

DIETARY EFFECTS ON RUMINANT LIVESTOCK REPRODUCTION WITH PARTICULAR REFERENCE TO PROTEIN

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INTRODUCTION

The process of reproduction is a coordinated function of many tissues, cell types and regulatory systems which is possible only when animals are provided with sufficient quantities of dietary nutrients. The livestock industry is faced with different situations as far as protein nutrition is concerned in different countries. In most of the Third World countries, animals survive on poor quality roughages and crop residues which are deficient in many essential nutrients. The major constraint in such feeds is protein deficiency because the digestible crude protein content of these roughages is very low. In certain Asian and African countries, animals generally graze without much feed supplement (Leng, 1990). Thus, the availability of nutrients, particularly protein, remains inadequate most of the year except during the rainy season or for some period thereafter and it is during this period that regular oestrous cycles are normally exhibited. Crossbreeding programmes have been adopted in some of the developing countries and thus a considerable population of improved cows has emerged. They require balanced nutrition for exploitation of their genetic potential so far as milk production is concerned. To some extent protein deficiency

is being overcome by mixing urea or other non-protein nitrogen substances in the total diet or by treating crop residues with these substances. A limit to urea feeding is necessary, however, otherwise ammonia levels in the rumen and blood may increase and have a detrimental effect on reproduction.

In developed countries, where feeds of higher protein content are given to increase milk production, the situation is quite different. However, too high a level of dietary protein can result in reduced fertility in dairy cows (Khasan *et al.* 1989) and decreasing the protein supply to 80% of National Research Council (Pangborn, 1978) or 75% of Agricultural Research Council (Treacher *et al.* 1976) recommendations can lead to improved fertility. This question of optimal protein content has been partly resolved by considering the extent of degradation of dietary proteins in the rumen. Thus, two types of protein requirements have been suggested for ruminants (Agricultural Research Council, 1980; National Research Council, 1989): the requirements of the animal itself and of the rumen microbial population. In this review the effect of protein nutrition on various reproductive functions in ruminant animals is discussed, including likely mechanisms.

EFFECTS OF PROTEIN NUTRITION ON REPRODUCTION PUBERTY

Female animals

Improving the fertility and lifetime efficiency of dairy animals is of great concern. It is well documented that the age at puberty is lower in rapidly growing animals (Arije & Wiltbank, 1971; Dufour, 1975; Shokamoto *et al.* 1975). The concept of target weight developed by Lamond (1970) is highly pertinent because puberty is a function of live weight rather than age which is evident both in cows and buffaloes (Dufour, 1975; Kaur & Arora, 1989). In other words, it is a rapid achievement of body size and weight which are prerequisites for the prompt onset of puberty. Even fetal growth is important because it has a bearing on birth weight which is correlated with growth rate. In semi-arid zones of the tropics, puberty is usually delayed in grazing cattle because grasslands do not provide enough protein and other nutrients (Topps, 1977). This low protein content of tropical grasses leads to insufficient production of rumen microbial protein to support optimum growth rate (Oyedipe *et al.* 1982). Poor growth rate due to low plane of nutrition delayed puberty in cows (Day *et al.* 1986) and goats (Doney *et al.* 1982). In temperate zones also, hill grazing is reported to be insufficient to support the potential growth in sheep and goats, resulting in a delay of puberty of up to one year (Dýrmundsson, 1987; Loudon, 1987).

Murrah buffalo calves given 37.0% less crude protein and 16.2% less total digestible nutrients than National Research Council (1978) requirements gained 397.5 g/d as compared to 570.2 g/d in control calves. The weight at first oestrus averaged 343 and 341 kg respectively, but underfed heifers exhibited a delay of 210 days in attaining first oestrus (Kaur & Arora, 1989). Similarly, Malik (1987) indicated that buffalo heifers maintained on a higher plane of nutrition showed first oestrus at an early age due to a higher growth rate. Therefore, the onset of puberty seems to be determined by weight gain achieved during the postweaning period, rather than by the age of the animal.

