

*A Review of Metabolic and Endocrinological Systems Governing Cow Body Weight
and Body Condition in Lactating Beef Cattle*

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Introduction:

According to the Alberta Cattle Commission (2000), there are approximately 4.75 million beef cows in Canada of which 1.9 million are in Alberta. These animals are maintained under a variety of management and environmental conditions and wean an annual calf crop estimated at 80 % (AAFRD, 1998). Data reported in the last beef cow/calf audit (AAFRD, 1998); suggest first cycle conception was less than 48%. The main contributing factor to this statistic may relate to the fact that less than 55% of replacement heifers and 40% of thin cows are fed separately from the mature cow herd. Complicating matters further, only 25% of Alberta beef producers condition score their cows (AAFRD, 1998).

If Canadian producers could achieve a 90% calf crop, they could market an additional 475 thousand calves. A 10% increase in the production efficiency to the Alberta and Canadian beef industry would represent a huge economic improvement. There are a number of reasons for the overall 20% shortfall in the total potential calf crop. The first 10% loss can be related to factors like, calving and post-calving calf mortality. However by far the greatest factor for the additional 10% are the poor management practices that contribute to poor conception rates within the cowherd (Weder, 2000).

Postpartum nutrition with respect to rebreeding has long been recognized as an important factor in influencing cow conception rates. The majority of the reproductive shortfalls in the beef industry are attributed to under-nutrition due to feed shortages, poor-quality feeds and (or) management. Many of the findings and reviews of under-nutrition affects on reproduction point to an extension from calving to the first postpartum estrus,

which is commonly referred to as the postpartum interval (PPI). The economic implications to beef producers of an increased PPI on the following years calf crop can vary. First, there will be reduced weaning weights if the weaning date is held consistent with the previous year. Secondly the producer can experience increased supplemental costs and increased cow open rates due to an increase in the length of the calving season and the inability for certain cows to breed back within the set breeding season. Cow body weight (BW) and cow body condition (BC) have long been recognized as having enormous effects on the length of PPI. Understanding how these two factors influence conception rates is key, if we are to make improvements within the Canadian beef industry.

Reproductive Controls:

Cow Body Weight & Body Condition:

Relationships between energy intake and BC in terms of reproductive success have been documented for centuries. These observations have stimulated countless research trials studying the relationship between nutrient intake and body fatness and the subsequent effects on reproductive variables (Bellows et al., 1974; Short and Adams, 1988). Dietary restriction during late pregnancy that result in BW and BC reductions, increase the time interval needed for cows and first-calf heifers to return to first estrus (Whitman, 1975; Deziuk and Bellows, 1983). Similar results have been reported when dietary restrictions occur during the postpartum period (Richards et al., 1986). Regression equations relating energy status, as expressed by BW change, against reproductive performance were developed by Dunn and Kaltenbach (1980) from data published by a number of researchers. They also developed regression equations by taking the average

length of the PPI and comparing it against the average prepartum BW change. When no prepartum weight losses occurred, 91% of multiparous and 64% of primiparous cows would be predicted to be in estrus by 60 days postpartum.

The concept of a target BW and or BC at the time of calving was first proposed by Lamond (1970). Whitman (1975) found that cows calving at body condition scores (BCS) of 6 to 8 (range of 1 to 9) were capable of returning to estrus within 60 days of parturition regardless of pre- or postpartum change in BW. Reviewers have concluded that prepartum nutrition is more important than postpartum nutrition in determining the length of the postpartum interval (Dunn and Kaltenbach, 1980; Deziuk and Bellows, 1983). These authors indicate that this minimum BC will ensure that body stores of nutrients are adequate for postpartum reproductive performance. In fact, recent findings by Lalman et al., (2000) found that post-calving energy supplementation only served to enhance milk production in primiparous heifers and that precalving BC had a greater influence on PPI than post calving energy levels.

Weaning has also been the focus of many research trials as a management tool to manipulate BC and BW. In Australia research on weaning strategies for emergency drought management showed that there are significant advantages in improving BC, reducing lactation stress and increasing reproductive rates (Schlink et al. 1988; McSweeney et al. 1993a, 1993b). In fact in more extensive studies, “Early Weaning” has dramatically reduced dry season BW and BC loss and increased pregnancy rates (Schlink et al. 1988, 1994; Sullivan et al. 1992). Bellows and Short (1974) found that early weaning primiparous heifers in poor BC significantly ($P < .01$) improved BC and shortened the PPI compared to normal weaned heifers (205 days).

Early weaning has also shown significant advantages as a management tool for mature cows. Even under pasture, situations there will come times when the nutrients supplied will be insufficient to maintain good milk production as well as sustain adequate BW and BC of the dam. When this scenario exists, early weaning may yield considerable advantages as a cow management tool (Richardson et al. 1978; Lusby et al. 1981). In fact if the cost of lactation in a 600 kg cow, producing 10 kg milk / day is looked at, it represents a 33% increase over maintenance in energy requirements and a 40% increase in protein requirements (NRC, 1996).

