The Role of Energy Balance and Metabolism on Reproduction of Dairy Cows

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Introduction

Over the last several decades, large increases in milk production capability among dairy cows have been associated with declining fertility. Conception rate in large commercial dairy herds in the USA stands at 25-40 % for mature cows (Butler, 2003).

In high genetic merit cows, feed intake and energy balance begin decreasing prepartum that results in mobilization of body fat as nonesterified fatty acids (**NEFA**) into the blood (Butler et al., 2006). The onset of lactation after calving is associated with a prolonged period of negative energy balance (**NEBAL**) during which energy intake lags behind the energy requirements of rapidly increasing milk production.

With regard to fertility to AI, there is a strong positive association between early commencement of postpartum ovulatory cycles and subsequent pregnancy (Butler, 2000; Galvao et al., 2010). This important relationship has focused research attention on the regulation and re-initiation of ovarian activity and ovulatory cycles in early lactation prior to the breeding period. Energy balance, re-initiation of ovarian activity, and metabolic health status are inter-connected in transition cows.

ENERGY BALANCE-RELATED FACTORS AFFECT RESUMPTION OF OVARIAN ACTIVITY IN TRANSITION COWS

Relationships during the Transition Period

The transition period is considered to extend from 3 wk before calving through the first 3 wk of lactation. During late pregnancy elevated plasma levels of steroid hormones (estradiol and progesterone) suppress the release of pituitary gonadotropins (LH and FSH) and ovarian follicular activity. Following calving, steroids are reduced and increased secretion of FSH and LH pulses become re-established to stimulate development of large ovarian follicles and ovulatory ovarian cycles. With the onset of lactation, the liver must support a heavy and rapidly increasing metabolic load for glucose production and fatty acid oxidation. The liver plays an important role as a site of NEFA metabolism and as the primary source of insulin-like growth factor-I (**IGF-I**) that stimulates development of ovarian follicles. The functional activity of these various tissues is negatively influenced by NEBAL (Butler, 2003). Changes in dry matter intake (**DMI**) begin prepartum and are the most important determinant of energy status.

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Decreasing DMI is associated with lower blood concentrations of the metabolic hormones, insulin and IGF-I (Butler et al., 2006).

Metabolic Hormones and Re-initiation of Ovarian Activity Postpartum

Negative energy balance, acting through the combined metabolic signaling of low blood glucose and insulin concentrations along with elevated NEFA, β-hydroxybutyrate (**BHBA**), and liver accumulation of triglycerides delays the increases in LH and FSH necessary for stimulation of ovarian follicles, estradiol production, and ovulation (Butler et al., 2006). Low blood insulin concentrations are responsible for low IGF-I production from the liver (Butler et al., 2003) which together reduce responsiveness of ovarian follicles to gonadotropins. Physiologically the metabolic and gonadotropin signals controlling early follicle development are interrelated: FSH stimulates granulosa cells in follicles to develop receptors for insulin, growth hormone and IGF-I; insulin and IGF-I then provide the hormonal stimulus for full development of preovulatory ovarian follicles (Kawashima et al., 2007; Shimizu et al., 2008; Sudo et al., 2007).

The changing profile of metabolites and metabolic hormones that evolves during NEBAL also provide important signals and cues for pulsatile LH secretion. The degree of NEBAL alters whether LH pulse frequency during the first follicular wave is sufficient to stimulate high estradiol production for ovulation (Beam and Butler, 1999). Inadequate LH pulse frequency results in follicular atresia and delays the occurrence of first ovulation for several weeks. Overall, FSH secretion does not seem to be inhibited by NEBAL, but more biologically effective isoforms are produced in cows with less severe NEBAL (Butler et al., 2008).

By way of various metabolic factors, interactions and responses, NEBAL shifts the course of postpartum ovarian activity and strongly influences the resumption of ovulatory cycles. At least one large follicle develops on the ovaries in all dairy cows by 6-8 d after calving. What is different among cows is that this first large follicle has 3 outcomes which relate to the variation among cows in days to first ovulation:

a) Ovulation occurs successfully in about 45% of cows by around d 20 of lactation;
b) Atresia (death) of the follicle occurs; <u>or</u>
c) The follicle becomes cystic.

In either case b *or* c, first ovulation is delayed at least an additional 3-4 wk (Beam and Butler, 1999).

