Effects of excess dietary protein on fertility in the beef herd

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Introduction

It has been well documented that a negative relationship exists between blood, plasma, or milk urea nitrogen and fertility in dairy cattle, with increased concentrations of plasma urea nitrogen (PUN; > 19 mg/dL) and milk urea nitrogen (MUN; > 15.4 mg/dL) being associated with suppressed fertility. Although this relationship is not fully understood, likely contributing factors have been suggested including altered sperm transport, impaired oocyte competence, and uterine environment. In the beef industry, while largely unfounded, it has been widely accepted that a similar negative relationship between plasma or blood urea nitrogen and fertility exists. While definitive cause-and-effect relationships are sparse, recent research indicates that excess dietary protein may have no negative impact on reproductive processes and fertility in beef cows.

Effects of protein restriction

In the beef industry, one of the most important factors impacting reproductive success is nutrition. Nutrition influences reproductive functions from follicular development to ovulation, hormone production, fertilization and ultimately pregnancy (Short and Adams, 1988). Restricting dietary nutrients prepartum have been shown to lengthen postpartum interval, decrease conception rates, and subsequently, pregnancy rates of beef cows as reviewed by Randel (1990). Cows with restricted energy intake are likely to lose body weight (BW) and body condition score (BCS), induced by a negative energy balance (Perry et al., 1991). Dziuk and Bellows (1983) and Richards et al. (1986) suggest calving cows at a BCS of ≥ 5 (on a 1-9 scale; Wagner et al., 1988) allows the female enough energy reserves to support milk production, maintenance and subsequent reproductive functions. Nutrient restriction and the resultant negative energy state suppresses the function of the hypothalamic-pituitary-gonadal axis by decreasing the pulsatile release of LH into circulation, which may interrupt proper ovarian activity (Short and Adams, 1988).

More specifically, protein is a key nutrient that may often be overlooked in ration formulation, especially in cow-calf production settings where low quality forages are commonly consumed. Restricting protein intake of cows reduces first service conception rates and pregnancy rates compared to cows fed adequate protein intake. In a study by Sasser et al. (1989), cows fed rations deficient in crude protein (CP; 0.32 kg/d) had first service conception rates of 25% and season pregnancy rate of 32%, which was significantly reduced compared to conception rates of their counterparts fed adequate CP (0.96 kg/d; 75% first conception and 74% overall pregnancy rates).

Dietary protein overview

While overfeeding protein in the form of legume-based hay and pastures does occasionally occur in the beef industry, consequences of over-supplementing CP was rarely a concern prior to the mass availability of ethanol coproduct feeds such as distillers grains, as it was economically impractical to supplement protein beyond the requirement of the cow. However, with continued expansion in the ethanol industry, meeting protein requirements is not as expensive as it once was due to the growing supply of protein supplements available through ethanol coproducts. As ethanol coproducts are both a cost-effective energy and crude protein source for ruminants, utilizing DDGS as an energy substitution for corn, and thus overfeeding protein has become more commonplace.

Dietary CP is composed of rumen degradable and rumen undegradable protein; defined by the amount of protein available for degradation into AA and peptides by rumen microbes. Pichard and Van Soest (1977) described a series of fractions which make up dietary protein including fractions A, B1, B2 and C, based on the degradability of the dietary protein source. Fractions A and B1 are rapidly degraded in the rumen, while B2 is more slowly degraded and C is insoluble in the rumen. Many coproducts such as corn distillers grains and brewers grains, are marketed as dried products, and thus are exposed to heat which can cause a Maillard reaction to occur. The Maillard reaction is a process that occurs with intense heat exposure which affects the aldehyde and amino group of a protein, thus decreasing the digestibility and rendering it less soluble (Ferguson, 1975). However, generally these coproducts do not undergo heat damage severe enough to completely bind proteins; thus, rumen undegradable protein fractions are still available for digestion and potential absorption in the small intestine (Waldo and Goering, 1979).

