INTERACTIONS OF NUTRITION WITH REPRODUCTIVE PERFORMANCE IN THE SOUTHEAST

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Introduction

Fertility of the cow herd is 10 times more important than carcass traits and twice as important as growth traits in terms of economic merit for a cow-calf operation (Trenkle and Willham, 1977). Of all the factors potentially capable of influencing fertility, nutrition is undoubtedly the most common. Although many nutrient deficiencies, including protein, minerals and vitamins can depress reproductive performance, energy deficiencies are generally first-limiting and can have a devastating effect on fertility. The purpose of this paper is to: 1) briefly review what is known about the effects of energy deficiency on reproductive performance, with particular attention to the environmental conditions and production practices of the southeast, 2) suggest likely mechanisms whereby nutrition regulates reproduction and 3) introduce new areas of research attempting to solve the nutrition/reproduction puzzle.

Energy Deficiency Before or After Calving

Body condition scoring is a management tool used to estimate the amount of energy reserves in the form of fat that a cow is carrying at any given time. A body condition score (BCS) of 1, for example, designates a cow that is emaciated, whereas a BCS of 9 designates a cow that is extremely obese. With short-haired cattle and in environments where cows don't typically develop a heavy winter hair coat, BCS can be visually assigned. In cooler climates or with long-haired cattle, BCS is determined by feeling for fat cover. A combination of both methods is presented in Table 1.

Research has consistently shown that cows calving in thin body condition and(or) who lose more than 1 BCS unit after calving have a longer interval from parturition to onset of normal estrous cyclicity, a lower first service pregnancy rate and a lower pregnancy rate after a short breeding season (Table 2). The consensus of most researchers, then indicates that mature cows should calve in a BCS $\geq$ 5 and should maintain their condition at a score of 5 or greater during the postpartum period (see reviews by Dunn and Kaltenbach, 1980; Randel, 1990; Dunn and Moss, 1992) in order to obtain optimal reproductive performance.

While BCS at calving determines the length of postpartum anestrus, condition scoring cows at calving does not allow managers sufficient time to markedly change body condition in the cow herd. Therefore, cows should be scored at the time of pregnancy determination such that managers have at least 90 to 120 days before the start of the calving season to get cows in adequate condition by calving. About half of Florida's cow-calf producers manage their cattle to calve in the fall, while the other half of the producers manage cattle to calve in the winter (Beef Survey, 1986). Forage quality, but generally not quantity, during the fall is insufficient

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TABLE 1. SYSTEM OF BODY CONDITION SCORING (BCS) FOR BEEF CATTLE[a]

Group	BCS	Description
Thin Condition	1	EMACIATED - Cow is extremely emaciated with no palatable fat detectable over spinous processes, transverse processes, hip bones or ribs. Tail-head and ribs project quite prominently.
	2	POOR - Cow still appears somewhat emaciated but tail-head and ribs are less prominent. Individual spinous processes are still rather sharp to the touch but some tissue cover exists along the spine.
	3	THIN - Ribs are still individually identifiable but not quite as sharp to the touch. There is obvious palpable fat along spine and over tail-head with some tissue cover over dorsal portion of ribs.
Borderline Condition	4	BORDERLINE - Individual ribs are no longer visually obvious. The spinous processes can be identified individually on palpation but feel rounded rather than sharp. Some fat cover over ribs, transverse processes and hip bones.
Optimum Moderate Condition	5	MODERATE - Cow has generally good overall appearance. Upon palpation, fat cover over ribs feel spongy and areas on either side of tail-head now have palpable fat cover.
	6	HIGH MODERATE - Firm pressure now needs to be applied to feel spinous processes. A high degree of fat is palpable over ribs and round tail-head.
	7	GOOD - Cow appears fleshy and obviously carries considerable fat. Very spongy fat cover over ribs and around tail-head. In fact "rounds" or "pones" beginning to be obvious. Some fat around vulva and in crotch.
Fat Condition	8	FAT - Cow very fleshy and over-conditioned. Spinous processes almost impossible to palpate. Cow has large fat deposits over ribs, around tail-head and below vulva. "Rounds" or "pones" are obvious.
	9	EXTREMELY FAT - Cow obviously extremely wasty and patchy and looks blocky. Tail-head and hips buried in fatty tissue and "rounds" or "pones" of fat are protruding. Bone structure no longer visible and barely palpable. Animal's motility may even be impaired by large fatty deposits.

