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Nutritional Effects on Dairy Cattle Fertility

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ABSTRACT

Dairy cow fertility has declined in recent decades, coincidental with large increases in milk production. The problem is often considered being nutritional and can be corrected through dietary adjustment. The interaction between nutrition and reproduction is poorly tuned, and study results are often contradictory. Nutrition is an important component of successful reproduction, but dietary change to improve pregnancy rates is complicated, and merely offering pastured cows a supplement is unlikely to result in large effects, say authors. The effect of energy balance, carbohydrate type, protein and fat on reproductive outcomes will be considered.

Keywords- diet, energy balance, fatty acids, non-structural carbohydrates, protein.

I. INTRODUCTION

Dairy cow fertility has declined in recent decades, coincidental with large increases in milk production (Royal et al. 2000; Lucy 2001; Berry et al. 2008; Friggens et al. 2010). Cows take longer to return to oestrus (Lucy 2001), display poorer signs of oestrus, may have poorer conception rates and have greater early embryo loss (Table 1; Lucy 2001; Diskin 2008b; Friggens et al. 2010). For example, in the 1990s:

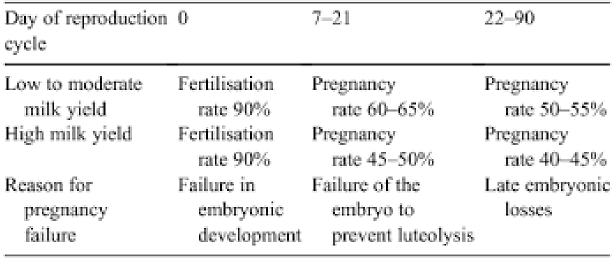
- in the USA, inter-calving interval increased 7.5% (1.0 month) and cows required 33% more services/conception (0.75 services: Lucy 2001),
- in the UK, calving rate to first insemination declined from 56 to 40% (Royal et al. 2000),
- in Ireland, the number of inseminations/conception increased from 1.54 to 1.75 (Mee et al. 2004), and

Nulliparous heifers have superior pregnancy rates compared with primipara OUS and multiparous cows. It is important to note that the extent of the decline in fertility is not uniform across countries. The decline reported in pasture-based countries, where the selection for milk production was not as intensive, was coincidental with the importation of HF sires from dairy systems intensively selecting on milk production. The same evolutionary mechanisms are likely to remain in play, resulting in declining fertility with increasing milk production, as seen in this article. To view the full article, please visit the page you came from. Back to the page that was originally published on 14 December 2010. This article was first published as an online-only, free-to-read article. We are happy to share the findings with the author’s publication.

Decline infertility is a problem of increasing importance on dairy farms because of the associated considerable financial loss. This effect is arguably the clearest in seasonal pasture-based dairy systems. Maximizing the proportion of the diet as grazed grass matters in minimizing production costs. Evans et al. (2006) modeled the infancy of calving spread and replacement rate changes between 1990 and 2003 in a seasonal-calving pasture-based system and reported a decline in a proper part of e150/ha. Decline in reproductive performance is primarily manifested as a lower pregnancy rate and more days from calving to conception. The problem is often considered to be a result of the greater negative energy balance (EBAL) associated with cows intensively selected for milk production. Care must be taken not to confuse inductive reasoning from observations (hypothesis generation) with experimental evidence of cause and effect. Because something is associated with a particular reproductive outcome does not necessarily mean the outcome will be different if steps are taken to alter the associated factor.

In this review, I will outline the perceived nutritional problems associated with grazed forages. I will discuss the underlying physiology associated with reproductive failure and the factors associated with this physiology. Nutrition treatments to alter.

Table 1. Reproduction outcomes in low to moderate- and high- producing dairy cows (adapted from Diskin *et al.* 2006)



Day of reproduction cycle	0	7–21	22–90
Low to moderate milk yield	Fertilisation rate 90%	Pregnancy rate 60–65%	Pregnancy rate 50–55%
High milk yield	Fertilisation rate 90%	Pregnancy rate 45–50%	Pregnancy rate 40–45%
Reason for pregnancy failure	Failure in embryonic development	Failure of the embryo to prevent luteolysis	Late embryonic losses

Intensively grazed forages can be of high quality, but feed supply at different times of the year can affect fertility. Cow potential DMI relative to actual, negative EBAL in supplemented grazing cows relative to supplemented grazing cows and the composition and nutrient balance of the most commonly grazed. We have suggested forages as contributors.

II. TEMPORAL PATTERNS OF SUPPLY

Although herbage growth patterns and rates will vary with climate conditions, the basic principles of a pasture-based system are consistent. In temperate and Mediterranean-type climates, with or without irrigation, herbage production is characterised by a spring peak that typically exceeds DMI requirements of the herd. Climate, stocking rate, nitrogen fertiliser, and herbage-production potential of the soil class are important factors. Roche et al. (2009c) provide a stylised representation of the dairy cow requirement/herbage production interaction.

The start of breeding to maintain a 365-day inter-calving period coincides with the spring rush in herbage growth and adequate herbage provision in moderately stocked pasture-based dairy farms. Climatic conditions are variable, however, even in relatively stable climatic zones. Average herbage supply may not always equal dairy cow feed demand during breeding. The impact of periods of underfeeding and, therefore, provision of supplements on reproduction outcomes will be discussed further.

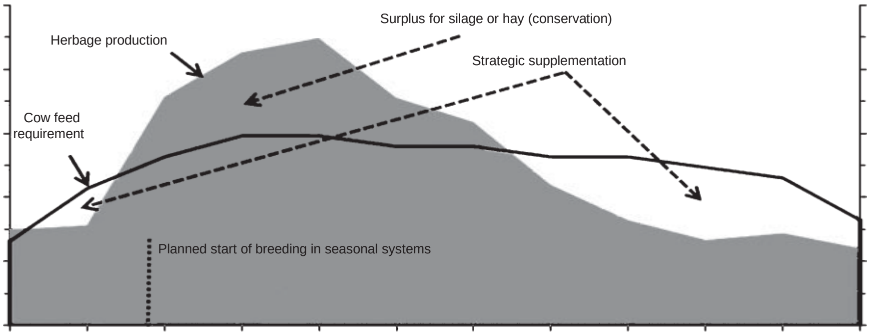


Fig. 1. A stylised relationship between daily dairy cow feed requirement (per ha) and herbage production (per ha), (shaded area = herbage supply, solid line = cow demand assuming a stocking rate of 3.3 cows/ha).