Rumen degradable protein

Protein sources that can be broken down in the rumen to be absorbed as amino acids (AA) for microbial protein synthesis, include urea (also known as non-protein nitrogen) and rumen degradable protein (RDP). Solubility of degradable protein can range anywhere from 100% degradable (urea) to less than 25% (blood meal), along with intermediate RDP products such as soybean meal (SBM; 75%; NRC, 2000). The soluble fraction of RDP will be metabolized into amino acids and peptides by protease enzymes, before being utilized as energy for rumen microorganisms (Butler, 1998). The amino acids can then be further broken down into organic acids, carbon dioxide, ammonia, and VFAs (Staples et al., 1993). Depending on energy availability in the rumen, AA can be incorporated into microbial protein or deaminated into VFAs (Bach et al., 2005). Non-protein nitrogen contributes to the N pool and can be incorporated into ammonia, DNA, RNA, AA or small peptides and is also used for microbial protein synthesis (Bach et al., 2005). If more ammonia is present than microorganisms can use, it is absorbed through the rumen wall into to the portal vein, where it becomes detoxified into urea by the liver. From the liver, the urea can be released into blood circulation for recycling or excretion. Ruminants have the unique capability of N recycling through saliva to return to the rumen for breakdown to ammonia, which is why research supports that cows do not need protein supplementation every day, but rather can be fed a weekly allotment on 2 or 3 days during a week. However, when there is adequate urea in the rumen, it is secreted in the urine and milk (Staples et al., 1993).

Rumen undegradable protein

After the rumen degradable portion of a protein source is broken down by the rumen microbes, the remaining portion of feed protein that is undegradable to the rumen will pass to the intestine and is primarily termed rumen undegradable protein (RUP). Rumen undegradable protein is passed to the small intestine where it is broken down by peptidase enzymes into peptides and AA. Once RUP is broken down, the resulting AA and peptide are available for absorption though the intestinal wall and utilized directly by the animal to support milk production, growth, fetus development, etc. (Ruminant Nitrogen Usage, 1985). In addition, approximately 50-80% of the protein escaping the rumen is rumen synthesized microbial crude protein (MCP; discussed later) synthesized in the rumen from peptides, AA, and ammonia being joined by peptide bonds. Fractions of RUP and MCP that remain undigested or incapable of being absorbed through the intestine into blood circulation, is passed on to the remainder of the digestive tract.

Metabolizable protein

Overall, the goal of protein supplementation is to supply adequate RDP to feed the microbial population of the rumen and adequate MCP and RUP to support production and life processes of the animal. This is commonly accomplished by formulating diets to meet metabolizable protein (MP) requirements. According to the NRC (2000), MP is defined as the amount of protein that becomes absorbed in the small intestine. The composition of MP can include MCP, rumen undegradable protein, and bypass protein. The quantity of MP passing to the small intestine is highly affected by dietary factors such as dry matter intake and type of feedstuff (forage or concentrate), which in turn affect passage rate and pH of the rumen. Cows with low DMI have slower rumen turnover, allowing a larger degree of protein to be degraded in the rumen. Whereas with high DMI, rumen turnover occurs more frequently; thus, less protein is degraded in the rumen and passage rate to the small intestine increases. Furthermore, at more acidic pH, bacteria N flow to the intestine increases (Hoover and Stokes, 1991). In order to increase MP reaching the small intestine, additional RUP may be included in the diet. Therefore, managing type of protein supplementation is a more efficient method to increase the amount of protein reaching the SI than attempting to manipulate MCP passage rate (Ruminant Nitrogen Usage, 1985; Canfield et al., 1990).

Plasma urea nitrogen

Urea N is a product of protein catabolism and is small enough to become incorporated into a variety of body cells, tissues and fluids such as plasma and milk, which has been associated with impaired reproductive function in dairy cows (Butler et al., 1998). When Urea N is produced from detoxification of ammonia from RDP or deamination of AA after excess RUP consumption, it increases concentrations in plasma and milk which comes at an energetic cost to the female (Staples et al., 1993). Compared to excess RDP, excess RUP supplementation was shown to reduce PUN (Carroll et al., 1994; McCormick et al., 1999). However, when excess RUP was supplemented, concentrations of PUN were increased compared to baseline concentrations (Gunn et al., 2014a; 2014b) but not the extent of excess RDP diets (17 and 10 mg/dL vs. 19 mg/dL). Thus regardless of source, excess CP may provide energetic expenditure on the animal by altering PUN which have been linked to suppressed fertility in dairy cows.

Still, while indulging in excess protein has shown to be undesirable, it may potentially be used for other reproductive parameters including increasing energy status and milk production (McCormick et al., 1999). Therefore, excess CP seems to be more likely to adversely affect reproduction if energy is in a deficit, but when metabolizable energy requirements are met, excess CP may be beneficial to reproductive functions.

Protein and reproduction

The effects of nutrient deficiency on ruminant reproductive functions have been thoroughly investigated and reviewed (Short and Adams, 1988; Randel et al., 1990; Perry et al., 1991; Robinson et al., 2006). In addition, protein requirements have been established for growth and maintenance (NRC, 2000) and recently revised (National Academies of Sciences, Engineering, and Medicine, 2016); however, protein requirements for reproduction have not been fully characterized and the impacts of excess supplementation on reproduction are yet to be established in beef cows. Furthermore, studies evaluating the effects of excess protein supplementation on ovarian function and consequently reproductive functions have elicited inconsistent results.

