Exploring the Genetics of Reproduction and Nutrition Efficiency: How do we select and feed for optimal dairy efficiency?

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Key points

- Non-lactational secondary traits (longevity, health, reproduction, etc.) are being included in selection indices worldwide by decreasing the emphasis on production.

- Greater emphasis on non-lactational secondary traits reflects the industry desire for more functional and efficient dairy cattle.

- The traditional view of an "efficient cow" was one that mobilized body fat in early lactation so that peak milk production was maximized. This approach to efficiency has apparently antagonized reproduction through changes in metabolic hormones.

- Dairy cattle in other systems may have differently shaped lactation curves. Changing the shape of the lactation curve so that peak milk production is less and persistency of lactation is greater may improve reproductive function while maintaining total lactation yield.

Introduction

Dairy cattle have been traditionally selected for milk production and milk components (fat and protein). The traditional approach made sense because farmers are paid for milk. Dairy selection has changed in the past decade. A compilation of dairy selection indices worldwide shows that the weighting given to production has declined from 79% to 57% from 1996 to 2004 (Wesseldijk 2004; Figure 1). At the same time, the weight of secondary traits such has longevity, health, and reproduction has grown from 6 to 27%. Thus, secondary traits are being included in indices by specifically decreasing the emphasis on production.

Greater emphasis on non-production traits reflects the industry desire for functional dairy cattle. Progress in any one trait (for example milk solids production) diminishes as the selection index is grown to include additional traits. The hope is that appropriate economic weightings are placed on secondary traits so that slowed progress in milk production is offset by improved farm economics created by more functional cows. Few will argue that high fertility and mastitis resistance have value. The real question is how much value (economic weight) do they have? This later question is particularly difficult when one considers that selection indices are designed for use by the national dairy herd that is comprised of increasingly diverse production systems.

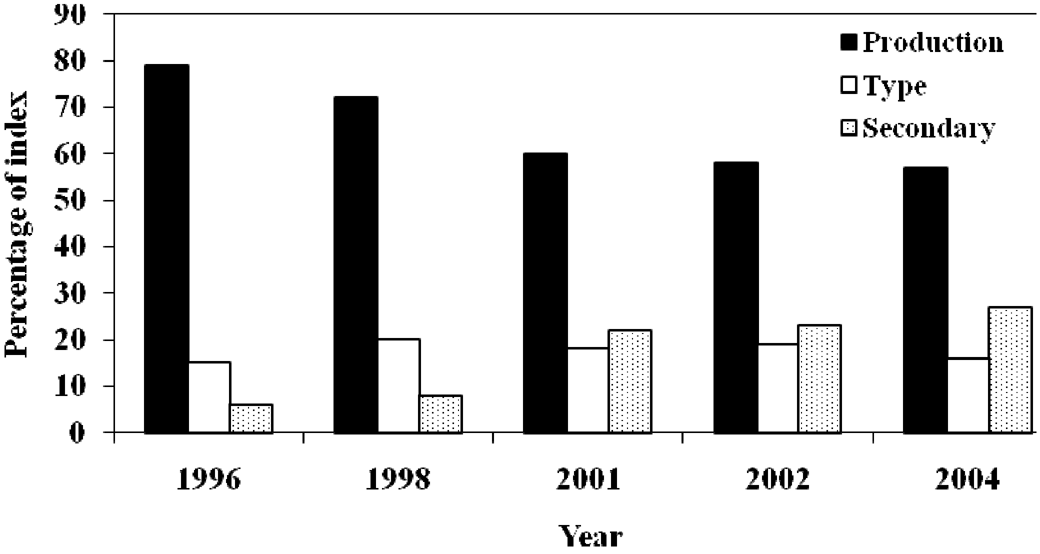

Figure 1. World selection index (composition of dairy selection indices worldwide) from 1996 to 2004 for production traits (lactation), type traits, and secondary (non-lactation traits). Data are from Wesseldijk 2004.

Efficiency traits of importance to dairy production

What constitutes an "efficient" dairy cow in North America?

North American-style Holstein cattle are large cows. The large body size reflects the strong correlation between TMR feed intake and milk production (Hristov et al 2005). Selecting for milk production in a confinement system favors large cows that can consume the largest amount of feed. This is because TMR is fed for ad libitum consumption and the biggest cows (consuming the most feed) will generally produce the most milk. This approach to genetic selection only works if there is a bias against high body condition score (BCS) cows. This bias has existed in US herds for a long time; fatter cows in a TMR system are viewed unfavorably because they do not fully partition nutrients toward milk production. Although the maintenance requirements for large cows may seem excessive, the argument is made that the maintenance energy required for a single high producing cow is less than two lower producing, smaller cows that produce an equivalent sum of milk. Thus, in the North American system the large high producing cow is viewed as the most efficient.