Prepartum Differences in DMI, Energy Balance and Metabolic Hormones Associated with Postpartum Follicle Outcome

In a recent study, follicle development was monitored beginning 1 wk postpartum for determination of ovulatory or nonovulatory outcome and comparison, retrospectively, with differences in prepartum DMI, energy balance, and metabolic hormone profiles (Butler et al., 2006). The main difference between ovulatory or nonovulatory follicles is their capacity to produce large amounts of estradiol. As early as 3 wk prepartum, the nonovulatory low estradiol cows would have lower DMI, energy balance, and plasma concentrations of insulin and IGF-I. Negative energy balance was more severe for nonovulatory cows. Overall, NEBAL is minimized in cows that maintain high DMI until the day of calving and rapidly increase their intake, thereafter, over the first several weeks of lactation. It is well established that DMI on d 21 of lactation is directly related to DMI on the day before calving (Grummer, 1995; Trevisi et al., 2002). Figure 1 summarizes changes in DMI throughout the transition period and body weight loss ie. NEBAL for cows ovulating (**OV**) early after calving or with nonovulatory follicles (**NOV**).

Variation between cows in the extent of NEBAL is directly related to differences in DMI and whether decreases in DMI occurs early or late relative to calving (*e.g*., -9 d *vs*. -1 d*).* Body condition score (**BCS**) is one major cow factor related to decreased DMI during the close-up dry period. Overconditioning (BCS > 4) reduces DMI (Drackley et al., 2005) and increases the risk of metabolic disorders. Maintaining moderate BCS (~3.00) until calving is currently recommended.

NEBAL, BCS Loss and DMI in Early Lactation

In early lactation dairy cows, the extent of NEBAL is apparent from degree of BCS loss. Cows with more severe NEBAL lose more BCS during the first 30 d of lactation and experience longer intervals to first ovulation (Butler, 2005). The variation in the degree of NEBAL among individual cows is explained largely by differences in energy intake rather than milk yield (Villa-Godoy et al., 1988; Zurek et al., 1995). The importance of DMI is demonstrated by grouping cows by days to first postpartum ovulation and calculating gross efficiency of milk production. Cows with the lowest efficiency ratio (milk production/DMI) have the shortest interval to first ovulation. Conversely, the most efficient cows (highest milk production compared to DMI) have extended delays to first ovulation (Figure 2). Since the energy efficiency of milk production is similar in all cows, the cows producing more milk per unit DMI experience more severe NEBAL as more of the energy requirement for milk is derived from body reserves rather than dietary intake. This is an unusual situation where ***high efficiency is not beneficial*** because delayed onset of ovulatory cycles results in lower fertility.
The bottom line - high producing cows that increase DMI to better match requirements for milk production will have better energy status and likelihood of higher fertility during breeding.

CARRYOVER EFFECTS OF EARLY NEBAL ON FERTILITY

Prolonged Anovulatory Periods

Using cows that lose ≤ 0.5 BCS during the first 30 d of lactation as an example, more than 90% will initiate ovulatory cycles by 60 d of lactation (DIM; see Figure 3, left panel). However, by comparison as many as 30-40% of cows losing more than 0.5 BCS in early lactation may remain anovulatory. Cows remaining anovulatory beyond 50 DIM have increased risk of non-pregnancy by 225 DIM with the consequence of being culled at the end of lactation (Figure 3, right panel).

Conception Rate to AI

Delayed ovulation and insemination provides some explanation for the observed low pregnancy rate; however, as loss of BCS becomes more extensive, the reduction in conception rate to AI becomes greater (See Butler, 2003 and Roche et al., 2009 for reviews). Cows losing one unit or more BCS (5 point scale) during early lactation are at greatest risk for low fertility. As a guideline, conception rate decreases about 10% per 0.5 unit BCS loss (Butler, 2001; Santos et al., 2009). Extended calving to conception intervals were associated with low BCS by wk +7 and greater peak milk yield (Patton et al., 2007; Wathes et al., 2007).

Oocyte and Embryo Quality

Another possible carryover effect of early NEBAL may be that oocytes are imprinted by deleterious conditions within the follicle during their development period of 60-80 d. Evidence has been reviewed on the metabolic environment during NEBAL that may impair oocyte development and embryo quality (Leroy et al., 2008a; Leroy et al., 2008b). One consequence of more severe NEBAL on fertility is through reduced circulating levels of IGF-I. Cows which failed to become pregnant despite multiple AI had low IGF-I in the week after calving and continuing low plasma IGF-I values through the breeding period (Taylor et al., 2004). Another study found a high incidence of inferior embryo quality and viability in normal healthy high-producing cows in early lactation as compared to embryos from non-lactating cows (Sartori et al., 2002). One novel approach has been to compare conception rates in lactating cows following AI (n=227) *vs.* embryo transfer (ET, n=160) using good quality embryos from non-lactating cows. Pregnancy rate (d 42) was higher with ET (47%) *vs.* AI (34%) suggesting that high milk production is associated with lower oocyte/embryo viability, *ie.* the cows' own oocyte (Demetrio et al., 2007). Therefore, these collective results indicate a detrimental impact of NEBAL on oocyte competency for embryo development, but metabolic effects may be exerted continuously during high milk yield.