When excess CP is incorporated into the diet, PUN and/or MUN is dramatically increased. In dairy cows, a dramatic increase in PUN that results in concentrations above 19 mg/dL has been reported to be related to a decrease in artificial insemination (AI) pregnancy rates by nearly 20% (Butler et al., 1996). More recent data suggests that milk urea nitrogen (MUN) concentrations above 15.4 mg/dL may result in a reduced probability of pregnancy success in dairy cows (Rajala-Schultz et al., 2001). However, contrary to previous studies, Guo et al. (2004) only reported a negative relationship between increased MUN and pregnancy success during the first insemination. Authors in that study were unable to find any relationship between MUN and subsequent service conception rate, which supports data of Ferguson et al. (1993) who published similar findings. In addition, there is evidence that long term supplementation can allow cows to adapt to elevated urea concentrations, which resulted in no negative effects on embryo development

(Dawunda et al., 2004; Gath et al., 2012).These data would suggest the cow adapts to excess CP over time and thus, negative impacts of CP on fertility may be temporary. Nonetheless, reports of Guo et al. (2004) and Ferguson et al. (1993) seem to have fewer supporters, as it is generally accepted that elevated PUN concentrations are negatively correlated with pregnancy success.

While not fully elucidated, multiple data sets suggest pathways by which excess protein may impair fertility. The majority of these hypotheses center on excess dietary protein via rumen degradable protein and resulting effects of urea formation. The first theory relates to the ability of urea to interrupt signaling between the hypothalamus and ovary by decreasing gonadotropin release and subsequent hormone responses (Jordan and Swanson, 1979a).

Another theory postulates that excess CP consumption results in an abundance of ammonia and urea in the reproductive tract, changing the uterine secretions (Jordan et al., 1983) and pH (Elrod and Butler, 1993) which alter the uterine environment, perhaps resulting in a hostile environment for early embryonic development. This reduction in uterine pH as a result of elevated PUN concentrations was later reconfirmed by Rhoads et al. (2004), where cows that were subjected to jugular infusion of urea established a lower uterine pH within 12 h post-infusion compared with a saline infused control. This is further supported by Meza-Herrera et al. (2009) who reported that high concentrations of periconceptional protein resulted in reduced uterine pH and reduced fertility rate but did not affect luteal function at 15 days post-insemination. Moreover, increased uterine fluid concentrations of urea (Jordan et al., 1983) and both ammonia and urea (Hammon et al., 2005) have been noted in cows with elevated PUN concentrations. This is of concern as both urea and ammonia have been shown to be detrimental to early embryonic development in vivo (Ocon and Hansen, 2003).

It should also not be overlooked that any shift in uterine pH around the time of insemination could impact sperm transport as postulated by Perry and Perry (2008). Elrod and Butler (1993) reported that uterine pH is lesser (6.8) on day of estrus than on d 7 of the estrous cycle, with day 7 pH values ranging from 6.9 to 7.2. Moreover, Perry and Perry (2008) reported that uterine pH decreased to approximately 6.8 during the proestrus period and quickly rebounded to luteal levels within 6 hours after onset of estrous. Because bull semen has a normal physiological pH of approximately 6.8 (Salisbury et al., 1978), and sperm motility has been shown to increase linearly with a concurrent increase in pH from 6.6 to 7.8 (Goltz et al., 1988), it would make sense that the uterus undergoes physiological changes in pH around the time of estrus to support sperm transport up to the oviduct. Jones and Bavister (2000) reported that while acidic conditions can completely suppress sperm motility, motility can be regained with a concurrent rise in pH if such a manipulation occurs within 24 h of sperm immobilization, suggesting that a period of low pH exposure may extend the lifespan of the spermatozoa. However, Acott and Carr (1984) found that prolonged exposure to acidic conditions irreversibly arrested sperm motility. Therefore, if cows with increased PUN concentrations have a more acidic baseline for uterine pH prior to estrus, it is feasible that the uterine environment of those females could retard or completely inhibit sperm motility at insemination, resulting in the inability for fertilization to occur.