III. DRY MATTER INTAKE

One of the greatest limitations of dairy systems based on grazed forages is the low DMI of cows relative to their potential intake. It is not possible to determine with certainty the reason for the difference in DMI between grazing cows and TMR-fed cows. We can infer plausible explanations from what I know about cow behavior and intake regulation. They supplement when grazing cows with a low fire cereal grain, time spent grazing and forage intake decline by at least as much as would occur if a high apart concentrate was offered. In situations where access to the pasture is time-limited, cows have longer grazing bouts and greater DMI/grazing bout, suggesting that physical factors are not wholly responsible for the cessation of grazing. The difference in DMI is more likely the result of evolutionary constraints and energy accounting by cows. Cows are naturally diurnal and have innate evolutionary programming to time feeding to limit the possibility of predation. The 'drive' to eat is regulated by a complex neuroendocrine accounting system that estimates the costs and benefits associated with acquiring more feed. Grazing is expensive from an energy perspective, and there comes a point when the acquisition of additional feed would not justify the energy expense. Cows can remove more herbage, but they 'choose' not to. This, and that there is likely an evolutionary-limited grazing duration, means that grazing cows, even when supplemented, will not achieve their genetic potential DMI. The difference in D MI can be only partially corrected through supplementation.

IV. ENERGY BALANCE

All mammals have developed to use stored reserves postpartum. The timing of the loss relative to re-breeding and the degree and duration of the body condition score (BCS) loss is of particular interest from a reproduction perspective. We associate increased selection for milk production with a greater loss of body reserves. There is concern that grazing dairy cows experience an even greater negative EBAL than TMR-fed cows because of their lower DMI (Mulligan et al. 2007). It could, therefore, be hypothesized that grazing cows would benefit, from a reproduce perspective, from the provision of high-quality supplements. However, the data do not support this effect of nutrition in early lactation on EBAL. The rate of BCS loss until 30–40 days in milk is similar in cows grazing perennial-ryegrass-dominant pastures and those offered a TMR planned to maximize milk production. Supplementation with starch-based concentrates resulted in an earlier nadir BCS (3 days earlier BCS consumed/kg DM concentrate consumed/day) and a greater rate of BCS gain post-nadir. These effects of nutrition are consistent with other studies and do not affect the effect of stocking rate/herbage allowance on the rate of loss of the BCS score. The data highlight signs applicant effects of the nutritional regime. Delaby et al. (2009) fed cows either

16.3 or 20.4 kg DM of one of two TMR diets differing in the SC to NSC content but not energy density (i.e. MJ/kg DM) They reported no effect of diet on BCS loss during the rest month of lactation. cows on the higher DMI-higher NSC treatment reached nadir BCS earlier and gained BCS more quickly.

Physiological changes at parturition uncouple the somatotropic axis, facilitating increased growth hormone secretion and lipolysis. Cows offered a greater feed allowance or fed 3–6 kg DM/day of concentrates have increased concentrations of insulin and insulin-like growth factor-1 (IGF-1) and reduced growth hormone concentrations by 30–60 DIM. These are all homothetic adaptations that facilitate nutrient direction to milk production. The isometric axis becomes 're-coupled between 30 and 60 DIM, but feed allowance and dietary SC to NSC interact with DIM and genetic merit for milk production in the timing of this re-Coupling. Although supplementation in early lactation does not greatly affect EBAL, feeding level and feed constituents do alter circulating hormone and metabolite concentrations. This effect of nutrition on fertility requires further research.

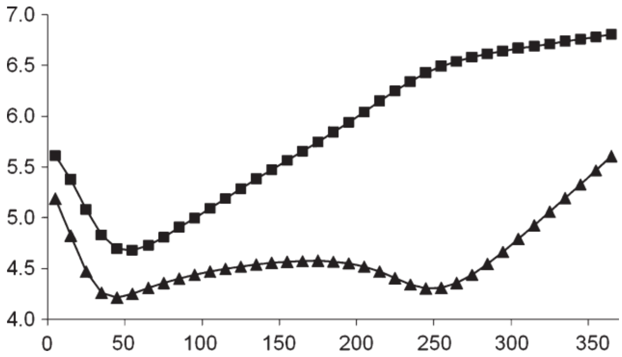


Fig. 2. Body condition score (BCS) profiles of cows of similar genetic merit for milk production either grazing a perennial ryegrass-dominant pasture (~) or offered a total mixed ration (&) in confinement. Profiles were produced from equations published by Roche *et al.* (2007*a*).

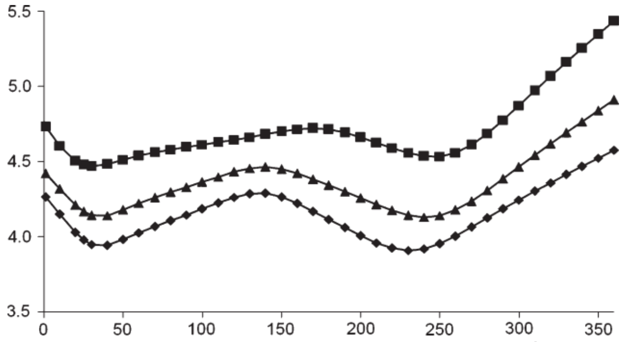


Fig. 3. Body condition score (BCS) profiles of cows stocked at 2.2 (&), 2.7 (~) or 3.7 (¤)cows/ha and grazing a perennial ryegrass-dominant pasture. Profiles were produced from equations published by Roche *et al.* (2007*a*).

V. FEED QUALITY

There are several primary ruminant nutritional-requirement systems. Dairy cow nutritional requirements are complex and dependent on multiple interacting factors. It presents these recommendations in Table 2. The quality of grazed forages is highly variable, with estimated repeat abilities within fortnight across years ranging from 22 to 54% for temperate forages. Optimally managed grass pastures have excess rumen degradable protein and surplus fibre. I have suggested the effectiveness of the pure component to be insufficiently 'effective' to stimulate rumination. These perceived deficiencies in grazed forages are often highlighted by nutritionists. Detailed experiments have failed to support a substitution of alternative feeds for grazed forages for milk production. Offering cows an easily consumed digestible supplement rarely increases DMI commensurate with the amount of supplement offered. In experiments where energy intake has been held constant, there has been no increase in milk energy output. Less than 12% (1.8 kg milk) of the difference in milk production (15.4 kg milk/day) could be attributed to a more balanced diet, according to Klover and Muller (1998) and estimated nutritional difference was associated with the excretion of excess nitrogen.