What constitutes an "efficient" cow in New Zealand?

Efficiency is viewed differently in other dairy systems. In this paper, the example of the New Zealand (NZ) system will be used to contrast the North American system. Whereas the North American system favors large cows, the NZ system places large cows at a disadvantage. The difference arises primarily from the feeding system. Feed energy limits production in pasture-based dairy systems (Waghorn and Clark 2004). The higher maintenance energy requirements for larger North American style cows in NZ come at a cost in terms of body condition and milk solids production (Kolver 2003). Although the North American cow has the ability to produce more milk, it cannot do so in NZ because the capacity to consume adequate energy through grazing pasture limits milk production. Thus the large negative weighting on mature body size in NZ makes sense given that energy is limiting and excessive maintenance requirements will drain body condition. A small negative weighting was placed on body size in the year 2000 within the US Net Merit system (VanRaden 2004).

Efficiency and body condition

Regardless of system, modern dairy cows are thinner than their ancestors. The decrease in body condition among modern cows reflects the continued emphasis on milk production traits (Berry et al 2003; Horan et al 2005). Given limited capacity to consume adequate dietary energy, dairy cows mobilize fat to support lactation (Bauman and Currie 1980). Improvements in milk production occur more rapidly than improvements in the capacity for cows to consume additional energy or the willingness of farmers to provide more feed. Thus, body fat is the obvious source of the additional energy.

Most of the available literature suggests that dairy cattle have a genetically-determined set point for body condition during lactation (Stockdale 2001; Contreras et al 2004). Once dairy cows begin lactation, they will migrate toward their body condition set point through the coordinated control of both feed intake and the depletion of adipose tissue. There is wide-spread consensus that the genetically-determined set point for BCS during lactation affects the reproductive performance of dairy cows. Cows with a high BCS during lactation have high fertility whereas cows with a low BCS during lactation have low fertility (Pryce et al 2001). The BCS at calving is unrelated to reproductive success because it does not reflect the actual BCS that will be achieved during early lactation (Contreras et al 2004). Although BCS during lactation is a valuable trait from a management perspective, it is not currently found in most selection indices. Its absence relates to the difficultly in collecting BCS data in a systematic manner on a large number of cows. There is a reasonable probability that BCS will be introduced into future genetic selection indices.

What about feed efficiency?

Feed efficiency is a complicated trait, particularly when viewed within the dairy scenario. Gross efficiencies (milk production per unit feed intake) are affected by a variety of factors including size of cow (maintenance requirement). Smaller cows producing equivalent milk to larger cows are clearly more efficient. Cows that lose body condition are initially viewed as efficient as well because energy and long chain fatty acids derived from adipose tissue increase milk production without additional feed consumed. Although this latter category of cow may be “efficient” there are clearly downstream effects of BCS loss on reproduction (see above).

Residual feed intake (RFI; the difference between an animal’s actual feed intake and its expected feed intake based on nutrient requirements) has been used as an index for identifying energetically efficient beef cattle. In their study of growing beef steers, Nkrumah et al. (2004) partitioned groups into high, medium and low RFI. Each group achieved an average daily gain of approximately 1.4 kg/day. Cattle in the low RFI group, however, consumed about 20% less feed per day when compared with the high RFI group. The difference in RFI was achieved without appreciable differences in body composition. A theoretical statistical analysis of RFI suggested that selection for RFI would be equivalent to selection on milk production and dry matter intake (Kennedy et al 1993). The RFI index (or a combination of selection on milk production and dry matter intake) has apparently not been applied to dairy selection. The utility of these energetic efficiency measures seem obvious given limited feed availability in pasture systems and high feed costs in confinement systems.

Genetic Improvements in Reproduction

Dairy cattle are inseminated and pregnancy is established during lactation. Unfortunately, recent changes in the genetics, productivity, and management of dairy cows have led to a worldwide decline in reproductive performance of lactating dairy cows (Lucy 2001). The energy required to ovulate a follicle, form a corpus luteum, and maintain an early pregnancy is small compared with the other energy demands of lactating cows. Nonetheless, reproductive tissues sense energy demands and function poorly during nutritional stress (Lucy 2003).