So why does body condition have such a profound effect on reproductive success? One theory that that has remained popular was that there is a “set point” of body fat or body composition, above or below which the adipose mass signals the central nervous system, that the body was either ready or not for cycling and pregnancy (Frisch, 1980). Research has demonstrated that there is a relationship between body fat and reproductive efficiency, however, there were many situations in which body fat content was negative, yet cycling was still positive (Dunn and Kaltenbach, 1980; Deziuk and Bellows, 1983). There was also even a theory that estrogen release from adipose tissue was the controlling factor behind reproduction (Frisch, 1980; Wade and Schneider, 1992).

Most research agrees though that ovulation is controlled by the release of LH, which is in turn regulated by GnRH, which are themselves related to the composition of the body (Wade and Schneider 1992; Rozeboom et al., 1993; Villa-Godoy et al., 1988). In Australia researchers found that a low BC at calving was associated with prolonged post-partum anoestrous intervals in suckled cows (Jolly et al., 1993). So is reproductive

cyclicality related to body condition or is it rather related to some other biochemical mechanism?

Blood Metabolites:

The measurement of blood metabolites may also be another useful indicator of nutritional status and potential rebreeding performance. The relationship between increased growth hormone (GH) and decreased insulin during early lactation suggests a role of metabolic hormones in promoting mobilization of adipose tissue stores to fulfill energy needs (Randel, 1990). Increasingly, more focus has been given to free glucose within the animal as to being a main precursor to reproductive success (McNamara, 1995; Short and Adams, 1988). It appears that serum GnRH and LH concentrations are related to glucose availability, which may not be related at all to BC. Wade and Schneider (1992), showed that there was a large release in GnRH and LH following an increase in energy in the diet of restricted hogs. The evidence now demonstrates that the release of GnRH and LH, and thus ovulatory activity, is affected by glucose supply. This would seem logical, since glucose is the only energy source utilized by the neural system, and since the neural-endocrine system is intimately involved in the control of reproduction and hormone secretion, blood glucose concentration would be the specific mediator for the effects of energy intake on reproduction (Short and Adams, 1988).

Although blood plasma glucose levels have long been thought of as having direct implications on the nutritional status of beef cows research evidence has been mixed. Selk et al., (1985) found that plasma glucose levels were correlated ($r^2 = .51$) with conception rates during the 1st year of a 2 year trial on PPI in first calf heifers. However in the 2nd year of the trial he found no correlations. Russel and Wright, (1983) measured

plasma glucose, 3-hydroxybutyrate and nonesterified fatty acids at various stages of the reproductive cycles of cows with different nutrient intakes. They found that glucose was not useful in evaluating energy status, 3-hydroxybutyrate was useful in pregnant cows, and nonesterified fats were useful in both pregnant and non-pregnant cows. McCaughey, (1985) studied intravenous infusion of glucose in postpartum beef cows. He found glucose infusion increased the levels of insulin ($P < .10$) and decreased the levels of lipolysis in early postpartum beef cows. Yet, glucose by itself did not improve the postpartum rebreeding of the cows in the trial. Garmendia et al., (1986) suggested that in beef cows insulin increases and lipolysis decreases in response to glucose infusion in an attempt to maintain relative constant glucose concentrations. This would imply that glucose would not be the limiting factor in determining postpartum rebreeding, suggesting that should there be a depression in the blood glucose levels the opposite would occur, and we would see an increase in lipolysis. This tendency of the animal to maintain relatively constant glucose concentrations in the blood may explain partially the lack of a consistent relationship between circulating glucose concentrations and reproductive performance. Circulating glucose concentrations may regulate reproduction at a threshold level with no advantage above the threshold but severe consequences like increases in PPI and anoestrous in beef cows, should levels fall below it. More importantly than glucose - gluconeogenesis may better explain the mechanism by which nutrition alters reproductive performance in cattle (Randel, 1990). In this context, glucose levels will be controlled by the sympathetic nervous system (SNS), which will be controlled by digestive absorption, gluconeogenesis, mammary gland requirements, and BC. Thus it may be the pattern of intake of specific nutrients in early lactation, and not

the total energy intake, which relates most closely to the reproductive status in domestic livestock (Wade and Schneider, 1992). Leers-Sucheta et al. (1994), found high rates of glucose absorption caused greater responsiveness of LH release to infusions of GnRH in lactating beef cattle.

Even though, free glucose has lately received more attention as to being a main precursor to reproductive success the level of BC at the time of parturition is still vitally important. First BC is an indicator of energy reserves and recent nutritional and physiological history; it allows us the flexibility to make nutritional management decisions. The second and even more importantly relates to the metabolic biology of the body. Body condition regulates glucose flux in the adipose tissue and helps to control the mixture of metabolic fuels available for the rest of the body. In this manner, BC is essential to ensure reproductive success.

However, the physiological and biological state of lactation does not fully explain all the differences in the ability for a cow to gain BW and BC. To clearly understand their roles we must look at and understand how nutrients are partitioned within lactation and how the system is regulated.

Nutrient Partitioning:

Ruminants have a unique niche in animal agriculture because they have the ability to convert low-quality roughages into useful products – meat and milk. Secondly, excess nutrients can be stored during periods of excess and retrieved later during periods of poor availability to maintain production. However during periods of limited nutrient availability, production may decrease due to insufficient energy reserves.

