ANIMAL FACTORS INFLUENCING FORAGE INTAKE IN MATURE BEEF COWS

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LITERATURE REVIEW

Introduction

Beef production is a large enterprise in the United States, with over 35 million beef cows grazing pastures and rangeland (NASS, 1997). This vast enterprise is responsible for converting forage into a high-quality human food product. The ability of the forage to meet the animal's nutritional requirements is affected by many interacting genetic and environmental factors such as forage species, maturity, growing conditions, and developmental stage at harvest. In situations where it is anticipated that grazed or harvested forage will contain inadequate nutrients to support the beef cow, producers typically provide a supplemental nutrient source to maintain acceptable animal growth and reproduction. Recent reviews of economic records from cow-calf operations indicate that feed costs represent over 33% of total production costs (Lankister et al., 1999) and that feed cost is the most critical control point for optimizing profitability for cow-calf producers (Miller et al., 2001).

For producers to properly manage grazing pressure on native and improved pastures, the amount of available forage must be determined as well as the quantity of forage that a cow will consume. Of these two factors, the most difficult to estimate is forage intake of the beef cow. Researchers study forage intake based on the premise that increasing intake would increase animal performance, efficiency, and productivity of livestock enterprises. Furthermore, forage intake has the single greatest impact on nutrients available to the animal as well as supplementation needs (Lalman and Lardy, 1998). However, feed intake regulation is a complex biological process that is influenced by many factors that relate to the animal, feed, management, and environment (Figure 1). As a result, feed intake in ruminant systems can be a challenging field of study, particularly with beef cattle that are more extensively managed than their dairy counterparts.

It is important to understand the animal and forage factors that potentially influence intake, in order to accurately estimate forage intake. The objective of this review is to describe how intake is measured and to identify key forage and animal factors that influence forage intake and the potential mechanisms of action.

Quantifying Dry Matter Intake in Ruminants

Estimating the amount of forage consumed by grazing ruminants is essential for nutritionists to make nutritional inferences (i.e. supplementation programs) and predict subsequent animal performance. Yet, intake of the grazing ruminant is difficult to measure directly and is therefore estimated indirectly (Moore and Sollenberger, 1997). Direct and indirect measures of intake have their respective advantages and disadvantages and the following discussion addresses these various approaches to quantifying forage intake.

Direct Measures

Direct intake measurement is the ideal method for measuring intake. Most commonly trials are conducted in confinement settings, feeding harvested forages (hay or silage). The forage is offered to the animal at a predetermined level (generally ad libitum) and the refusal is collected. However, these confinement studies do not mimic actual production settings, as they are typically climate controlled (or sheltered) and the forages are chopped. By chopping forages, selectivity is reduced (Zemmelink and Mannetje, 2002) and passage rate is increased, which may result in inflated intake values.

While directly measuring intake in a confinement setting is achievable, a problem arises in extrapolating data collected in this manner to actual grazing situations. This stems from the forages fed in these confinement settings being harvested forages. Moisture content can impact forage intake as water content can decrease forage intake at moisture contents in excess of 80% (Minson and Wilson, 1994). Since harvested forages typically have less moisture than growing pastures, applying intake data from confinement studies where hays were fed to grazing situations involving lush forage is difficult.

In contrast to confinement feeding trials, directly measuring forage intake in the grazing ruminant is difficult. Some researchers have attempted to quantify forage intake directly in grazing ruminants by several methods. One method is to weigh the animal either during grazing or before and after eating (Horn, 1981; Penning and Hooper, 1985). The primary limitation with weighing animals before and after the grazing session is the need to account for weight loss due to defecation and urination during the grazing period. Another method is to measure herbage mass prior to and following grazing. The reduction in herbage mass can then be divided by the number of animals in the pasture and the number of grazing days to provide an estimate of daily forage intake (Burns et al., 1994). However, this method of estimating intake assumes that the decline in forage mass is entirely due to consumption. Forage intake can be overestimated if non-experimental animals consume forage (wildlife) or there is loss of herbage mass due to trampling or defecation. Another consideration with measuring herbage mass to estimate intake is that the sward will continue growing during the grazing period. Therefore, grazing time must be regulated to minimize the potential for intake underestimation if the sward is growing during the experimental period. Furthermore, to accurately estimate herbage mass, numerous samples must be taken prior to and following grazing. The number of samples needed is related to the size of the pasture and the variation in sward growth throughout the pasture.

While these methods attempt to directly measure intake in grazing situations, the challenges associated with waste loss (weighing method) or with the time and quantity of samples required to accurately estimate herbage mass make these methods impractical. Therefore, these challenges associated with direct measuring forage intake in grazing situations has led to the use of indirect methods.

Indirect Measures

A marker is a substance that is assumed to be neither digested nor absorbed by the animal and can fall into two categories, internal and external. Internal markers are most commonly used to estimate digestibility and are inherent to the feedstuff. Some commonly used internal markers are acid detergent insoluble ash, indigestible fiber components (NDF and ADF), and lignin (Pond et al., 1986). External markers are generally used to estimate fecal output and are exogenous to the feed. Chromic oxide, chromium-mordanted fiber, rare earth elements, and polyethylene glycol have been used extensively in research (Pond et al., 1986).

Intake can be indirectly estimated if digestibility and fecal output are known. Intake, fecal output, and feed digestibility interact in such a manner that when two of the items are know the third can be calculated (Figure 2). For example, if the forage digestibility is known and an indigestible marker is used to estimate fecal output, then intake can be estimated by the following equation (Mayes et al., 1995):

$$\text{Intake} = \text{Fecal Output} / (1 - \text{Digestibility})$$

Markers can provide valuable information as to the relative differences between dietary treatments, however when compared to directly measured data, marker estimated data can be highly variable (Cochran et al., 1986).

Feed Intake Regulation in Ruminants

Feed intake regulation in the ruminant is a complex biological process that incorporates managerial, feed, and animal factors (Figure 1). Many theories attempt to explain intake regulation, but most are limited in the scope of factors that are described as factors regulating forage intake. Research has proposed that intake is regulated via mechanisms including physical fill, chemostatic controls, and the need to maximize metabolic efficiency.

In a recent review, Pittroff and Kothmann (1999) described the current predominating theory of intake regulation in the ruminant as "the two-phase hypothesis" (Figure 3). This theory states that intake of low digestibility feedstuffs (i.e. roughages) is limited by the capacity of the gastrointestinal tract to degrade the feed, whereas intake of higher digestibility feeds is regulated through metabolic controls. This review will discuss the factors involved in the control of physical fill and metabolic control, as well as some recently proposed alternative hypotheses of intake regulation.

Voluntary dry matter intake of low digestibility feeds is considered limited by physical distention of the gastrointestinal tract. The reticulorumen is the primary site at which distention limits forage intake (Campling and Balch, 1961; Allen, 1996). Low-quality forage diets result in situations where energy is limiting animal performance (Mertens, 1994). Researchers have established a nonlinear relationship between forage intake and digestibility of the diet (Blaxter et al., 1961; Conrad et al., 1964; Van Soest, 1965). As digestibility of a diet increases, physical distention of the gastrointestinal tract becomes less important in regulating intake. Conrad et al. (1964) suggested that there is a break point in digestibility at which voluntary dry matter intake stops being controlled by physical fill and is replaced by the need to satisfy energy demand. However, this break point may be related to voluntary dry matter intake being controlled by the integration of multiple stimulatory and inhibitory inputs from the gastrointestinal tract to the brain (Forbes, 1996). Stretch receptors located in the rumen wall signal the degree of distention (fill) to the brain via the vagus nerve (Leek and Harding, 1975). In low-quality forage diets, the stretch receptors in the reticulorumen may provide the stimulus to the satiety center of the hypothalamus that determines the end of a meal (Forbes, 1996). Thus, as diet quality (i.e. digestibility) increases, the effects of physical fill on intake decrease due to reduced stimulation of the stretch receptors in the reticulorumen.

The region of the brain that is most directly associated with the control of feed intake is the hypothalamus (Baile and Mayer, 1969). Peptides and volatile fatty acids can act as neurotransmitters to stimulate/inhibit feeding behavior in animals. Neuropeptide Y has been shown to be an intake stimulant in sheep and rodents (Miner, 1992). Morley et al. (1984) described an extensive peripheral peptide satiety system that includes cholecystokinin, bombesin, gastrin-releasing peptide, glucagon, and somatostatin. The volatile fatty acids, acetate and propionate, have been determined to play a role in short-term intake regulation via depression of intake (Battacharya and Alulu, 1975; Baile and McLaughlin, 1987; Quigley and Heitmann, 1991).

Recently, Ketelaars and Tolkamp (1992a, 1992b, 1996; Tolkamp and Ketelaars, 1992) have challenged the predominating "two-phase" intake theory regarding physical and physiological constraints. Their primary arguments are against the physical fill constraints on intake. These authors refer to the fact that smaller ruminants have larger gastrointestinal tracts relative to their body mass, therefore why would large ruminants evolve to have relatively small gut size, if gut size limited capacity to use forages? Ketelaars and Tolkamp (1992a, 1996) also challenge the fact that during increased performance demands like lactation, the satiety set point likely changes, resulting in increased animal intake. They ask the question, why does the animal not always eat to their full capacity at all times? Most researchers would answer this question as the animal's intake reflects changes in energy requirements of the animal. Yet, researchers have not been able to provide an explanation for this change in satiety set point.

Reviews by Ketelaars and Tolkamp (1992a, 1992b, 1996) and Tolkamp and Ketelaars (1992), caused them to conclude that feed consumption is a balance between costs and benefits to the animal. They base this theory on the free radical theory of aging. In this theory, reactive oxygen species that come from the use of oxygen for ATP production, cause damage to cell structures. These damages accumulate with age, causing loss of cell function (Ketelaars and Tolkamp, 1996). If animals were to reduce oxygen consumption, theoretically the damage caused from free radicals would be minimized, however, oxygen consumption is vital to life. Therefore, an animal's system must balance between the benefits (oxygen consumption that is needed) and the costs (excess byproducts from oxygen consumption). The bottom line to Ketelaars and Tolkamps proposed theory of intake regulation is that animals function to optimize not necessarily maximize, feed intake.

Theories such as the two-phase hypothesis and intake optimization likely work in concert with each other, one predominating over the other, depending upon plane of nutrition of the animal and diet type. The factors behind intake regulation are dynamic and interact in such a manner that individual isolation may be challenging. However, by understanding how components such as fill, energy demand, and metabolic controls interact to control intake, more accurate models and prediction equations can be developed.