Geneticists have reacted to the worldwide decline in dairy fertility by including fertility traits in selection indices. It is impossible to capture each of the individual fertility components listed above. Instead, time to pregnancy (the most meaningful outcome) is measured. The US has adopted Daughter Pregnancy Rate (DPR) for fertility weightings (VanRaden et al 2004). The DPR is based on days open (the number of days from calving to conception). A 1% increase in DPR is equivalent to 4 days open. In untreated cattle, the DPR captures cyclicity, estrous expression, and fertility (conception rate) in a single measure. The DPR breeding value for North American Holstein cows has declined since 1960 but appears to have stabilized and is improving (Figure 2). The improvement may be explained by the inclusion of longevity and DPR in selection indices.

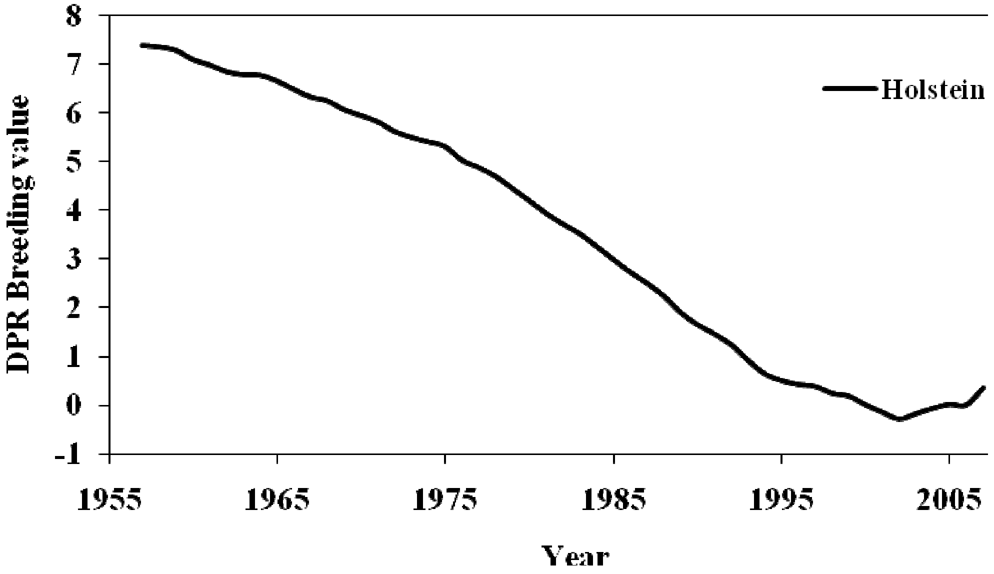

Figure 2. Daughter pregnancy rate (DPR) breeding value for United States Holstein cows from 1957 to 2007 (USDA Animal Improvement Programs Laboratory; http://aipl.arsusda.gov).

Physiological Mechanisms that Link Efficiency with Reproduction

Genetic selection can be applied to quantitative traits but the link between successful genetic selection and the underlying physiological mechanisms sits inside a black box. A limited number of genes may control any one trait but these key genes are often fixed by years of selection. There are hundreds of other genes that act on the trait of interest but these are more difficult to find because their contribution is much smaller. A simple reproductive trait (interval to first ovulation) will be used to illustrate the complexity of physiological processes.

Growth hormone, IGF1, and insulin

Growth hormone (GH) is a pituitary hormone that controls the growth of a variety of tissues. Insulin-like growth factor-I (IGF1) is released from liver and is believed to control tissue growth as well. Growth hormone is an anabolic hormone that has the capacity to antagonize insulin action (Etherton and Bauman 1998). Antagonizing the actions of insulin has a nutrient partitioning effect through which the production of milk is favored.