Regulation of nutrient partitioning involves two types of controls - homeostasis and homeorhesis (Bauman and Currie, 1980; Bauman et al., 1989) Homeostasis involves the operation of multiple compensatory mechanisms functioning to maintain physiological equilibrium. Homeostasis was originally defined as "the condition of relative uniformity which results from the adjustments of living things to changes in their environment"(Bauman and Currie, 1980). Thus, homeostatic controls operate on a minute-by-minute basis so that, despite acute challenges from the external environment, the internal environment remains unchanged. There are many well-established examples of homeostasis. One example for nutrient partitioning deals with the absorptive and post-absorptive periods following the consumption of a meal. In the short-term, homeostatic controls (primarily insulin and glucagon) maintain a relatively constant supply of nutrients to peripheral body tissues by promoting the storage of nutrients following a meal and the mobilization of these nutrients during the post-absorptive period.

The second type of control is called homeorhesis and was defined as the "orchestrated changes for priorities of a physiological state" (Bauman and Currie). Homeorhetic control involves the coordination of metabolism, resulting in the directed partitioning of nutrient utilization for the processes of growth, pregnancy and lactation (Bauman and Currie, 1980; Bauman et al., 1989). Thus, homeorhetic mechanisms provide chronic regulation, while homeostatic controls operate on an acute minute-by-minute basis to maintain a steady state and, in life-threatening situations, may even override the long-term regulation to preserve vital functions.

The first priority in any animal is to maintain its basal metabolism. Therefore, all energy stored or ingested will first be directed at maintaining basal metabolism. From

there on all energy needed for other activities is allocated according to importance. The approximate order of priority for partitioning of nutrients is as follows. 1) Basal metabolism, 2) Activity, 3) Growth, 4) Basic energy reserves, 5) Pregnancy, 6) Lactation, 8) Reproduction 9) Excess reserves (Example: Figure 1; Short et al., 1990).

Energy reserves (glycogen and fat) in ruminants can constitute as much as 50% of the animal's maximum possible weight (Short et al., 1990). In fact, the inadequacies of BW in describing the physiological status of beef animals is why we depend on BC scoring systems (Bellows et al., 1982). The effect of nutrition on postpartum reproduction depends somewhat on whether nutritional inadequacies exist before or after calving. Obviously if there has been an energy deficit during lactation, weaning will allow energy to be moved to reserves – since it is down in priority from lactation.

