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A review of recent developments on the effect of nutrition on ovulation rate (the flushing effect) with particular reference to research at Ruakura

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ABSTRACT

The results in this field over the last 10 years at Ruakura and relevant international data is reviewed. The nutrients involved have been defined and a likely mechanism of action indicated. Pasture allowance experiments indicated effects of pasture quality and a series of pellet feeding trials defined effects of both energy (linear) and protein (threshold) intakes. The threshold effect of protein was confirmed by the abomasal infusion of protein. Analyses of changes in blood concentrations of amino-acids indicated the involvement of the branched-chain amino-acids (BCAA) and this has been confirmed by an increased ovulation rate after intravenous infusion of BCAA. It is concluded that the static and dynamic liveweight and the immediate nutrient effects are the same response measured at different times. The rate at which the response develops is dependant on the type of feedstuff.

Studies into the mechanism of action in both intact and ovariectomised ewes have ruled out effects on pituitary release of FSH either directly or via interference with negative feedback influences. This indicates that the effect is at the ovarian level and is mediated either by direct action of the BCAA or indirectly via a metabolic hormone.

Keywords Nutrition, ovulation, branched chain amino acids, ewes, protein, energy, FSH, negative feedback, insulin.

INTRODUCTION

Nutrition is one of the most significant environmental influences on reproductive performance of sheep. For at least 90 years there have been scientific publications dealing with the influence of nutrition on fertility and ovulation rate of ewes. Although the general principles of the response, such as the empirical relationship between liveweight and ovulation rate are well recognised, the mechanisms of effect of the ovulatory response is not well understood.

Research at "Ruakura" has attempted to:

(1) define the nutritional inputs required to obtain the "flushing response" both in terms of amount and type of nutrient and the duration of feeding. This has ranged from trials involving pasture allowance, through feeding of formulated diets in pellet form, to abomasal and intravenous infusion of specific nutrients; and,

(2) determine the route of action by which the input of nutrients perturbs the endocrinological

mechanisms controlling ovulation rate. This has involved studies on changes in circulating levels of gonadotrophins in both intact and ovariectomized ewes and also the trials investigating changes in liver enzyme levels.

The time frame and interconnection of these research efforts are shown in Figure 1.

LIVEWEIGHT RELATIONSHIPS

All the so-called liveweight effects are reflections of differences in nutrition at some prior stage in the animal's life. The definition of the liveweight effect and distinction of the relative contributions of the "static" and "dynamic" components (Coop, 1966) have received considerable attention. The effect of the ewe's body reserve status is shown in the well-established and repeatedly documented relationship between liveweight immediately prior to mating and an increase in ovulation rate (Morley *et al.*, 1978). This static liveweight effect has been compartmentalized into the effects of body size and body condition (Ducker and Boyd, 1977) and,

liveweight and body condition together predict ovulation rate better than liveweight alone. The "dynamic effect" of liveweight change or "flushing" effect has been much less repeatable because of the lack of precise quantitative descriptions of the level and type of diet being offered to, and consumed by, the ewe.

ACTIVITY	YEAR							
	78	80	82	84	86	88	90	92
PASTURE ALLOWANCE.	■	■	■					
PELLET FEEDING		■	■	■	■			
ABOMASAL INFUSION.					■	■	■	■
JUGULAR INFUSION.							■	■
bGH INJECTION						■		
LAPAROSCOPY	■	■	■	■	■	■	■	■
LIVER ENZYMES					■	■	■	■
BCAA LEVELS			■	■	■	■	■	■
FSH LEVELS (INTACT EWE)				■			■	■
FEEDBACK FSH (OVX EWES)							■	■
OVARIAN INFUSION.								■

FIG 1 Gantt chart of the research programme at Ruakura on the effects of nutrition on ovulation rate.

At Ruakura Rattray *et al.* (1978, 1980a, 1981) found increases in ovulation rate of ewes presented with a greater pasture mass, less dead material, higher clover content and lower utilization, thus reflecting the importance of diet quality in grazing ewes. These workers also produced considerable data to support the dynamic response and showed that for ewes at any given mating liveweight their ovulation rate depended on the liveweight change that had taken place in the previous 3-6 weeks (Fig. 2).