Male animals

An inverse relationship between growth rate and age at puberty also exists in males (Waddad & Gaili, 1985). Low protein feeding has been shown to delay puberty by about five months in Nigerian bulls and their Friesian crosses (Rekwot *et al.* 1987) and such bulls

had poor testicular development and smaller ejaculates as compared to their normal counterparts (Rekwot *et al.* 1988). Young bulls kept on grazing plus concentrate feed showed better growth rate than those on grazing alone, with an earlier age at puberty and a greater scrotal circumference (Perry *et al.* 1991; Tegegne *et al.* 1992). Even at maturity, the size of the testicles is smaller in underfed animals resulting in a lower sperm concentration in the semen (VanDemark *et al.* 1964). It has also been reported that the seminal vesicles contain less fructose and citric acid as well as smaller Leydig cells and seminiferous tubules, and decreased testosterone level under protein stress conditions (Nolan *et al.* 1990). Even older bulls were susceptible to low dietary protein and showed decreased testicular size and reduced fertility than those adequately fed (Lindsay *et al.* 1982; Rekwot *et al.* 1988). Restriction of both protein and energy also prevented Merino lambs from reaching puberty in their first potential breeding season (Ketut Sutama & Edey, 1985), with reduced testicular size and sperm concentration in the ejaculate (Parker & Thwaites, 1972; Oldham *et al.* 1978; Foote, 1978; Alkass *et al.* 1982). Feed restriction also reduced libido in rams (Parker & Thwaites, 1972).

OESTROUS CYCLE

Deficiency of protein and/or energy has been reported to result in cessation of oestrous cycles (Louw *et al.* 1988; Richards *et al.* 1989), a loss of 15% body weight being critical to cause infertility in cows. The phenomenon of cessation of oestrous cycles has been observed in cows in winter months and in buffaloes in summer months. The proportion showing oestrus was only 63% in winter months and 43% in summer months in underfed buffaloes as compared to oestrus detection of 100 and 89% respectively in well fed buffaloes. The mean anoestrous period was 21.8 and 159.8 d in buffaloes at optimum and deficient levels respectively (Kaur & Arora, 1982). The anoestrous period recorded in cows was 170.3 d in a deficient group and 36.3 d in normal animals (Juneja & Arora, 1990). Such an effect may be due to ovarian dysfunction resulting in a very low progesterone level both in cows and buffaloes. The disruption of pulsatile luteinizing hormone (LH) release affects follicular development and leads to an anoestrous condition. The day of the cycle at which progesterone peaked was 13.7 in the case of malnourished cows as compared to 12.6 in well fed animals, showing a slower development of the corpus luteum during the luteal phase. Oestrous cycle length has also been observed to increase as a result of dietary protein deficiency, reported as 21.4 d in deficient as compared to 19.4 d in normal cows (Juneja & Arora, 1989). In buffaloes, oestrous cycle length in deficient animals has been recorded to be 23.2 d as compared to 22.7 d in normally fed animals (Kaur & Arora, 1982). Sasser *et al.* (1988) reported a 29% reduction in oestrous cycles on a low dietary protein intake of 320 g as compared to control given 960 g daily.

Following severe undernutrition, optimal feeding rapidly restores pituitary and gonadal functions. Foster *et al.* (1988) observed that suppression of LH and follicle stimulating hormone secretion in undernourished lambs was reversed within 2 d of changing their feeding level. Kaur (1981) reported an increase in plasma progesterone concentration within 8 d of a shift to optimum feeding in an underfed buffalo. An increase in progesterone concentration was also recorded a few days prior to the onset of oestrus after a long anoestrous period. It has been suggested that the increase in progesterone concentration is of intraovarian luteal tissue origin (Berardinelli *et al.* 1979) and is required to stimulate the frequency of LH pulses (Smith & Day, 1990). The initial LH surge may cause luteinization of follicles rather than ovulation. Subsequent LH surges may be followed by ovulations and oestrous cycles of normal length (Schillo *et al.* 1992).