Table 2. Simple[A] nutritional recommendations[B] (g/kg DM unless otherwise stated) for high production dairy cows and the corresponding nutritional evaluation of temperate[C] and tropical[D] pastures under optimal management

		Recommended	Temperate	pasture
CP	–	180, 160, 140, 120[G]	223	204
NDF	–	Minimum 280–320	425	616
ADF	–	Minimum 200[E]	228	239
NSC	–	Maximum 380	113	53
Starch	–	Maximum 300	–	–
Fat	Unprotected	Maximum 30	42	21
	Rumen protected	Maximum 30	–	–
	w-6[F]	261	92	–
	w-3[F]	112	573	–

[A] Distilled from international nutrient requirement recommendations (ARC 1980; NRC 2001; CSIRO 2007) into simple extension messages.
[B] CP = crude protein (nitrogen · 6.25); NDF = neutral detergent fibre; ADF = acid detergent fibre; NSC = non-structural carbohydrate; w6 = omega-6 fatty acids; w3 = omega-3 fatty acids.
[C] Primary source: Roche *et al.* (2009*c*).
[D] Primary source: Reeves *et al.* (1996).
[E] Using ADF as a proxy for effective NDF.
[F] Actual fatty acid content of total mixed ration formulated to maximise milk production. Primary source: Kay *et al.* (2005).

[G] Four values reflect recommendations in early, mid, and late lactation and during the non-lactating period for mature cows.

Conclusion

Although domesticated forages used for intensive pasture-based dairy production are very digestible and supplementation does not greatly influence the degree of negative EBAL in the 4–6 weeks following calving, availability of supply is not certain and periods of restriction may occur if supplements are not provided. Provision of additional NSC after 30 DIM reduces the period of BCS loss and increases BCS gain, reflecting a more positive EBAL than if the cow were not supplemented. In addition, different dietary ingredients result in different rumen fermentation patterns and differences in post-ruminal products of digestion. On entering the blood, these products can have marked effects on blood ammonia, urea, and glucose concentrations, which, in turn, can affect hormone concentrations and the balance of hormone axes and, possibly, follicular and uterine fluid composition. The effects of EBAL and differences in these nutrition-derived physiological subtleties and their effect on reproduction will be discussed further

Physiological processes underpinning fertility and sub-fertility

1) The chain of reproduction events between when a cow calves and re-calves is long and complex, but can, for all intents and purposes, be split in two when considering the interaction with nutrition: Pre-ovulatory reproductive failure, with nutrition possibly influencing the timing of return to oestrus and, therefore, submission rate; and

2) Post-ovulatory reproductive failure, when nutrition might influence fertilisation and/or embryo survival and, therefore, conception rate.

Pre-ovulatory reproductive failure is primarily a function of the timing of return to oestrus postpartum. An early resumption of estrous cycles following calving is important, as delays result in reduced conception rates and pregnancy rates. A nutritional intervention might ease some of this loss. The effects and timing of such an intervention will probably be different for both components and need to be tailored to the individual cow. The physiological processes underpinning the postpartum return to Oestrus and the effect of nutrition on these processes must, therefore, be understood.

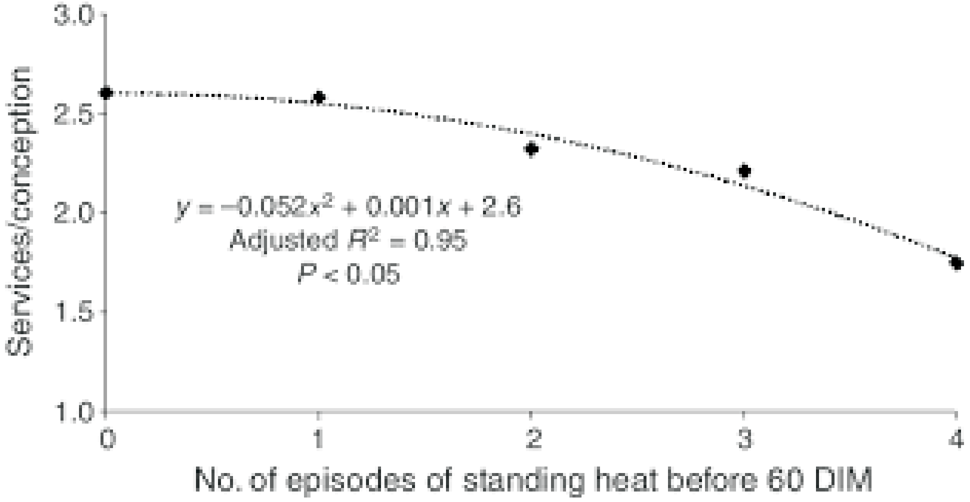


Fig. 4. Services/conception for cows exhibiting 0, 1, 2, 3 or 4 heats in the first 60 days postpartum (Thatcher and Wilcox 1973). DIM, days in milk.

Reproduction by numbers

Successful reproduction at the herd level can be described mathematically. This makes it easier to determine whether problems are pre-or post-ovulatory. For example, a herd that averages 90% submission rate and 60% conception rate will have 96% of cows pregnant in 12 weeks (4% empty) In comparison if a herd averages only 70% submission. rate, the empty rate would be 11% in very fertile cows (conception rate of 60%) but could be as high as 27% in cows with. Additional post-oVulatory sub-fertile characteristics (i.e. cows in heat) This review will not discuss the association between management and reproductive failure, but acknowledges the importance of staff training and encouragement.

Ovulation and postpartum anoestrus:

Extended anovulatory-anoestrus remains a major cause of 'sub-fertility' in pasture-based dairy herds. We have recognized it as an important contributory component of increased milk production. The interval from calving to detected oestrus is typically 10–14 days longer than the interval to first ovulation. A study found that 35% of cows that had calved within 4 weeks of the planned start of mating were having ovulatory cycles, but only 35% were detected as having estrous cows. In mature cows, a similar pattern of 'reproductive recovery' is clear in mature cows (McDougall and Rhodes 1999, 2001) The study concludes that cows that calve late within the seasonal calving period and those slow to recover physiologically post-calving are less likely to have achieved their greatest potential for re-establishing pregnancy. They published the results of the study in the Journal of Dairy Research, vol. 3, at page 2 (April 2010).