Although impaired uterine environment has gained the largest following as the primary reason for which cows with elevated PUN concentrations may not conceive, the indirect effect of PUN on oocyte quality and early embryonic development is also of concern. Specifically, shifts in PUN are mimicked by similar shifts in follicular fluid urea and ammonia (Hammon et al., 2005), which may negatively impact early embryonic development as expressed by retarded cleavage and blastocyst formation rates after insemination (Iwata et al., 2006). This concept is supported by Rhoads et al. (2006) who conducted a reciprocal, single-embryo transfer 7 days after insemination between cows with high or moderate PUN concentrations. Embryos from high PUN donors resulted in fewer pregnancies than those from moderate PUN donors, with PUN categorization of the recipient found to be insignificant. In summary, these data insinuate that excess protein, resulting in increased concentrations of PUN, may be negatively impacting fertility through altered oviduct function, compromised fertilization, impaired oocyte quality and early embryonic development, altered uterine environment, or a combination thereof. It should be noted however, not all researchers have reported a negative relationship between excess CP and reproduction of dairy and beef cows (Howard et al., 1987; Rusche et al., 1993; Lents et al., 2008, Geppert et al., 2016 a,b; Gunn et al, 2016).

Excess rumen degradable protein

Lactating dairy cows have commonly been the subject of interest when analyzing how overfeeding highly degradable protein effects reproduction, as increasing RDP is a common practice to stimulate greater milk production (Butler et al., 1981). However, while greater RDP intake maximizes milk production, reproductive efficiency is usually sacrificed. Jordan and Swanson (1979a) observed a negative correlation between excess RDP and reproductive efficiency (services per conception and days open) when CP increased from 12%, 16% to 19% in the diet.

In multiparous beef cows supplemented with either 1.2 kg/d or 2.5 kg/d of a 42% CP soybean meal based supplement, Lents et al. (2008) found no difference in AI pregnancy rates of postpartum lactating cows. In addition, when primiparous beef heifers were supplemented with soybean meal at 100% or 150% of CP requirements, PUN concentrations were greater with more RDP intake but no differences in conception rate existed (Rusche et al., 1993). Thus, excess RDP does not appear to be related to suppressed pregnancy in beef females to the extend as is noted in dairy females; however, as both classes of females are typically under lactational stress near breeding, any extra energy expended to metabolize excess protein may cause females to fall into a negative metabolic energy status, reducing the amount of energy available for reproductive functions (Staples et al., 1993) if diets are only designed to meet and not exceed energy requirements.

Lactating dairy cows consume more dry matter (DM) than non-lactating cattle in order to support milk production (NRC, 1989). This substantial dry matter intake (DMI) increases liver blood flow. By increasing blood flow, metabolism of steroid hormones (estrogen and progesterone; Sangsritavong et al., 2002) also increases. Thus, DMI may reduce circulating levels of these hormones, ultimately affecting the feedback mechanisms driving successful reproductive functions. Jordan and Swanson (1979b) further investigated reduced progesterone concentrations in lactating dairy cows consuming excess RDP and discovered potential competitive action of urea interrupting binding of LH to LH receptors on the corpus luteum (Haour and Saxena, 1974). Furthermore, hormone production may be mediated by stage of production as lactating cows had reduced concentrations of progesterone after excess RDP consumption (Jordan and Swanson, 1979b; Sonderman and Larson, 1989; Staples et al., 1993), but progesterone concentrations of non-lactating cows were not affected by amount of RDP in the diet (Elrod and Butler, 1993; Garcia-Bojalil et al., 1994).

Excess rumen undegradable protein

While excess dietary RDP is commonly linked to suppressed reproductive function, excess RUP supplementation has been commonly linked to more positive effects on reproduction by shortening postpartum interval (Figueroa et al., 1992; Sinclair et al., 1994) and improving conception rates in dairy cows (Armstrong et al., 1990; Bruckental et al., 1989). In addition, studies which compared excess supplementation of highly undegradable to degradable feedstuffs, greater RUP supplementation increased first service conception rate in beef heifers (Wiley et al., 1991; Martin et al., 2007) and overall pregnancy rates in dairy cows (McCormick et al., 1999). When gestating beef heifers (Gunn et al., 2014a) and primiparous beef heifers (Rusche et al., 1993) were supplemented with 100% or 150% RUP, similar AI and overall breeding season pregnancy rates were observed.

Since AA and peptides from degraded RUP is absorbed in the intestine and is readily available to the ruminant, excess RUP has shown to stimulate the pancreas to increase insulin production (Sletmoen-Olson et al., 2000; Schroeder et al., 2005). Insulin affects ovarian tissues by enhancing LH receptor synthesis and actions of the pituitary through these receptors (Butler and Canfield, 1989). Kane et al. (2002) suggested that undegraded protein works to improve reproduction by mediating LH and FSH production. Although Wiley et al. (1991) and Rusche et al. (1993) observed no difference in insulin or LH parameters between beef cows fed excess RUP or RDP, perhaps through a coupling of mechanisms, greater RUP may have the potential to increase insulin which may enhance gonadotropin synthesis, early embryonic development, and potentially improve reproductive efficiency. Enhanced gonadotropin synthesis is supported in part by recent research by Geppert et al. (2016 a,b) which identified beef cows consuming excess concentrations of RUP increased ovulatory follicle size and number of antral follicles during the ovulatory wave.

