7.10 Vitamin A

The signs of vitamin A deficiency are lachrymation, photophobia, diarrhoea, dull coat and night blindness (Campbell, 1983). Kirk et al. (1971) demonstrated in store cattle that there were sufficient stores in the liver to protect the animal for at least 100 days. Green foliage, from weeds, trees and bushes is always available even during the dry season so this is also a relatively inexhaustible source of carotenoids.

8 LIPID METABOLISM

The usual diets fed to ruminants contain from 0% in dry older pastures to 10% of the dry matter in forages as a leafy material-containing lipid where animals are able to select leaf tip materials to graze. The majority of lipids from pasture plants are phospholipids and glycolipids with the major long chain fatty acid components being linolenic (50%), linoleic (10%) and palmitic 15% (Hawk, 1973).

Once in the rumen the complex lipids are rapidly hydrolysed by bacterial lipases to long chain fatty acids, galactose and glycerol, the last two being fermented to VFAs. The long chain fatty acids are quickly absorbed onto particles in the rumen where they are hydrogenated by the microorganisms. Hawke and Silcock (1969) state the organisms involved are the lipolytic bacteria while protozoa may not be capable of lipolytic activity (Girard and Hawke, 1978). When natural feedstuffs are fed, the two major lipid factions entering the small intestine are free fatty acids (85-90%) and phospholipids (10-15%). The phospholipids are transported as part of the microbial cell membrane while the free fatty acids attach to feed particles as well as other particulate matter and move with these materials to the lower gut (Davis, 1990).

9 THE REPRODUCTIVE PROCESS

The implication of nutrition on the reproduction process in the female is related to three physiological stages :-
1. The production of gametes, viable ovum.
2. The development of the reproductive organs, uterus and placenta and the growth of the foetus (pregnancy).
3. The development of the mammary tissue and the consequent secretion of milk (lactation).

The nutrient demand for the production of ova production is small, but is critical for the hormones produced, to stimulate growth and release of the ovum. The nutrient demand for pregnancy is moderate, until late pregnancy, where as the demands for lactation are large. However, if the production of ova is superimposed upon the needs for lactation, especially at a time when the animal is under nutritional stress, gamete production will be affected so that oestrus does not occur or is not detectable (lactation anoestrus) (Butler and Smith, 1989; Harrison et al. 1989). The gametes can also be affected after ovulation and fertilisation, where embryonic death occurs before implantation into the uterus of the developing embryo (McClure, 1973).

9.1 The bovine oestrus cycle

Excellent reviews of the events of the bovine oestrus cycle are available (Roberts, 1956; McDonald et al. 1991; Short and Adams, 1988; McClure, 1994). A summary of events will be given here of the oestrus cycle of the cow.

The average breeding cycle of the cow is 21 days in cows and 20 days in heifers, with the range 17–25 days (Hopkins, 1988). Adsell (1964) states that oestrus cycles average 20–21 days with 85% varying from 18–24 days. During oestrus the female exhibits outward signs of accepting copulation and actively seeks out the male. The length of time the female will stand for copulation is short, approximately 18 h. During oestrus the ovaries contain one or two follicles that have increased in size markedly and the uterus has become turgid and oedematous with high levels of secretions occurring from the vagina and cervix. The developing follicle(s) sheds the ovum after the animal is no longer receptive to the male, this is usually about 28 h after the onset of oestrus (Hopkins, 1988). The area from where the follicle ruptures in the ovary, fills up with blood and, over the next 50 to 62 h, the cells
associated with the collapsed area where the ovum was shed begin secreting hormones. This structure is now called the corpus luteum and marks the beginning of the luteal phase and the corpus luteum continues to grow for about 10 d following oestrus. The secretory function (progesterone) continues until the next ovulation, but if the cow is fertilised the progesterone secretion continues until superseded by the production of progesterone from the placenta in the uterus.

If fertilisation occurs, the fertilised ovum divides daily reaching the uterus at 72-84 h in a 8–16 cell stage of development and begins to attach to the endometrium at 22 d, with the interdigitation between foetal and maternal tissues occurring by day 30 (King et al. 1979). Pregnancy lasts 282 ± 5.6 days.

Figure 21. Hormones of the oestrus cycle of the cow
The function of the reproductive endocrine system is modulated by nervous signals from other hypothalamic nuclei and higher centers, the ovarian hormones oestradiol, progesterone and inhibin as well as the endogenous opioid peptides (McQueen and Fink, 1988; Sprangers and Pacsek, 1988). In the 21-day cyclic cow the concentration of progesterone falls from its peak of 19–25 nmol/ml at 16–19 d after oestrus to <3.0 nmol/ml at ovulation. The plasma oestradiol 17-β concentration rises from its minimum of < 10 pg/ml (mean 3.6 pg/ml) to a peak of 15–25 pg/ml on the day before next oestrus and falls to its basal level within 2 to 5 h after the beginning of oestrus. The concentration of LH in the plasma rapidly increases from its basal level of 2–3 ng/ml to >10–15 ng/ml for 8 h with a peak of 10–65 ng/ml corresponding to the onset of oestrus.

Progesterone appears in the blood in appreciable quantities five days after oestrus and continues to increase until about the 16–17th day, by which time it has reached its peak of 19–25 ng/ml (Stabenfeldt et al. 1969) (see Fig. 22).