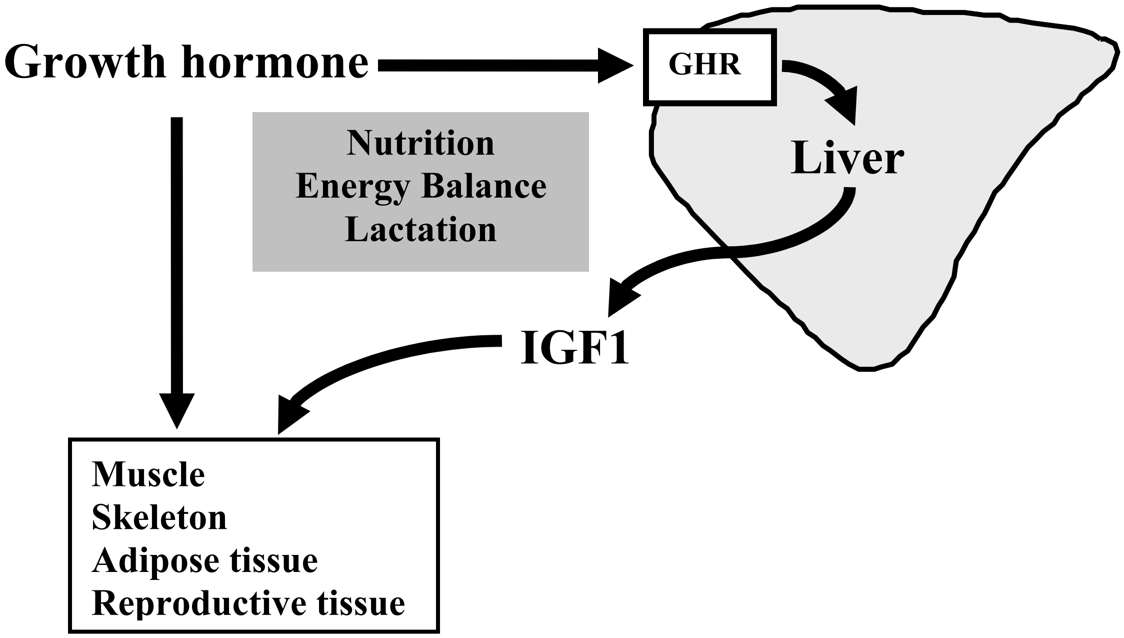

Figure 3. The growth hormone (GH), insulin-like growth factor-I (IGF1) endocrine axis. This endocrine axis controls many aspects of growth, lactation, body condition, and reproduction in dairy cattle. Central to the axis is the liver where expression of growth hormone receptor (GHR) is controlled by nutrition, energy balance and stage of lactation. Negative energy balance in early lactation leads to an increase in GH but low liver GHR expression and low blood IGF1 concentrations. This early lactation hormonal milieu antagonizes reproduction.

High producing dairy cows have high concentrations of GH and low concentrations of insulin (Bauman 1999). Dairy cows also appear to suffer from insulin resistance (insensitivity to insulin manifested at the tissue level). Growth hormone promotes lipolysis while antagonizing lipogenesis and blocking insulin-dependent glucose uptake in peripheral (non-mammary) tissues (Etherton and Bauman 1998). There is a large increase in circulating GH concentrations during early lactation. This initial increase in GH drives BCS loss. After this initial period of GH action, there is a second period where GH remains elevated in high producing dairy cows. The steady-state blood GH concentrations may ultimately determine the BCS for the individual cow because GH antagonizes lipogenesis. Cows in US herds are supplemented with recombinant GH (Bauman 1999). The recombinant GH acts in a manner that is consistent with the normal effects of GH (antagonizing insulin action and preventing lipogenesis). The net effect on the cow is greater milk production through the nutrient partitioning effect of GH.

How do metabolic hormones (GH, IGF1, and insulin) affect reproduction?

Many of the mechanisms that control reproduction are linked directly to the nutrition of the animal. The reader is referred to reviews for more information on specific topics (Lucy 2000; Lucy 2003).Follicular growth in postpartum cattle is controlled by a combination of luteinizing hormone (LH) and follicle stimulating hormone (FSH). Follicle stimulating hormone is viewed as responsible for initiating follicular growth and LH is responsible for final maturation of the dominant/preovulatory follicle. Secretion of LH and FSH is controlled by GnRH from the hypothalamus.

Postpartum cyclicity depends on body condition and negative energy balance. The negative energy balance in early lactation depresses LH pulsatility. Postpartum cows will begin to cycle when energy balance improves and LH pulsatility reaches a critical level. The increase in LH pulsatility stimulates the maturation of a dominant follicle. The dominant follicle produces estradiol that reaches a threshold level to trigger estrus, the LH surge, and ovulation.

Insulin and IGF-I concentrations gradually increase postpartum. Cows in negative energy balance have lower blood concentrations of insulin and IGF-I. Insulin and IGF-I stimulate GnRH secretion from the hypothalamus and LH secretion from the pituitary. The hormonal control of GnRH and LH, therefore, arises from the metabolic and nutritional status of the animal via insulin and IGF-I. It does make sense that these peripheral metabolic hormones will act on the hypothalamus to convey information from metabolically important tissues. A variety of metabolites (glucose, fatty acids, etc.) and other hormones may also be involved.

The same metabolites and hormones that influence GnRH secretion and ultimately LH and FSH secretion may act directly on the ovary to influence the sensitivity of the ovary to LH and FSH. Thus, the effects of nutrition on reproduction are manifested at the ovary and at the pituitary and hypothalamus through metabolic hormones (GH, IGF1, and insulin) that are essential for nutrient partitioning. In addition to the follicle, the corpus luteum, uterus, and embryo respond positively to insulin and IGF1.