Forage Factors Influencing Intake by Ruminants

Two primary factors drive nutrient availability for forage fed livestock: forage availability and forage nutritive value. Vegetative tissues of the plants commonly fed to ruminants contain a large percentage (35-80%) of their organic matter in the cell walls (Jung and Allen, 1995). For beef cattle on low-quality forage diets, high cell wall concentration and consequently low digestibility of the forage (nutritive value) often limit forage intake. Therefore it is imperative to understand how these factors impact forage intake and what additionally factors can influence forage nutritive value.

Cell Wall Components

In 1963, Van Soest proposed the use of detergents for the analysis of fiber fractions of forages. The resulting fractions were based on nutritional availability to the animal and included cell contents, neutral detergent fiber (NDF), and acid detergent fiber (ADF). Cell contents are readily available to the animal and include soluble starches, sugars, pectin, and protein. Neutral detergent fiber includes hemicellulose, cellulose, and lignin, and the ADF fraction includes only cellulose and lignin (Maynard et al., 1979). Fiber has been related to the theory of physical fill as the fiber ferments and passes more slowly from the reticulorumen, as compared to non-fibrous constituents of feeds. The detergent fiber fractions (ADF and NDF) and lignin are negatively correlated to voluntary dry matter intake of ruminants. Reid et al. (1988) conducted feeding trials with 170 forages in three forage classes, tropical grass, temperate grass, or temperate legume, offered ad libitum to cattle, over a 20-yr period. From these data, correlations were determined between dry matter intake and the detergent fiber fractions. Both NDF and ADF were negatively correlated (-0.41 and -0.52, respectively) with dry matter intake of cattle. Horn et al. (1979) evaluated the impact of nitrogen fertilization on bermudagrass pasture chemical composition in Oklahoma. These authors reported that forage intake was negatively correlated with lignin concentration of the bermudagrass. The literature indicates that the structural components of forages (hemicellulose, cellulose, and lignin) are negatively associated with forage intake in ruminants. Yet, several factors including forage type and maturity influence the concentration of the fiber fractions in forages and thus potentially influence forage intake.

Forage Type

Reid et al. (1988) evaluated 428 forages fed to sheep and 170 forages fed to cattle over 20 yr. Forages fell into three classes including temperate grasses, tropical grasses, and legumes. Intake was greater for legumes compared with both grass types. Legumes are eaten in greater quantities than grasses of similar digestibility, likely due to legumes having shorter retention time in the rumen than grasses (Thornton and Minson, 1973). Tropical grasses also result in lower intakes by ruminants than their temperate counterparts, due to lower digestibility of the dry matter (Minson and Wilson, 1980). Varel and Kreikemeier (1999) evaluated alfalfa hay and brome hay as to intake potential and found that mature cows consumed more organic matter from alfalfa hay as compared to brome hay. The anatomical differences between legumes and grasses is likely responsible for their results. Holloway et al. (1979) utilized high and low quality fescue pastures to evaluate grazing animal intakes. The high quality fescue pasture was overseeded with red clover and lespedeza and the low quality pasture was a monoculture of tall fescue. Mature cows consumed more digestible dry matter from the high quality pasture as compared to the lower quality pastures, which may be driven by the influence of legumes in the high quality pastures in this study.

Forage Maturity

Forage maturity is a large determinant of forage nutritive value. As forages mature, cell wall concentration increases and cell contents decrease. In 1984, Vona et al. conducted a study to evaluate the effects of forage maturity on the voluntary dry matter intake of cattle and sheep. Regardless of cultivar, intake decreased with advancing stages of maturity of the forage. Additionally, as forages mature there is an increasing proportion of stem and decreasing proportion of leaves. Research has shown that forage leaves are retained in the rumen a shorter time than forage stems (Laredo and Minson, 1973; Poppi et al., 1981), thus more mature forages with increased stem would be retained longer in the rumen, slowing the rate of passage and potentially limiting intake.

Forage Availability

Forage availability for the grazing ruminant can be determined by calculating herbage mass or measuring pasture sward height. Intake can be expressed as the product of biting rate, intake per bite, and grazing time. It has historically been viewed that as sward height declines, so does intake per bite, however biting rate usually increases in an attempt to compensate for the decline in forage availability (Hodgson, 1985). Grekara et al. (2001) conducted a study to evaluate the effects of pasture sward height and supplement on intake and grazing behavior of lactating beef cows. Cows on the lower sward height (4 to 8 cm) consumed similar amounts of forage as compared to animals on the higher sward height pastures (8 to 11 cm), but spent an additional 1.3 h/d grazing to do so. Results from this study indicate that although pastures had different sward heights, forage availability was not limiting intake, the animals merely adjusted grazing behavior to meet the needed intake.

Forage factors that influence intake by beef cattle are numerous and complex. It is imperative to develop further understanding of these factors and their interactions to better develop methods of estimating forage intake in both confinement and grazing situations.

Animal Factors Affecting Forage Intake by Beef Cows

Numerous animal factors can influence forage intake by beef cows as demonstrated by the variety of factors incorporated into models. Many models of feed intake contain animal factors such as body weight, age, physiological status, and genetic merit for production (Conrad et al., 1964; Forbes, 1977; NRC, 1996), due to the influence of these factors on energy requirements for the animal.

Age

The majority of research considering the effect of animal age on forage intake has been conducted in sheep. Egan and Doyle (1982) reported that when feeding high quality forage, lambs consumed more forage than aged wethers. In contrast, when low quality forage was fed, the lambs could not be sustained for long periods, likely due to their increased energy requirement, per unit of body weight, as compared to older animals. Varel and Kreikemeier (1999) evaluated forage utilization by heifers (10 months of age) and mature beef cows (7 to 9 years old). Cows consumed more feed (expressed per unit of metabolic weight) and more efficiently utilized the forages, as compared to heifers. This was attributed to cows having a smaller ruminal fluid fill that turns over faster, thus increasing ruminal fiber digestion and potentially intake. In the high-yielding dairy cow, the intake capacity of primiparous heifers is approximately 80% of mature, multiparous cows (Ingvartsen and Andersen, 2000). However, comparisons of young beef cows (2, 3 years of age) with more mature counterparts have not been established.

Physiological Status

Physiological status has been more extensively studied than cow age, in regards to forage intake. Both cows (Ovenall et al., 1991; Stanley et al., 1993; Marston and Lusby, 1995) and heifers (Vanzant et al., 1991) have been evaluated for changes in forage intake during the transition period from pregnancy to lactation (Table I). Vanzant et al. (1991) compared first calf heifers that were pregnant and lactating with non-pregnant control heifers and found that during both pregnancy and lactation, the pregnant/lactating heifers consumed approximately 18-20% more forage than non-pregnant counterparts. Additionally, lactating heifers consumed 13% more forage than they did during late gestation. Ovenall et al. (1991) evaluated the effects of lactational status on forage intake of beef cows. Lactating cows ate 11% more DM than their nonlactating contempories. Stanley et al. (1993) evaluated changes in forage intake during the transition period from gestation to lactation in beef cows consuming alfalfa hay. During late gestation, intake was fairly constant, however, by 22 d postpartum, intake increased in excess of 30% over the prepartum period. In 1995, Marston and Lusby evaluated the effect of protein and energy supplementation on forage intake of mature beef cows during late gestation and early lactation. On average, cows in early lactation consumed 18% more forage DM than during the late gestation period. Across four studies, the literature is consistent that lactating females consume more forage than non-lactating females (Table I). The extent of this difference may be influenced by forage quality and other animal factors including age and production potential.

Milk Production

A beef cow's nutritional requirements peak during early lactation. During lactation, her maintenance energy requirements increase by 20% as compared to her requirements during late gestation (NRC, 1996). Furthermore, maintenance energy requirements are positively associated with genetic potential for lactation (Ferrell and Jenkins, 1985). For beef cows, each kg of milk requires approximately 0.72 Mcal NEm/d and 34 g CP/d (NRC, 1996). Therefore, not only are the beef cow's maintenance energy requirements increasing, her production energy requirements also increase proportionally to the level of milk that is produced. As a result, the increased energy requirements due to lactation may drive the increased intake that is observed as beef cows make the transition from gestation to lactation.

Wagner et al. (1986) estimated the daily forage organic matter intake of beef breeds differing in milk production potential. Hereford, Angus, and Simmental cows and the various crosses of these breeds were used to evaluate organic matter intake and there was no difference among breed crosses for body weight and size. With increasing proportion of Simmental (up to 50%), milk production also increased. Cows that were greater than 50% Simmental consumed more forage than straightbred Hereford, Hereford x Angus, and low percentage Simmental cows. Hatfield et al. (1989) compared forage intake for cows of differing potential for milk production, using Hereford x Angus cows as low, Red Poll x Angus cows for medium, and Milking Shorthorn x Angus cows for high milk production potentials. These researchers did observe linear increases in milk yield in these cows during early and late lactation. Forage DMI increased linearly with increased milk production for both early and late lactation for these groups of cattle.

Montano-Bermudez et al. (1990) worked with cows of similar breeding to the Hatfield study, and determined that the high and medium milk production potential cows required 12% more energy per unit of metabolic body weight for maintenance, as compared to the low milk production potential cows. Ferrell and Jenkins (1982) evaluated the efficiency of cows of different size and milk production and determined that cows having higher milk production potential had higher maintenance requirements per unit of metabolic body size than cows having lower milk production potential. The observed increases in forage intake by cows with increased genetic merit for milk production (Table II) is likely due to increased maintenance energy requirements in addition to the increased energy demand associated with increased milk production.

The previously discussed studies utilize breed crosses to generate their differences in milk production potential. Some potential problems with using breed crosses include heterosis effects (if comparing to straightbred animals) and differing mature size and/or growth rate. Within a breed, expected progeny differences (EPD) can be used to predict differences in calf weaning weight due to milk production of the dam. Researchers have demonstrated that this statistical tool is successful (Diaz et al., 1992; Marston et al., 1992; Mallinckrodt et al., 1993; Minick et al., 2001). Minick et al. (2001) demonstrated that females selected for high milk production had lower body condition scores throughout the lactation as compared with the females selected for low milk production. This indicates that females producing more milk may not be meeting their nutrient demand and therefore are mobilizing body tissues to maintain increased levels of milk production. The relationship between predicted genetic merit for milk production via sire EPD and feed intake has not been established in the literature. It can be hypothesized that if EPDs are successful in predicting differences in calf weight due to milk production, and that intake and milk production are positively related, then selecting females for increased milk production would increase nutrient intake of the cows.

