Prepartum and postpartum nutritional management to optimize fertility in high-yielding dairy cows in confined TMR systems

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The 6 to 8-week period centered on parturition, known as the transition or periparturient period, is critical to welfare and profitability of individual cows. Fertility of high-producing cows is compromised by difficult transitions. Deficiencies in either nutritional or non-nutritional management increase risk for periparturient metabolic disorders and infectious diseases, which decrease subsequent fertility. A primary factor impeding fertility is the extent of negative energy balance (NEB) early postpartum, which may inhibit timing of first ovulation, return to cyclicity, and oocyte quality. In particular, pronounced NEB during the first 10 days to 2 weeks (the time of greatest occurrence of health problems) is critical for later reproductive efficiency. Avoiding over-conditioning and preventing cows from over-consuming energy relative to their requirements in late gestation result in higher dry matter intake (DMI) and less NEB after calving. A pooled statistical analysis of previous studies in our group showed that days to pregnancy are decreased (by 10 days) by controlling energy intake to near requirements of cows before calving compared with allowing cows to over-consume energy. To control energy intake, total mixed rations (TMR) must be well balanced for metabolizable protein, minerals and vitamins yet limit total DM consumed, and cows must uniformly consume the TMR without sorting. Dietary management to maintain blood calcium and rumen health around and after calving also are important. Opportunities may exist to further improve energy status in fresh cows. Recent research to manipulate the glucogenic to lipogenic balance and the essential fatty acid content of tissues are intriguing. High-producing cows that adapt successfully to lactation can have high reproductive efficiency, and nutritional management of the transition period both pre- and post-calving must facilitate that adaptation.

Keywords: transition period, reproduction, nutrition, metabolic disorders

Implications

Nutritional strategies and feeding management during pre-calving and post-calving periods impact health, productivity and fertility of high-producing dairy cows. Formulating diets to meet requirements of the cows but avoid over-consumption of energy may improve outcomes of the transition period and lead to improved fertility. Management to improve cow comfort and ensure good intake of the ration is pivotal for success. Impacts of the transition program should be evaluated in a holistic way that considers disease occurrence, productivity and fertility.

Introduction

Reproductive success is critical to the profitability and sustainability of dairy farms using confined total mixed ration (TMR)-based systems. Successful reproduction depends on a coordinated series of physiological events, including resumption of ovarian cyclicity postpartum, development and ovulation of a viable oocyte, fertilization, restoration of the uterus, embryo development and implantation, and maintenance of pregnancy until fetal maturation (Butler, 2003; Garnsworthy et al., 2008). Dietary formulation and feeding management during the dry period, peripartal period, and early postpartum (fresh) period may facilitate or interrupt many of these steps before pregnancy is established and maintained (Butler, 2003; Garnsworthy et al., 2008; Thatcher et al., 2011). In high-producing dairy cows, conception rates for normally cycling cows are high (>70%) but many cows (>50%) undergo early embryonic loss and fail to maintain the pregnancy (Diskin and Morris, 2008). A major point of emphasis in relating nutrition and reproduction in dairy cows is the extent and duration of negative nutrient status and negative energy balance (NEB) in early lactation, which is influenced heavily by nutritional and environmental management during the period of transition from pregnancy to lactation.
The 6 to 8-week period centered on parturition, known as the transition or periparturient period, is critical in determining welfare and profitability of individual cows during the subsequent lactation (Drackley et al., 2005). Suboptimal transition management programs lead to a high rate of production disease in dairy herds (Mulligan and Doherty, 2008). Disturbances of metabolism during the transition may have direct or indirect influences on fertility, and difficult transitions have negative impacts on subsequent reproduction (Chapinal et al., 2012). A variety of nutritional strategies to facilitate the metabolic and physiological adaptations from gestation to lactation have been proposed (Friggens et al., 2004; Roche et al., 2013).

The objectives of this paper are to review the causes of NEB and its resulting metabolic disturbances, to relate how these outcomes influence reproduction, and to consider how different nutritional strategies prepartum and postpartum may affect NEB and adequacy of other nutrients. Our central theme is that prepartum and postpartum management that promotes high dry matter intake (DMI) of properly balanced diets after calving is the unifying factor between transition success and reproductive success. Because of space limitations, we emphasize energy intake, with the recognition that adequacy or balance of many other nutrients can modulate fertility. Our review will focus on newer information relating to the roles of nutrition and inflammation during the transition.