Nutrient partitioning for greatest milk production occurs when blood GH is elevated and blood insulin and IGF1 are low. Improvements in reproduction occur under a contrasting hormonal milieu (i.e., high blood insulin and IGF1 concentrations). It is difficult, therefore, to consistently achieve good reproduction in cows that undergo extremes in nutrient partitioning and have low insulin and IGF1.

Nutrient Partitioning in New Zealand versus North American Cattle

We recently completed a trial where dairy cows with diverse genotypes were studied in a common pasture grazing environment in New Zealand (Lucy et al 2009). Three genetic strains and two different feed allowances were studied. One question that we asked related to the performance of cows with modern North American (NA) genetics relative to modern New Zealand (NZ) genetics in a pasture-based system. The data reported here quantified this comparison as it related to milk production, energy balance, and the uncoupling of the somatotropic axis.

Reproductive success is closely tied to BCS during early lactation. A primary objective of the study, therefore, was to examine mechanisms controlling BCS loss during early lactation. The NA cows lost more BCS during early lactation than NZ cows (Figure 4). The predominant period of BCS loss was the first eight weeks after calving. Afterwards (wk 9 to 16), the NA cows continued to lose BCS, but at a slower rate. In comparison, the NZ cows gained BCS during this period (after 8 wk postpartum). Excessive BCS loss for cows with predominately NA genetics has been reported previously in studies comparing these strains. The difference in BCS for NA90 cows relative to NZ70 (approximately 1 BCS unit by 16 wk of lactation on the 10-point BCS scale) is equal to approximately 0.3 units on the NA 1 to 5 BCS scale.

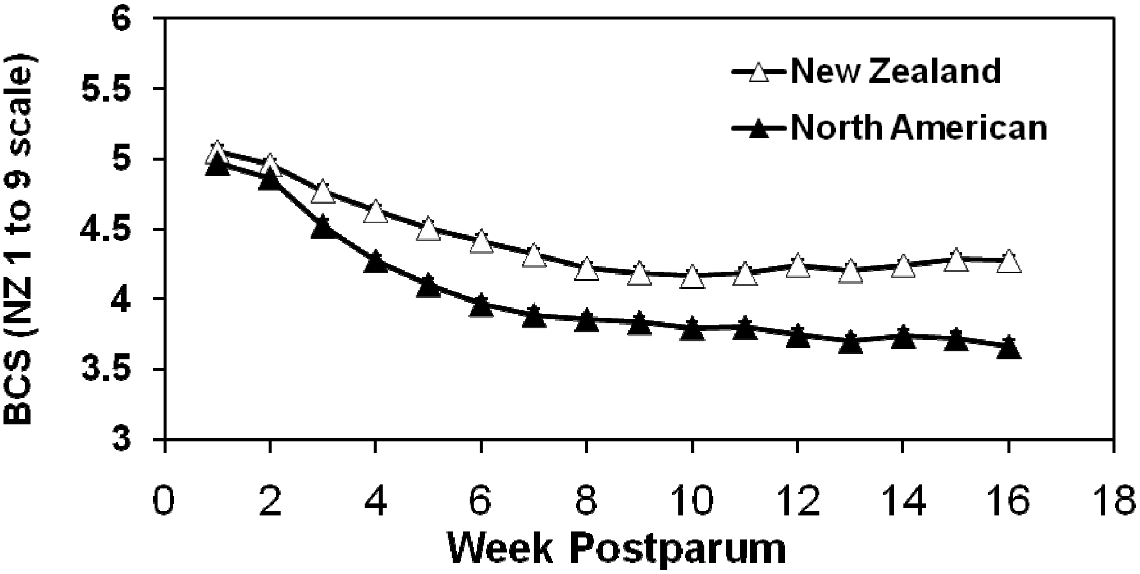

Figure 4. Body condition score (BCS) of New Zealand and North American cows on NZ pasture. Data are from Lucy et al (2009).

Milk production was expressed as Mcal NE_L in milk, based on kg protein, fat, and lactose. Although total milk NE_L during the first 16 wk was nearly identical for the NA and NZ cows, there appeared to be a distinct difference in the shape of the NE_L profile for the two strains. The NA cows ascended to peak milk energy production rapidly after calving and maintained greater milk energy production than NZ cows from 2 to 6 wk postpartum (Figure 5). This period of greater milk energy production coincided with the period of greatest BCS loss in NA cows. The differences in milk energy production were relatively minor (about 10%) and short-lived (approximately 4 wk). Nonetheless, the difference in milk energy production could account for most of the BCS loss in NA90 cows because the additional NE_L for milk (36 Mcal) was approximately equal to the predicted Mcal provided by the BCS loss (35 Mcal; Figure 4).