Recent developments

As previously discussed, not all data support an inverse relationship between dietary protein and fertility. To the contrary, little, if any research in beef cattle support the data derived from dairy cattle. In particular, blood urea nitrogen concentrations do not appear to be linked to fertility at all in beef cows. In a study by Bryant et al. (2011), heifers grazing wheat pasture in Oklahoma prior to and through the early breeding season recorded PUN concentrations in excess of 20 mg/dL during synchronization and AI and noted no differences in pregnancy to AI or season-long pregnancy rates when compared to heifers fed in a drylot with PUN concentrations less than 10 mg/dL. Similarly, Amundson et al. (2015) noted no difference in pregnancy rates of heifers maintained on a high nitrogen diet compared to control when diets were fed 60 days prior to, through the reminder of the breeding season. In that study urea was the primary source of excess protein, with PUN concentrations averaging 23.4 mg/dL and 13.3mg/dL for high protein and control treatments, respectively. Finally, recent research by Gunn et al. (2016) suggests that in beef cows and heifers adapted to their plane of nutrition for at least 21 days prior to the breeding season, PUN is not negatively related to AI pregnancy rate. To the contrary, on 1,331 animals analyzed, PUN tended to have a weak positive relationship with AI pregnancy rate (P = 0.06; Figure 1). It should be noted, that in all three of these studies, cattle were adapted to their diets prior to the beginning of the breeding season. Thus, it is plausible that abrupt changes in diet resulting in excessive dietary protein around the time of breeding may negatively impact fertility. However, this area warrants further research.

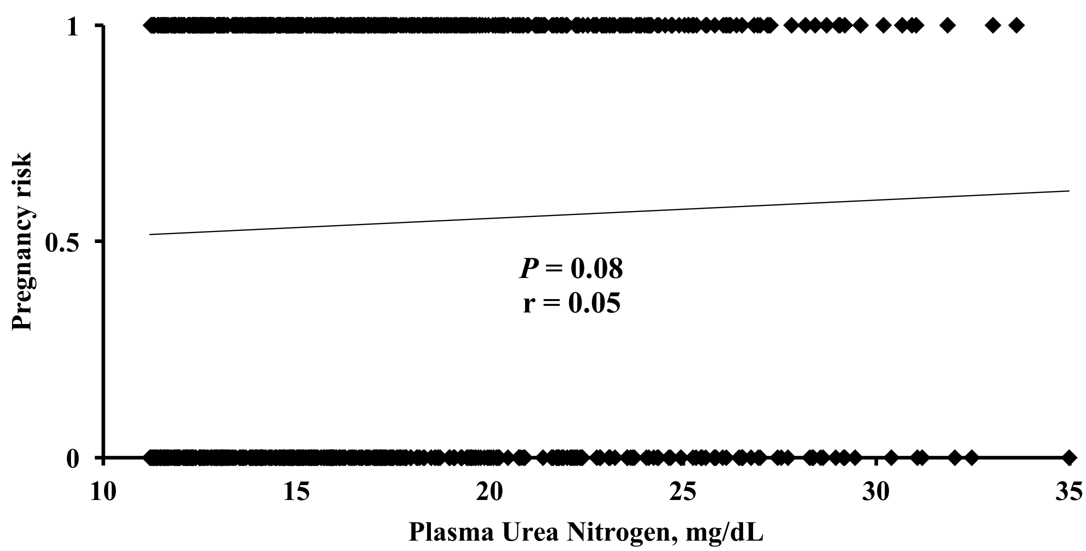

Figure 1. Relationship between circulating blood or plasma urea nitrogen concentration and first service pregnancy risk.

Summary

The amount of data in the dairy literature relating excess dietary protein to suppressed fertility, primarily through increased concentrations of urea impacting reproductive function is undeniable. These observations are likely exacerbated by metabolic stressors and negative energy balances often created during peak lactation, which often coincides with timing of AI in many herds. However, more recent research in beef cattle suggest that when metabolizable energy is not a limiting factor, excess dietary protein does not negatively impact reproductive processes and fertility. However, future research should be conducted on the effects of abrupt changes in diet around the time of insemination that result in acute increases in dietary protein.

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