OVULATION RATE

Adequate nutrition during prenatal and postnatal periods is essential in all species for optimum ovulation rate (Doney *et al.* 1982; Henniawati & Fletcher, 1986). Ewes are usually provided with extra food for a few weeks before mating (flushed) to increase the proportion of multiple ovulations and multiple births (Smith, 1988; Teleni *et al.* 1989; Abecia *et al.* 1993). Conversely, feeding low protein diets has an adverse effect on ovulation rate (Davis *et al.* 1981; Stewart & Oldham, 1986; Nottle *et al.* 1988). Ewes maintained on temperate hill grazing or in the arid or semi-arid zones are usually deficient in protein and energy and their ovulation rate has been reported to average less than one in a single oestrous period (Rhind *et al.* 1986). An increase in ovulation rate by 8–25 ovulations per 100 ewes given protein supplement before mating had been observed and the blood levels of leucine, isoleucine and valine were about twice those in the protein supplemented group (Waghorn *et al.* 1990). Abecia *et al.* (1993) did not observe any effect of protein supplementation (120 v. 95 g/head daily) after weaning in the month of July on the onset of breeding or ovulation rate at first oestrus in ewes, but the effect was evident at mid term in subsequent oestrous cycles in the month of September. An increase in the protein level during the transitional period from anoestrus to the onset of the breeding period did not raise the ovulation rate in the first cycle in contrast to the results obtained within the breeding season (Radford *et al.* 1980; Smith *et al.* 1990; Pearse *et al.* 1991). Ewes exhibiting multiple ovulations in the first cycle after weaning experienced advanced onset of breeding (Baird & McNeilly, 1981; Karsch, 1984). The higher ovulation rates in ewes in good body condition reflect their greater number of large ovarian follicles in the late luteal phase of the preceding oestrous cycle (Rhind & McNeilly, 1986; Rhind *et al.* 1989; Xu *et al.* 1989). The changes that determine the number of ova to be released in response to variation in the level of dietary protein intake are still not clear. It seems that higher protein levels increase the concentration of insulin (Smith, 1988), which enhances the activity of certain hepatic enzymes; in consequence there is likelihood of increased catabolism of steroid hormones (Thomas *et al.* 1987) resulting in reduced circulatory levels. Thus, the negative feedback effect of steroids on the anterior pituitary is reduced, leading to increased gonadotrophin secretion (Ritar & Adams, 1988) resulting in a higher ovulation rate.

CONCEPTION

Protein inadequacy has an important bearing on survival of embryos and development of the fetus during pregnancy in domestic animals (Folman *et al.* 1983; Robinson, 1990). Lower conception rates have been observed as a result of underfeeding in cows (Meaker, 1976; Kaim *et al.* 1983; Baruah *et al.* 1986; Fletcher *et al.* 1987) either due to fertilization failure or some other ovarian dysfunction. In buffaloes, the conception rate at first service has been reported to be 66.7% in normal as compared to 16.7% in protein deficient animals (Kaur, 1993). In another study, 2.66 inseminations were recorded in normally fed as compared to more than 4.00 inseminations per conception in protein deficient buffalo heifers (Kaur & Arora, 1989). Likewise Juneja & Arora (1986) reported 2.25 services per conception in protein deficient as compared to 1.50 inseminations per conception in normal cows, while Sasser *et al.* (1988) reported conception rates of 32% in deficient cows and 74% in normal protein counterparts. Such reports of lower conception rate have also appeared in ewes (Abdul-Wahid *et al.* 1986). The effects of protein deficiency on conception rate may be confounded due to overlapping of events such as peak milk production and return to cyclic sexual function in lactating animals (Stevenson & Call, 1988; Swanson, 1989). Feeding of high protein diets has been found useful in increasing the dry matter