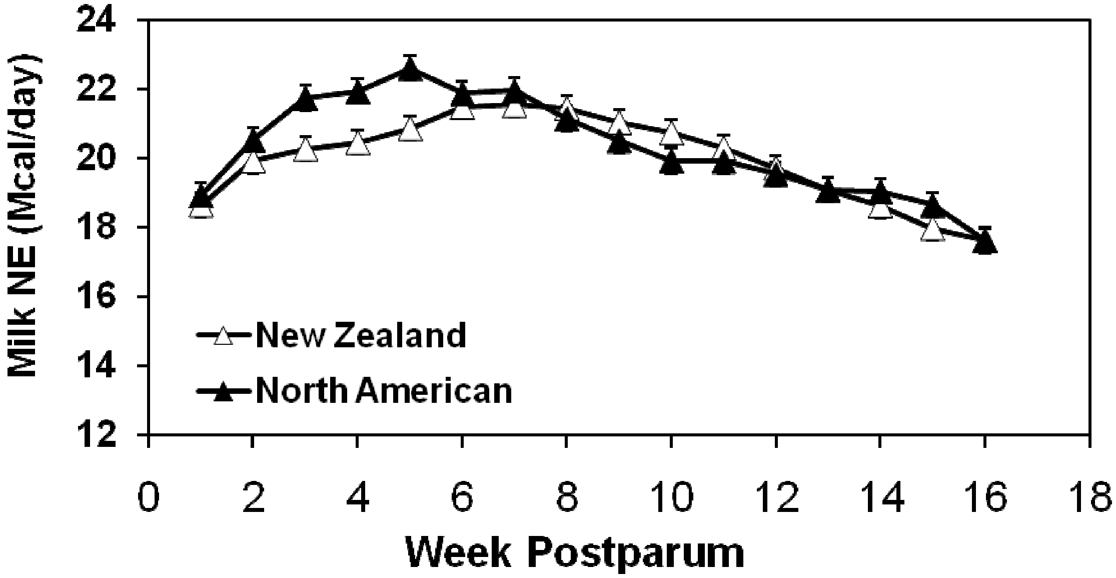

Figure 5. Milk net energy (NE) of New Zealand and North American cows on NZ pasture. Data are from Lucy et al (2009).

Excessive BCS loss in early lactation is a characteristic of NA cows under pasture management systems. It is also a characteristic of NA cows in the traditional NA system where negative energy balance during early lactation is considered necessary to support a high level of milk production. Components of the somatotropic axis were examined to determine if GH was coordinating the changes in BCS in this study. Growth hormone concentrations were greater in NA cows, particularly during the first 9 wk of lactation (Figure 6, upper panel). Growth hormone facilitates lipolysis during early lactation. The greater loss in BCS for NA cows, therefore, perhaps could be explained by the greater plasma GH concentrations in NA cows. The elevated plasma GH concentrations were associated with greater BCS loss in NA90 cows.

Plasma IGF1 concentrations are an indicator of postpartum energy balance and the extent of the uncoupling of the somatotropic axis. In high producing dairy cows, the somatotropic axis is uncoupled shortly after calving (Lucy et al 2001). Recoupling of the axis requires heightened liver GHR expression and the re-establishment of liver IGF-I synthesis and secretion (Figure 3). The recoupling event depends on nutrition and energy balance (better nutrition and more positive energy balance leads to liver GHR expression and liver IGF-I synthesis and secretion). The NA cows apparently stayed within a more catabolic state (negative energy balance) during early lactation because their IGF1 concentrations were less than NZ cows (Figure 6, lower panel). Perhaps maintenance requirements and the capacity of the mammary gland to produce milk exceeded nutrient availability in NA cows. Physiologically, the NZ cows had the capacity to recouple their somatotropic axis earlier postpartum because they shifted toward a more anabolic state. This shift toward an earlier anabolic state was apparently related to a slower rise to peak milk production (Figure 5).