Fertility, milk yield and peripartal health problems

A widespread assumption is that fertility of modern dairy cows is decreasing, particularly for Holstein–Friesian genetics, at least in part because of unintended consequences of continued selection for high milk production. This assumption has been challenged recently (LeBlanc, 2010; Bello et al., 2012). There is a wide distribution of reproductive success both within and among herds. For example, within five California herds encompassing 6396 cows, cows in the lowest quartile for milk yield in the first 90 days postpartum (32.1 kg/day) were less likely to have resumed estrous cycles by 65 days postpartum than cows in quartiles two (39.1 kg/day), three (43.6 kg/day) or four (50.0 kg/day); milk production did not affect risk for pregnancy (Santos et al., 2009). Changes in management systems and inadequacies in management may be more limiting for fertility of modern dairy cows than their genetics per se.

Dairy cows are susceptible to production disorders and diseases during the periparturient period and early lactation (Mulligan et al., 2006; Ingvartsen and Moyes, 2013; Roche et al., 2013). There is little evidence that milk yield per se contributes to greater disease occurrence. However, peak disease incidence (shortly after parturition) corresponds with the time of greatest NEB, the peak in blood concentrations of non-esterified fatty acids (NEFA), and the greatest acceleration of milk yield (Ingvartsen et al., 2003). Peak milk yield occurs several weeks later. Disorders associated with postpartum NEB also are related to impaired reproductive performance, including fatty liver (Rukkwamsuk et al., 1999; Jorritsma et al., 2003) and ketosis (Walsh et al., 2007; McArt et al., 2012). Cows that lost >1 body condition score (BCS) unit (1 to 5 scale) had greater incidence of metritis, retained placenta, and metabolic disorders (displaced abomasum, milk fever, ketosis) as well as a longer interval to first breeding than cows that lost <1 BCS unit during the transition (Kim and Suh, 2003).

Indicators of NEB are highly correlated with lost milk production, increased disease and decreased fertility (Ospina et al., 2010; Chapinal et al., 2012). However, the extent to which NEB is causative for peripartal health problems rather than just a correlated phenomenon must be examined critically (Roche et al., 2013). For example, in transition cows inflammatory responses may decrease DMI, cause alterations in metabolism, and predispose cows to greater NEB or increased disease (Bertoni et al., 2008; Graugnard et al., 2012 and 2013; Ingvartsen and Moyes, 2013). Inducing a degree of calculated NEB in mid-lactation cows similar to what periparturient cows often encounter does not result in marked increases in ketogenesis or other processes associated with peripartal disease (Moyes et al., 2009). Nevertheless, early postpartal increases in NEFA and decreases in glucose concentrations were strongly associated with pregnancy at first insemination in a timed artificial insemination (TAI) program (Garverick et al., 2013). Although concentrations of NEFA and glucose were not different between cows that ovulated or did not before TAI, probability of pregnancy decreased with greater NEFA and increased with greater glucose concentrations at day 3 postpartum (Garverick et al., 2013). In support of these findings, early occurrence of subclinical ketosis is more likely to decrease milk yield and compromise fertility. McArt et al. (2012) found that cows with subclinical ketosis detected between 3 and 7 days after calving were 0.7 times as likely to conceive to first service and 4.5 times more likely to be removed from the herd within the first 30 days in milk compared with cows that developed ketosis at 8 days or later.

Cows that successfully adapt to lactation (Jorritsma et al., 2003) and can avoid metabolic (Ingvartsen et al., 2003) or physiological imbalance (Ingvartsen and Moyes, 2013) are able to support both high milk production and successful reproduction while remaining healthy. Decreased fertility in the face of increasing milk production may be attributable to greater severity of postpartal NEB resulting from inadequate transition management or increased rates of disease. Competition for nutrients between the divergent outcomes of early lactation and subsequent pregnancy will delay reproductive function. Because NEB interrupts reproduction in most species, including humans, inappropriate nutritional management may predispose cows to both metabolic disturbances and impaired reproduction. Cows must make ‘metabolic decisions’ about where to direct scarce resources, and in early lactation nutrients will be directed to milk production rather than to the next pregnancy (Friggens, 2003).
NEB and impaired fertility

Cows cannot consume sufficient energy-yielding nutrients from voluntary DMI after calving to meet energetic requirements for milk production. Consequently, NEB occurs for a period of days to weeks during early lactation. Although studies have demonstrated a weak and variable relationship between the degree of NEB and impaired fertility, the time to NEB nadir and the direction and/or rate of change in NEB appear to be stronger indicators (Whitaker et al., 1993; Butler, 2003; Reist et al., 2003). Possible mechanisms for detrimental effects of NEB on reproduction include (1) delayed resumption of ovarian cyclicity, through effects on hypothalamic, pituitary and ovarian function, (2) impacts on oocyte or corpus luteum (CL) ‘quality’, viability, or function, sometimes referred to as ‘follicular memory’ and (3) development of fatty liver (hepatic lipidosis).