intake of high yielding animals (Davis, 1978; Wohlt & Clark, 1978) with a resultant increase in milk production (Leng & Nolan, 1984). On the other hand, Oldham (1984) reported that high crude protein levels which promoted milk production have an adverse effect on subsequent fertility. In many other studies, higher crude protein intake either had no effect or it led to more services per conception (Howard *et al.* 1987; Khasan *et al.* 1989). Ferguson & Chalupa (1989) applied logistic regression analysis to the existing data on protein effects on reproduction in lactating cows in order to find out the impact of rumen degradable protein (RDP) and undegradable dietary protein on conception rate. They suggested that an intake of RDP in excess of rumen requirements is associated with decreased conception rate in dairy cows. Ferguson *et al.* (1988) recorded an increase in conception rate from 23.0 to 46.2% in dairy cows when the dietary protein was reduced from 184 to 160 g/kg and its RDP content from 67 to 62%.

EMBRYO SURVIVAL

Prolonged underfeeding has been reported to cause a significant reduction in the survival and development of embryos in cows and sheep (Parr *et al.* 1982, 1986; Robinson, 1986). Rhind *et al.* (1989) did not observe any difference in fetal size between days 21–26 in ewes maintained on 50 and 150% of their maintenance protein needs in early pregnancy. However, a higher plane of nutrition has been reported to reduce embryo survival rate in ewes (Parr *et al.* 1987). Higher protein or energy intakes have a stimulatory effect on hepatic blood flow which influences the metabolic clearance rate of progesterone (Symonds & Prime, 1989) causing its decrease to an extent that may compromise embryo survival and growth (McKelvey & Robinson, 1986). In this context, Parr *et al.* (1987) demonstrated that the reduction in the rate of embryo survival arising as a result of a higher plane of protein and energy nutrition can be avoided by administration of exogenous progesterone. Differences in circulating progesterone level due to dietary protein status may bring about changes in the production of either trophoblastic proteins or endometrial secretory proteins (Stone, 1987). Levels of ten such endometrial proteins have been shown to increase during early pregnancy with the administration of exogenous progesterone (Ashworth & Bazer, 1989) in animals fed on a higher plane of nutrition which might be an essential mechanism for embryo survival (Thatcher *et al.* 1989; Bazer, 1989). It may also be possible that a low plane of nutrition and in consequence higher progesterone level may modify the secretory pattern of IGF binding proteins from the blastocyst and this requires further investigation of its involvement in embryo survival (Corps *et al.* 1989).

In embryo transfer experiments, a positive relationship has been established between embryo quality and feeding level as evidenced through maternal blood glucose concentration from the time of ovulation up to embryo recovery from the donor ewes (McKelvey & Robinson, 1988). Waghorn & Smith (1990) synchronized oestrus in 20 ewes and divided them into two groups for feeding low and high protein (133 v. 271 g/kg) diets. The number of ova recovered per ewe increased from 1.47 to 1.89 in the high protein group and from 1.35 to 1.50 in the low protein group.

FETAL GROWTH AND NEONATAL VIABILITY

Maternal dietary protein restriction during pregnancy can affect fetal growth through lack of supply of certain amino acids to the fetal tissues and may reduce the birth weight of offspring (Dunn, 1980; Robinson, 1983, 1990). During late pregnancy in cows, the protein and energy requirements are 1.5 times the maintenance needs and any deficiency may lead

to restricted growth (Wright *et al.* 1986; Topps *et al.* 1989). Additional dietary protein intake to the extent of 0.3–0.5 times above maintenance during pregnancy proved adequate in ewes (Robinson & McDonald, 1989). Restriction of feed intake to 0.15 times maintenance requirement showed arrested growth of the fetuses in ewes during early pregnancy, resulting in a specific effect in the proximal tibial metaphysis with consequent lower lamb live weight at birth (Vincent *et al.* 1985). The condition of the uterus at the time of mating is also important for placental and fetal growth and this is dependent on the level of feeding (Faichney & White, 1987). Both quantity and quality of protein influence fetal growth in ewes as feeding of lupin grains, a source of extra protein, in late pregnancy has resulted in better lamb birth weight (Kleemann *et al.* 1988). Ewes bearing triplets, maintained only on high quality pastures, may even suffer from a deficiency in the supply of certain amino acids (Barry & Manley, 1985), particularly cystine and histidine (Robinson *et al.* 1985).