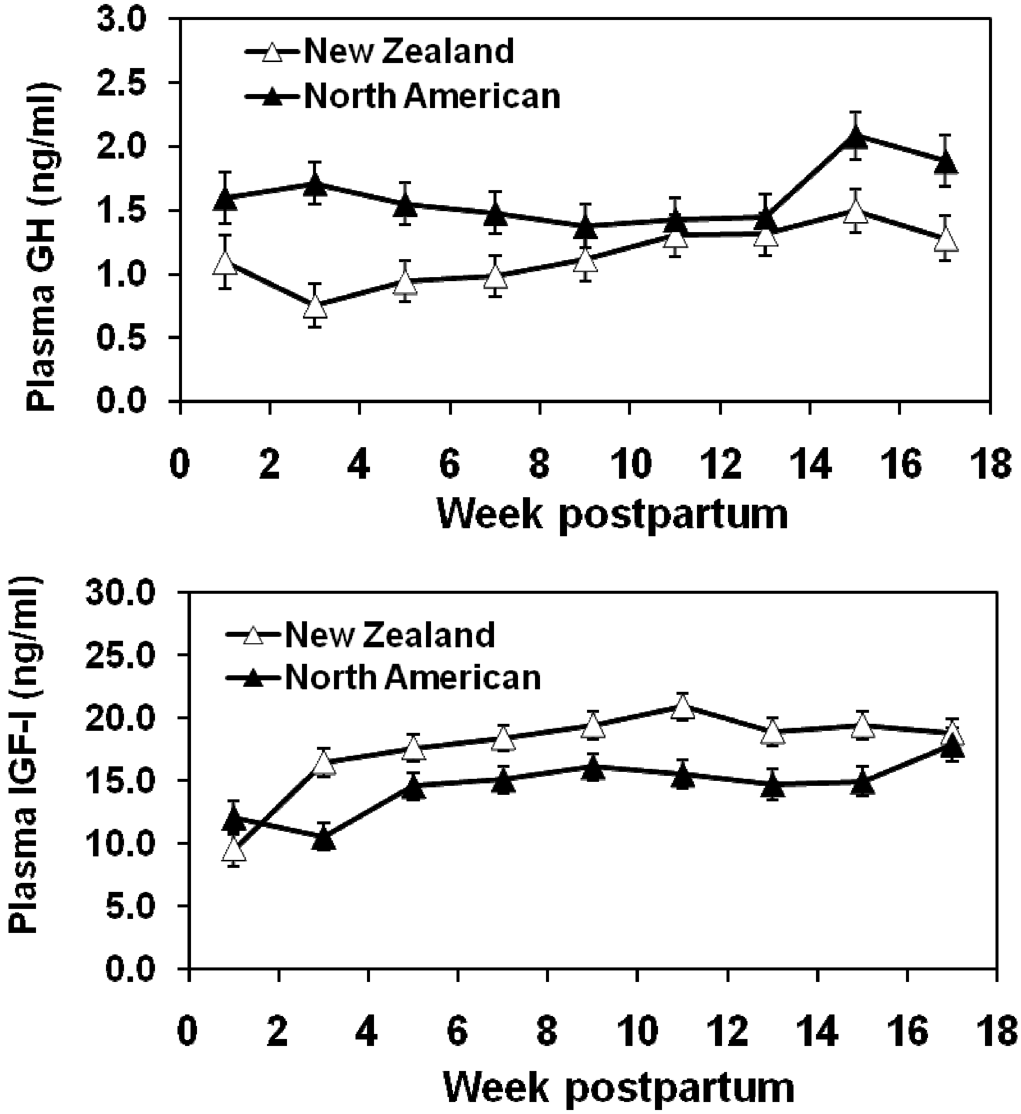

Figure 6. Plasma GH (top graph) and IGF1 (bottom graph) from New Zealand and North American cows on NZ pasture. Data are from Lucy et al. (2009).

Rethinking the Lactation Curve of North American Dairy Cattle

Figure 5 (above) shows that the NZ cows produced less milk in early lactation. This may represent a distinct physiological difference between NZ and NA cows. Less early lactation milk production in NZ cows apparently leads to less BCS loss in early lactation. This may explain why NZ cows are superior to NZ cows in terms of postpartum reproduction (cows in better body condition typically have better reproductive rates).

An interesting question that could be raised is whether or not the US dairy industry should attempt to change the lactation curve of the cow to relieve some of the BCS loss in early lactation (Figure 7). If peak milk production was less and persistency was greater then the overall level of production across the entire lactation may not change (loss of milk at peak being compensated by greater production in later lactation). Manipulating the lactation curve in this manner for the purpose of alleviating BCS loss is not a new concept and was proposed in 1985 (Ferris et al. 1985). Peak milk production, ascent to peak production, and persistency are traits with moderate heritability so the shape of the lactation curve can theoretically be changed. Nonetheless, Ferris et al (1985) concluded that genetic improvement in total milk production is difficult when peak milk production is not emphasized. Subsequent recent publications have again raised the possibility of increasing persistency and decreasing peak milk yield as a means to alleviate BCS loss (Macciotta et al. 2006).