In general, fertility is greater in cows that ovulate sooner after parturition (Butler, 2003; Bossaert et al., 2008; Galvão et al., 2010b). During early postpartum NEB, the pulse frequency of LH release, the size and development rate of follicles, concentrations of estrogen and progesterone, and size of the CL all are decreased (Jorritsma et al., 2003; Garnsworthy et al., 2008). Successful ovulation depends on estrogen production by the dominant follicle, restoration of pulsatile LH secretion, and responsiveness of the ovary to LH. The state of postpartum NEB is associated negatively with reproductive performance in part because it interrupts these three factors (Butler, 2003). Insulin, concentrations of which generally reflect energy status and dietary adequacy, may be a primary link between the metabolic and reproductive systems. Insulin is necessary to increase synthesis of IGF-1 in the liver in response to elevated concentrations of somatotropin (growth hormone; GH), to increase oestriol production by the dominant follicle and to increase LH receptors for insulin (growth hormone; GH), to increase estrodiol production by the dominant follicle, and to increase LH receptors for insulin. Changes in the endocrine and neuroendocrine systems drive the altered partitioning of nutrients from foetal maturation to milk synthesis between late pregnancy and early lactation (Ingvartsen, 2006). During the dry period, concentrations of insulin and leptin reflect energy balance and generally are higher than in late lactation (Janovick et al., 2011). These hormones promote and respond to, respectively, energy storage in adipose tissue. During the last 3 weeks of pregnancy, nutrient demands by the foetal calf and placenta are at their greatest (Bell et al., 2000). Cows should be able to meet these requirements from the diet, although DMI may be decreased by 10% to 30% compared with intake during the early dry period. Although stressors and severe limitations in DMI can lead to NEB before calving, the degree is much less than what occurs following parturition.

Secretion of GH increases near parturition, with the timing of increase dependent on nutrient status (Grum et al., 1996). In the face of decreasing concentrations of insulin prepartum, GH promotes mobilization of stored nutrients (primarily fat from adipose tissue) to support milk production (Lucy, 2000). Marked decreases in the primary GH receptor in liver (GHR-1A) lead to sharply decreased hepatic secretion of IGF-1.
This ‘uncoupling’ of the somatotropic axis prevents feedback inhibition of GH secretion by IGF-1, thereby maintaining elevated concentrations of GH (Lucy, 2000).

**Lipid metabolism**

The profile of low insulin and high GH concentrations orients the adipose tissues toward mobilization of stored triacylglycerols (TAG). Lipogenesis is almost completely inhibited, which decreases re-esterification of NEFA within adipocytes. Decreased insulin also removes an important anti-lipolytic influence on adipose tissue. Sensitivity and response to catecholamines in adipose tissue is increased by GH, resulting in greater lipolysis of TAG (Drackley et al., 2001 and 2005; Roche et al., 2013). In addition, other factors secreted in response to infection, stress or trauma, most likely the cytokines (tumor necrosis factor-α (TNFα), interleukin-1 and interleukin-6, among others) result in increased concentrations of NEFA in blood and TAG in liver (Contreras and Sordillo, 2011). Consequently, stressors and poor nutritional management that decrease voluntary DMI will result in large increases in TAG mobilization and consequently NEFA concentrations immediately after calving. Increased ketogenesis, which occurs when glucose supply is limited during NEB, can result in ketosis (Drackley et al., 2001). Fatty acids taken up in excess of what can be oxidized to CO₂ or ketone bodies are re-converted to TAG. Because ruminant animals are unable to effectively export TAG from the liver as very low density lipoproteins, TAG can accumulate and cause fatty liver (Drackley et al., 2001).

**Glucose and protein metabolism**

Dairy cows rely extensively on hepatic gluconeogenesis from propionate to meet their glucose requirements. Limited DMI after calving limits the supply of propionate for glucose synthesis, and therefore increase conversion of amino acids from the diet or from skeletal muscle, particularly alanine and glutamine, and glycerol from mobilized adipose TAG to glucose. Gluconeogenic activity of liver tissue increases around and after calving to help maintain supply of glucose to the mammary gland and prevent hypoglycoemia (Drackley and Cardoso, 2001).