Physiological and Metabolic Changes during Transition from Gestation to Lactation

Digestive Tract Morphological Changes

Lactation results in increased feed intake by ruminants. Associated with this change are various changes in the morphology of the gastrointestinal tract. Increased hypertrophy of the liver, intestine, and rumen epithelium occur during lactation (Kelly et al., 1991). In rodents (rats and mice) increased hypertrophy and hyperplasia of the gastrointestinal mucosa occurs during lactation and has been associated with an increase in food intake (Campbell and Fell, 1964; Crean and Rumsey, 1971; Lichtenberger and Trier, 1979). In addition to increased cell numbers and cell growth, absorptive capacity of the gastrointestinal is also impacted. Increased amino acid and glucose uptake has been shown to occur in the small intestine of rats (Cripps and Williams, 1975). Amino acids and sugars are absorbed into intestinal epithelial cells via active transport systems that utilize the electrochemical Na^+ gradient at the brush border. The enzyme, Na^+, K^+-ATPase, is necessary to maintain the electrochemical gradient. McBride and Milligan (1984) concluded that Na^+, K^+-ATPase activity accounts for 55% of total mucosal respiration at peak lactation in dairy cows. During mid lactation and the dry period, Na^+, K^+-ATPase respiration dropped to approximately 35% of the total mucosal respiration. Research in lactating ewes has shown that hepatic Na^+, K^+-ATPase respiration accounts for 45% of the total liver oxygen consumption, which was 24 to 37% higher than during late lactation and the dry period (McBride and Milligan, 1985). These adaptations in the gastrointestinal tract may facilitate the increased nutrient demands that occur during lactation.

Nutrient Metabolism

It has been documented in beef and dairy cattle that as cows approach parturition, intake decreases, with the lowest intake on the day of calving. Shortly after calving intake begins to increase until maximum intake is reached, typically after peak milk yield has been achieved (Figure 4). Many changes occur in nutrient metabolism to attribute to the increased intake of lactating females (Table III).

By the end of seven months of gestation, the bovine conceptus has achieved approximately 40% of its birth weight (Bauman and Currie, 1980). During the last two months, glucose and amino acid requirements for the conceptus increase dramatically. To accommodate the increased nutrient needs of the conceptus, the cow must alter carbohydrate, protein, and lipid metabolism within her own body. To provide sufficient glucose to the conceptus, the cow's whole-body glucose production must increase, generally in the form of hepatic gluconeogenesis (Bell, 1995). The extent of increased glucose production is related to level of feed intake. Animals on higher quality or non-restricted diets have more substrate to utilize to meet the conceptus requirements, however even animals on restricted diets show increased hepatic gluconeogenesis (Steel and Leng, 1973). Bell (1995) suggests that there is evidence for pregnancy-induced reduction in glucose uptake by the dam's peripheral tissues. Furthermore there is evidence of greater lactate production and Cori cycling in pregnant ruminants to provide substrate for gluconeogenesis (Baird et al., 1983). In an effort to spare glucose, circulating levels of nonesterified fatty acids (NEFA) and ketones are elevated during late pregnancy, particularly close to term (Bell, 1995). Levels of NEFA begin to rise 2 to 3 weeks prior to parturition and peaks at calving or during the first week of lactation (Ingvartsen and Andersen, 2000). This mobilization of body reserves is what drives the negative energy balance that ruminants are in during early lactation, until feed intake levels increase to support nutrient demand. The bovine works to spare glucose through the use of her own body reserves for her energetic needs.

Endocrine Changes

During the transition from gestation to lactation, endocrine profiles change to accommodate the new demands for lactation. As dairy cows make the transition from late gestation to early lactation, plasma insulin decreases and growth hormone levels increase (Kunz et al., 1985). The shift in insulin and growth hormone indicates a shift to gluconeogensis rather than glucose storage. Thyroid hormone (T4 and T3) concentrations increase gradually during late gestation, drop by 50% during parturition, and then recover and increase during early lactation (Kunz et al., 1985). The increase in thyroid hormones indicates lipolysis increases to increase circulating NEFA levels to provide energy for the cow. Estrogen levels increase during late gestation, but decreases immediately at parturition. Furthermore, progesterone levels, which are elevated to maintain the pregnancy, decline rapidly approximately 2 d prior to calving (Chew et al., 1979). It appears that endocrine status changes to accommodate the need to mobilize body tissues as the cow prepares for lactation.

Summary

Forage intake regulation is a complex, dynamic system that involves feed, animal, and environmental factors. Research efforts to understand and predict changes in forage intake have had limited success due to the complexity of regulatory mechanisms. Within the animal, metabolic control works in concert with physical characteristics of the feed to control intake. The beef cow has many factors that can influence her feed intake. Among these are age and/or size, physiological state, and genetic merit for milk production. In the dairy cow, multiparous cows consume more feed on an absolute basis than primiparous heifers. Little research has been conducted in the beef cow to evaluate the impact of cow age or parity on forage intake. Additionally, genetic merit for milk production influences intake. Cows with greater genetic merit for milk production consume more forage, however most of this data has been generated using various breed crosses. This may be confounding due to differences in body weight or growth rate among various breed crosses. During lactation, nutrient demands increase. As a result, during early lactation, physiological and endocrinological changes occur within the cow to mobilize her own body tissues to meet the increased energy demands. Intake is sensitive to changes in physiological state and genetic merit for lactation, but within breed comparisons of changes in intake have not been established in the literature. To properly manage grazing resources and develop supplementation programs for cow-calf operations, it is imperative to understand the relationships of cow age or parity, physiological stage, and genetic merit for milk production.

TABLE I. Effect of physiological status on forage intake in beef cows.

Study	Cow Type	Weight (kg)	Forage	Physiological Status	Intake	Intake Method
Ovenall et al., 1991[a]	Hereford (H) x Angus (A) cows	487	Prairie Hay	Non Lactating	1.87	Direct
		453		Lactating	2.11	
Vanzant et al., 1991[b]	H x A heifers	487	Tallgrass Prairie (KS)	-55	9.0	Marker
	H x A heifers (open-control)	439		-55	7.2	
	H x A heifers	485		-12	9.8	
	H x A heifers (open-control)	432		-12	9.7	
	H x A heifers	423		+26	10.8	
	H x A heifers (open-control)	443		+26	8.9	
Stanley et al., 1993[b]	H x A cows	568	Alfalfa hay	-61	8.8	Direct
				-48	9.5	
				-34	10.0	
				-20	10.4	
				-6	11.0	
				+8	12.2	
				+22	14.9	
Marston and Lusby, 1995[ac]	H x A cows	485	Native grass hay (OK)	Gestation	1.64	Direct
		418		Early Lactation	2.01	

[a] Intake expressed as percent of body weight, on a dry matter basis.
[b] Physiological status represented in relation to days pre- or post-calving, where calving = d 0. Intake expressed as kg of DM/d
[c] Cow weights averaged across supplement treatments.

TABLE II. Influence of milk production and genotype on forage intake in cows.

Study	Cow Type	Weight (kg)	Forage	Milk Prod. (kg/d)	Intake	Intake Method
Wyatt et al. 1977[a]	Hereford (H)	388	Tallgrass Prairie (OK)	6.1	100	Marker
	H x Holstein (HO)	385		9.6	113	
	HO	445		11.7	130	
Kronberg et al. 1986[b]	H	460	Summer Range (MT)	N/A	1.7	Marker
	75% Simmental (S) x 25% H	573		N/A	1.9	
Wagner et al. 1986[c]	H	535	Foothill range (MT)	8.2	2.3	Marker
	25% S x 75% H	543		9.2	2.2	
	Angus (A) x H	537		7.9	2.5	
	S x H	564		14.1	2.6	
	75% S x 25% H	548		13.8	2.8	
Hatfield et al. 1989[b]	H x A (low milk prod.)	560	Meadow hay (NE) Early Lactation	8.4	2.6	Direct
	Red Poll (RP) x A (med. milk prod.)	502		9.4	2.9	
	Milk Shorthorn (MS) x A (high milk)	538		10.6	3.0	
	H x A (low milk prod.)	573	Meadow hay (NE) Late Lactation	6.4	2.7	
	RP x A (med. milk prod.)	510		7.3	3.1	
	MS x A (high milk prod.)	546		8.6	3.2	

[a] Intake averaged across supplementation treatments and expressed as % change from the Hereford group (base is 100).

[b] Intake expressed as percent of body weight, on a dry matter basis

[c] Intake expressed as percent body weight, on an organic matter basis

Table III. Partial list of metabolic changes associated with lactogenesis in ruminants (Bauman and Currie, 1980)

Physiological Function	Metabolic Change	Tissues involved
Milk Synthesis	Increased synthetic capacity	Mammary
	Increased blood flow	
	Increased nutrient uptake and use	
Lipid Metabolism	Increased lipolysis	Adipose
	Decreased lipogenesis	
	Increased use of lipid as energy	Other body tissues
Glucose Metabolism	Increased gluconeogenesis	Liver
	Decreased glucose use (spare glucose)	Other body tissues
Protein Metabolism	Increased protein metabolism	Muscle and other body tissues
Mineral Metabolism	Increased absorption	Gut
	Increased mobilization	Bones
Intake	Increased consumption	Central nervous system
Digestion	Increased hypertrophy of GIT	Digestive tract (including liver)
	Increased capacity for nutrient absorption	