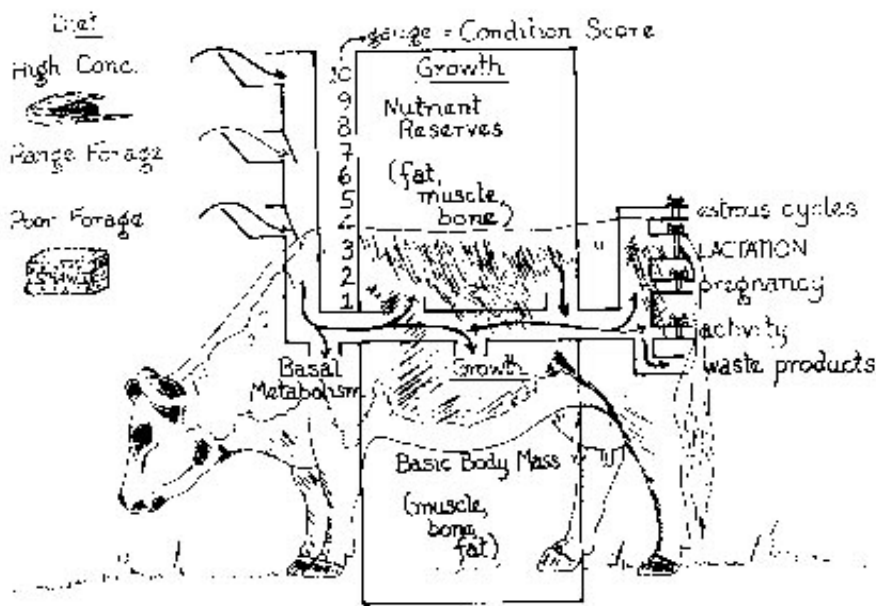


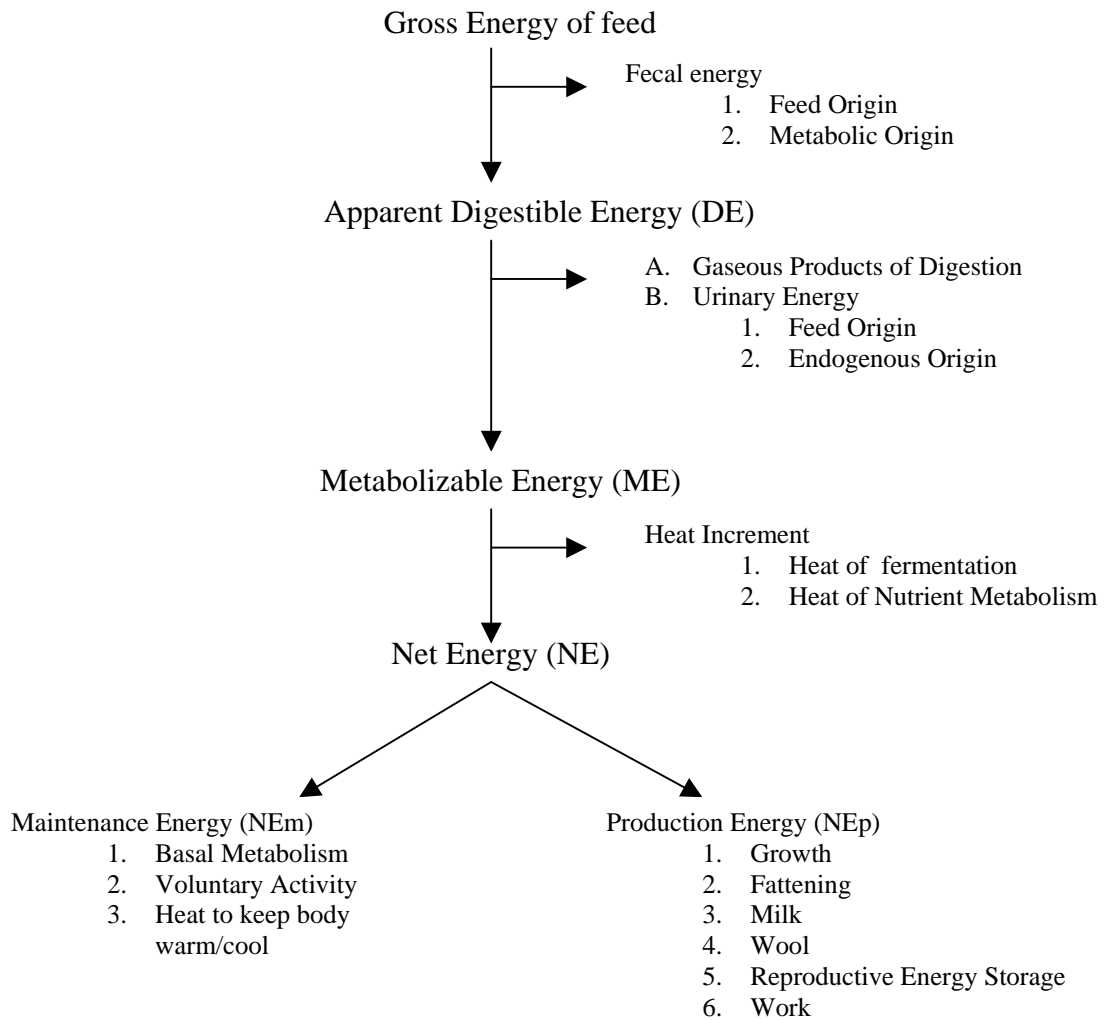
Figure 1. Nutrient Partitioning in Bovines; Short et al., 1990.

Nutrient Partitioning - Maintenance:

There are many definitions of maintenance; biologically it is the process of maintaining the weight / body composition of a non-producing mature animal without

changing its energy status. Measuring the amount of digestible energy (DE) necessary for maintaining the same equilibrium in a nursing or pregnant animal is level is more difficult. The difficulty arises due to the problem of determining the energy directed toward maintenance versus production. This concept can be better understood if we review Figure 2. – The conventional scheme of energy utilization in Ruminants.

Figure 2. The conventional scheme of energy utilization in Ruminants. NRC 1996



The main problem in determining maintenance levels in pregnant and lactating animals lies in understanding the changes in body tissue metabolism brought on by these

biological states. These biological states often increase the size and energy needs of certain organs like the liver and digestive system. Therefore, if the biological definition of a non-pregnant/non-lactating animal is used to determine the maintenance energy needs for a pregnant/lactating animal, it would severely underestimate its energy needs.

For most tissues, blood flow per unit mass parallels energy expenditure per unit, of weight, (ie., ratios of 5 and 6 to 1 for nervous tissue; Baldwin et al., 1985). The close match between energy expenditure and blood flow reflects very precise, local regulation of blood flow according to need. This may be explained, by an increased need for oxygen – which indicates higher levels of energy metabolism and an increased demand for more energy metabolites (Baldwin et al., 1985). For example, energy expenditure per unit mass of the liver is 25 times greater than for muscle. This implies that there could be a relatively small change in tissue weights but greater basal energy expenditure that occurs as a ruminant moves from growth to pregnancy and then to lactation. As an example, a 50% increase in liver weight compensated by a similar weight decrease in muscle could cause a 10% increase in basal energy metabolism. In fact some research has indicated that just the change in organ weights brought on by pregnancy alone, could cause an overall increase in the animals energy needs by 9.5% (Baldwin et al., 1985).

TABLE 1. Effect of lactation on organ weights and estimated energy expenditures in lactating cows; Baldwin et al., 1985.

Organ	<u>Non-Lactating</u>		<u>Lactating</u>	
	(% BW)	(Mcal/d)	(% BW)	(Mcal/d)
Digestive Tract	3.8	1.1	4.9	1.4
Heart	0.35	1.5	0.45	1.8
Liver	1.3	3.4	1.7	4.2
Adipose	7.3	0.75	6.0	0.61
Carcass	58.0	3.9	54.0	3.6
Total	71.0	10.6	67.0	11.6

The change in organ weights may provide a partial explanation of the energy kinetics left unanswered by conventional scientific energy models (Metabolizable and California Energy Systems). As a result of weaning the improvements seen in cow BC, may simply be related to changes in organ weights, as the cow switches from lactation to non-lactation. The underlying assumption would then be that after weaning, nutrients could be redirected, due to a decrease in organ nutrient demand.