Physiological processes involved in pre-ovulatory reproductive failure and possible interactions with nutrition

A myriad of physiological and neuroendocrine events are required for a cow to resume normal oestrous activity postpartum. The timing of these events relative to each other is presented in Fig. 5. The major points of control are the:

1) Gonadotropin releasing hormone pulse generator, located in the hypothalamus, which regulates the pulsatile pattern of gonadotropin releasing hormone release,

2) Gonadotropin (follicle stimulating hormone: FSH; luteinising hormone: LH) synthesis and secretion, which respond to gonadotropin releasing hormone pulses, and

3) Responsiveness of ovarian antral follicles to the gonadotropins. A feedback loop is involved, whereby ovarian follicle secretions (i.e. steroids and inhibins) regulate secretion of FSH and LH.

In pasture-grazed cows, a wave of antral follicular development with one follicle exceeding 9 mm in diameter (the 'dominant follicle') has been recorded between 6 and 17 days postpartum. Ovulation only occurs when circulating oestradiol concentrations suffice to stimulate the pre-ovulatory LH surge. The number of follicular waves to first ovulation and the PPAI are highly correlated (R2 = 0.93; Burke et al. 1995), because the intervals between successive waves of follicle development are consistent ~10 days. Any factor that affects test radio production will, therefore, affect the P PAI. The decline in blood concentrations of progesterone and estrogen post-calving removes the negative feedback of these hormones on gonadotropin synthesis and secretion after calving, and FSH secretion begins shortly after calving. The dominant follicle may ovulate, or become atretic and be replaced by one or more subsequent dominant follicles, or may continue growth and become cystic (Rhodes and Rhodes, 2003).

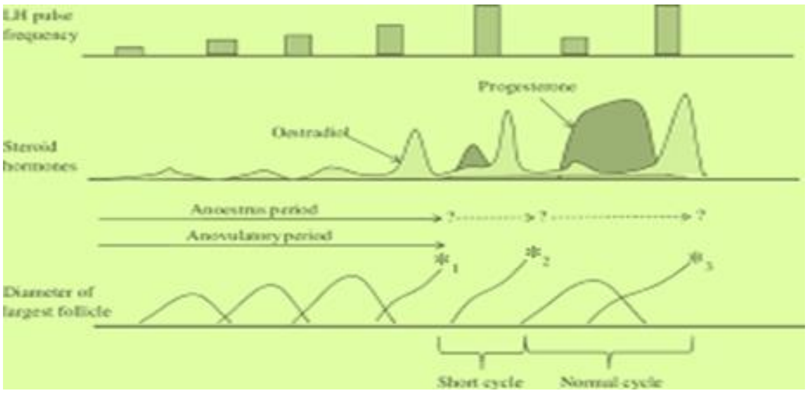


Fig. 5. Schematic representation of key physiological events and endocrine patterns between calving and the end of the first normal cycle in cattle (adapted from Rhodes *et al*. 2003).

Conclusions

Successful reproduction requires cows to have ovulated and displayed signs of oestrus. We must nurture the developing embryo through maternal secretions. The uterine endometrium must undergo extensive development/remodelling to facilitate implantation. The innate immune system must be sufficiently suppressed to allow embryo development. Perturbations to the endocrine environment and the timing of endocrine events are common feature in sub-fertility. We will discuss further the potential effects of nutrition on these variables.

Calving body condition score

Calving BCS and, therefore, nutrition/EBAL during the previous lactation and non-lactating periods affects ovarian follicles. BCS has a negative effect on gonadotropin (FSH, LH) secretion and follicular responsiveness to gonadotropic substances. The effect of BCS on PPAI is influenced by cow genetics, which can be deduced from breed and number of follicular waves. NZ HF cows were treated for anoestrous than North American HF cows, despite the fact that BCS loss is reportedly greater in the North American strain. The contrasting difference in genetic susceptibility to a nutrition/ EBAL-related delay in ovarian follicular development during early lactation has not been further elucidated. It points to effects of genetic selection on the duration of PPAi and not energy balance per se, even when the two are coincidental (McNaughton et al. 2003). Research and Discussion. Researchers found a negative association between calving B CS and days to first oestrus was associated with delayed ovarian activity, infrequent LH pulses, poor follicular responses to. gonadtropins and reduced functional competence of the follicle.

The physiology underpinning the effect of BCS state on PPAI is not completely understood. BCS at calving is negatively associated with the length of the P PAI. Calving BCS may be important in conception rate. Nadir BCS was positively associated with pregnancy rate at 42 and 84 days after planned start of mating. The optimum BCS is probably 5 on a 10-point scale, with heifers and second calvers being in better body condition at Calving. Such a BCS will minimise the duration of postpartum anoestrus, thereby improving the likelihood of a successful pregnancy. In comparison, a greater calving B CS will result in excessive BCS loss in early lactation, while thinner than this will extend the PPAi. Further research is required to understand the effect. of energy status (i.e. B CS at a point in time) on conception rate and to separate this from cow. genetics.