During pregnancy oestrogen and progesterone are secreted by the placenta and circulate in the maternal blood, inhibiting the secretion of gonadotrophin releasing hormone (GnRH) by the hypothalamus (McClure, 1994). The gonadotrophin secreting cells of the adenohypothysis are then deprived of sufficient stimulation to maintain the synthesis of follicle stimulating hormone (FSH) and lutenising hormone (LH). These have to be restored after calving before normal cycles can commence (Nett, 1987). Restoration is completed by Day 10 post partum (Moss et al. 1985) and episodic release of LH normally commences on Day 13 post calving (Peters et al. 1981; Wagner and Hansel, 1969). Episodic release of LH reaches a peak mean concentration and frequency 2 weeks before the first oestrus after calving, which normally occurs between Day 17 and Day 42 post-partum (Humphrey et al. 1983).

**9.2 The requirements for reproduction**

The metabolism of the cells of the reproductive organs, ovum and foetus appear similar to those of other systems with the energy for cellular metabolism is derived from ATP, which is replenished by the terminal oxidative pathways in the tricarboxylic acid (TCA) cycle from glucose and free fatty acids. Availability of oxaloacetate (from glucose) appears to be the rate-limiting factor for the incorporation of free fatty acids (FFA) into the TCA cycle. Glucose and
FFA are derived from propionate, lactate, acetate, butyrate and amino acids that have been absorbed. The cells of all reproductive organs, ovum, embryo and foetus metabolise glucose or the products of glycolysis for the replenishment of ATP (Brinster, 1967; Mazur and Younglai, 1986). Insulin is required to assist the entry of glucose into all cells other than nerve cells, e.g. luteal cells require insulin for maximal progesterone production (Poff et al., 1988). The hypothalamus, ovum, embryo and foetus have an obligatory requirement for glucose and because late pregnant and heavily lactating cows have difficulty in maintaining glucose homeostasis, any reduction in availability of glucose is likely to affect their metabolism and possibly the survival of the ovum and embryo (McClure, 1994). Acetate and amino acids may have a significant, but as yet undefined role as an alternate energy source for the adenohypothysis and ovary (Teleni et al., 1985; Downing and Scaramuzzi, 1991).

9.3 Amino acids as substrates for ATP generation

The role of amino acids as building blocks for body protein is well recognised; however, amino acids are also metabolised via ketogenic or glucogenic intermediaries (Kelly et al., 1993). Windemueller and Spaeth (1978) suggested that in the ruminant some tissues, such as the intestine, preferentially utilise amino acids over carbohydrates as oxidisable substrates. Because carbohydrates undergo fermentation in the rumen, ruminants absorb little glucose from their small intestine in comparison to monogastrics. The primary sites for the production of blood glucose are the liver and kidney and glucose is essential for synthesis in the mammary gland and in the brain. Propionate and amino acids are the major absorbed gluconeogenic precursors. The amino acid store in skeletal muscle can provide a carbon source that may be mobilised to support the generation of energy substrates. With respect to energy utilisation, mechanisms regulating the degradation of muscle proteins and the resultant release of amino acids appear similar to the mobilisation of glycogen and triglyceride from the liver and adipose tissue (Smith, 1986).

Black et al. (1990) measured the rate and extent of oxidation of each amino acid in lactating cows using radiolabelled amino acids and quantified the CO₂ expired. It was shown that only four amino acids (glutamate, glutamine, aspartate and alanine) were substantially oxidised during a three-hour post-injection period.
Some of the intermediates of protein metabolism, e.g. alanine and glutamine are also direct and important intermediates in energy transactions in the whole body. This is also true in the rumen where microbial utilisation of free amino acids for fermentation as well as the synthesis of amino acids for cell proliferation occurs (Kelly et al. 1993).

9.4 The effect of diet on glucose production

Owing to the fermentative nature of their digestion, ruminants normally absorb little dietary hexose (Bergman et al. 1970; Lomax and Baird, 1983). Even when ruminant diets contain high amounts of concentrate, the absorption of glucose from the gut accounts for less than one third of the whole body glucose turnover (Bergman, 1973; van der Walt et al. 1983).

Since the rate of absorption of sugar from the gut is low, the ruminant liver has little need to remove glucose from the portal blood. The ruminant has adapted and has little or no glucokinase and little hexokinase activities in the liver (Ballard et al. 1969). The three organs that release glucose into the blood are gut, kidneys and liver (Brockman, 1993). The liver is the most important glucose-producing organ, accounting for 85-90% of whole-body glucose turnover in animals on a roughage diet or during fasting (Bergman et al. 1970). Since the liver takes up only small amounts of glucose and always has a net output of glucose (Bergman et al. 1970; Brockman, 1983) its glucose needs must be met by gluconeogenesis even in the fed state. The main mechanism of regulating hepatic glucose metabolism is to regulate the diversion of excess glucogenic substrates away from the liver. During fasting, glycogen is mobilised from extrahepatic sites for use in gluconeogenesis. Glucose production is linearly related to the availability of its precursors in plasma (Lindsay, 1976). Animals grazing fibrous pastures, low in nitrogen and minerals, can suffer deficiencies in energy intake due to low microbial numbers and poor digestibility of the forage (see Section 4.2) and so the potential to improve fertility through supplementation that will increase microbial numbers is obvious. Furthermore, the potential to affect fertility by improving glucose generation and measuring the increased fertility, would also provide the way to measure more precisely the effect of such supplements.