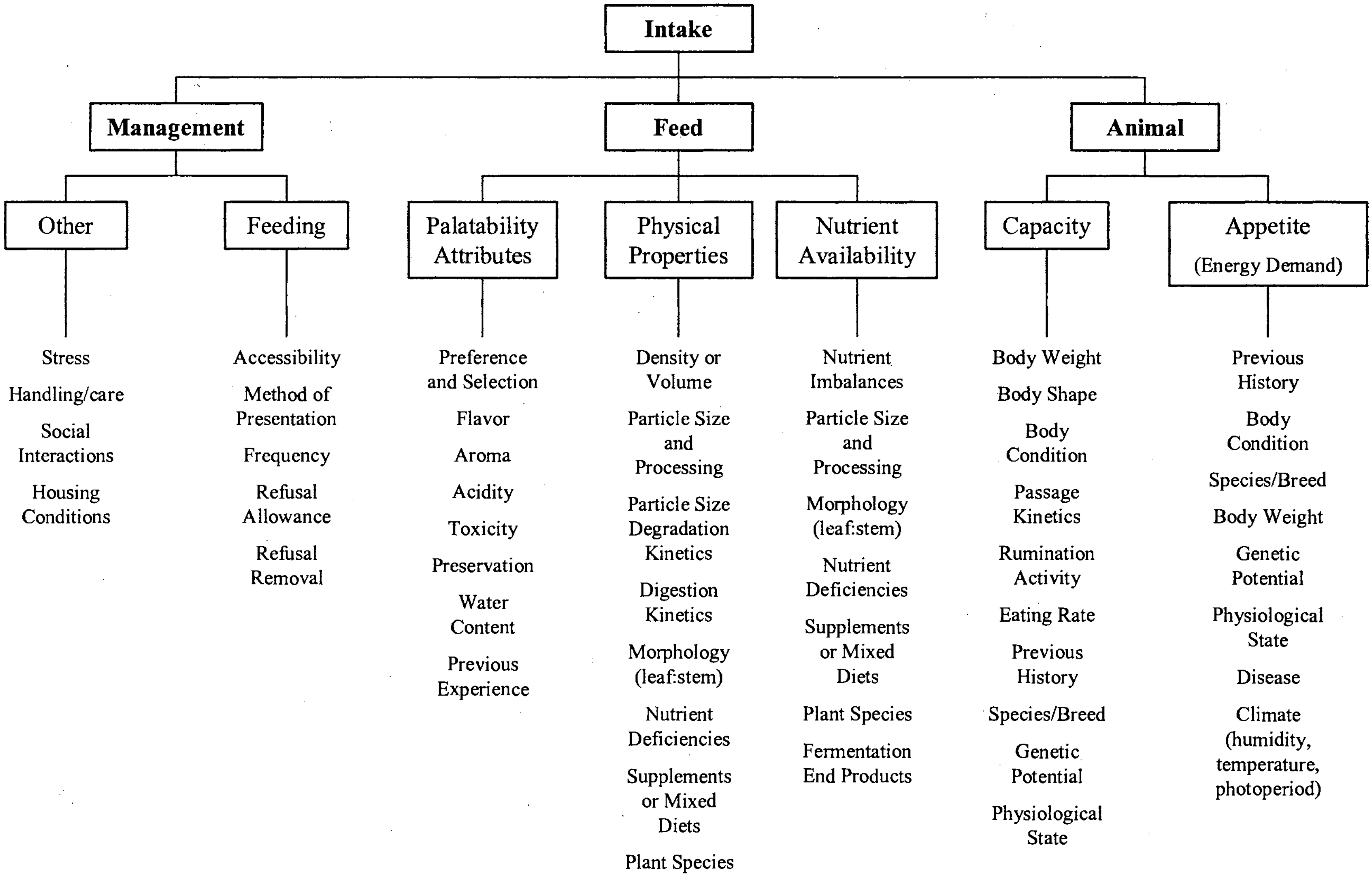

Figure 1. Classification of factors affecting feed intake by ruminants (adapted from Mertens, 1994)

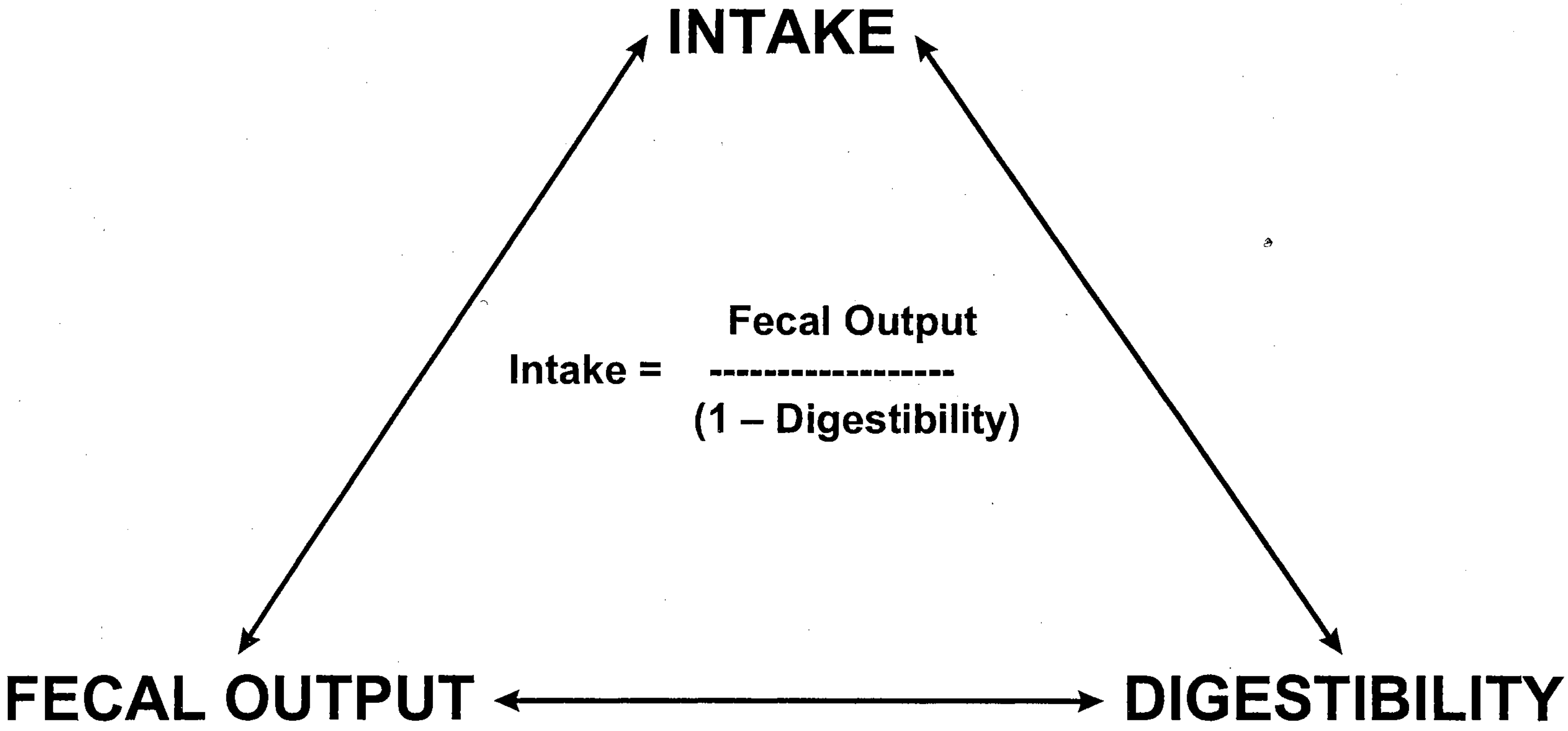

Figure 2. Interactions of intake, fecal output, and forage digestibility. Fecal output and feed digestibility can be used to indirectly estimate intake.

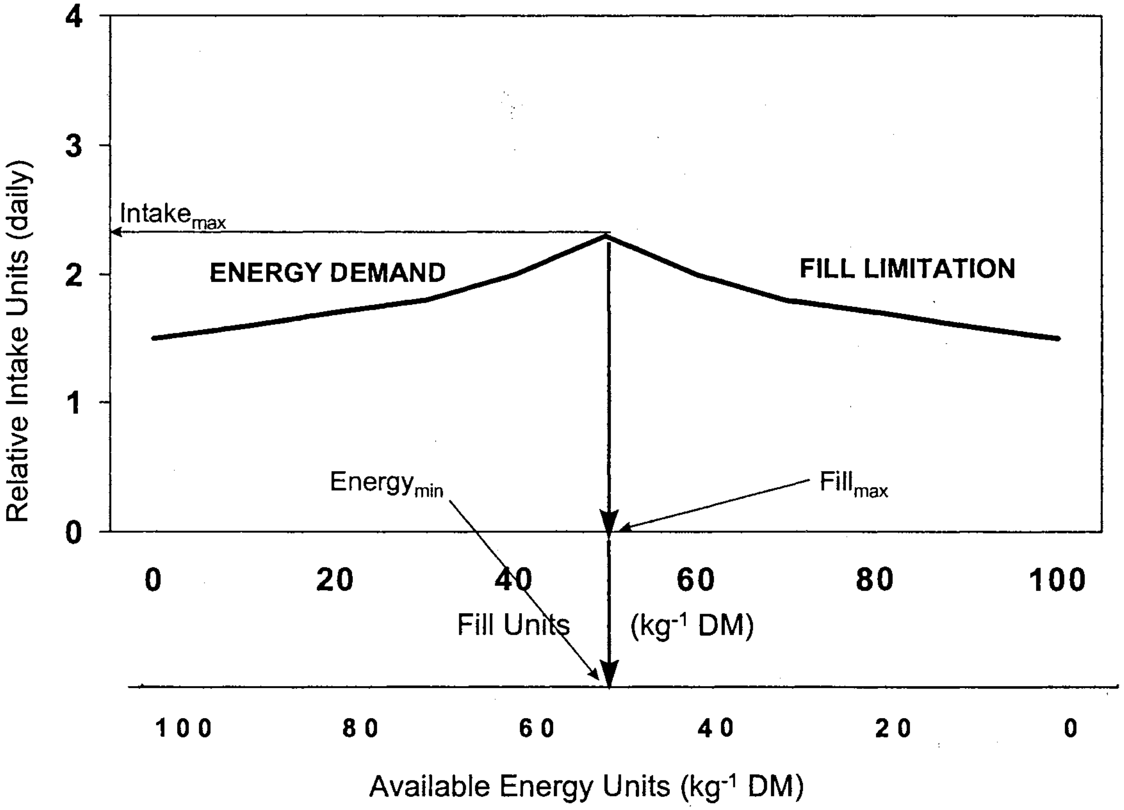

Figure 3. Illustration of the relationship between physical fill and energy demand on the regulation of forage intake in ruminants. Maximum intake occurs at maximum ruminal fill and minimum available energy that meets the animal's energetic requirements (adapted from Mertens, 1994).