If the animal prior to weaning were fed at a level that maintained its body weight and body condition, weaning would simply change the energy balance so that the animal would now have a net energy surplus. Herein lies the problem of determining the maintenance expenditure of pregnant lactating animals - how is energy directed towards maintenance versus production? In fact the ability to partition energy between organs may partially explain why some cows may have lower maintenance requirements and yet still support lactation without compromising body condition (Baldwin et al., 1985).

Similarly, as metabolizable energy availability increases, more energy can be diverted into lipogenesis. The uncertainty regarding the distribution of energy between milk and body tissue is referred to as the "Partitioning Problem" (Moe and Tyrrell, 1975). The extent of body fattening is a function of both the genetic potential of the animal and the total energy within the diet. In addition the nature of the diet and or the type of diet can strongly influence the energy partition between milk production and body fat accretion (Moe and Tyrrell, 1975). As diets decrease in their metabolizable energy content the ability for animals to convert fat becomes compromised and may in fact call for a mobilization of fat reserves to sustain milk production (Randel, 1990). This is often seen as the case in the Canadian and Western United States cow/calf production systems,

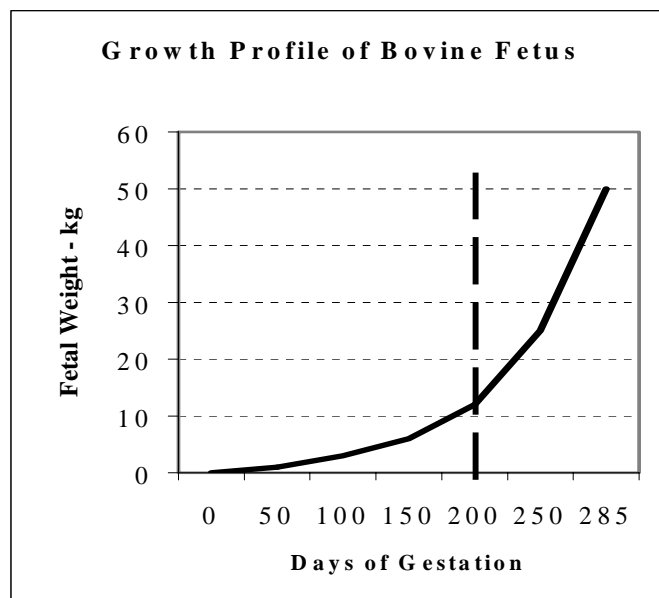
where there is a rapid decrease in forage quality during the later stages of the growing season while the cow is still trying to lactate (Weder, 2000).

Nutrient Partitioning - Pregnancy:

Pregnancy imposes a great nutritional strain on an animal and can be as much as 75% greater for a pregnant animal as opposed to a non-pregnant animal of the same weight (Bauman and Currie, 1980). Thus in keeping with the concept of partitioning a great deal of homeorhesis must occur in order to direct the nutrients needed to sustain pregnancy. This is more clearly demonstrated by looking at the growth curve of the bovine fetus during pregnancy.

Figure 3, shows that the fetus achieved only 40% of its birth weight during the first 7 months (broken Line) of gestation. The bulk of the weight gain falls during the last two months and clearly shows the need for substantial energy partitioning in order to maintain a healthy pregnancy. The nutrients required to do so can equalate to about 4.5-kg milk/day (Bauman and Currie, 1980).

Figure 3. Growth profile of bovine fetus during pregnancy; Bauman and Currie, 1980.



Not shown on the table is the growth in the mammary tissue. The bulk of mammary tissue development also happens to coincide at precisely the same time as maximal fetal growth. This development only adds more to the metabolic burden of pregnancy.

One thing that differentiates the bovine fetus from those of many other species is that the bovine cannot merely be classified as a “passenger” (Bauman and Currie, 1980). The ruminant fetus is more vulnerable than that of many species to swings in maternal nutrition, and severe retardation can result from chronic malnutrition. Thus, nutrient partitioning during the later stages of gestation by homeorhetic signals is of vital importance. Typically, 50-70% of the glucose required for fetal growth in the bovine is supplied by oxidative metabolism, however within 2 days that level can be cut in half should there be maternal starvation.

Nutrient partitioning - lactation:

Following parturition, the partitioning of nutrients during lactation takes on a much more complicated role. There are many systems involved in the initiation, regulation and maintenance of this biological function, however understanding the regulatory mechanisms is important to understand how they effect body condition and subsequent reproductive performance.

Somatotropin:

One of the most important hormones that alters nutrient partitioning during lactation is somatotropin. Somatotropin (ST) is a homeorhetic control that shifts the partitioning of nutrients in an animal so that lactation and milk synthesis can be

sustained. Lactation involves the metabolic coordination of various body organs and tissues and includes the metabolism of all nutrient classes - carbohydrates, lipids, proteins and minerals (Monsanto, 1995). The adaptations of ST can be broadly divided into two segments – first the direct effects on the mammary tissues and secondly the indirect effects on the system mediated by the insulin-like growth factor (IGF-1).