POSTPARTUM ANOESTROUS INTERVAL

Reduction of the postparturient anoestrous period has received greatest attention in lactating animals. Protein and/or energy deficiency are common predisposing factors for prolonging the postparturient interval to first oestrus. Regaining threshold body weight is necessary for animals to come into regular oestrous cycles (Doney *et al.* 1982). The cows showing poor body condition exhibited extended postpartum oestrus intervals compared with those which were in good condition (Wright *et al.* 1987; Richards *et al.* 1989; Houghton *et al.* 1990). In developing countries, cattle and buffaloes kept mainly on grazing exhibited longer anoestrous periods extending from January to August due to inadequate availability of nutrients. During the late monsoon months (August & September), grasslands show improvement with a flush of nutrients, leading to the so-called 'onset of breeding' season. Kaur & Arora (1982) observed that the seasonal anoestrous period could be reduced to a great extent by improving the nutritional status of the animals. In Australia, the interval from calving to first oestrus was reduced from 75 to 40 d in grazing cows by giving a protein supplement along with phosphorus (Little, 1975). Sasser *et al.* (1988) reported an 11 d increase in postpartum oestrus interval in cows maintained on a low protein diet. On the other hand, intake of dietary protein above the feeding standards for maximizing milk yield have resulted in prolongation of the time from the day of calving to conception (Folman *et al.* 1981). It is expected that a large supply of undegradable dietary protein, that enhances milk yield and in turn stimulates the mobilization of body fat in early lactation, may accentuate the energy deficit and delay rebreeding (Ferguson & Chalupa, 1989). Higher amounts of RDP may also extend the postpartum anoestrous period by delaying uterine involution (Carroll *et al.* 1988). Ducker *et al.* (1985) emphasized that maximum or peak milk yield at the time of insemination is detrimental to conception. Goodall & McMurray (1984) predicted financial advantages or disadvantages of reducing the rebreeding interval by considering different feeding strategies, calving dates and reproductive performance values. Nutritional status affects the timing and magnitude of various hormones secreted during late pregnancy and early lactation and thus affects the postpartum anoestrous period. The mechanism is likely to be an alteration in the frequency of episodic release of LH necessary for fostering ovarian follicular development and ovulation. Alternatively, protein or energy deficiency in early lactation may render ovarian follicles less responsive to the gonadotrophin stimulus (McCann & Hansel, 1986). The interval to first ovulation in the postpartum period therefore depends upon the process of recovery in the normal functions of the brain pituitary-ovarian axis and the genital tract.

POSSIBLE MECHANISMS OF EFFECTS OF PROTEIN NUTRITION ON REPRODUCTION

Low as well as high levels of protein intake seem to be associated with reproductive disturbances in animals. Few mechanisms based on the amount of dietary protein intake, its digestion and metabolism can be postulated.

PUBERTY

Attainment of a particular body weight has been accepted as a pre-requisite for the onset of puberty. Acquisition of a minimum level of body fat is also considered to trigger pubertal endocrine changes (Randel, 1990), though there are reports that heifers reared on different planes of nutrition do not attain puberty at a consistent level of body fat (Brooks *et al.* 1985). Simpson *et al.* (1991) reported that prepubertal heifers which deposited more fat reached puberty at a later age. Hence, it is apparent that minimum body fat alone is not sufficient to trigger puberty. The important event leading to onset of puberty has been identified as the pre-pubertal increase in luteinizing hormone (LH) pulse frequency which results from a decrease in responsiveness of the hypothalamic-pituitary axis to oestrogen negative feedback (Kinder *et al.* 1987). Undernutrition might delay puberty by inhibiting the pulsatile release of gonadotrophin releasing hormone (GnRH) from the hypothalamus and thus might influence the pulsatile LH secretion (Moss *et al.* 1985; Foster & Olster, 1985; Day *et al.* 1986), which is required to stimulate the development of ovarian follicles to the preovulatory stage. On GnRH injection in such underfed heifers, LH pulses were observed to be similar to those of normal animals (Kurz *et al.* 1990; Kile *et al.* 1991).