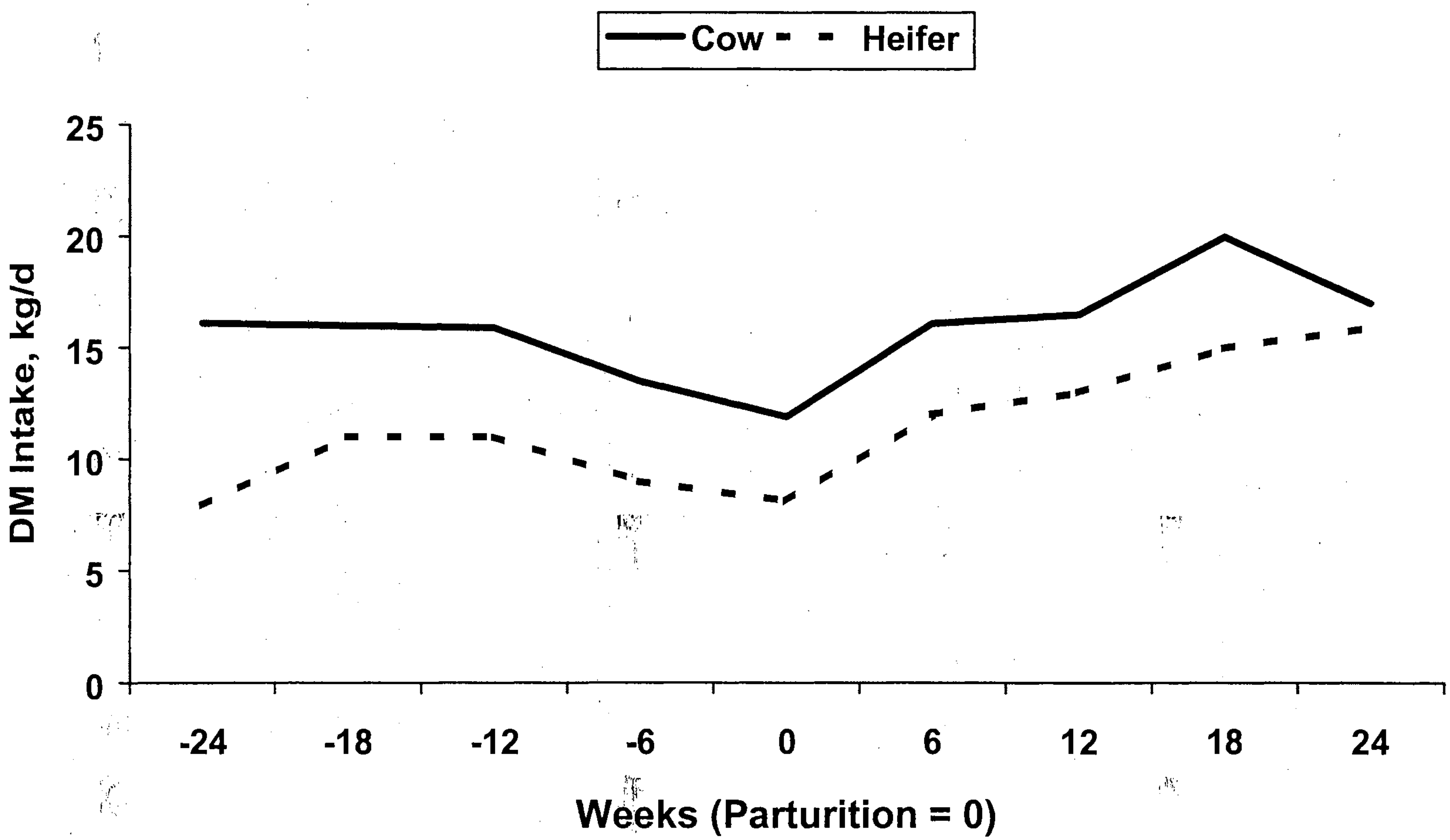

Figure 4. The pattern of intake around calving in dairy cows and heifers (Ingvartsen and Andersen, 2000).

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CHAPTER TWO

INFLUENCE OF MILK PRODUCTION POTENTIAL ON FORAGE DRY MATTER INTAKE OF MULTIPAROUS AND PRIMIPAROUS BRANGUS FEMALES

Abstract

Brangus females (n = 24) were used in three experiments to evaluate the effects of parity (multiparous vs primiparous; COW vs HFR) and potential genetic merit for milk production (MEPD; HIGH vs LOW) on forage DM intake (DMI) during late gestation, early lactation, and late lactation. Females were selected for MEPD based upon their sire's EPD for milk production. Low quality (5.3% CP and 75.9% NDF) hay was offered ad libitum (130% of previous 2-d average intake) and cottonseed meal was supplemented to ensure adequate degradable intake protein. All females were adapted to diets at least 7 d and individual intakes were collected for 9 d. During the lactation trials, actual milk production was determined using a portable milking machine, following a 12-h separation from calves. During late gestation, COW consumed 24% more ($P = 0.01$) forage DM than HFR. However, parity class did not influence forage DMI when intake was expressed relative to BW. Furthermore, MEPD class did not influence forage DMI during late gestation. During early lactation, COW produced 66% more ($P < 0.001$) milk than HFR, and HIGH tended ($P = 0.1$) to produce more milk than LOW. Multiparous cows consumed 19% more ($P < 0.0001$) forage DMI than HFR, when expressed on an absolute basis, but not on a BW basis. High MEPD cows consumed 8% more ($P < 0.05$) forage DM than LOW. During late lactation, COW produced 84% more milk than HFR, but MEPD class did not influence ($P = 0.4$) milk yield. Also, COW consumed 17% more ($P < 0.01$) forage DM per day than HFR, but when intake was expressed relative to BW, neither parity nor MEPD influenced forage DMI during late lactation. Multiparous cows were 54 and 74% more efficient ($P < 0.01$) than HFR converting digestible OM to milk yield during early and late lactation, respectively. Milk yield (kg/d) and BW (kg) explained significant proportions of the variation in forage DMI during early and late lactation. Results suggest that multiparous cows and primiparous heifers consume similar amounts of forage DM, expressed per unit of BW, during late gestation and lactation. Selecting females for increased genetic merit for milk production increases forage DMI during early lactation.

Introduction

For cow-calf producers to optimize efficiency in their production systems, it is imperative for cows to calve 12-mo intervals. The primiparous beef heifer presents challenges to achieving this goal, as they may have increased postpartum intervals (Bellows and Short, 1978; Triplett et al., 1995) and lower pregnancy rates upon rebreeding (Rae et al., 1993) compared with multiparous cows. Reduced reproductive performance in cows and heifers can result from inadequate nutrient intake pre- or post-partum (Randel, 1990). Varel and Kreikemeier (1999) reported that mature cows consumed more forage than 10-mo old heifers, when expressed per unit of metabolic BW, but not per unit of BW. This difference was attributed to increased forage utilization by the mature cows. However, data comparing forage intake of primiparous and multiparous females during gestation and lactation are limited.

Selection for increased milk production based upon sire EPD results in increased milk production (Diaz et al., 1992; Marston et al., 1992; Mallinckrodt et al., 1993), however this increase may be at the cost of body nutrient reserves (Minick et al., 2001). Lactating females consume more forage DM than gestating females (Vanzant et al., 1991; Stanley et al., 1993; Marston and Lusby, 1995). Furthermore, as milk yield increases, so does forage DM intake (DMI; Wyatt et al., 1977; Wagner et al., 1986; Hatfield et al., 1989). However these researchers used various breed crosses of different biological types to establish different levels of milk production. The relationship between the predicted differences in milk yield, stage of production, and forage DMI has not been established. Therefore, our objective was to evaluate the influence of cow parity and predicted difference in milk production (EPD) on forage DMI in late gestation, early lactation, and late lactation.

Materials and Methods

Three experiments were conducted at the USDA-ARS Grazinglands Research Laboratory in El Reno, OK to evaluate the effects of parity and predicted genetic merit for milk production on forage dry matter intake in Brangus females. All three experiments used the same low-quality hay (Table IV). The hay was harvested at the USDA-ARS Grazinglands Research Laboratory during the summer of 1998, from a bermudagrass-native prairie pasture and was stored outside as round bales until feeding. Round bales were re-baled into small square bales to facilitate feeding the animals individually. During re-baling, the outer layer (15 cm) that appeared damaged was separated and discarded.

Selection Population

Females used in the following series of experiments were selected from a population consisting of 65 multiparous, purebred Brangus cows and 39 primiparous, purebred Brangus heifers. Within each parity class (cows vs heifers), females were ranked based upon sire EPD for milk production (MEPD). Within the multiparous cow population, 43 sires were represented with a range of sire EPD for milk of +6.6 to –11.4. The primiparous heifer population had 17 sires represented with a range of sire EPD for milk of +8.2 to –6.5. Experimental females (n = 12 per parity) were selected from the upper and lower 25% of represented sires for each parity population. Replacements were selected that had a similar sire EPD of the female being replaced.

Experiment 1 – Late Gestation

In December 2000, 12 multiparous cows and 12 primiparous heifers were selected as previously described for high and low MEPD prior to the initiation of Exp. 1. Cows averaged 61 d and heifers averaged 33 d prepartum. One cow was removed during Exp. 1 due to lameness and data from three heifers was excluded due to early calving. Females were weighed at the beginning and end of the feeding period. Average weight for the feeding period was used to express intake relative to unshrunk BW and metabolic BW ($BW^{0.75}$). Body condition scores (scale 1 – 9; Wagner et al, 1988) were determined by two independent evaluators at the beginning of each feeding period and average scores are reported.

Prior to initiating Exp. 1, a sample of the forage was analyzed for chemical composition to determine if degradable intake protein (DIP) supplementation would be needed. Animal and forage factors were incorporated into the 1996 Beef NRC Model, Level One and DIP balance was evaluated, assuming a microbial efficiency of 11% (Russell et al., 1992). Degradable intake protein was calculated to be limiting for all three experiments, therefore cottonseed meal (CSM) was supplemented so that all classes of females in each experiment had a calculated DIP balance of 150 g/d. These calculations led to CSM supplementation rates of 0.2% of BW per day for cows and 0.3% of BW per day for heifers during Exp. 1 (Table V).

Females were housed in a partially enclosed barn (18 x 73 m) equipped with pens measuring 4.6 x 4.6 m. Two females of similar weight and parity, representing high and low MEPD were allotted to a pen. Females were individually fed hay and supplement daily by using the Calan gate system (American Calan Inc., Northwood, NH) and were trained to the gates and adapted to the diet simultaneously. The training and adaptation period was 24 d followed by a 9-d intake collection period. All animals had ad libitum access to water and a trace mineralized salt block (contained not less than 93% NaCl, 3500 ppm Zn, 2800 ppm Mn, 1750 ppm Fe, 350 ppm Cu, 70 ppm I, and 70 ppm Co). Forage was offered ad libitum, which was determined to be 130% of the previous 2-d average. During the intake collection period, hay, CSM, and orts were sub-sampled at each feeding and hay and CSM were composited for the period, and orts were composited by animal.