Limited protein reserves exist in dairy cows, primarily in the form of skeletal muscle protein. Muscle protein mobilization, as estimated by plasma concentrations of 3-methyl-histidine, is increased during the first week after calving compared with prepartment values (van der Drift et al., 2012). Loss of muscle mass may begin before calving and before the initiation of fat mobilization (van der Drift et al., 2012). Maintenance of maternal stores of protein is important for long-term health, productivity and reproduction (Bell et al., 2000). Deficiency in metabolizable protein supply may be linked to ketosis (van der Drift et al., 2012; Lean et al., 2013a) and other peripartal diseases (Roche et al., 2013), which in turn may decrease fertility.

**Immune system function**

Function of the immune system is depressed during the transition period (Ingvarsten and Moyes, 2013). Decreased ability of the immune system to respond to infectious challenges likely is responsible for the high incidence of environmental mastitis around calving, as well as the high incidence of metritis. Retained placenta also has been linked to failure of the immune system to recognize the placenta as a foreign tissue (Kimura et al., 2002). Reasons for the decreased immune function are not clear. Vitamins A and E as well as trace minerals (selenium, copper, zinc) play a role in immune function. Cows that seem to be the most stressed by nutrition and environmental factors, as judged by excessive loss of BCS, are the most likely to become ill. Negative balances of energy or metabolizable protein may be a major contributing factor (Ingvarsten and Moyes, 2013). Galvão et al. (2010a) found that glycogen content of neutrophils (reserve of glucose, the main fuel for neutrophil functions) was lower in early postpartum cows, and was associated with decreased functions of those cells. An inadequate supply of metabolizable protein has been related to impaired function of the immune system (Houdijk et al., 2001).

**Calcium metabolism**

The sudden onset of milk synthesis results in a tremendous demand for calcium. As a result, concentrations of calcium in blood can drop precipitously at calving, leading to milk fever. Subclinical hypocalcaemia is more common, with more than 40% of cows entering the second or greater lactation affected (Reinhart et al., 2011). Subclinical hypocalcaemia contributes to disorders such as displaced abomasum and ketosis by decreasing smooth muscle function critical for normal function of the digestive tract (Horst et al., 1997), which can result in decreased DMI. Hypocalcaemia may compromise function of immune cells (Kimura et al., 2006). Until the ability of the digestive tract to absorb calcium can increase, calcium must be obtained from bone resorption. Metabolic acidosis caused by a negative dietary cation-anion difference (DCAD) favors mobilization of calcium from bone, whereas high dietary potassium concentrations and positive DCAD suppress mobilization (Horst et al., 1997; Lean et al., 2013b). Magnesium participates in the regulation of bone resorption (Horst et al., 1997).

Nutritional intervention to help prevent hypocalcaemia likely must be instituted at least 14 days before calving to be effective (Horst et al., 1997). De Garis et al. (2010) reported that increasing the number of days cows consumed a close-up diet before calving increased pregnancy rates in two of three commercial herds, and tended to increase the proportion of cows pregnant at 6 weeks and 21 weeks after beginning the insemination period.

**Nutritional management to control NEB and optimize fertility**

Postpartal NEB results from initiation of milk synthesis, but the degree of NEB in individual cows is poorly related to milk production or milk energy secretion. The depth and duration of NEB are highly related to DMI (Zurek et al., 1995; Drackley et al., 2005). Consequently, feeding and management strategies for dry cows, transition cows and
fresh cows should seek to meet nutrient requirements but promote appetite and vigorous DMI after calving (Grummer et al., 2004). In TMR systems, a diet must be formulated to meet the nutrient needs of most cows within the group rather than allotting amounts of concentrate based on milk production. Proper nutritional formulation of the diet is essential to ensure that supply of all nutrients will be in balance.

Some important factors to promote good appetites and high DMI after calving include (1) minimizing environmental stressors and keeping cows comfortable, (2) avoiding excessive BCS, (3) preventing over-consumption of energy relative to requirements during the dry period, (4) ensuring adequate intake of forage effective fiber and avoiding excessive intakes of rapidly fermentable starch in the post-calving diet, (5) reducing the DCAD before calving but increasing it in the fresh cow diet and (6) nutritional support of the immune system (see earlier section). Nutritional strategies proposed to assist cows in making these adaptations have been reviewed (Friggens et al., 2004; Beever, 2006; Ingvartsen, 2006; Drackley and Dann, 2008; Lean et al., 2013a and 2013b; Roche et al., 2013). Selected aspects are discussed in the following sections.