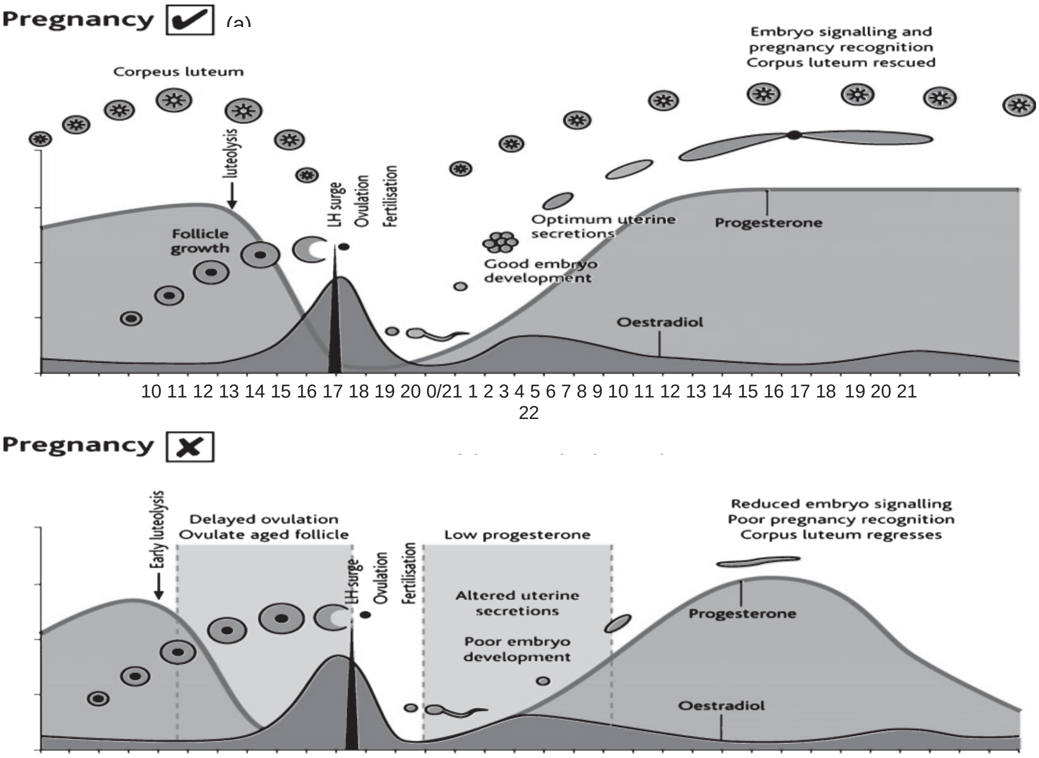


Fig. 6. Schematic representation of endocrine changes and pre-ovulatory events during the estrous cycles and early pregnancy in fertile (*a*) and sub-fertile (*b*) cows (source: Meier and Burke 2010). LH, luteinizing hormone

Early lactation negative energy balance

Early lactation EBAL is negatively associated with PPAI, with shorter durations to rest ovulation associated with a more positive EBAL. We have reported a poor nutritional state to extend the interval between � Lapin ovulation and detection of oestrus in mature cows. In mature cows subjected to a severe feed restriction, the 6-week pregnancy rate was 8% lower in restricted cows. These data are consistent with recent results from Burke et al. (2010b) in mature dairy cows that were subject to a 45% feed restriction for the 2 weeks of mating. This outcome was a combination of a 4.2% reduction in the 3-week submission rate and a 5.6% reduction of the conception rate to RAfst service. It is not clear how much of this effect is because of reduced submission rates.

Negative EBAL affects ovarian activity by impinging on the pulsatile secretion of LH and reducing follicular responsiveness to LH and FSH. It also suppresses follicular oestradiol production. Large, aged follicles are less fertile and, therefore, negative EBAL may reduce subsequent conception rate. Embryo competency is compromised shortly after fertilisation in cows in negative EBAL. For example, Leroy et al. (2005) reported a 40–50% reduction in the number of grade-1 embryos recovered from lactating dairy cows compared with beef cows and non- lactating heifers. In addition to the effect of EBAL on time to first ovulation and oocyte/embryo quality, a negative EBAL in early lactation can delay the elimination of bacteria from the uterus (Lewis 1997), reduce the innate immune response (van Knegsel *et al.* 2007) and alter the necessary postpartum uterine inflammatory response, thereby, delaying uterine repair (Wathes *et al*. 2009). As a result, the uterine environment will take longer to be in a receptive state, a key component in ensuring the successful establishment of pregnancy (Hansen 1995; Walker *et al*. 2009, 2010).

IGF-1 is produced primarily in the liver under the action of growth hormone (the somatotropic axis) This axis is significantly influenced by EBAL, with a negative EBAL causing the axis to become 'uncoupled' (a physiological state in which elevated growth hormone concentrations do not result in commensurate increases in IGF-1 production) A positive EBAL resulting in an insulin-mediated 'recoupling' is thought to be responsible for PPAI and conception rate-related effects. There was no association between plasma IGF- 1 concentration in early lactation and pregnancy rate in our study. IGF-2 has been reported to alter follicle follicles.

IGF has been implicated in uterine receptivity and embryo implantation. A negative EBAL in early lactation is reported to alter the IGF system in the oviduct and endometrium. The effects of IGF-1 and -2 on in vitro embryo development and IFNt production are inconsistent. It is reasonable to conclude that factors that result in disturbances within the IGF systems are detrimental to follicle and embryo development. These factors may, perhaps, provide a mechanism for reduced fertility in these animals. Further research is necessary to determine if nutritional intervention to alterIGF-1 production or stability will improve reproduction. To help people with fertility issues, contact The Fertility Project at 1-800-273-8255.Although the severity and duration of negative EBAL is a contributing factor to reduced submission rates and pregnancy rates (Roche *et al*. 2009*a*), how greatly early lactation negative EBAL can be influenced by nutrition must be considered. Postpartum loss of stored reserves is a mammalian adaptation for nurturing the neonate and is facilitated by peripartum homoeorhetic adaptations (Roche *et al*. 2009*a*).

Recent experiments have explored the effect of nutrition on the inter- lactation profile of BCS change. Concentrate feeding in early lactation did not affect the rate of B CS loss. The greater post-nadir BCS gain with increasing concentrate supplementation concurs with this hypothesis. There is limited evidence that manipulating dietary rumen degradable protein content influences BCS loss, but the aforementioned studies do not support this theory. Treatment with grazing cows that are restricted or provided with additional supplementary feeds has failed to affect pregnancy rate in some experiments. The general conclusion is that lipolysis is primarily regulated genetically while lipogenesis is environmentally controlled.

Non-structural carbohydrate supplementation

Postpartum hormones are increased when animals are fully fed before calving and/or calving BCS is optimal. Burke and Roche 2007: PPAI reduced in multiparous cows from increasing the NSC to SC ratio. Circulating IGF-1 concentrations were not affected by diet in the study reported by Garnsworthy et al. (2008) Diet did not affect the onset of FSH production, the timing of recruitment of the first dominant follicle, the pattern of subsequent follicle development, or the number of follicles detected during each follicular wave. Nevertheless, the high starch diet reduced the interval from calving to �akiarst ovulation and increased the proportion of cows ovulating within 50 days of calving (Gong and Gong 2002); unpublished data from our laboratory also indicate a reduction in P PAI length with increasing plasma insulin, but the proportion explained is <3%. The physiological mechanisms for the reported effects of feeding high-energy supplements to increase LH secretion. likely involves the induction of insulin spikes, but increasing NSC in isoenergetic diets would be expected to increase circulating insulin concentrations.