[a]From Richards et al., 1986.

TABLE 2. EFFECT OF BCS AT CALVING AND DURING THE POSTPARTUM PERIOD ON COW FERTILITY.

Citation	Interval to Estrus (days)		1st Service Preg. Rate (%)		Pregnant in first 40 days	
	Thin[1]	Adeq.[2]	Thin	Adeq.	Thin	Adeq.
Houghton et al., 1987	79[b]	47[a]	98	72	---	---
Richards et al., 1986	60[b]	46[a]	65	67	69[a]	81[b]
Rutter & Randel, 1984	60[b]	32[a]	---	---	---	---
Wiltbank et al., 1962	---	---	38	66	50[a]	95[b]
Wiltbank et al., 1964			54[a]	83[b]	72	92

[a,b]Values in the same column within cow condition without common superscripts differ, $P < .05$.
[1]Thin = BCS < 5.0.
[2]Adequate = BCS ≥ 5.0.

to meet the needs of a last-trimester cow and(or) of a lactating female. Forage quantity and quality are both limiting during the winter in southeastern states. Therefore, supplementation programs must be designed to meet the cow's nutrient demands depending on the season of the year and the cow's own physiological state.

In summary, we know that energy deficiency impairs reproductive performance. However, the effect of energy deficiency on reproduction is indirect, as the calculated nutrient requirements needed for growth of a follicle, transport of sperm and eggs and secretion of reproductive hormones is negligible compared to the energy required for day-to-day functioning of vital organs and other normal physiological processes. Yet, a cow that has insufficient body energy stores or who loses a significant amount of fat experiences depressed fertility. The key to unravelling the mystery, then, lies in the way a cow perceives nutritional inadequacy and what metabolic signal(s) turn the reproductive system on or off.

Mechanisms of Nutritional Regulation of Reproduction

Metabolic pathways: Cows receiving inadequate dietary energy intake to meet production demands undergo characteristic changes in blood concentrations of nutrient metabolites and metabolic hormones (for review, see Bauman and Currie, 1980). Blood metabolic profiles during the postpartum period from a selected experiment are shown in Figure 1. Fat is mobilized from body reserves as reflected by elevated serum concentrations of fat metabolism products, such as β-hydroxybutyrate, glycerol and(or) fatty acids, and by an elevation in the pulsatile secretion of growth hormone, a metabolic hormone involved with fat mobilization. At the same time, blood levels of insulin, the metabolic hormone involved with cellular uptake of glucose and fat deposition into adipocytes, is reduced along with a reduction in insulin-like growth factor-I (IGF-I), which is thought to act in a autocrine/paracrine manner at the cellular level to influence specific cell functions. Glucose levels in the blood may or may not be decreased by inadequate dietary energy, which is likely dependent on the severity and length of energy shortage. In cases of severe energy deficiency, blood levels of urea nitrogen may also be elevated due to catabolism of muscle tissue.