Experiment 2 – Early Lactation

In March 2001, 12 multiparous cows and 12 primiparous heifers were assigned to two feeding periods such that each period was balanced for parity and MEPD. Females in Period 1 averaged 63 d postpartum with a range of 53 d and the females in Period 2 averaged 60 d postpartum with a range of 52 d. Cows averaged 47 d and heifers averaged 76 d postpartum as the heifers were bred to calve earlier than the cows. Peak lactation has been reported to occur between 49 and 90 d, with an average of about 60 d, depending upon breed, nutrition, and age (Marston et al., 1992; Mallinckrodt et al., 1993; Minick et al, 2001).

All animals were placed in a drylot for a 7-d adaptation to the diet (prior to measuring milk production). Each pen housed a single cow-calf pair and cow-calf pairs were randomly allotted to pens (same facilities as Exp. 1). Each pair was individually fed for a 7-d adaptation period and 9-d data collection period. Forage was offered ad libitum and CSM was fed at 0.4% and 0.5% of BW for cows and heifers, respectively. Supplement was offered and subsampled daily and forage and ort samples were collected every two d. Calves were assumed to consume minimal forage, however data are reported as cow-calf pair intakes, since the calf was not separated.

On d 7, milk production was determined directly using a single-cow portable machine (Brown et al., 1996). Cows and calves were separated at 1900 h on the evening prior to milking. Hay and water were provided during the 12-h separation. Milking began at 0700 h the next morning. Approximately 10 min prior to milking, cows were sedated with 1.5 mL of acepromazine maleate (10 mg/mL, i.m.; Phoenix Pharmaceutical, Inc., St. Joseph, MO) and 1.0 mL of oxytocin (20 USP units/ml, i.m.; Phoenix Pharmaceutical, Inc., St. Joseph, MO) to induce milk let-down. Daily milk yield was estimated as the net weight of milk adjusted to a 24-h basis (Brown et al., 1996).

Experiment 3 – Late Lactation

In July 2001, 12 multiparous cows and 12 primiparous heifers were assigned to two feeding periods such that each period was balanced for parity and MEPD. Females in Period 1 averaged 162 d postpartum with a range of 53 d and the females in Period 2 averaged 165 d postpartum with a range of 52 d. Cows averaged 149 d and heifers averaged 178 d postpartum as the heifers were bred to calve earlier than the cows.

Similar to Exp. 2, all animals were placed in a drylot for 7-d prior to measuring milk production and then each cow-calf pair was randomly allotted to a pen. The barn in this experiment had enclosed sides and measured 15 x 73 m and each pen measured 3.7 x 3.7 m. Milk production was determined as previously described. Due to the expected increase in calf forage intake, the feeding regime differed from the previous two experiments. All pairs were separated and cows were offered hay for two 4-h feeding bouts at 0730 and 1800 h, similar to the experiment of Ovenell et al. (1991). Forage was offered ad libitum, as described previously. Cottonseed meal feeding levels were determined as described in Exp. 1. Cottonseed meal was offered at 0800 h to each female and was fed at the rate of 0.4% and 0.45% of BW for cows and heifers, respectively. While separated, calves were offered ad libitum access to water, hay, and a 14% CP creep feed. Daily intake data are reported as the sum of two 4-h feeding bouts.

Forage, Feces, and Supplement Analysis

Forage, orts, and fecal samples were dried at 55°C in a forced-air oven and were ground to pass a 2-mm screen. Dry matter and ash determinations were conducted in accordance with approved methods of the AOAC (1996). Nitrogen content of forage, supplements, and feces was determined by combustion (LECO-NS2000, Leco Corporation, St. Joseph, MO) in accordance with AOAC (1996). Samples were analyzed for NDF and ADF using ANKOM technology (ANKOM^{200} Fiber Analyzer, Ankom, Fairport, NY). Forage lignin concentration was determined by digesting ADF residue in 72% w/w sulfuric acid (AOAC, 1996). Degradable intake protein of the forage was estimated (Roe et al., 1990) by measuring nitrogen disappearance during a 48-h incubation in a borate-phosphate buffer containing protease type XIV from *Streptomyces griseus* (P-5147, Sigma Chemical Co., St. Louis, MO). Total digestible nutrient concentration of the forage was determined by the summative equation of Weiss et al. (1992). Tabular values for DIP, crude fat, and TDN for CSM were used (NRC, 1996).

Fecal output of the cows was estimated using acid detergent insoluble ash (ADIA) as an internal marker. During each experiment, fecal samples were collected daily for five d and composited. Acid detergent insoluble ash was determined as the residue following complete combustion of the ADF residue (Van Soest et al., 1991). Total diet organic matter digestibility was calculated as described by Cochran and Galyean (1994).

Statistical Analysis

Data in Exp. 1 were analyzed as a split plot arrangement using least squares analysis of variance (PROC MIXED; SAS Inst. Inc., Cary, NC). The main effects of parity (cows vs heifers) and MEPD (high vs low) and the interaction were included in the model. Pen was also included in the model as a random effect and was nested within parity and within the parity x MEPD interaction to test the main effects and interaction, respectively. Data in Exp. 2 and 3, were analyzed as a 2 x 2 factorial arrangment using least squares analysis of variance (PROC MIXED; SAS Inst. Inc., Cary, NC). Period was treated as a random effect and the fixed effects of parity, MEPD, and the interaction were included in the model. Regression analysis was conducted using multiple regression analysis (PROC REG; SAS Inst. Inc., Cary, NC). Forage DMI was regressed on milk yield (MY), MY^2, MY^3, BW, $BW^{0.75}$, BCS, and parity class and all possible regression equations were evaluated. The best fitting model was determined by evaluating change in R^2 and the Mallows C(p) statistic (MacNeil, 1983). Data from females that were maintained through all three experiments were pooled and evaluated incorporating stage of production into the model. Data were analyzed using repeated measures analysis (PROC MIXED; SAS Inst. Inc., Cary, NC) and effects in the model included MEPD, stage of production, and the interaction. The covariance structure was modeled using the spatial power law structure due to the unequally spaced time points (stage of production) for these experiments.

Results and Discussion

Late Gestation

When forage DMI was expressed on an absolute basis (kg/d) mulitparous cows consumed 24% more forage than primiparous heifers ($P = 0.014$; Table VI). Yet, when forage DMI was expressed relative to BW (kg/100 kg BW) or metabolic BW (kg/100 kg $BW^{0.75}$), neither parity nor MEPD affected forage DMI (Table VI).

Varel and Kreikemeier (1999) compared forage intake and utilization of mature cows and 10-mo old heifers fed alfalfa and brome hay. Forage intake did not differ between cows and heifers when expressed per kg of BW, yet when expressed per unit of

$BW^{0.75}$, mature cows consumed 21% more alfalfa and 33% more brome hay than the heifers. Additionally, these researchers observed that mature cows had faster rates of ruminal NDF digestion, which may have been attributed to a smaller ruminal fluid fill that turns over more rapidly. We did not observe a difference in intake when expressed per unit of $BW^{0.75}$. One explanation may be that the first calf heifers used in this study were older and closer to their expected mature weight compared to the 10-mo old heifers used by Varel and Kreikemeier (1999).

Fiss and Wilton (1992) evaluated various breeding systems from 1980 to 1988, including straightbred Herefords and crossbred systems involving Angus, Gelbvieh, Pinzgauer, Tarentaise, Charolais, Simmental and Maine Anjou. Cows were fed a 50% corn silage and 50% haylage diet on a DM basis. The crossbred females produced 47% more milk during lactation than the straightbred Hereford cows, indicative of increased genetic potential for milk production. These authors reported total energy intake for gestation, which was considered the time from weaning through parturition. The crossbred cows consumed 18% more feed energy (Mcal of ME/d) during gestation. Their increase in feed intake during gestation may have been a function of BW as the crossbreds also were heavier at weaning compared to the straightbred Herefords. In our study, divergent selection for milk production did not influence forage DMI during late gestation.

Lactation

Milk Production. Cows selected for high and low MEPD tended to differ in milk yield during early lactation with high MEPD producing 21% more milk than low MEPD

($P = 0.097$; Table VII). This difference was not observed ($P = 0.398$) during late lactation (Table VIII). Our data concur with previous research that indicates selection for sire milk EPD successfully predicts differences in milk yield of the daughters (Diaz et al., 1992; Marston et al., 1992; Mallinckrodt et al., 1993). Additionally, cows that produce more milk tend to have faster declines in yield after achieving peak milk production (Mallinckrodt et al., 1993; Minick et al., 2001).

Multiparous cows produced 66% and 84% more milk than primiparous heifers during early ($P < 0.001$; Table VII) and late lactation ($P < 0.001$; Table VIII), respectively. These data concur with literature that indicates that beef cows do not reach peak milk production until approximately 4-5 yr of age (Hansen et al., 1982; Clutter and Nielsen, 1987; Mallinckrodt et al., 1993).

Forage Intake. During early lactation high MEPD females consumed 8% more ($P < 0.001$; Table VII) forage DM than low MEPD cows. When DMI was expressed relative to BW and $BW^{0.75}$, high MEPD consumed 7% more forage compared to low MEPD ($P = 0.027$ and $P = 0.011$, respectively). However, during late lactation (Table VIII), MEPD class did not influence forage DMI on either an absolute or BW basis. Hatfield et al. (1989) evaluated the relationship between beef cows of varying milk production potential and forage intake during early and late lactation. The cows used in their experiment were F_1 crosses produced from Hereford, Red Poll and Milking Shorthorn sires with Angus dams. These breed crosses were designed to create differences in milk production potential, but maintain similar growth and mature size. These authors observed a quadratic increase in intake expressed per unit of BW as milk production levels increased during both early and late lactation. Furthermore, Wagner et al. (1986) used cows with increasing percentage of Simmental, but maintained similar BW, to generate a range in milk production and measured forage intake using an external marker. As proportion of Simmental increased in the cows, so did milk production and forage intake expressed as a percent of BW. From these experiments and the results of our study, a positive relationship between forage DMI and milk production is apparent.