However Smith *et al.* (1982), summarised a series of grazing experiments conducted at Ruakura, and found that ewe liveweight at mating, and pre-mating liveweight change accounted for only 42.0% and 18.5% respectively, of the variation in ovulation rate. Moreover, other workers showed that increased nutrition can increase ovulation rate without increasing liveweight (Oldham and Lindsay, 1984).

DURATION OF FEEDING PERIOD AND TIME OF CYCLE

The period for which a supplement must be fed to elicit an increase in ovulation rate appears to be dependent on the type of supplement. Ovulation rate responses to increased allowance of pasture were not observed for at least 3 weeks (Smith *et al.*, 1983) and ewes needed to be fed a high energy supplement for at least one oestrous cycle. Ovulation rate increased after four days when ewes were fed a high protein supplement, such as lupins (Stewart and Oldham, 1986). The different critical duration of feeding the two types of supplement may provide clues to the mechanism of effect of nutrition on ovulation rate.

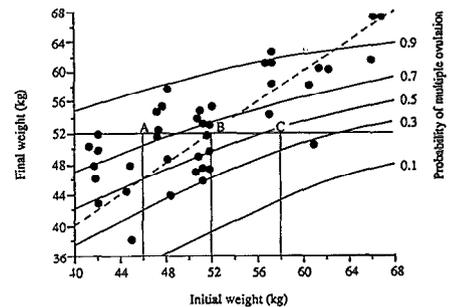


FIG 2 Curves of probability of ewes having a multiple ovulation and the association with initial (LW1) and final liveweights (LW2). Dotted line represents zero liveweight change (static) over a 6 week period. Points A, B, and C indicate the different probabilities of having multiple ovulations for groups of ewes with the same final weight (52kg) but with different liveweight changes in the preceding 6 weeks. (Point A represents a gain of 6 kg and 75% multiple ovulations; B represents no gain and 60% multiples; C represents a 6 kg loss and 45% multiples). Adapted from Smith *et al.*, (1982).

Stewart and Oldham (1986) identified the critical time as Days -8 to -5 before the next ovulation (Day 0) and this was confirmed by Nottle *et al.* (1986). Feeding supplements after Day -5 either had no effect on ovulation rate (Stewart and Oldham, 1986) or decreased it (Stewart, 1990). The timing of the critical period shows that the ovary requires at least 4 days to respond to a change in intake. This is not surprising, as Coleman and Dailey (1983) found it took four days for preovulatory follicles to develop.

EVALUATION OF ROLE OF VARIOUS NUTRIENTS

Interest in the contributions of protein and energy to ovulation rate was stimulated by the responses to supplementation with lupin grain (Knight *et al.*, 1975). These workers ascribed the effect to the higher protein content of the lupin grain. Moreover, the work of Rattray *et al.* (1981) which showed the additional response to pasture with higher clover content also indicated a possible role for additional dietary protein.

Smith (1985) presented data from a series of trials conducted at Ruakura in an attempt to define the effects of protein and energy on ovulation rate. The design of the experiments provided for animals to receive different levels of protein intake at any one level of energy intake and also different energy intakes at similar protein intakes.

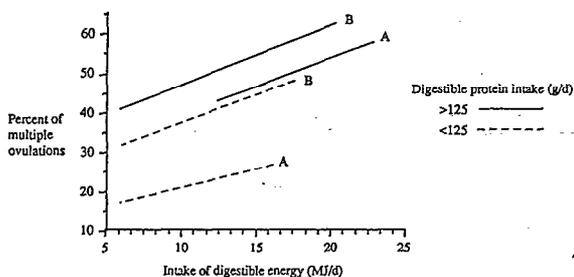


FIG 3 Effect of intake of digestible energy (MJ/d) and digestible protein (g/d) on the percentage of ewes having multiple ovulations in two trials A and B. From Smith (1985).