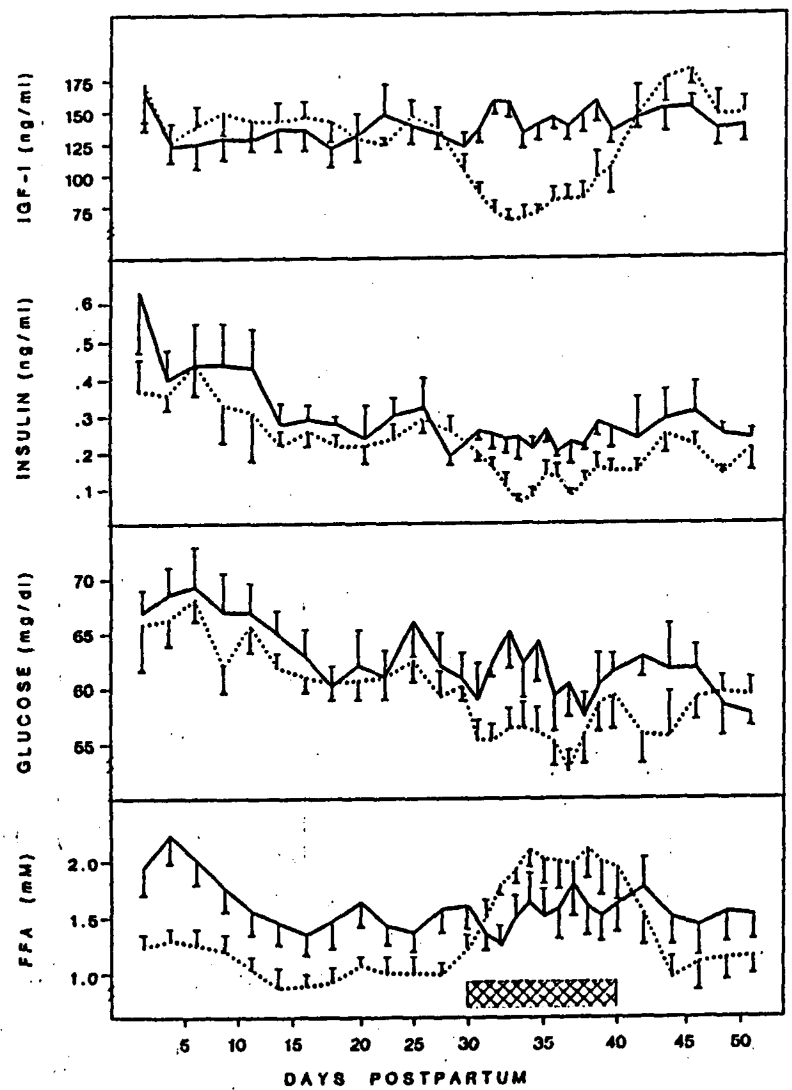

Figure 1. Serum concentrations of IGF-I and insulin and plasma concentrations of glucose and FFA in postpartum beef cows fed ad libitum (-) or restricted to 50% of ad libitum feed intake (----) for 10 d (cross-hatched bar) during the postpartum period. Standard error bars (T) are given for each daily mean. From Rutter et al., 1989.

Attempts to discover the metabolic signal regulating reproduction: Because cows receiving inadequate dietary energy undergo well-documented changes in circulating nutrient metabolite and metabolic hormone levels, it may be reasonably assumed that one or a combination of the metabolites or hormones acts as a metabolic signal to the reproductive system. Early work focused on glucose as a potential signal for the following reasons: 1) glucose is an essential nutrient for normal brain function in the ruminant, as the ruminant cannot substitute other metabolites, such as ketones like monogastrics can; 2) ruminants absorb little, if any, glucose from the diet, but must manufacture this essential nutrient from the ruminal volatile fatty acid, propionate, or from carbon chains released when certain body tissues are degraded; and 3) diets which elevate ruminal propionate concentrations, such as grain feeding or the use of ionophores, have a positive effect on fertility.

To test the hypothesis that glucose was the metabolic signal responsible for nutritional effects on fertility, a number of experiments were conducted. The first experiment used prepuberal heifers abomasally infused with propionic acid to mimic the effect of a grain diet or a diet fed with addition of an ionophore. After 21 days of infusion, heifers receiving propionate had a significantly greater release of pituitary luteinizing hormone (LH) following stimulation by gonadotropin-releasing hormone (GnRH) than heifers receiving saline infusion (figure 2). Propionate-infused heifers also had greater circulating concentrations of glucose compared to saline-infused heifers. These results indicated that glucose could be mediating nutritional effects on fertility potentially by enhancing pituitary production of LH or by increasing the sensitivity of the pituitary to a GnRH stimulus. In the next experiment, postpartum cows were infused with glucose or saline for 7 days beginning at 26 days postpartum (McCaughey et al., 1985). Although glucose infusion significantly increased circulating concentrations of glucose and insulin and decreased free fatty acid levels, glucose had no effect on secretion of LH or on the number of cows ovulating by 53 days postpartum. It was concluded from this study that supplying extra energy to cows in adequate body condition does not enhance reproductive hormone secretion. The following two experiments took a different approach such that, instead of adding glucose to a system already adequate in energy, we would specifically drain glucose from the system with a compound called phlorizin which selectively inhibits glucose uptake by the renal tubules, thereby "dumping" glucose into the urine (Rutter and Manns, 1987, 1988). The amount of phlorizin infused was calculated to cause a daily glucose loss similar to the amount normally found in milk (about 500 g/day). Phlorizin-infused cows showed the characteristic metabolic response to energy deficiency by decreased concentrations of insulin and glucose and elevated concentrations of free fatty acids (figure 3). These two studies showed specifically that a glucose drain reduced LH pulse amplitude, but not frequency of LH pulse release. LH pulse frequency is indicative of the frequency of GnRH release from the hypothalamus to stimulate the pituitary, and LH pulse frequency is thought to be responsible for growth of ovarian follicles. LH pulse amplitude, on the other hand, is indicative of the strength of the hypothalamic stimulus or the ability of the pituitary to respond to a given stimulus. LH pulse amplitude is thought to be involved in the final maturation of a follicle towards ovulation. The lower LH pulse amplitude found with a glucose drain, then, could mean that the quantity of GnRH released by the hypothalamus is insufficient to stimulate normal LH release or that other factors such as ovarian steroids are inhibiting the ability of the pituitary to respond to an appropriate GnRH signal. The end result of this change in LH secretion is a delay in resumption of normal estrous cyclicity in the postpartum cow.