Cows consumed 19% more forage DM and OM than primiparous heifers on an absolute basis during early lactation ($P < 0.001$; Table VII) and during late lactation ($P = 0.002$; Table VIII). Yet, when expressed per unit of BW or $BW^{0.75}$, both groups consumed similar amounts of forage DM. During both stages of lactation, heifers had approximately 5% higher OMD than cows ($P = 0.046$ and $P = 0.004$ for early and late lactation, respectively). However, the observed increase in OMD did not offset the lower forage OM intake of heifers as compared with the cows. As a result cows consumed approximately 9% more digestible OM than heifers, at both stages of lactation.

Forage DMI regression equations for early and late lactation are shown in Tables IX and X, respectively. Initial regression analysis indicated minimal benefit in using $BW^{0.75}$ in our models as compared with BW, therefore BW was used for all regressions. During early lactation, BW was the best single variable for predicting forage DMI ($R^2 = 0.6768$; Table IX). However during late lactation, MY was the best single predictor ($R^2 = 0.6366$; Table X). During both stages of lactation, the best two variable equation incorporated MY and BW with $R^2 = 0.8202$ for early and $R^2 = 0.7289$ for late lactation. Anderson et al. (1983) reported prediction equations for TDN intake that included BW, weight change, and milk yield that had an R^2 of 0.77. They reported little benefit by incorporating BW^x (where x = various exponents to express metabolic BW) as compared with BW. In contrast, Hatfield et al. (1989) found $BW^{0.75}$ better correlated with DMI than BW. Previous research and the results of our analysis indicate that measures of BW and milk yield can explain significant portions of the variation in DMI during lactation in beef females.

Efficiency. Efficiency was expressed as the ratio of milk (kg/d) to TDOMI (kg/d). Cows were 54 ($P = 0.002$) and 74% ($P < 0.001$) more efficient than primiparous heifers during early and late lactation, respectively. No effect of MEPD was noted for either stage of lactation. Marshall et al. (1976) evaluated weaning data from individually fed 2-, 3-, and 4-yr old Angus, Charolais, and reciprocal cross cows and calves. Efficiency was calculated as the ratio of total TDN intake of the cow-calf unit to the weaning weight of the calf. Those females that produced more milk had heavier calves at weaning and were more efficient in converting TDN intake to kg of calf. In contrast, other researchers have demonstrated that cows that have lower genetic potential for milk production are more efficient, both biologically (Montano-Bermudez and Nielsen, 1990) and economically (van Oijen, et al., 1993).

In our study, primiparous heifers consumed similar amounts of forage compared with mature cows, when intake was expressed relative to BW. Yet, the heifers are less efficient in converting energy intake to milk production. Lalman et al. (2000) demonstrated that increasing dietary energy to thin, primiparous beef heifers increases the net energy requirements for lactation. Significant increases in weight gain were not observed except for when high energy diets (2.7 Mcal ME/kg DM) were fed. Perhaps heifers partition more dietary energy to maintenance and/or gain in addition to lactation, therefore reducing efficiency of milk production as compared with older females.

Stage of Production. Data were pooled from females that completed all three experiments (n = 15) to evaluate the effect of stage of production. All females were treated as a contemporary group in between intake trials. Weather effects could not be separated from stage of production and therefore are confounded within stage of production. All data are expressed relative to BW and $BW^{0.75}$ to eliminate the effect of parity class, since these differences were not significant when analyzed for each individual experiment. Body condition score tended to be influenced by both stage of production ($P = 0.07$; Table XI) and MEPD class ($P = 0.12$). Body condition was greatest during late gestation and tended to decrease as lactation progressed. Females selected for low MEPD tended to have 0.27 units greater BCS, averaged across all three stages of production. Minick et al., (2001) reported a similar trend in that females selected for higher milk production had lower BCS throughout lactation, regardless of breed. Regardless of how intake was expressed (BW or $BW^{0.75}$), high MEPD cows consumed 6% more DM than low MEPD, when averaged across all three stages of production ($0.1 < P < 0.06$). Stage of production affected DMI ($P < 0.0001$). Females consumed 31 and 18% more forage DM during early and late lactation as compared with late gestation. As females progressed from early to late lactation, DMI dropped by approximately 17%. Vanzant et al. (1991) reported increases in total and forage OM intake of primiparous heifers at d 26 of lactation of 9 and 13% over late gestation. Other researchers have demonstrated that lactating cows during early lactation consume 11 to 36% more feed than cows during late gestation (Ovenell et al., 1991; Stanley et al., 1993; Marston and Lusby, 1995).

A beef cow's nutritional requirements peak during early lactation (NRC, 1996). During lactation, the maintenance requirements of cows are estimated to be about 20% higher than nonlactating females (NRC, 1996). Ferrell and Jenkins (1985) suggested that maintenance energy requirements are positively associated with genetic potential for production. Furthermore, Montano-Bermudez et al. (1990) determined that crossbred cows with high and moderate genetic potential for milk production required 12% more energy per unit of metabolic weight than cows with low genetic potential for milk production to maintain body weight. Research has demonstrated that ion pumping across biological membranes is a large contributor to the energy expenditure of animals (Milligan and McBride, 1985). In dairy cattle, Na^+, K^+-ATPase-dependent respiration was 31% greater for intestinal epithelium from lactating cows as compared with dry cows (McBride and Milligan, 1984). Thus, increases in forage intake during lactation, particularly early lactation, are likely responses to increased maintenance in addition to increased productive energy requirements of the beef cow.

Implications

Within a breed, selecting females for increased milk production increases forage intake during early lactation, when nutrient requirements are highest for the beef cow. When intake is expressed relative to body weight, intake is similar between multiparous cows and primiparous heifers. However, multiparous cows were more efficient in converting energy intake to milk production, regardless of genetic merit for milk production. Body weight and actual daily milk yield explained a large proportion of the variation in dry matter intake. These factors should be considered in nutritional models used to estimate nutrient requirements or diet adequacy. However, more research is needed to clarify the relationships between body condition and milk yield on forage intake in the beef cow.

Table IV. Chemical composition of hay and cottonseed meal for all experiments (DM basis unless specified)

	Hay	Cottonseed Meal
OM	87.9	85.1
CP	5.3	44.6
Degradable intake protein, % CP	45.0	57.0[a]
NDF, ash-free	75.9	33.3
ADF, ash-free	47.9	24.9
Acid detergent insoluble ash	3.7	0.5
Lignin, % DM	6.4	--
Neutral detergent insoluble CP	2.0	--
Acid detergent insoluble CP	0.9	--
Crude fat	2.0	3.2[a]
TDN	52	75[a]

[a] Values from Nutrient Requirements for Beef Cattle (NRC, 1996)

Table V. Descriptive variables for females used for Exp. 1 through 3.

	High MEPD[a]		Low MEPD	
Variable	Cows	Heifers	Cows	Heifers
	--Late Gestation (Exp.1)--			
n	6	5	5	4
Avg. sire milk EPD[b]	+4.3	+4.9	-6.1	-5.0
Age, mo	46	23	61	22
Cottonseed meal, kg DM/d	1.6	1.4	1.6	1.4
Wt, kg	578	502	599	468
BCS[c]	4.4	4.8	4.9	4.8
	--Early Lactation (Exp. 2)--			
n	6	6	6	6
Avg. sire milk EPD	+4.3	+4.8	-5.7	-5.7
Age, mo	50	27	71	22
Cottonseed meal, kg DM/d	2.0	2.0	2.0	1.9
Wt, kg	549	459	557	434
BCS	4.3	4.1	4.6	4.2
	--Late Lactation (Exp. 3)--			
n	6	6	6	6
Avg. sire milk EPD	+4.3	+4.8	-5.7	-5.7
Age, mo	53	30	74	29
Cottonseed meal, kg DM/d	1.9	2.0	1.9	1.8
Wt, kg	540	467	559	454
BCS	4.3	4.3	4.5	4.2

[a] MEPD = predicted genetic merit for milk production

[b] Milk EPD is expressed as kg weaning weight in offspring due to maternal milk

[c] BCS = body condition score, scale 1-9

Table VI. Least squares means for forage intake and digestibility of cows during late gestation (Exp. 1)

Variable	High MEPD[a]		Low MEPD		SEM	P[b]		
	Cows	Heifers	Cows	Heifers		Parity	MEPD	X[c]
			--Intake--					
Forage DMI, kg/d	10.1	8.1	10.3	8.4	0.70	0.014	0.726	0.879
Forage DMI, kg/100 kg BW	1.76	1.59	1.71	1.73	0.13	0.511	0.729	0.426
Forage DMI, kg/100 kg $BW^{0.75}$	8.6	7.6	8.5	8.1	0.60	0.198	0.722	0.500
Forage OM intake, kg/d	8.9	7.1	9.0	7.3	0.62	0.014	0.726	0.879
Forage OM intake, kg/100 kg BW	1.56	1.40	1.50	1.52	0.12	0.511	0.729	0.426
Forage OM intake, kg/100 kg $BW^{0.75}$	7.6	6.6	7.4	7.1	0.52	0.198	0.722	0.500
NDF intake, kg/d	8.1	6.6	8.2	6.8	0.54	0.019	0.732	0.916
NDF intake, kg/100 kg BW	1.40	1.31	1.36	1.41	0.10	0.774	0.727	0.427
Total digestible OM intake (TDOMI), kg/d	5.5	4.8	5.8	4.7	0.32	0.016	0.748	0.510
TDOMI, kg/100 kg BW	0.96	0.96	0.97	0.98	0.06	0.940	0.760	0.893
TDOMI, kg/100 kg $BW^{0.75}$	2.60	2.51	2.65	2.54	0.15	0.453	0.749	0.944
Total energy intake, Mcal NEm/kg BW	1.83	1.88	1.90	1.86	0.17	0.971	0.805	0.633
Total energy intake, Mcal NEm/kg $BW^{0.75}$	9.0	8.9	9.4	8.7	0.50	0.417	0.787	0.469
		--Apparent Digestibility--						
Total diet OM digestibility, %	56.0	57.9	58.0	55.4	0.93	0.692	0.733	0.020
CP digestibility, %	63.7	70.1	64.2	65.4	3.3	0.211	0.456	0.381
NDF digestibility, %	58.0	60.5	60.3	55.7	0.97	0.282	0.118	0.002

[a] MEPD = predicted genetic merit for milk production

[b] *P*-value for differences due to effects in the model

[c] X = interaction of parity and MEPD

Table VII. Least squares means for milk production, forage intake, and digestibility of cows during early lactation (Exp. 2)