The direct actions of ST appear to be primarily concerned with the coordination of metabolic processes primarily within the adipose tissue. Adipose tissue has two main functions, lipogenesis and lipolysis. Specifically ST alters adipose tissue response to homeostatic signals affecting lipid synthesis and lipid mobilization. Somatotropin reduces the ability of insulin to stimulate lipogenesis and enhances the ability to stimulate lipolysis. Somatotropin does not alter the attachment of insulin to its binding site but rather inhibits or prohibits its synthesis. The inhibitory effect of ST on lipogenesis works by blocking protein synthesis within the adipose tissue. The mechanism is in fact consistent with the existence of secondary messengers, which arise from the somatotropin receptor binding sites, which biologically inhibit the response to insulin. The secondary messenger will then enter the adipocyte and inhibit the insulin protease necessary for the normal action of insulin (McNamara, 1995). This theory has been tested and it was found that the adipose tissue from pregnant and lactating cows possess a specific insulin protease which shares the same characteristics as insulin protease from other sources (Marinchenko et al., 1992). Blocking the release of prolactin during early lactation not only stopped the synthesis of milk in dairy cattle but also resulted in an increase in lipogenesis and decreased the rates of lipolysis (Bauman and Currie, 1980). If a cow is in a positive energy balance in terms of energy intake when ST is initiated, then the body

will not necessarily have to redirect fat stores in order to support the energy needs of milk synthesis. However, if the cow is near zero or in negative energy balance, ST will force the animal to rely on body fat reserves that are mobilized to support the nutrient needs for milk synthesis. In this case the animal will either have to increase its voluntary feed intake, feed quality or reduce lactation in order to return to a positive nutrient balance (Monsanto, 1995).

Insulin like Growth Factor-1:

Somatotropin also indirectly effects the mammary gland via the actions of the insulin like growth factor-1 and together they play vital roles in the regulation of lipogenesis (Jolly et al. 1993). In late pregnancy and early lactation, adipose tissue becomes resistant to the normal actions of insulin and in fact there is a reduction in lipogenesis (McNamara, 1995). The enzyme that is primarily responsible for the action of insulin and somatotropin is acetyl-COA carboxylase, which is the primary rate-limiting enzyme in fatty acid synthesis from glucose or acetate. Thus, the theory that weaning simply diverts energy from milk production to fat production is far too basic. Lipogenesis is regulated hormonally and ST and IGF-1 play a vital role in its regulation.

Besides the immediate hormonal influence of ST and IGF-1, lactation will also be effected by several other factors, which also have a profound effect on the nutrient partitioning within the animal. These factors will include the:

- Genetic potential for milk production*
- Nutritional history of the animal*
- Stage of lactation*
- Level of nutrition*
- Type of diet*

The influence and impact of these factors will vary, however at this time little research has been done as to the direct impacts of these factors within the partitioning equation of beef cattle. In fact, total milk production calculated for beef cattle has typically been done without isolating these factors and so it is difficult to establish their cumulative effect. However it is well known by nutritionists that manipulation of the last two factors through ration and feed changes can have profound effects on total milk yield (Moe and Tyrrell, 1975).

Lipogenesis:

Lipogenesis is the process related to the conversion of glucose and its intermediates like pyruvate, lactate and acetyl CoA to fat. The main factors controlling the rate of lipogenesis are related to the nutritional status of the animal. Rates of lipogenesis are greater in well-fed animals, versus a calorie deficient or insulin deficient animal (Diabetes). For lipogenesis to occur there must be a high concentration of free fatty acids (McNamara, 1995). The source of the long chain fatty acid can either be a dietary lipid or synthesized from Acetyl-CoA, which would be derived from a carbohydrate. In the adipose tissue, fatty acids may be oxidized to acetyl-CoA (beta-oxidation) or esterified to acylglycerols. Typically, fats are stored as a triacylglycerol (Chapman, 1996).

The triacylglycerol stores in adipose tissue are continually undergoing lipolysis (hydrolysis) and reesterification. Both of these pathways involve different reactants and enzymes. This allows many of the nutritional, metabolic, and hormone factors that regulate the metabolism of adipose tissue to work on the process of lipogenesis or on lipolysis. The end products of these two processes determines the amount of free fatty

acids in adipose tissue and the level of free fatty acids circulating in plasma (Chapman, 1996).

Lipolysis:

Lipolysis, which is the degradation of adipose tissue, is no less complicated than lipogenesis and in fact involves many of the same factors as lipogenesis. In high producing dairy cattle, where lactation peaks at 3 to 4 weeks post-partum lipolysis is often the sole source of energy that can sustain such high peaks in lactation beyond the caloric content of the ration being fed. In many incidences, a zero energy balance is not achieved until milk production returns to 80% of peak production. During the first 10 weeks of lactation the NE deficiency can be the energy equivalent of 50 kg of pure lipid (Bauman and Currie, 1980). Bauman and Currie (1980) proposed that up to an 80% glucose turnover is required during maximum mammary secretions. Under normal management conditions the cow will have to make up for this BW and BC loss over the last third of her lactation in order to replenish her body reserves in preparation for her next lactation. But what governs and controls lipolysis?

Lipolysis regulation may be partially accounted for by the insulin resistance of adipose tissue during early lactation (Bauman and Vernon et al., 1993). However, insulin concentration or binding alone can not account for the wide variation in rates of lipolysis throughout lactation. As in lipogenesis, somatotropin plays a vital role in lipolysis. Somatotropin increases the responsiveness of the adipose tissue to beta-adrenergic agents by increasing the amount of beta-receptors. This makes the adipose tissue more responsive to adenosine. Although adenosine limits lipolysis, the somatotropin may be

acting to partially remove this limitation and thus increase lipolysis during early lactation (McNamara, 1995). Simply put if lipogenesis is inhibited, lipolysis is accelerated.

