were unavailable for 1983. Intake and body weight analysis of variance tables are given in Appendix tables 8 and 9.

1984 Trial

Breed ($P < .01$) and month ($P < .06$) influenced intake of the five breeds in 1984 (Appendix table 10). Intake values between breeds and months are shown in table 2. When averaged across months, intakes for 1S3H, HH, AH, SH, and 3S1H were 2.2, 2.3, 2.5, 2.6, and 2.8% BW/d respectively. When averaged across breeds, intake in June declined from 2.9% BW/d to 2.2% BW/d in August. When milk production, body weight, and wt:ht ratios were added as covariates in the intake model, milk production accounted for approximately 60% of the variation in intake between breeds ($P < .01$). This was determined by designing a linear contrast using breed deviations from the overall least squares

Table 1. 1983 Daily forage intake (% BW OMB) for lactating cows.

Breed	June ¹	July	August	Mean
HH	3.1 ± .2 ^a	3.0 ± .1 ^a	2.2 ± .2 ^a	2.8 ± .1 ^a
3S1H	2.8 ± .2 ^a	3.1 ± .1 ^a	2.3 ± .2 ^a	2.7 ± .1 ^a
Mean ²	3.0 ± .2 ^a	3.0 ± .1 ^a	2.3 ± .2 ^b	

¹Means within a column followed by a common superscript are similar (P<.07).

²Means within the row followed by a common superscript are similar (P<.07).

Table 2. 1984 Daily forage intake (% BW OMB) for five cow breeds

Breed	June ¹	July	August	Mean
1S3H	2.6 ± .2 ^a	2.2 ± .1 ^a	1.9 ± .2 ^a	2.2 ± .1 ^a
HH	2.7 ± .2 ^{ab}	2.2 ± .1 ^{ab}	2.1 ± .2 ^{ab}	2.3 ± .1 ^{ab}
AH	3.0 ± .2 ^{bc}	2.4 ± .1 ^{ab}	2.2 ± .2 ^{bc}	2.5 ± .1 ^{bc}
SH	3.0 ± .2 ^{bc}	2.5 ± .1 ^{bc}	2.2 ± .2 ^{bc}	2.6 ± .1 ^{cd}
3S1H	3.2 ± .2 ^c	2.8 ± .1 ^c	2.4 ± .2 ^c	2.8 ± .1 ^d
Mean ²	2.9 ± .2 ^a	2.4 ± .1 ^b	2.2 ± .2 ^b	

¹Means within a column followed by a common superscript are similar (P<.07).

²Means within the row followed by a common superscript are similar (P<.05).

mean for milk production. The sums of squares generated by this contrast accounted for about 60% of the intake sums of squares for breed. Body weight was significant ($P < .05$) in explaining intake differences among breeds as well.

Within-breed variation in intake was partially explained by body weight ($P < .01$) and wt:ht ratio ($P < .05$), but milk production was nonsignificant.

Milk Production

Mean monthly milk production for all breeds used in 1984 are shown in table 3. The SH and 3S1H breeds produced 5.5 kg/day more milk during the summer than the 1S3H, HH and AH breeds. Monthly values decreased significantly ($P < .01$) from June to August for all breeds with the 1S3H, 3S1H, SH, HH, and AH decreasing by 14.2, 13.8, 11.5, 9.9, and 7.6 kg respectively. The analysis of variance table for milk production is given in Appendix table 11.

Body Measurements

Mean body weights and wt:ht ratios did not differ among the breeds used in 1984 ($P > .10$) (Table 4). Body weights for the HH, AH, 1S3H, 3S1H, and SH averaged 535, 537, 543, 548, and 564 kg respectively and wt:ht ratio averaged 4.14 kg/cm for all breeds. Body weight and wt:ht ratio increased ($P < .01$) during June, July and August for all breeds from 528 to 550, and 557 kg and from 4.03 to 4.18, and 4.21 respectively. The analysis of variance table for body weight and wt:ht ratio is given in Appendix table 12.