Maximize cow comfort and minimize stressors
Non-nutritional management that maximizes cow comfort and welfare plays a huge role in transition success. Bach et al. (2008) found that non-nutritional management accounted for >50% of the variation in mean milk production (20.6 to 33.8 kg/day) among 47 herds fed exactly the same TMR. Although not demonstrated directly in dairy cows, a common feature of environmental or behavioral stress in other animals is disruption of barrier function of the gastrointestinal epithelia, which may allow translocation of endotoxins and cause systemic inflammation (Pearce et al., 2013). Ametaj et al. (2005) found a strong relationship between blood indicators of inflammation (acute phase proteins, TNFα) and hepatic lipid accumulation in dairy cows. Emmanuel et al. (2007 and 2008) demonstrated that increasing amounts of barley grain increased concentrations of endotoxin in rumen fluid, and at low rumen pH the transfer of endotoxin across the rumen epithelium was increased. Intermittent administration of endotoxin triggered metabolic and inflammatory responses typically associated with displaced abomasum and retained placenta (Zebeli et al., 2011). These findings raise the fascinating prospect that at least some periparturient diseases result from adverse ruminal conditions caused by excessive grain in the precalving or fresh cow diet, perhaps aggravated by overcrowding, heat stress or other stressors. Others also have implicated inflammatory responses in alterations of metabolism, occurrence of health problems and impaired reproduction (Bertoni et al., 2008; Graugnard et al., 2012).

Non-nutritional stressors may decrease DMI and predispose cows to postpartum health problems. Cows that developed metritis (Hammon et al., 2006; Huzzy et al., 2007) or ketosis (Goldhawk et al., 2009) after calving had lower DMI or reduced feeding behavior before calving. Lower prepurpartum DMI per se likely is not causative, because individually fed cows restricted to 80% of their energy requirements (fed in two meals daily) did not have greater occurrence of metritis or ketosis (Dann et al., 2005 and 2006; Douglas et al., 2006; Janovick et al., 2011).

Optimize BCS
The role of excessive BCS in contributing to transition problems and impaired subsequent reproduction is well established and has been discussed by many authors (Drackley et al., 2005; Garnsworthy et al., 2008; Roche et al., 2013). Cows with excessive body lipid reserves mobilize more of that lipid around calving, have poorer appetites and DMI before and after calving, have impaired immune function, have increased indicators of inflammation in blood and may be more subjected to oxidative stress (Contreras and Sordillo, 2011). What constitutes ‘excessive’ BCS relative to the cow’s biological target remains controversial. Garnsworthy (2007) argued that the average optimal BCS has decreased over time with increased genetic selection for milk yield, perhaps related to correlated changes in body protein metabolism. Recommendations for optimal BCS at calving have trended downward over the last two decades, and in the authors’ opinion a score of about 3.0 (1 to 5 scale) represents a good goal at present. Adjustment of average BCS should be a longstanding project and should not be undertaken during the dry period.

Prevent over-mobilization of body lipid
Health disorders related to excessive mobilization of body TAG stores have been studied for many years but remain a problem in many dairy herds. Such problems actually are more relevant in modern TMR-fed dairy herds, particularly with the increasing reliance on corn (maize) silage as a primary forage in many areas of the world. For example, in four large commercial herds (over 10 000 cows sampled), McArt et al. (2012) found that peak incidence and prevalence of subclinical ketosis (blood BHBA 1.2 to 2.9 mmol/l) was at 5 days postpartum, suggesting that problems in transition may be highly involved in etiology. High concentrations of NEFA before and after calving can decrease DMI, lead to hepatic lipid accumulation and ketosis, negatively affect the immune system, lead to oxidative stress and inflammation, and are negatively associated with return to reproductive function (Bosseart et al., 2008; Contreras and Sordillo, 2011). In addition to management-related stressors and excessive BCS, dietary energy management during the dry period and prepurpartum period is important.