However, the biochemical reaction of somatotropin is not the only regulatory system governing lipolysis. The function and influence of the thyroid system is another. The thyroid system plays an integral part in regulating the amount of cyclic adenosine mono phosphate - cAMP. In fact, this has been measured in dairy cattle. Cyclic AMP levels were 3 times greater per gram of adipose tissue and 5 times greater per mg of cellular protein in dairy cattle in the first 2 months postpartum of lactation compared to the last month prepartum (McNamara et al., 1992). Thus, one of the mechanisms by which adipocytes increase their sensitivity to lipolytic stimulation during lactation may be a tighter molecule connection between cAMP, protein phosphorylation, and hormone-sensitive lipase activity.

Gluconeogenesis:

Ruminants only absorb limited quantities of glucose from the gastrointestinal tract – the majority of metabolites are absorbed as volatile fatty acids (VFA's). Of all the VFA's - propionate is the primary gluconeogenic VFA absorbed (Bergmann, 1973). Abomasal infusion of propionate has been shown to enhance blood glucose concentrations and release of LH following a GnRH challenge in prepuberal heifers (Rutter et al., 1983).

The feeding of ionophores, such as lasalocid and monensin has long been demonstrated as another effective way of shifting VFA ratios. In fact feeding ionophores will shift the VFA proportion to greater levels of propionate (Moseley et al., 1977; Short and Adams 1988). Results of feeding ionophores to replacement heifers and growing

bulls have demonstrated a reduction in the age and weight at puberty (Moseley et al., 1977; McCartor et al., 1979). Similarly changing a ration from a high roughage component to greater amounts of concentrates will also result in a shift of VFA production to greater amounts of propionate (McCartor et al., 1979).

Propionate increases the ovarian response to endogenous and exogenous gonadotropins and enhances the release of LH following a challenge with either GnRH or estrogen (Randel, 1990). Randel, (1990) demonstrated this hypothesis in a trial where monensin was fed to lactating postpartum beef cows. He found that the ionophore decreased the release of LH following GnRH challenge and enhanced release of LH following an estradiol challenge and that the cows returned to estrus sooner (Randel, 1990).

It is postulated that an increase in gluconeogenesis occurs when there are elevated levels of propionate (Randel, 1990). With an increased level of propionate, dependency upon amino acids for gluconeogenesis would be decreased. Freeing up more amino acids would have a direct effect at the hypothalamic-pituitary-ovarian axis, which would result in an increase in the secretion of GnRH from the hypothalamus and an increase in the pulsatile secretion of LH from the pituitary.

Nutrition and Pituitary Function:

Mean serum concentrations of LH are lower in postpartum cows losing BC rather than those that maintaining (Randel, 1990). Diets that are either low in energy or protein, lead to lower pulsatile releases of LH, indicating that an increased concentration of gonadotropin is stored in the pituitary gland and cannot be released following a GnRH challenge. Data indicates that hypothalamic release of GnRH is being suppressed, which

proves that the nutritional status of the postpartum cow alters pituitary release of LH following a GnRH challenge (Randel, 1990).

Increased pulsatile secretion of LH from the pituitary stimulates ovarian function and results in the return to estrus with ovulation and subsequent development of a functional corpus luteum. The compound or compounds that are detected by the hypothalamic-pituitary-ovarian axis may be energy-related compounds, amino acids or catabolites (Randel, 1990).

Other evidence indicating that nutrition affects the hypothalamic release of GnRH has been obtained by the use of estrogens to stimulate the release of LH (Randel, 1990). In early postpartum stages and in severely restriction diets, cattle have had complete failure responding to a challenge of estradiol-17B. The reduced ability of cows receiving diets with lower energy levels to respond to estradiol suggests that the hypothalamic responsiveness is due to a decrease in estradiol receptors as well as faulty synthesis, storage and secretion of hypothalamic GnRH. This suggests that the nutritional control over postpartum rebreeding in cattle would be controlled by the hypothalamus (Randel, 1990).

Sympathetic Nervous System:

Another mechanism regulating the metabolism of glucose and fatty acids in the adipose tissue is the sympathetic nervous system (SNS) (Landsberg, 1990). When the intake of energy is decreased, the release of norepinephrine (NE) from the SNS to brown and white adipose tissue is altered, theoretically to conserve energy. In rats, where the NE was artificially decreased by injection of alfa-methylparatyrosine (AMPT) which blocks the synthesis of NE, there was an increase in lipogenesis. In obese rats, the accumulation

of fat has been linked to lower levels of NE (Knehans and Romsos, 1983). This further suggests that the SNS plays a vital role in the regulation of lipolysis during lactation. Whether this adaptation plays an important role in early lactation remains unclear; however the rise in SNS release of NE later in lactation is consistent with the elevated rates of lipolysis found this time in rats and cows.

Table 2., shows the results of a study in which the activity of SNS was estimated by measuring the turnover of NE, using alpha-methylparatyrosine (AMPT), a blocker of NE synthesis. In that experiment it was clearly shown that the SNS had a strong influence in controlling NE synthesis (McElroy et al., 1986).