There are plausible physiological mechanisms for a positive effect of NSC-enhanced plasma insulin on PPAI. Increased insulin enhances the responsiveness of ovarian follicles to gonadotrophic stimulation and supports general hepatic production of IGF-I. Insulin and IGF-1 are required for hypothalamic and pituitary function. It is unclear whether these hormones have a direct action on stimulating Gonadotrophin. The effect of glucogenic/insulinogenic precursors on PPAI is not consistent. Studies have found no effect of concentrate feeding on postpartum return to oestrus. The effect of EBAL and dietary NSC content on post-ovulation fertility appears to be negative. Glucose infusions before superovulation in ewes have resulted in reduced quality embryos and reduced pregnancy rate. Such a diet would require a high NSC diet until they achieve Oestrus, followed by a diet that did not promote insulin secretion until the end of the breeding season. In comparison, feed restrictions or fermentable are we have reported supplements to benefit embryo development. These data show that the nutrient requirements for an early resumption of ovarian cycles, follicle development, and embryo development may be quite different, regarding a potential advantage to alter dietary ingredients through early lactation to ensure early resuspension of oestriol and excellent quality embryos. The physiological mechanisms involved remain poorly understood but appear to be under the infancy of glucose or glucose-derived metabolites or hormones (e.g. insulin or IGF-1) . The authors compared an insulinogenic and non-insulinogenic diet to 120 DIM. Results were not entirely convincing. The insulinogenic diet in early lactation did not result in an earlier resumption of the ovarian activity or earlier detection of oestrus. However, cows offered the insulin-inducing diet until estrous followed by the non-infective diet had greater pregnancy rates at 120 DIM.

Dietary protein

The effect of glucogenic/insulinogenic precursors on PPAI is not consistent. Studies have found no effect of concentrate feeding on postpartum return to oestrus. The effect of EBAL and dietary NSC content on post-ovulation fertility appears to be negative. Glucose infusions before superovulation in ewes have resulted in reduced quality embryos and reduced pregnancy rate. Such a diet would require a high NSC diet until they achieve Oestrus, followed by a diet that did not promote insulin secretion until the end of the breeding season. In comparison, feed restrictions or fermentable are we have reported supplements to benefit embryo development. These data show that the nutrient requirements for an early resumption of ovarian cycles, follicle development, and embryo development may be quite different, regarding a potential advantage to alter dietary ingredients through early lactation to ensure early resuspension of oestriol and excellent quality embryos. The physiological mechanisms involved remain poorly understood but appear to be under the infancy of glucose or glucose-derived metabolites or hormones (e.g., insulin or IGF-1). The authors compared an insulinogenic and non-insulinogenic diet to 120 DIM. Results were not entirely convincing. The insulinogenic diet in early lactation did not result in an earlier resumption of the ovarian activity or earlier detection of oestrus. However, cows offered the insulin-inducing diet until estrous followed by the non-infective diet had greater pregnancy rates at 120 DIM.

Pre-ovulatory effects of dietary crude protein are inconsistent. Jordan and Swanson (1979) reported fewer days to rest observed oestrus in cows receiving a high crude protein ration. Barton et al. (1996) reported a delay of 4 days in the time to augment in cows on a diet containing 200 g/kg DM crude protein compared with one containing 130 g/ kg DM. Most studies suggest a negative effect of excess rumen degradable protein on the probability of conception. High blood UN and associated elevated concentrations of blood ammonia have been implicated in embryo degeneration and alterations to the uterine environment (Butler 1998, 1998, 1999) High bloodUN and associated high ammonia have also been implicated for embryo degenerating. The effect of crude protein on pregnancy rate is much more consistent, with most studies suggesting it has little effect on follicle development and time to the postpartum oestrous activity. nutritional strategies to reduce blood UN are unlikely to result in a greater submission rate, however, as blood UN is not directly related to protein degradability, which is thought to be a key indicator of ovulatory function. Ã. Westwood et al. (2000) reported a lower conception rate to first service in cows receiving a diet high in rumen degradable protein. Treatment not affected blood UN.

The majority of studies have been undertaken in cows being fed a TMR containing low to moderate dietary crude protein concentrations relative to the crude protein content of temperate pastures. Cows grazing temperate pastures often have blood and milk UN well in excess of the ‘ideal’ concentrations reported previously. For example, Roche *et al.* (2005) reported blood UN concentrations of 42.0 mg/dL and milk UN concentrations of 40.5 mg/dL in dairy cows grazing high crude protein pastures (286 g/ kg DM) in early lactation. Similarly, Kolver and Macmillan (1994) reported blood UN concentrations rising from 28.5 mg/ dL at calving to 42.0 mg/dL 8 weeks in milk and Ordóñez *et al.* (2007) noted blood UN of more than 60 mg/dL in early lactation cows grazing nitrogen-fertilised pastures. If dietary crude protein or rumen degradable protein, or blood UN were negatively associated with reproductive outcomes, these data suggest that the problem should be greatest in grazing cows. Pregnancy rates, however, tend to be high in such systems (Horan *et al*. 2004; Burke *et al*. 2008) and do not appear to be influenced by dietary crude protein content or blood UN concentration. Kenny *et al.* (2001, 2002) investigated the effect of dietary crude protein and fermentable energy supplementation on pregnancy outcomes in beef heifers. They concluded that although blood urea concentrations were 77% greater in their high crude protein treatments (29.9 vs 16.9 mg/dL), embryo survival was not affected and, in fact, embryo weight was greater in heifers receiving the high crude protein diet (Kenny *et al.* 2001). Ordóñez *et al.* (2007) also reported no difference in embryo survival in dairy cows grazing 254 or 216 g/kg DM crude protein pastures, despite the very large differences in blood UN (55 vs 36 mg/dL). Consistent with these data from grazing systems, Garcia-Bojalil *et al.* (1994) reported no difference in numbers or percentages of normal embryos, abnormal or retarded embryos, and unfertilised ova in non-lactating cows offered either 123 and 274 g/kg DM crude protein diets (blood UN = 9.8 and 21.3 mg/dL, respectively).