While use of ‘steam-up’ or ‘close-up’ diets before calving has been widely recommended for many years, there is an almost uniform lack of positive effects on health, production or reproduction in the literature. The simplest and most easily defended principle of nutrition for dairy cows during the dry period and transition is to feed to meet but not greatly exceed requirements (Drackley and Dann, 2008). Although not new, this concept has been incorporated into practical systems suitable for modern dairy management practices on both small and large dairies.
Manage pre-calving energy intake

Our research group has shown that controlling energy intake during the dry period to near calculated requirements leads to better transition success (Grum et al., 1996; Dann et al., 2005 and 2006; Douglas et al., 2006; Janovick et al., 2011; Graugnard et al., 2012 and 2013; Ji et al., 2012). Our research drew from earlier reports that limiting nutrient intakes to requirements of the cows was preferable to over-consumption of energy (e.g. Kunz et al., 1985). Cows fed even moderate-energy diets (1.50 to 1.60 Mcal NEL/kg DM) will easily consume 40% to 80% more net energy for lactation (NEL) than required during both far-off and close-up periods (Dann et al., 2005 and 2006; Douglas et al., 2006; Janovick and Drackley, 2010). Cows in these studies were all <3.5 BCS (1 to 5 scale) at dry-off, and were fed individually TMR based on corn silage, alfalfa silage and alfalfa hay with some concentrate supplementation. We have no evidence that the extra energy and nutrient intake was beneficial in any way. More importantly, our data indicate that allowing cows to over-consume energy even to this degree may predispose them to health problems during the transition period if they face stressors or challenges that limit DMI.

Our studies indicate that prolonged over-consumption of energy during the dry period can decrease post-calving DMI (Dann et al., 2006; Douglas et al., 2006; Janovick and Drackley, 2010). Over-consuming energy results in negative responses of metabolic indicators, such as higher NEFA and BHBA in blood and more TAG in the liver after calving (Douglas et al., 2006; Janovick et al., 2011). Alterations in cellular and gene-level responses in liver (Loor et al., 2006 and 2007) and adipose tissue (Ji et al., 2012) potentially explain many of the changes at cow level. Over-consumption of energy during the close-up period increases the enzymatic ‘machinery’ in adipose tissue for TAG mobilization after calving, with transcriptional changes leading to decreased lipogenesis, increased lipolysis and decreased ability of insulin to inhibit lipolysis (Ji et al., 2012). Controlling energy intake during the dry period also improved neutrophil function postpartum (Graugnard et al., 2012) and so may lead to better immune function.

Our data demonstrate that allowing dry cows to consume more energy than required, even if cows do not become noticeably over-conditioned, results in responses that would be typical of overly fat cows. Because energy that cows consume in excess of their requirements must either be dissipated as heat or stored as fat, we speculated that the excess is accumulated preferentially in internal adipose tissue depots in some cows. Moderate over-consumption of energy by non-lactating cows for 57 days led to greater deposition of fat in abdominal adipose tissues (omentum, mesenteric, and perirenal) than in cows fed a high-bulk diet to control energy intake to near requirements (Drackley et al., 2014). The NEFA and signaling molecules released by visceral adipose tissues travel directly to the liver, which may cause fatty liver, subclinical ketosis and secondary problems with liver function.

Data from our studies support field observations that controlled-energy dry cow programs decrease health problems (Beever, 2006). Other research groups (Rukkwansuk et al., 1998; Holcomb et al., 2001; Holtenius et al., 2003; Vickers et al., 2013) have reached similar conclusions about controlling energy intake during the dry period, although not all studies have shown benefits (Winkleman et al., 2008). Application of these principles can be through controlled limit-feeding of moderate energy diets or ad libitum feeding of high-bulk, low-energy rations (Janovick and Drackley, 2010; Janovick et al., 2011; Ji et al., 2012) as proposed by others (Beever, 2006).

Effects of controlling prepartum energy intake on fertility

Individual studies such as these lack statistical power to accurately determine effects of diet on milk production, disease incidence and reproductive success. Therefore, Cardoso et al. (2013) conducted a pooled statistical analysis of seven studies (cow was the experimental unit) at the University of Illinois to investigate associations between prepartum energy feeding regimen and reproductive performance. Days to pregnancy (DTP) was the dependent variable to assess reproductive performance. Individual data for 408 cows (354 multiparous and 54 primiparous) were included in the analysis. The NEL intake (NELI) was calculated from each cow’s respective dietary NEL density and average DMI. Nutritional treatments applied prepartum were classified as either controlled energy (CE; median NELI = 13.7 Mcal/day) or high energy (HE; median NELI = 22.1 Mcal/day) diets fed during the far-off (FO) or close-up (CU) dry periods.