Table 2. Norepinephrine content and turnover in adipose tissue of virgin, pregnant, or lactating rats. McElroy et al., 1986.

Adipose Tissue	<u>Day 18 Pregnancy</u>		<u>Day 21 Lactation</u>	
	Basal	3 hours after AMPT	Basal	3 hours after AMPT
Perimetrial				
Virgin	31.8	13.8	19.6	12.9
Bred	16.2*	11.1**	38.5*	24.6**
Retroperitoneal				
Virgin	22.2	12.7	12.6	15.3
Bred	15.4*	7.7**	32.2*	23.2**

*Bred vs. virgin and pregnant vs. lactating, P<0.05.

**Rate of turnover due to injection of AMPT different between bred and virgin, P<0.05.

Number of animals was 5 to 7 for each group.

In dairy cattle, rates of lipolysis remain deviated after peak lactation, even though feed intake has increased, somatotropin has decreased, energy balance is positive, and rates of lipogenesis are markedly increased (McNamara, 1994). This apparent uncoupling of regulation leads to the belief that the SNS plays a vital role in fine tuning the regulation of lipolysis and lipogenesis to meet both the needs of the lactating animal and the need to increase adipose reserves after peak lactation. The adaptation of the SNS seems to be a secondary adaptation to extending lactation, and is probably acting in addition to the regulation by insulin and the somatotropin.

The Influence of Suckling:

Biologically suckling has a wide effect on domestically farmed species. The effects range from complete anoestrous in pigs, to no effect on ewes, to an intermediate effect in cattle (Williams, 1990). Suckling is still however a very important factor determining PPI and BC in cows (Short et al., 1990). Suckling has shown to prolong the postpartum anoestrous period in beef and dairy cattle (Wetteman et al., 1978; Zalesky et al., 1984). In some instances, research has shown that PPI is even proportional to the sucking frequency (Zalesky et al., 1984; Jaeger et al., 1987). The exact mechanism by which suckling extends the postpartum anoestrous period remains unclear. The possible relationship of nutritional intake and lactation stress coupled with the need for continued body growth and hormonal signals spurred on by suckling, may all play as factors. However to fully understand the implications of suckling, a differentiation needs to be made between lactational stress and the physical aspect of suckling.

A well-known study by Short et al., (1972) compared postpartum intervals of suckled, non-suckled and mastectomized cows. The PPI for the in the experiment was 65 d, vs. 25 d and 12 d respectively. By adjusting nutrient intake to maintain constant BW among groups, these authors concluded that both suckling and the presence on mammary glands could delay postpartum estrus independent of lactational energy demands.

Although most research dealing with the impact of suckling frequency has focused on PPI, little research has focussed on suckling and its implications on hormonal changes that effect the nutritional status of the dam. The hormonal studies that have been done have mostly focused on suckling and the implications on the reproductive type hormones, specifically LH and GnRH. Work done on these hormones, has conclusively

established that suckling suppresses the release of LH from the anterior pituitary gland during the early postpartum period (Carruthers and Hafs, 1980; Carruthers et al., 1980). The fluctuations in the release of LH during the postpartum period are thought to be a direct reflection of the release of leutenizing release hormone (LHRH) from the hypothalamus (Carruthers et al., 1980).

Jaeger et al., (1987) found that the response of the bovine pituitary to GnRH during the post-partum period was not influenced by the act of suckling but was rather effected by the post-parturition time. On the other hand Wetteman et al., (1978) and Randel (1981) demonstrated that suckling intensity was a major contributing factor to the length of the PPI. More than likely though it would seem that some form of nutrient partitioning would explain the differences in these trials. Particularly since the majority of experiments that have shown positive results have involved primiparous beef heifers (Bellows et al., 1974). These experiments have also shown the greatest benefits of early weaning has been shown on poorer conditioned first and second calvers, by reducing the lactation stress and thereby improving their overall conception rates (Laster et al., 1973; Randel 1981).

Conclusion and Review:

Understanding the metabolism of energy-yielding compounds in adipose tissue is pivotal to understanding the demands that lactation and pregnancy put on animals. A clear picture has been drawn about the importance of maintaining adequate BW and BC for optimizing the reproductive status of beef cattle. In identifying the physiological

differences between lactating and non-lactating pregnant animals it is key that we understand the role of lipogenesis and lipolysis and how these processes are regulated.

However not all the differences between a pregnant/lactating and a pregnant/non-lactating animal can be explained by these biochemical reactions. In fact, a good proportion of the metabolic difference may lie in the ration quality and type as well as phenotypical differences. These may include genetic parameters for the partitioning of nutrients to different organ and in the relationship of nutrient utilization. Regulation of nutrient partitioning to support fetal development and milk synthesis is complex. The role of the sympathetic nervous system in body function regulation is one that I feel has not been studied enough. There has been much research focused on PPI up until the point of conception but little concerning post-conception metabolic control parameters. Herein lies the key to understanding how suckling affects the whole system of lipolysis/lipogenesis. Improvement in this area will require a coordinated effort to understanding both the physiological and quantitative parameters that control lipogenesis and lipolysis. We need to know and better understand the regulatory mechanisms, to better plan prevention and intervention methods of management cow BW and BC.

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