In addition, hypothalamic luteinizing hormone releasing hormone (LHRH) level was the same both in underfed and *ad lib.* fed lambs which suggested that the effect of feed restriction was on central mechanisms controlling LHRH release rather than on LHRH synthesis. It is further evident that *N*-methyl-D-aspartate activates the release of accumulated GnRH from the hypothalamus which is inhibited as a result of undernutrition (Ebling *et al.* 1990; I'Anson *et al.* 1990), suggesting that the central nervous system was responsible for the release of GnRH (Dunn & Moss, 1992). Since dietary protein:energy ratios influence intermediary metabolism leading to changes in the circulatory concentrations of insulin, certain amino acids and non-esterified fatty acids (Brockman & Laarveld, 1986; Howard *et al.* 1987; Patil, 1993), it is proposed that these metabolites may act as nutritional signals influencing LH secretion. Schillo (1992) reported that insulin and tyrosine enhance and non-esterified fatty acid inhibit the pulsatile secretion of LH in young sheep and that neurones controlling the pulsatile release of LHRH are responsive to the availability of these substances.

Insulin has been shown to bind with insulin specific receptors in the arcuate nucleus and median eminence areas of the brain to control GnRH secretion in mammals (van Houten *et al.* 1980; Duffy & Pardridge, 1987; Wallum *et al.* 1987). Tyrosine administration has been shown to enhance the onset of puberty along with increased litter size in rats in some cases (Hammerl & Muller, 1988), and in adult cows ovarian activity has been induced by tyrosine administration (Hammerl, 1986). The theory behind this action of tyrosine is increased synthesis of a catecholamine neurotransmitter in the central nervous system of rats and monkeys (Kalra & Kalra, 1983; Terasawa *et al.* 1988; During *et al.* 1989). To elaborate further, Hall *et al.* (1990) studied the effect of tyrosine infusion for 22 days in ovariectomized feed restricted lambs and reported higher concentration of tyrosine in blood and hypothalamic tissue along with higher frequencies of LH pulses. It is therefore evident that any disruption in LH pulse frequency due to reduced supply of amino acids

or energy may delay the onset of puberty in animals, though further research is still required to identify other metabolites which may mediate the effects of nutrition on LHRH release.