The Cox proportional hazard model revealed a significant difference in DTP between HE and CE during the CU period (median = 167 and 157 days; hazard ratio = 0.696; Figure 1). Cows fed HE diets during the last 4 weeks prepartum lost more BCS (1 to 5 scale) in the first 6 weeks postpartum than those fed CE (−0.43 and −0.30, respectively). Cows fed CE during the FO period had lower concentration of NEFA in weeks 1, 2 and 3 of lactation compared with cows fed HE. Higher NEFA concentration in week 1 postpartum was associated with a greater probability of diseases (n = 251; odds ratio = 1.176). Cows that were fed HE during the dry period had greater odds of experiencing displaced abomasum or ketosis than cows that received CE.

Cows fed the CE regimen during the FO period had greater concentrations of glucose in plasma during weeks 1 and 3 after calving than HE cows. In the first 2 weeks after calving, cows that received HE in the FO period had higher concentrations of total lipids and TAG and greater TAG : glycogen in liver than CE. The positive effect of CE during the CU to decrease DTP may be explained by increased NEL intake during the first 4 weeks postpartum and lower incidence of peripartal diseases. In addition, lower BCS loss during the first 6 weeks postpartum and slightly higher glucose concentration at week 3 likely contributed to improved reproductive performance.

Our current working hypothesis to explain these results is that cows over-consuming energy (especially from starch)
begin to display metabolic characteristics similar to human type II diabetes or metabolic syndrome (Janovick et al., 2011). Cows were in moderate to low BCS, but their metabolic profiles resembled those seen in over-conditioned cows. Cows that over-consumed during the first 5 weeks of the dry period had similar blood glucose but greatly elevated insulin (indirectly suggesting insulin resistance), and during the close-up period had greater concentrations of NEFA and BHBA than cows fed restricted amounts of the same diet or a bulky low-energy diet (Dann et al., 2006). Although insulin receptor function in adipose tissue was not impaired, insulin’s anti-lipolytic signals were down-regulated so that there was less suppression of TAG lipolysis (Ji et al., 2012). Along with increased lipolytic gene expression (Ji et al., 2012), this would lead to increased NEFA and then to decreased DMI according to the hepatic oxidation theory of intake control (Allen et al., 2009). Schoenberg and Overton (2011) demonstrated that cows fed to slightly above requirements had greater decreases in plasma NEFA in response to a glucose challenge compared with cows that over-consumed energy, which agrees with our in vitro metabolic data (Ji et al., 2012). We are currently following up on several aspects related to these phenomena.

**Management of CE diets**

It is important to note that nutritionally complete diets must be fed and that the TMR must be processed appropriately so that cows do not sort the bulkier ingredients (Janovick and Drackley, 2010). Feeding bulky forage separately from a partial TMR or improper forage processing will lead to variable intake among cows, with some consuming too much energy and some too little. Underfeeding relative to requirements, where nutrient balance also is likely limiting, leads to increased incidence of retained placenta and metritis (Mulligan et al., 2006). Merely adding a quantity of straw to a diet is not the key principle; rather, the diet must be formulated to limit the intake of energy (~1.3 Mcal NEL/kg DM, to limit intake to about 15 Mcal/day for typical Holstein cows, or 9 MJ ME/kg DM to limit intake to about 100 MJ/day) but meet the requirements for protein, minerals and vitamins. Reports of increased transition health problems or poor reproductive success (Whitaker et al., 1993) with ‘low-energy’ dry cow diets must be examined carefully to discern whether nutrient intakes were adequate.

**Postpartum (fresh cow) dietary considerations**

Less is known about diet formulation for the immediate postpartum period to optimize transition success and subsequent reproduction. Increased research is needed in this area. Proper dietary formulation during the dry period or close-up period will maintain or enable rumen adaptation to higher grain diets after calving. Failure to do so may compromise early lactation productivity. For example, Silva-del-Rio et al. (2010) attempted to duplicate the dietary strategy of Dann et al. (2006) by feeding either a low-energy far-off diet for 5 weeks followed by a higher-energy diet for the last 3 weeks before parturition, or by feeding the higher-energy diet for the entire 8-week dry period. They found that cows fed the higher-energy diet for only 3 weeks before parturition produced less milk than cows fed the diet for 8 weeks (43.8 v. 48.5 kg/day). However, the far-off dry period diet contained 55.1% alfalfa silage and 38.5% wheat straw but no corn silage. In comparison, the higher-energy dry period diet and the early lactation diet both contained 35% corn silage. Ruminal adaptation likely was insufficient for cows fed the higher energy diet for only 3 weeks.