These results indicated effects of both protein and energy intake. The linear (energy) response is in general agreement with that seen with increasing intake of ewes supplemented with pasture silage (Rattray *et al.*, 1980b). Significant responses to increased protein intake were obtained at all but the lowest levels of energy intake. The threshold level of digestible protein intake (approx. 125 g/day) in the trials of Smith (1985) is close to the levels at which Davis *et al.* (1981) found a response. This "threshold" effect of digestible protein intake provides a basis on which we can rationalize the variability in responses that have been obtained in many flushing or feed-supplementation experiments. The

failure to obtain an increase in ovulation rate following supplementation could be due to:

- (1) the protein level of the basal diet being sufficient to meet the threshold requirement; or,
- (2) the total protein intake from both basal diet and supplement being insufficient to meet that requirement.

It has been suggested (Knight *et al.*, 1975) that the benefit obtained from feeding lupins may be due to its lower level of ruminal degradation (Hume, 1974). However, attempts to increase the post-ruminal supply of protein by the treatment of casein with formaldehyde have given variable results and caused considerable debate on the role of various nutrients (Teleni *et al.*, 1985; Nottle *et al.*, 1988). The conflicting conclusions in many of the experiments maybe at least partly due to the techniques used to modify the supply of protein and energy by changes in diet formulation and/or level of food intake and creating the possibility of variable rumen fermentation. At Ruakura Cruickshank *et al.* (1988) infused ewes with protein or glucose via the abomasum for 10 days to avoid this effect and obtained significant increases in ovulation rate with two protein sources while an isocaloric infusion of glucose gave only an intermediate result. These results confirmed the threshold protein effect suggested by Smith (1985).

Waghorn (1986) fed the same diets as Smith (1985) to study the correlations between ovulation rates, (calculated for his intake levels from the equation of Smith, 1985), and a range of nutritional and physiological parameters. The strongest relationship was between ovulation rate and the plasma concentrations of the branched-chain amino acids (BCAA), valine, leucine and isoleucine. There were no significant correlations between ovulation rate and either a glucose tolerance test or with plasma insulin levels, although insulin levels were higher in the animals fed the high protein diets. More recently, analysis of the changes in concentrations of BCAA in the blood of ewes fed a low protein (11%) diet followed by a high protein (22%) diet indicated a positive link to changes in ovulation rate (Waghorn and Smith, 1990; Waghorn *et al.*, 1990). Concentrations of non-essential (NEAA), BCAA and other essential (EAA) amino acids in the

blood of ewes on a low protein diet did not differ between those with single or multiple ovulations. When changed to the high protein diet, the concentrations of NEAA did not change, but the BCAA differed with the ovulatory response to increased feeding. When the dietary change resulted in increased ovulation, the increases in blood concentration of BCAA was at least twice that measured in ewes which showed no change in ovulation rate. Also, the increase in blood BCAA concentration in ewes which changed from 2 to 3 ovulations was twice that seen in ewes changing from 1 to 2 ovulations. These results indicate that the BCAA have a role in influencing the mechanisms controlling ovulation rate. This has been confirmed by the finding that intravenous infusion of BCAA, but not other amino acids, produced an increase in ovulation rate (Downing and Scaramuzzi, 1990; Downing *et al.*, 1990; J.F. Smith, unpublished). It is noteworthy also that sheep placed on supplemental dietary energy for a period of 2 or more weeks had elevated levels of the branched chain amino acid, leucine (Nissen and Ostaszewski, 1985). This could indicate a common route for the effects of both protein and energy supplements.

It is important to note that most of the Ruakura trials involved supplementation of, or nutrient substitution in, ewes that were already on a maintenance or above maintenance plane of nutrition. This contrasts with many other studies overseas where the supplementation is made to ewes in either, or both, protein and energy deficiency. Recognition of the base level of nutrition of the experimental animals must be made in the interpretation of the results obtained.