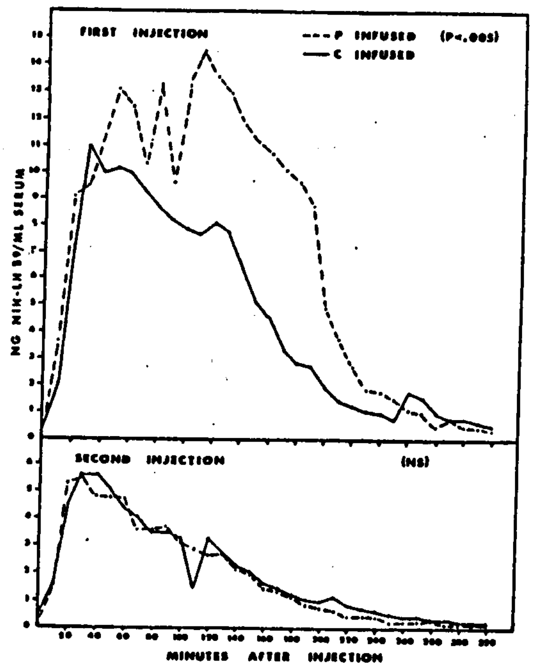

Figure 2. Mean plasm luteinizing hormone (LH) concentrations after two 100-*ug* injections of gonadotropin releasing hormone (GnRH) administered at 6-h intervals to heifers previously infused with propionate (P) or water (C) for at least 21 d. Magnitude of the LH response was similar ($P > .10$) for each treatment group in periods designated NS. From Rutter et al., 1983.

However, the nagging question of the specific metabolite or hormone signalling the reproductive system was not answered in these series of experiments. In fact, the data were pointing away from glucose itself as the signal because added glucose did not stimulate the reproductive endocrine system and, although circulating glucose levels did drop in some cases, glucose levels never changed very much in response to a given treatment. It was concluded that the metabolic hormones involved in intermediary energy metabolism, such as insulin, IGF-I and perhaps growth hormone, were more likely candidates for acting as a signal to the reproductive system. Work has been underway for the past five years or so in several labs following up on the approach of a metabolic hormone link to the reproductive system. Research with rats and pigs indicates that IGF-I has a direct effect on the ovary's ability to produce reproductive steroids (Veldhuis and Demers, 1985; Adashi et al., 1986; Hammond et al., 1988) which in turn may influence the pituitary's response to GnRH and(or) quality of an ovulated egg. Research in cattle is less definitive at this point, although insulin and(or) IGF-I may still have some as yet undefined role (Spicer et al., 1988; Alpizar et al., 1992; Rutter et al., 1992).