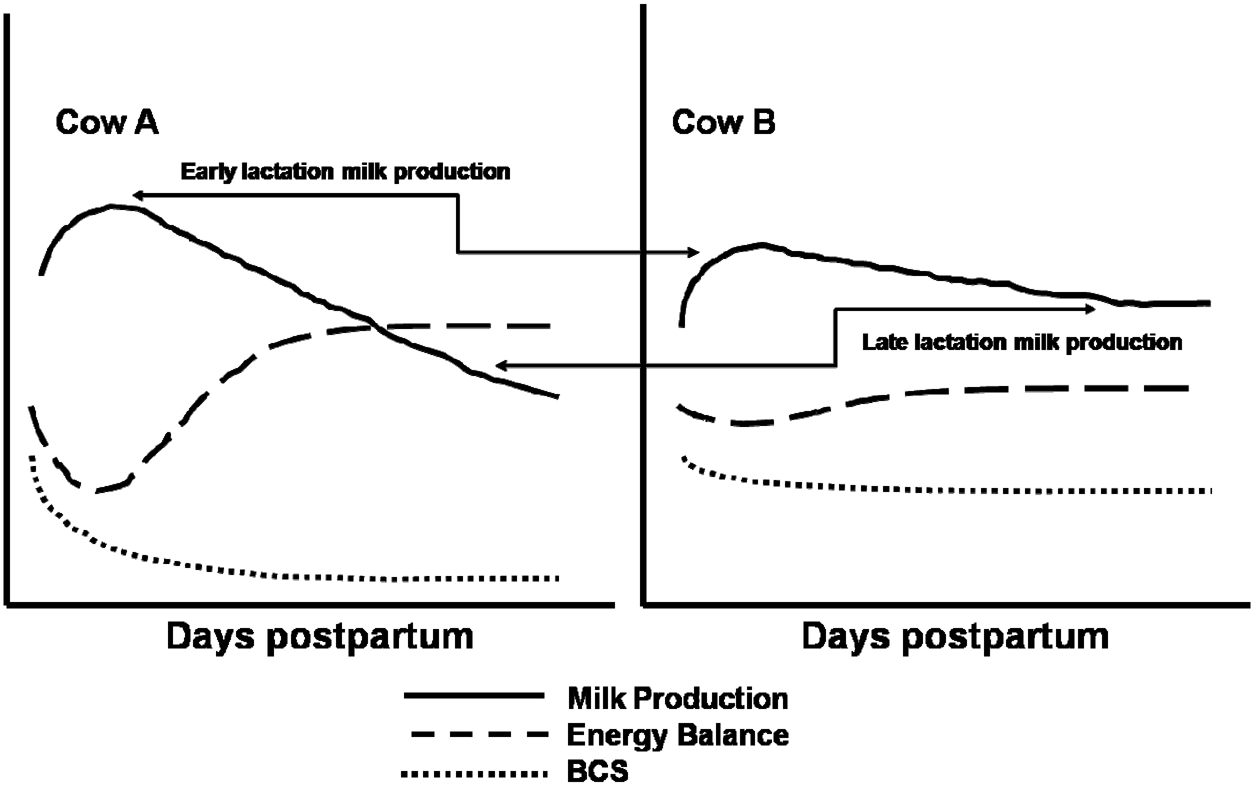

Figure 7. Theoretical model of milk production, energy balance, and body condition score (BCS) in two dairy cows. Peak milk production in early lactation is greater in Cow A. This greater milk production is achieved through negative energy balance and body condition mobilization (BCS loss). The loss of BCS antagonizes reproduction. In Cow B, peak milk production is less in early lactation. Negative energy balance and BCS loss is also less (similar to NZ cow). This cow may have better reproduction because BCS loss is less. Increased persistency may be one means of offsetting lost milk production in early lactation.

Conclusions

Non-lactational secondary traits (longevity, health, reproduction, etc.) are being included in selection indices worldwide by decreasing the emphasis on production. Greater emphasis on non-lactational secondary traits reflects the industry desire for more functional and efficient dairy cattle. The traditional view of an "efficient cow" was one that mobilized body fat in early lactation so that peak milk production was maximized. This approach to efficiency has apparently antagonized reproduction through changes in metabolic hormones. Dairy cattle in other systems may have differently shaped lactation curves. Changing the shape of the lactation curve so that peak milk production is less and persistency of lactation is greater may improve reproductive function while maintaining total lactation yield.

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