LOW PROTEIN FEEDING EFFECTS ON FERTILITY

Protein deficient cows develop hypoalbuminaemia which has been shown to correlate inversely with number of services per conception (Payne *et al.* 1970). Low protein diets reduce the efficiency of metabolizable energy utilization (MacRae *et al.* 1985) accompanied by reduced glucose entry rate and plasma glucose concentration (Linzell & Peaker, 1971). Teleni *et al.* (1989) observed an increase in glucose entry rate in sheep when additional protein was presented to the small intestine by abomasal infusion of casein. Decreased plasma glucose concentration in protein restricted animals results in decreases in plasma insulin levels both of which can inhibit the pulsatile release of LH (Foster *et al.* 1989). Deficiency of certain amino acids may lead directly to alterations in the levels of certain hormones and their releasing factors. Intravenous infusion of amino acids or abomasal infusion of casein or increased intake of dietary protein have all been shown to elevate blood insulin, glucagon and glucose levels (Chew *et al.* 1984; Ladenheim *et al.* 1984; Blauwiel *et al.* 1986; Cohick *et al.* 1986; Rutter & Manns, 1987) and insulin in turn has been found to increase follicle stimulating hormone and progesterone in cultured pituitary and luteal cells (Adashi *et al.* 1981; Ladenheim *et al.* 1984). Moreover, immunoreactive insulin and insulin specific receptors have been identified in the arcuate nucleus and the median eminence areas of the brain (Havrankova *et al.* 1978; van Houten *et al.* 1980) which play an important role in the control of GnRH secretion in mammals. The normal frequency of LH pulses can be restored by either glucose infusion to severely diet restricted ewes (Foster *et al.* 1989) or by injections of GnRH (Vandalem, 1986). It is therefore evident that the decrease in the number of LH pulses is due to inhibition of the GnRH pulse generating stimulus rather than insufficiency of its synthesis and storage in the pituitary gland. However, full information on the mechanisms linking metabolic status to LHRH secretion is still lacking. A recently discovered peptide, neuropeptide Y (NPY), has been shown to provide a link between the control of feed intake and the secretion of GnRH. NPY infused cerebroventricularly suppresses the release of LH in ovariectomized rats, rabbits and monkeys (Kalra & Crowley, 1984; Khorram *et al.* 1987, McDonald *et al.* 1989; Kaynard *et al.* 1990). In this connection, m-RNA of NPY is believed to be elevated in feed restricted rats, and in consequence the concentration of NPY is greater in specific hypothalamic regions such as the paraventricular and arcuate nuclei (Sahu *et al.* 1988). It seems that this higher concentration of NPY is inhibitory to the release of LH in ovariectomized non-oestrogen-treated animals (Sabatino *et al.* 1989). In a study conducted in ovariectomized sheep, NPY injections into the lateral ventricle had inhibitory effects on LH release (Malven *et al.* 1990; McShane *et al.* 1992). The pathway of the effects of low protein intake on LH secretion is depicted in Fig. 1.

HIGH PROTEIN FEEDING EFFECTS ON FERTILITY

Feeding more than the recommended amounts of protein or inclusion of excess degradable protein in the diet adversely affect animal reproduction. On such diets it is likely that relatively more ammonia is released in the rumen through the process of deamination by bacterial enzymes (Visek, 1984). The excess ammonia or urea produced in the rumen can diffuse from the alimentary tract to the peripheral circulation and appear in the uterine secretions (Jordan *et al.* 1983), thereby disturbing endocrine functions (Ferguson *et al.*

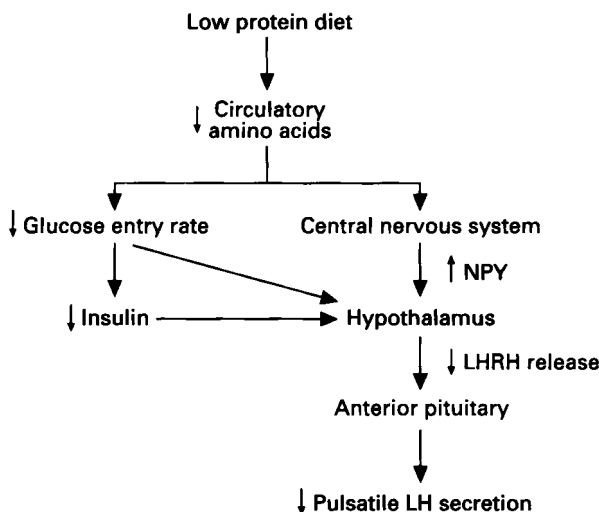


Fig. 1. Likely mechanisms for the effect of low dietary protein on pulsatile luteinizing hormone secretion. LH, luteinizing hormone; LHRH, luteinizing hormone releasing hormone; NPY, neuropeptide Y.