In summary, there are sound physiological reasons for a negative effect of metabolites originating from surplus rumen degradable protein on embryo survival, and there is consistent evidence for a negative association between blood UN and the probability of conception *in vitro* and in TMR-fed cows. Data from grazing systems, however, indicate a lack of effect of either dietary crude protein or blood UN on fertility outcomes. The reason for this inconsistency is not known but current data do not indicate a reproduction benefit to reducing dietary protein in pasture-based systems. A greater understanding of the physiological mechanisms that protect the grazing dairy cow from excess rumen degradable protein is required to improve our understanding of reproductive failure.

Dietary fat

The influence of dietary fat on reproductive performance is poorly understood because much of the published data come from studies having nutritional rather than reproductive objectives (Staples *et al*. 1998). The rationale behind altering dietary fat to improve reproduction outcomes is 2-fold:

1) Use of dietary fat supplements in early lactation to increase energy intake, reduce negative EBAL and, thereby, assist the physiological processes that are primarily responsible for ensuring a resumption of ovulatory cycles after calving (Lucy *et al*. 1992); and
2) Physiological effects of FA in reproductive tissues (Mattos *et al*. 2000; Wathes *et al*. 2007).

The potential benefit of fat supplementation on ovarian function was validated in early postpartum cows by Lucy *et al.* (1991), who reported enhanced growth and function of the dominant ovarian follicle in cows supplemented with 22 g/kg DM of calcium salts of long-chain unsaturated fatty acids (UFA: Megalac; Church and Dwight Co., Inc., Princeton, NJ, USA). These results were consistent with the effects of an improved EBAL on ovarian function. A further study, however, indicated that the positive effect of fat supplements in early lactation was not due to improved EBAL *per se*, but rather through a more direct effect of fat on follicular function (Lucy *et al*. 1993). A likely explanation for this mechanistic action of fat involves the ovarian requirement for cholesterol to synthesise steroids (Gwynne and Strauss 1982; Staples *et al*. 1998); dietary fat consistently increases plasma cholesterol concentration in cows (Grummer and Carroll 1991). The effect of fat on steroid production appears limited to long-chain UFA. Zachut *et al*. (2008) reported increased follicular androstenedione and oestradiol concentrations, and a greater expression of P450 aromatase mRNA in granulosa cells in cows supplemented with long- chain UFA but not those supplemented with saturated FA (SFA: C16:0 and C18:0).

In agreement with the hypothesis that UFA directly affect ovarian function, total number of follicles, the size of the pre- ovulatory follicle and non-esterified fatty acids and insulin contents in follicular fluid have all been increased in cows supplemented with long-chain UFA (Mattos *et al*. 2000; Lucy *et al*. 1993; Zachut *et al*. 2008). In addition, Fouladi-Nashta *et al*. (2007) reported improved blastocyst production from mature and cleaved oocytes in cows supplemented with long-chain UFA, even though there was no evident effect on oocyte quality; the fat also buffered oocytes against the negative effects that high milk yields have on oocyte development potential. In addition to the positive effect of UFA on follicular competency and oocyte quality, Scott *et al*. (1995) reported that a greater proportion of cows fed long-chain UFA displayed stronger signs of oestrus. These data reflect a positive effect of dietary UFA on pre- ovulatory and peri-oestrous physiology and create an expectation for an improved submission rate with UFA supplementation. The research, however, originates in relatively low-fat diets and there are few data available on likely implications for cows grazing fresh forages already high in polyunsaturated fatty acids (PUFA) (Kay *et al*. 2005; Wales *et al*. 2009). Kay *et al*. (2006) supplemented cows grazing perennial ryegrass-dominant pastures with one of two sources of rumen protected FA; the sources were isolipid (~0.52 kg added lipid) but differed in their SFA to UFA ratio (0.62 : 0.38 and 0.29 : 0.71 SFA to UFA, respectively); unpublished data from that experiment indicate no effect of supplementary FA or the composition of the FA supplement on the duration of the PPAI, although negative EBAL was less in supplemented cows. These results may reflect the already high PUFA content of a fresh forage diet (Kay *et al*. 2005; Wales *et al*. 2009), with additional UFA failing to add benefit, or it may reflect the lower milk production of grazing cows and the associated lower metabolic challenge.

In addition to the pre-ovulatory effects of UFA, there is evidence that dietary long-chain PUFA act as specific regulators of post-ovulatory reproductive processes also, but the effects are inconsistent *in vitro* and *in vivo*. Dietary FA can affect post-ovulatory reproductive function in two ways:

1) Through affecting oocyte and embryo quality; and
2) Through altering the maternal physiological processes involved in luteal regression, preventing the prostaglandin-induced termination of progesterone synthesis.