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**Figure 1** Survival function curves for days to pregnancy (DTP) for 332 Holstein cows fed either controlled energy (CE = blue) or high energy (HE = red) during the last 4 weeks before calving. Blue and red lines represent median values for DTP when 50% of the cows were pregnant. Drawn from data in Cardoso et al. (2013).
A major area of concern in the fresh cow period is sudden increase in dietary energy density leading to subacute ruminal acidosis (SARA), which can decrease DMI and digestibility of nutrients (Mulligan and Doherty, 2008). Adequate physical form of the diet, derived either from ingredients or mixing strategy, must be present to stimulate ruminal activity and chewing behavior (Zebeli and Metzler-Zebeli, 2012), although good methods to quantify 'adequacy' remain elusive. Dietary starch content and fermentability likely interact with forage characteristics and ration physical form. Dann and Nelson (2011) compared three dietary starch contents (primarily from corn starch) in the fresh cow period for cows fed a CE-type ration in the dry period. Milk production was greatest when starch content was moderate (23.2% of DM) or low (21.0% of DM) in the fresh cow diet compared with high (25.5% of DM). If SARA decreases DMI and nutrient availability to the cow, NEFA mobilization and increased ketogenesis may follow. In addition, rapid starch fermentation in the presence of NEFA mobilization leads to bursts of propionate reaching the liver, which may decrease feeding activity and DMI according the hepatic oxidation theory (Allen et al., 2009). A moderate starch content (ca. 23% to 25% of DM) with starch of moderate fermentability (e.g. ground dry corn rather than high-moisture corn or ground barley) along with adequate effective forage fiber may be the best strategy for fresh cows. Recent research also has demonstrated that high grain diets can lead to greater numbers of gram-negative bacteria such as Escherichia coli with resulting increases in endotoxin present in the rumen, which may decrease barrier function and inflammatory responses in the cow (Zebeli and Metzler-Zebeli, 2012).

As discussed in a previous section, insulin enhances ovarian follicle development but may impair oocyte quality and development. Garnsworthy et al. (2008) proposed that feeding a glucogenic diet (higher in starch) until cows resumed ovarian cyclicity followed by a higher fat (lipogenic) diet during the breeding period would improve reproductive success. In subsequent research, the number of cows pregnant at 120 days was greater for cows fed a glucogenic (high-starch) diet that increased insulin early postpartum followed by the lipogenic diet (higher fat) during the breeding period (Garnsworthy et al., 2009). More recent studies have not confirmed this effect (Dyck et al., 2011; Gilmore et al., 2011) although diets and experimental conditions differed and cow numbers were limited. The aim to increase early postpartum insulin by feeding higher starch diets must be tempered by the need to maintain optimal rumen health and digestion.

Supplemental fats have been widely investigated as a way to increase dietary energy intake and improve reproduction (Thatcher et al., 2011). A novel strategy to use polyunsaturated fatty acid (PUFA) supplements to improve reproduction has been reported (Silvestre et al., 2011). Cows fed calcium salts of safflower oil from 30 days before to 30 days after calving, followed by calcium salts of fish oil to 160 days postpartum, had greater pregnancy rates and higher milk production. The mechanism is believed to be provision of greater amounts of linoleic acid (n-6 PUFA) until early postpartum, which improves uterine health, followed by greater amounts of n-3 PUFA from fish oil to decrease early embryonic loss (Thatcher et al., 2011).

The effects of turbulent transitions on reproduction are established early postpartum, likely during the first 10 days to 2 weeks postpartum (Butler, 2003; McArt et al., 2012; Garverick et al., 2013). By 8 weeks postpartum, >95% of cows should be at or above energy balance (Sutter and Beever, 2000). Use of targeted prepartum and postpartum strategies may minimize health problems and lessen NEB, and thereby improve subsequent fertility. Combinations of strategies such as the glucogenic-lipogenic concept and the n-6/n-3 concept seem especially intriguing and worthy of continued investigation.

Conclusion

In TMR systems, formulation and delivery of appropriate diets that limit total energy intake to requirements but also provide proper intakes of all other nutrients before calving can help lessen the extent of NEB after calving. Effects of such diets on indicators of metabolism are generally positive, suggesting the potential to lessen effects of periparturient diseases on fertility. Strategies for diet formulation to improve DMI and lessen NEB of fresh cows are less well researched, but the balance between adequate physically effective fiber and starch fermentability is critical. Continued development of innovative strategies such as manipulation of glucogenic to lipogenic nutrients and essential fatty acid supply should pay dividends to fertility.

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