Uterine Conditions Postpartum

Uterine tissues were collected from cows 2 wk postpartum to evaluate gene expression and immune responses related to NEBAL. Cows in more severe NEBAL were still undergoing more active uterine inflammatory response compared to moderate NEBAL cows that had reached a more advanced stage of repair. Severe NEBAL prevents a more effective immune response to microbial challenge after calving, prolonging the time required for uterine recovery and compromising subsequent fertility (Wathes et al., 2009).

Subclinical endometritis (**SCE**) is characterized by an increased proportion of polymorphonuclear (**PMN**) cells in uterine fluid at 35-49 DIM. SCE is prevalent in high-producing dairy cows and has been associated with delayed resumption of ovarian cyclicity (Senosy et al., 2009) and extended intervals to pregnancy (Galvao et al., 2009; Gilbert et al., 2005; Sheldon et al., 2009).

NUTRITIONAL AND MANAGEMENT STRATEGIES

Increased Energy Intake to Improve Energy Balance

Dairy cow diets are supplemented with fat primarily to increase energy density and to enhance milk production and reproduction (recently reviewed in Santos et al., 2008). The benefits observed for reproduction are most likely mediated by unsaturated fatty acids (**FA**) available from the lipid sources, but this is difficult to predict because microbial activity in the rumen results in biohydrogenation of > 70-85 % of the unsaturated FA, even when fed as rumen inert calcium salts (Castaneda-Gutierrez et al., 2007; Santos et al., 2008). Data from multiple studies demonstrate that supplemental FA, whether more saturated or unsaturated, do not hasten resumption of postpartum ovulatory cycles in dairy cows. However, supplementation with unsaturated FA (trans-octadenoic and linoleic acids) have been shown to improve embryo quality and development, leading to overall higher pregnancy rates and reduced pregnancy losses (as reviewed by Santos et al., 2008; Cerri et al., 2009; Juchem et al., 2010). Perhaps by the same or a separate mechanism, feeding omega-3 unsaturated FA in fish oil exerted immunosuppressive effects during the breeding period in association with improved fertility in dairy cows (Silvestre et al., 2011).

Decreased Dry Period Length Reduces NEBAL and Improves Fertility

Nutritional strategies to improve energy balance during the transition period and early lactation have included supplemental dietary fat and higher nonfiber carbohydrate, but neither approach has shown consistent benefits. An alternative strategy of shortening the dry period has been proposed as a means to improve energy status of dairy cows after calving through enhanced DMI or moderate decreases in milk energy output (Grummer, 2007; 2011). As reviewed by Grummer and co-workers (Grummer et al., 2010), reducing the dry period length from 55 to 34 d decreased days to first ovulation after calving, percentage of anovulatory cows, and days to pregnancy. Reduction in days open was confirmed for older cows, but not for second parity cows. Shortening the dry period, especially for older cows appears to be a successful strategy for improving reproductive efficiency. Further research is necessary to investigate the optimum diets (high energy vs. high fiber) during shortened dry periods (Grummer, 2011).

Summary

Negative energy balance (NEBAL) may begin prepartum in association with declining feed intake. Excess body condition is one factor related to decreased feed intake. During the first 3 wk of lactation, NEBAL delays early ovulation and recovery of postpartum reproductive function and provides the major nutritional link to low fertility in lactating dairy cows. NEBAL may detrimentally impact the oocyte that is released after ovulation and exert other carryover effects on uterine conditions resulting in reduced conception rate to insemination. Reducing NEBAL is beneficial, but very difficult to achieve in cows being managed for high milk yield. Maintaining energy intake through the prepartum period to calving and increasing intake rapidly thereafter reduce NEBAL and the detrimental effects on coordinated ovarian and liver function. Utilization of FA supplements may provide a useful strategy to improve reproductive performance in lactating cows. Management of feed intake, nutrition, and metabolic health of lactating cows for improved reproductive performance begins in the transition period and continues through early lactation.

Conclusions

Metabolic changes in periparturient cows associated with onset of NEBAL appear most responsible for the coordinated detrimental effects on metabolic health and reproductive performance. Negative energy balance during early lactation is related to decreasing feed intake prepartum and provides the major nutritional link to low fertility in lactating dairy cows. Finally, negative energy balance delays early ovulation and recovery of postpartum reproductive function and exerts carryover effects (BCS, oocytes, uterus) that reduce fertility during the breeding period.