1986) and the corpus luteum (Garwacki *et al.* 1979), and may also reduce motility and survival of sperms as a result of a changed uterine environment. The toxic effects of ammonia, urea or other unidentified nitrogenous compounds influence the survival of ova, sperms and early developing embryos (Umezaki & Fordney-Settlage, 1975; Jordan *et al.* 1983; Sahlu *et al.* 1992). Excess protein, irrespective of protein source or degradability, decreases uterine pH on day 7 of the estrous cycle (Elrod & Butler, 1993) by decreasing the uterine Mg, K and PO₄ concentrations during the luteal phase (Jordan *et al.* 1983) which can in turn inhibit the endometrial carbonic anhydrase activity (Rowlett *et al.* 1991). The decrease in pH in the uterus adversely affects the activity and survivability of sperms in the reproductive tract (White, 1974). Ferguson *et al.* (1988) suggested that dietary protein intakes producing serum urea-N greater than 200 mg/l were indicative of excess protein intake, particularly RDP.

High protein intake may also influence the reproductive system as a result of activation of different mechanisms in the liver for hepatic detoxification and the increase of energy demand for deamination of excess amino acids (Visek, 1984). Excess ammonia may also disturb intermediary metabolism and thus increase blood concentrations of urea, glucose, non-esterified fatty acids and insulin. Smith (1986) reported that some nitrogenous end products might alter the functioning of the hypophyseal-pituitary-ovarian axis by decreasing LH pulse frequency and amplitude. Fig. 2 illustrates the mechanism of action of excess dietary protein on LH secretion.

CONCLUSIONS AND PERSPECTIVES

There is considerable current interest in the influence of protein nutrition on reproduction of farm animals particularly in developing countries where dietary protein deficiency is common. In the developed world, excess protein is often fed to obtain more milk from high yielding animals. Both aspects of protein nutrition have implications for the reproduction process in primiparous as well as pluriparous animals. It is essential that the animals should be given adequate protein during the postweaning period to get optimum growth and early puberty. It is also well recognized that an increase in prepubertal LH pulse frequency is an

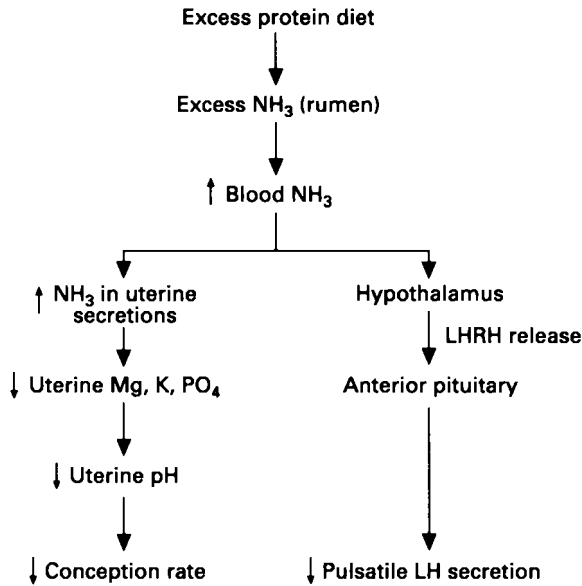


Fig. 2. Likely mechanisms for the effect of excess dietary protein on pulsatile luteinizing hormone secretion. LH, luteinizing hormone; LHRH, luteinizing hormone releasing hormone.

important event for the onset of puberty. Attention is now being paid to the cellular biochemical changes being mediated through certain amino acids which influence pulsatile LH secretion. Alterations in body metabolism as a result of deficiency of certain amino acids may influence the neuronal mechanisms linking nutritional status with the pulsatile release of LHRH. Further studies are required to identify the neurones controlling LHRH release from the hypothalamus with the generation of neuroendocrine signals.

In embryo biotechnology work, the influence of nutrition on donor and recipient animals needs to be investigated to promote ova recovery rate, embryo survival and embryo development, as this technique is now being used on a wider scale to generate superior progeny for increased milk production.

Studies are required to work out in detail the mode of action of feeding high protein diets on various events of the reproductive cycle. The results of such investigations may help to overcome failures in reproductive function without depressing milk yield. There is a distinct possibility of reducing the total protein by prescribing less RDP in the diet, so that no harm is done to the reproductive tract. Long term studies are also suggested to investigate the carry-over effects of different nutritional regimes, particularly dietary protein level.

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