MECHANISMS FOR INCREASED OVULATION RATE

There is evidence that liveweight and body condition influence ovulation rate by affecting the number of large follicles available for recruitment (Allen and Lamming, 1961). In recent experiments using a follicle mapping technique, Stewart (1990) showed that a short term (4 day) intake of lupin supplement increased the numbers of medium and small follicles visible on the ovary and the number of follicles growing (non-atretic) between 12 and 24 h after a prostaglandin injection.

Follicular recruitment and development is dependant on the neuro-endocrine feedback loop

between the hypothalamus-pituitary axis and the ovary (Martin and Thomas, 1990).

Because the gonadotrophins (LH and FSH) are essential for follicular growth it is possible that changes in the secretion and circulating levels of these hormones may mediate the influence of nutrition on ovulation rate.

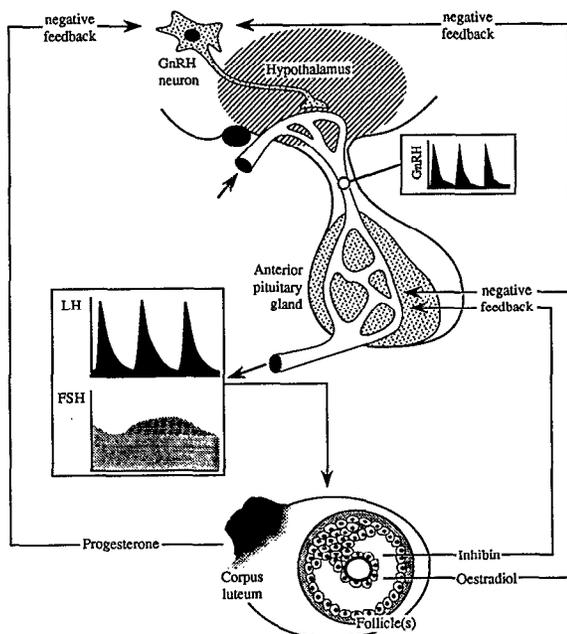


FIG 4 Endocrine links between the hypothalamus, pituitary gland and ovary. Important points to note: (a) the pulsatile nature of GnRH secretion; (b) the GnRH pulses are transposed into LH pulses on a one to one basis; (c) the GnRH pulses are not transposed into pulses of FSH so this hormone is secreted in a relatively continuous manner; (d) inhibin produced by the follicle acts only on the pituitary gland where in a synergistic effect with oestradiol, it selectively reduces the secretion of FSH (from Martin and Thomas 1990).

Treating ewes with exogenous FSH in the follicular phase increased ovulation rate (McNatty, *et al.*, 1985; Thompson and Smith, 1988) and the finding that twin ovulating ewes had greater concentrations of FSH than single ovulating ewes five days before ovulation (Davis, *et al.*, 1981; McNatty *et al.*, 1985) strongly support the suggestion that circulating levels of FSH may be involved in the control of ovulation rate. However, effects of nutrition on FSH levels during the

cycle appear equivocal (Smith, 1988; Smith, *et al.*, 1990c) and the data on effects of liveweight or body condition on levels of FSH is conflicting. There is also conflicting evidence for a role of LH in the control of ovulation rate. These data have recently been reviewed (Smith and Stewart, 1990).

WAYS IN WHICH NUTRITION COULD ALTER GONADOTROPHIN SECRETION

Effects of nutrition on circulating levels of gonadotrophins could be achieved in a number of ways (Fig. 5). Firstly, there is the possibility of a direct effect on the hypothalamic-pituitary axis; and, secondly via a reduction in the negative feedback effect of oestradiol and/or inhibin.