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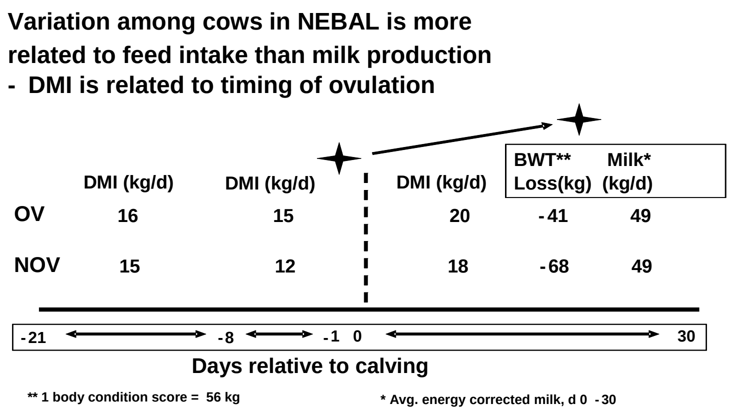

Figure 1. Comparison of changes in pattern of DMI and body weight (BWT) for cows with early (OV) ovulatory or nonovulatory (NOV) follicles after calving. + DMI d -1 is highly correlated to DMI at d 21. From Butler et al., 2006.

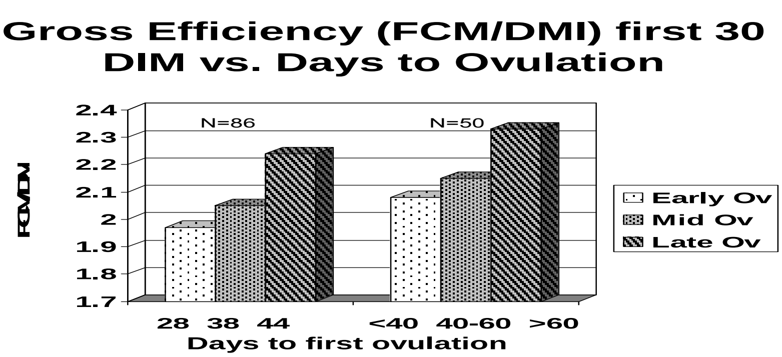

Figure 2. Gross efficiency: kg fat corrected milk (FCM) compared to kg DMI in early lactation dairy cows in two studies. Cows were grouped by days from calving to first ovulation. Cows with high efficiency had delayed ovulation because they were in more severe NEBAL and used more body reserves for energy requirement.

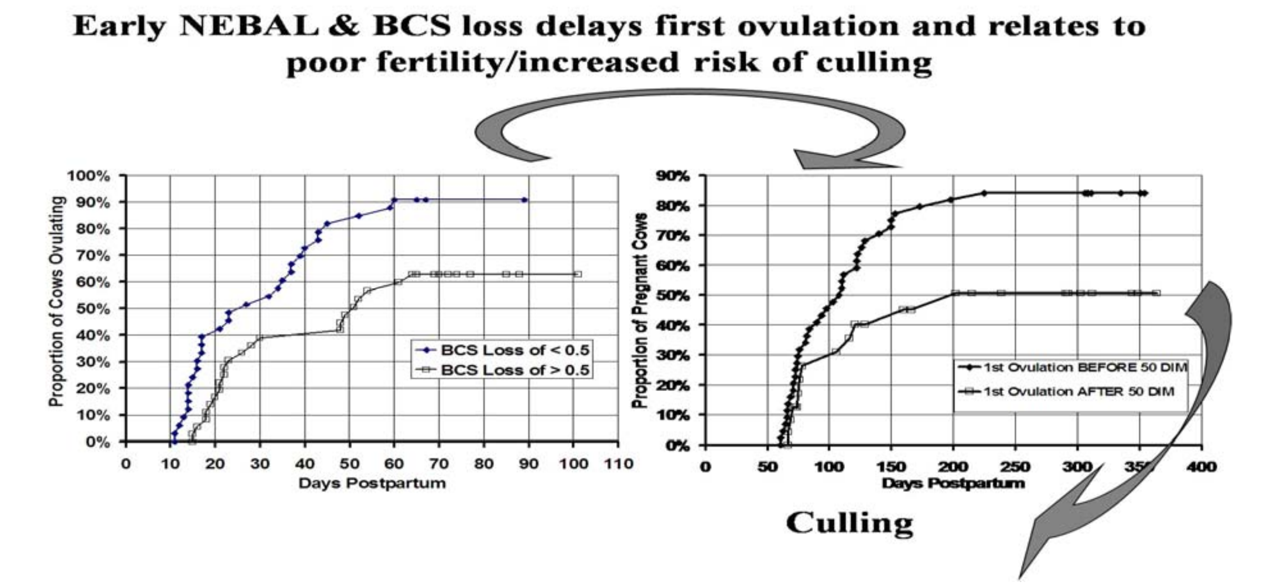

Figure 3. Negative energy balance (NEBAL) results in body condition score loss in early lactation dairy cows. Greater BCS loss (> 0.5 score by 30 days in milk) delays the timing of first ovulation. Among the cows that have delayed ovulation until after 50 days postpartum, pregnancy rate during lactation is reduced and cows remaining open after 225 days are likely to be culled. N = 72 cows in study.

SESSION_NOTES