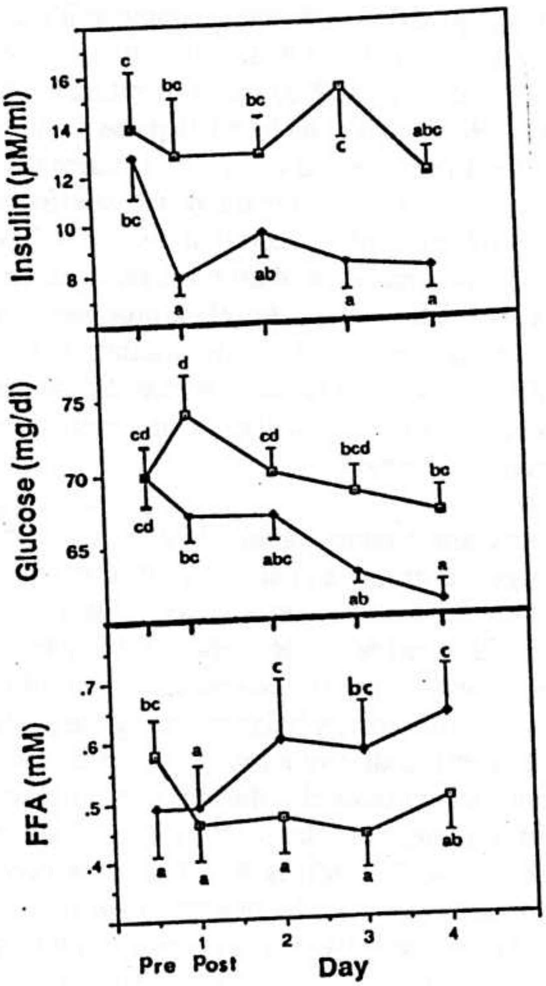

Figure 3. Effect of phlorizin infusion on mean daily plasma concentrations of insulin, glucose and free fatty acids (FFA). Two blood samples for each cow were used to determine mean concentrations before (PRE) and after (POST) the start of infusion treatment (saline = □; phlorizin = ■) on d 1. Values for d 2 to 4 were calculated from the mean of four samples per cow. Standard errors (horizontal bars) are represented for the mean of 10 cows/treatment. Means without common superscripts differ ($P < .05$). From Rutter and Manns, 1988.

New Areas of Research

Brain level: Two new approaches to nutritional effects on reproduction are underway or proposed at several labs. One approach is to identify amino acids acting as neurotransmitters that change in relationship to an animal's nutritional status. Using the growth-retarded ovariectomized lamb as a model, Hall et al. (1992) has shown that abomasal infusion of tyrosine increases hypothalamic tyrosine content and enhances LH pulse frequency. However LH pulse frequency was almost twice as great in lambs fed a 2X maintenance diet, indicating that tyrosine alone may not be sufficient to completely overcome the negative effects of undernutrition on LH release, that other neurons controlling GnRH secretion may not have been fully active and thereby unable to use tyrosine maximally or that tyrosine enhances both stimulatory and inhibitory inputs controlling GnRH secretion. Another proposed approach (Moss, personal communication) is to determine changes in hypothalamic/pituitary content or insulin and(or) IGF-I receptors and the IGF-I binding proteins in relation to nutritional status in postpartum cows. This proposal is an initial step in determining whether or not energy deficiency causes a change in the brain's receipt of a metabolic message.

Ovarian level: Attempts are continuing to identify a metabolic signal affecting the ovary's ability to respond to a gonadotropic signal. Use of ultrasound technology has enabled researchers to track development of follicles on a daily or weekly basis without subjecting animals to the stress of repeated surgery. Significant findings to date indicate that body condition at calving determines when during the postpartum period that a large follicle capable of ovulation will develop while negative energy balance during the postpartum period determines if a cow will develop a follicle capable of ovulation (Perry et al., 1992; Rutter et al., 1992). It appears that energy deficiency, particularly during the postpartum period, is retarding development of medium-sized follicles into large follicles. Future proposed research will investigate whether or not insulin, IGF-I and(or) IGF-I binding proteins are involved in this retardation. Another new area of research at the ovarian level involves the use of fat in cattle diets. Some researchers have shown a positive effect of fat feeding on postpartum fertility (Lucy et al., 1989; Williams, 1989; Wehrman et al., 1991). The proposed mechanism of action suggests that fat feeding increases blood levels of cholesterol, thereby supplying the ovary with substrate needed for steroidogenesis. However, other researchers (Carroll et al., 1990; Spitzer, personal communication) have not been able to duplicate the positive effects on fertility even though blood cholesterol levels have been elevated. Proposed research in Florida (Rutter and Kunkle, personal communication) will attempt to determine effects of feeding fat in a molasses-based slurry on postpartum reproductive performance.

Summary

By 1992, over 700 papers had been published regarding nutritional effects on reproduction. It has been well documented that poor body condition at or after calving reduces fertility in cattle, likely by suppressing hypothalamic GnRH secretion which in turn does not stimulate the pituitary to release an appropriate LH signal to the ovary to induce follicular growth and production of ovarian hormones. There are also good indications that nutrition can directly affect the ovary by suppressing ovarian response to a gonadotropic signal. Although many nutrient metabolites and metabolic hormones have the potential to link the metabolic and reproductive systems, none have yet been identified as the key signal whereby the reproductive system is turned on or off.

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