Endometrial FA reflect dietary FA (Bilby *et al*. 2006*b*; Childs *et al*. 2008*b*; Meier *et al*. 2009). For example, endometrial w-3 PUFA concentrations were more than 2-fold higher and eicosapentaenoic acid (w-3 C20:5) concentrations alone more than 7-fold higher in the endometrium of cows fed isolipid diets high in w-3 PUFA (500 g/kg FA) compared with cows fed diets low in w-3 PUFA (2 g/kg FA) (Coyne *et al*. 2008). Fresh forages contain a greater proportion of w-3 PUFA (linolenic acid: C18:3; Table 2) than TMR and this difference should be reflected in endometrial UFA concentration and in the ratio of w-3 to w-6 UFA. Consistent with this, Meier *et al*. (2009) reported a 50% greater w-3 to w-6 ratio in the endometrium of grazing cows than traditionally reported for cows fed TMR (from 10 to >15.5) (Bilby *et al*. 2006*b*; Childs *et al*. 2008*b*), consistent with the expected differences in dietary PUFA composition (see Kay *et al*. 2005). These data reflect a better FA composition in the diet of grazing dairy cows from a reproduction standpoint than cows fed an unameliorated TMR. The effect of dietary FA composition has been variable, with some reports of enhanced effects to changes in FA content and ratios on early embryo development and other reports concluding no effect and even negative effects. For example, Leroy *et al*. (2010) reported reduced developmental potential and greater mRNA expression for genes related to apoptosis and metabolism in embryos cultured in palm oil-derived hyperlipidaemic serum. This may have related to the source of FA used, as embryonic development was also reduced in HF cows fed SFA compared with those fed PUFA (Thangavelu *et al*. 2007), suggesting that FA composition is important. Marei *et al*. (2010) reported reduced oocyte development following the addition of linolenic acid (an w-3 PUFA) during *in vitro* maturation, consistent with the negative effect of the hyperlipidaemic diet presented by Leroy *et al*. (2010). In comparison, Cerri *et al*. (2009) reported that cows fed a diet rich in linoleic acid and other UFA had a greater proportion of excellent, good, and fair quality embryos than embryos from cows fed palm oil (primarily C16:0), and embryos from cows fed PUFA had a greater number of blastomeres. In other studies, supplementary PUFA failed to alter oocyte quality or subsequent embryo development (Bilby *et al*. 2006*a*; Fouladi-Nashta *et al*. 2007; Childs *et al*. 2008*a*), but the high fat diet improved blastocyst production from mature and cleaved oocytes (Fouladi-Nashta *et al*. 2007). In comparison, Petit *et al*. (2008) reported that supplementation with w-3 UFA (flaxseed oil: linolenic acid: C18:3) decreased embryo quality compared with feeding calcium salts of palm oil (SFA: C16:0). Despite this, they noted that treatment had

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no effect on the subsequent pregnancy rate of heifers receiving frozen grade-1 embryos. The reasons for the inconsistent effects of dietary fat content and FA composition on oocyte and embryo quality are not known and make recommendations to improve fertility impossible.

The other post-ovulatory mechanism in which FA may have a role is in oxytocin-induced prostaglandin synthesis. Twenty carbon PUFA are the precursors for physiological compounds called eicosanoids, of which prostaglandins are a key family. As prostaglandins play important roles in luteal regression and pregnancy maintenance, targeting a reduction in prostaglandin synthesis through modifying dietary PUFA content has been an area of increasing research interest as a potential means to improve fertility (see reviews by Mattos *et al*. 2000; Wathes *et al*. 2007). PUFA reduce prostaglandin (PGF_{2a}) synthesis in both endometrial explants (Cheng *et al*. 2001) and cells (Mattos *et al*. 2003) *in vitro*. Results from *in vivo* studies do not necessarily agree. For example, Cheng *et al*. (2005) reported that w-6 PUFA had a greater reducing effect on PGF_{2a} synthesis than w-3 PUFA, while Petit *et al*. (2004) reported an increase in PGF_{2a} secretion when cows were supplemented with w-6 PUFA. Studies examining the effect of dietary w-3 PUFA supplementation on PGF_{2a} secretion have also produced inconsistent results *in vivo*. Supplementation with fish oil reduced the oxytocin-induced secretion of PGF_{2a} in some studies (Thatcher *et al*. 1997; Mattos *et al*. 2004), had no effect elsewhere (Heravi Moussavi *et al*. 2007; Childs *et al*. 2008*a*), and led to an increase in PGF_{2a} and the expression of mRNA for prostaglandin E synthase in the endometrial tissues of cows in other experiments (Childs *et al*. 2008*a*; Coyne *et al*. 2008).

The inconsistent effects of dietary and tissue FA content on reproduction variables are difficult to interpret and few studies have reported the effect of fat supplements on either conception rate or early embryo mortality. Staples *et al*. (1998) examined 100 research papers where the effect of fat on reproduction was reported. Of those reporting conception rates, 11 studies observed positive effects or a tendency for a positive effect, whereas three studies reported strong negative effects. Since that review, one of the few studies reporting pregnancy losses, Ambrose *et al*. (2006) reported that a flaxseed (primarily w-3 PUFA: C18:3) supplement reduced pregnancy losses and increased conception rate to timed AI when compared with a sunflower seed (primarily w-6 PUFA: C18:2) supplement. A similar tendency for embryo mortality was observed by Petit and Twagiramungu (2006) when flaxseed was compared with other fat sources. These data indicate benefits of w-3 PUFA on pregnancy rate. More recently, Juchem *et al*. (2010) reported that a calcium salt rich in linoleic and other trans-octadecenoic acids resulted in greater pregnancy rates at 27 and 41 days after insemination compared with cows fed palm oil, suggesting a benefit of w-6 PUFA over SFA.

In summary, the effects of dietary fat and the type of fat consumed on reproductive outcomes is difficult to interpret. Supplementing cows receiving a low fat (<20 g/kg DM) diet with rumen-protected FA reduced PPAI. The effect of FA-type (saturated, mono-unsaturated, or polyunsaturated) or FA- grouping (w-3 or w-6) on reproduction variables is inconclusive. Reasons for the inconsistency in research results are unclear and the area requires further investigation. From what is known, cows grazing fresh forages tend to have high concentrations of dietary fat (>40 g/kg DM), of which more than 50% are w-3 PUFA and more than 25% are w-6 PUFA. The amount of fat and the balance of w-3 PUFA to w-6 PUFA would, therefore, appear sufficient for optimal ovarian function and to ensure maximum pregnancy rates. Supplementing grazing cows with FA is unlikely to be beneficial.

VI. CONCLUSIONS

Nutrition is a key factor in reproductive success and failure. Intake and energy balance, carbohydrate amount, degradation characteristics and the balance between structural and non- structural types, protein amount and the balance of rumen degradable to undegradable protein sources, and the amount of fat as well as the balance between saturated and unsaturated sources and w-3 and w-6 groupings have all been implicated in pre-ovulatory and post-ovulatory reproductive function. There is, however, inconsistency in the published literature on the impact of these dietary constituents on reproductive outcomes, with epidemiological associations not borne out in hypothesis- testing experiments and a failure of *in vitro* studies to mimic subsequent *in vivo* results. In addition, many of the nutritional recommendations aimed at improving reproduction are to modify hormones/metabolites that have been associated with fertility (e.g., IGF-1), with no evidence that a nutritional intervention (e.g., starch-based supplement) to alter said hormone/metabolite will positively affect reproduction. The reviewed data suggest that the primary focus of the nutritionist aiming to improve reproduction should be to ensure late lactation nutrition and lactation length are managed to achieve optimal calving condition.

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