	High MEPD[a]		Low MEPD			*P*[b]		
Variable	Cows	Heifers	Cows	Heifers	SEM	Parity	MEPD	X[c]
--Milk Production--								
Milk yield, kg/d	11.3	7.8	10.5	5.3	2.13	<0.001	0.097	0.392
Milk energy, Mcal NEm/kg BW	1.56	1.29	1.42	0.92	0.15	0.015	0.094	0.462
Milk energy, Mcal NEm/kg $BW^{0.75}$	7.5	6.0	6.9	4.2	0.71	0.005	0.091	0.437
--Intake--								
Forage DMI, kg/d	13.8	12.0	13.2	10.6	0.36	<0.001	0.010	0.293
Forage DMI, kg/100 kg BW	2.53	2.63	2.36	2.45	0.07	0.202	0.027	0.880
Forage DMI, kg/100 kg $BW^{0.75}$	12.2	12.2	11.5	11.2	0.31	0.576	0.011	0.659
Forage OM intake, kg/d	12.1	10.6	11.6	9.3	0.32	<0.001	0.010	0.293
Forage OM intake, kg/100 kg BW	2.22	2.31	2.08	2.15	0.06	0.202	0.027	0.890
Forage OM intake, kg/100 kg $BW^{0.75}$	10.7	10.7	10.1	9.8	0.27	0.576	0.011	0.659
NDF intake, kg/d	11.2	9.9	10.7	8.8	0.28	<0.001	0.012	0.281
NDF intake, kg/100 kg BW	2.05	2.16	1.92	2.02	0.05	0.070	0.028	0.896
Total digestible OM intake (TDOMI), kg/d	7.2	7.0	7.1	6.1	0.24	0.015	0.059	0.115
TDOMI, kg/100 kg BW	1.31	1.52	1.28	1.40	0.05	0.002	0.114	0.352
TDOMI, kg/100 kg $BW^{0.75}$	3.52	3.90	3.44	3.55	0.11	0.043	0.074	0.233
Total energy intake, Mcal NEm/kg BW	2.32	2.91	2.34	2.63	0.13	0.004	0.349	0.280
Total energy intake, Mcal NEm/kg $BW^{0.75}$	11.2	13.5	11.4	12.0	0.61	0.029	0.301	0.221
Efficiency as kg milk/kg TDOMI	1.58	1.13	1.48	0.86	0.14	0.002	0.218	0.587
--Apparent Digestibility--								
Total diet OM digestibility, %	51.5	55.8	53.1	54.7	1.37	0.046	0.855	0.334
CP digestibility, %	61.0	63.9	62.8	63.1	1.32	0.234	0.700	0.350
NDF digestibility, %	50.2	54.3	52.2	52.6	1.44	0.135	0.951	0.217

[a] MEPD = predicted genetic merit for milk production;

[b] *P*-value for differences due to effects in the model;

[c] X = interaction of parity and MEPD

Table VIII. Least squares means for milk production, forage intake, and digestibility of cows during late lactation (Exp. 3)

	High MEPD[a]		Low MEPD			P[b]		
Variable	Cows	Heifers	Cows	Heifers	SEM	Parity	MEPD	X[c]
	--Milk Production--							
Milk yield, kg/d	8.7	5.4	8.8	4.1	0.94	<0.001	0.398	0.335
Milk energy, Mcal NEm/kg BW	1.23	0.86	1.17	0.69	0.13	<0.001	0.363	0.551
Milk energy, Mcal NEm/kg BW$^{0.75}$	5.9	4.0	5.8	3.2	0.64	<0.001	0.363	0.491
	--Intake--							
Forage DMI, kg/d	11.7	10.8	12.0	9.4	0.47	0.002	0.225	0.085
Forage DMI, kg/100 kg BW	2.18	2.32	2.14	2.08	0.09	0.691	0.168	0.300
Forage DMI, kg/100 kg BW$^{0.75}$	10.5	10.8	10.4	9.6	0.42	0.536	0.151	0.197
Forage OM intake, kg/d	10.3	9.5	10.5	8.3	0.41	0.002	0.225	0.085
Forage OM intake, kg/100 kg BW	1.91	2.04	1.88	1.83	0.08	0.691	0.168	0.300
Forage OM intake, kg/100 kg BW$^{0.75}$	9.2	9.5	9.1	8.4	0.37	0.536	0.151	0.197
NDF intake, kg/d	9.6	8.9	9.8	7.8	0.37	0.002	0.249	0.087
NDF intake, kg/100 kg BW	1.78	1.91	1.76	1.73	0.07	0.537	0.173	0.309
Total digestible OM intake (TDOMI), kg/d	6.8	6.6	6.9	6.1	0.34	0.084	0.466	0.323
TDOMI, kg/100 kg BW	1.27	1.41	1.24	1.34	0.07	0.023	0.367	0.711
TDOMI, kg/100 kg BW$^{0.75}$	3.37	3.63	3.33	3.43	0.18	0.182	0.350	0.555
Total energy intake, Mcal NEm/kg BW	2.43	2.80	2.37	2.75	0.22	0.005	0.625	0.933
Total energy intake, Mcal NEm/kg BW$^{0.75}$	11.7	13.0	11.5	12.7	1.03	0.038	0.608	0.934
Efficiency as kg milk/kg TDOMI	1.30	0.82	1.29	0.67	0.17	<0.001	0.460	0.556
	--Apparent Digestibility--							
Total diet OM digestibility, %	56.3	58.4	55.8	60.8	2.45	0.004	0.382	0.190
CP digestibility, %	66.5	68.3	66.6	71.3	2.90	0.013	0.209	0.217
NDF digestibility, %	54.9	53.6	47.7	56.0	6.33	0.259	0.437	0.123

[a] MEPD = predicted genetic merit for milk production;

[b] *P*-value for differences due to effects in the model;

[c] X = interaction of parity and MEPD

Table IX. Sources of variation for forage dry matter intake (kg/d) of Brangus females during early lactation

Intercept	Milk[a]	Milk^2	BW[b]	BCS[c]	Parity[d]	R^2	C(p)
--Best Single Variable--							
2.864	--	--	0.0191*	--	--	0.6768	12.40
--Best Two Variable--							
0.821	0.7769*	-0.0392*	0.0164*	--	--	0.8202	2.02
--Three Variable--							
4.179*	0.1421*	--	0.0139*	--	0.0582	0.7347	10.59
4.476*	--	--	0.0167*	-0.1461	0.4299	0.6852	15.55
9.297*	0.1812*	--	--	0.2051	1.306*	0.6429	19.80
0.6564	0.7836*	-0.0396*	0.0162*	0.0529	--	0.8204	4.00
0.8163	0.7770*	-0.0081*	0.0164*	--	-0.0016	0.8202	4.02
6.490*	0.7371*	-0.0070*	--	0.4043	1.400	0.7062	15.45
4.4753*	0.1425*	--	0.0146*	-0.1389	0.0391	0.7363	12.43
--Four Variable--							
0.6696	0.7834*	-0.0082*	0.0162*	0.0532	0.0052	0.8204	6.00

[a] Milk yield expressed as kg/d and both linear and quadratic expressions are considered a single variable

[b] Body weight expressed in kg

[c] Body condition score scale 1 to 9

[d] Parity class where multiparous = 1 and primiparous = 0

[*] Significant in model at $P < 0.1$ level

Table X. Sources of variation for forage dry matter intake (kg/d) of Brangus females during late lactation

Intercept	Milk[a]	Milk^2	BW[b]	BCS[c]	Parity[d]	R^2	C(p)
--Best Single Variable--							
4.478*	1.612*	-0.0836*	--	--	--	0.6366	21.26
--Best Two Variable--							
1.234	1.353*	-0.0733*	0.0088*	--	--	0.7289	12.29
--Three Variable--							
2.111	0.3296*	--	0.0140*	--	-0.8550	0.6160	25.48
3.770	--	--	0.0119*	0.2096	0.6229	0.4721	41.02
1.188	0.4781*	--	--	1.576*	-0.4397	0.6270	24.29
-0.494	1.332*	-0.0677*	0.0053	0.7762	--	0.7613	11.78
-2.196	1.660*	-0.0844*	0.0141*	--	-1.404*	0.7862	9.09
-1.917	1.660*	-0.0762*	--	1.410*	-0.8349	0.7640	11.49
-1.326	0.4502*	--	0.0097*	1.146*	-1.124	0.6862	19.89
--Four Variable--							
-4.759*	1.675*	-0.0791*	0.0105*	0.9460*	-1.591*	0.8333	6.00

[a] Milk yield expressed as kg/d and both linear and quadratic expressions are considered a single variable

[b] Body weight expressed in kg

[c] Body condition score scale 1 to 9

[d] Parity class where multiparous = 1 and primiparous = 0

*Significant in model at $P < 0.1$ level

Table XI. Least squares means for body condition, milk yield, and intake of cows over three stages of production.

Variable	High MEPD [a]			Low MEPD			SEM	P [b]		
	-50 d [c]	62 d	163 d	-50 d	62 d	163 d		SOP [d]	MEPD	X [e]
n	9	9	9	6	6	6	--	--	--	--
BCS [f]	4.5	4.3	4.3	4.8	4.7	4.4	0.16	0.065	0.118	0.464
Milk Yield, kg/100 kg BW	--	1.98	1.50	--	1.60	1.29	0.20	0.002	0.243	0.450
Milk Yield, kg/100 kg $BW^{0.75}$	--	9.4	7.2	--	7.7	6.2	0.98	0.002	0.267	0.452
Total DMI, kg/100 kg BW	1.97	2.98	2.62	1.94	2.81	2.38	0.08	<0.0001	0.088	0.327
Total DMI, kg/100 kg $BW^{0.75}$	9.5	14.2	12.4	9.4	13.4	11.4	0.34	<0.0001	0.056	0.271
Forage DMI, kg/100 kg BW	1.76	2.60	2.24	1.73	2.43	2.01	0.08	<0.0001	0.0682	0.329
Forage DMI, kg/100 kg $BW^{0.75}$	8.5	12.4	10.6	8.4	11.6	9.6	0.34	<0.0001	0.058	0.289

[a] MEPD = predicted genetic merit for milk production
[b] *P*-value for differences due to effects in the model
[c] Average days relative to parturition (parturition = d 0)
[d] SOP = stage of production
[e] X = interaction of SOP and MEPD class
[f] BCS = body condition score, scale 1-9

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VITA 2

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