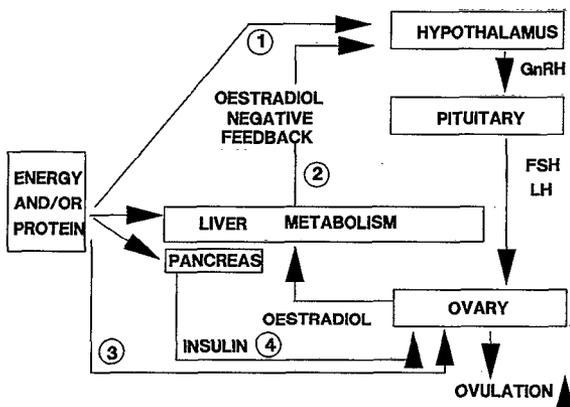


FIG 5 Possible pathways by which increased supply of nutrients could perturb the hypothalamic-pituitary and ovarian interrelationship and produce an increase in ovulation rate. (1) Direct effect on hypothalamic-pituitary axis leading to an increase in FSH/LH production. (2) Effect on liver metabolism of steroids reducing the negative feedback and increasing gonadotrophin release. (3) Direct effect of nutrients on the ovary increasing sensitivity to FSH. (4) Effect of a metabolic hormones (insulin) on the ovary having a synergistic effect with the gonadotrophins.

Direct Effect at Hypothalamic-Pituitary Level

It is possible that changes in intake could induce a change in the rates of neurotransmitter turnover, and consequently influence the hypothalamic regulation of gonadotrophin secretion. Downing and Scaramuzzi (1990) tested this hypothesis by infusing ewes with

aromatic amino-acids. This treatment had no effect either on ovulation rate or on levels of FSH or LH, suggesting that this is an unlikely route of action.

Alternatively, a nutrient could have a direct effect on the pituitary. Although support for this mechanism should be derived from a study of the effect of nutrition on the secretion of the gonadotrophins in ovariectomised ewes, the results are equivocal, (Nottle *et al.*, 1988; Ritar and Adams, 1988). At Ruakura, Cruickshank *et al.* (1990) found no effects on peripheral plasma levels of FSH with abomasal infusion of protein into ovariectomised ewes.

Modification of the Negative Feedback Effects

Nutrition could have an indirect effect on the secretion of FSH by a reduction in the negative feedback of oestradiol and/or inhibin. Oestradiol-17 β depressed ovulation rate in the ewe and also lowered plasma FSH levels (Webb and Gauld, 1985; Payne *et al.*, 1990). The concentration of oestrogen receptors in the uterus of ovariectomised ewes varies inversely with liveweight (Adams and Ritar, 1986; Atkinson and Adams, 1988). Since the concentration of receptors is also determined by oestrogen, these data indicate that liveweight can affect oestrogen levels.

A major site of oestrogen metabolism is the liver; in particular, the cytochrome P450 enzymes in the endoplasmic reticulum. These enzymes may therefore be important in the control of ovulation rate. Diet has been shown to alter the catabolic pathways for oestrogen in man (Anderson *et al.*, 1984) and manipulation of the level of hepatic microsomal enzyme activity in the ewe with phenobarbital has proved successful in altering ovulation rate (Smith *et al.*, 1986; Payne *et al.*, 1987; Thomas *et al.*, 1987; Thomford and Dzuik, 1988). Payne and co-workers at Ruakura, showed that the effect of protein intake on ovulation rate was relatively greater than the effects on enzyme levels (Payne *et al.*, 1991). However, the phenobarbital-induced increase in ovulation rate was not accompanied by increased concentration of FSH (Davis *et al.*, 1989; Smith *et al.*, 1990a); and neither did phenobarbital or high protein treatments ameliorate the depression in ovulation rate produced by subcutaneous implants of oestradiol-17 β (Payne *et al.*, 1990). The mechanism by which phenobarbital increased ovulation rate remains

unresolved.

Investigations using ovariectomised ewes has shown a range of nutritional effects. Using oestradiol-17 β implanted ovariectomised ewes, Ritar and Adams (1988) found no increase in FSH levels with lupin feeding. Wright *et al.* (1988) found no difference in the FSH levels of ovariectomised ewes fed at different levels, but the depression in FSH produced by oestrogen implants was significantly less in the ewes on the higher level of feeding. This suggested an effect of nutrition on oestrogen-feedback systems. However at Ruakura, Smith *et al.* (1990b) using the abomasal infused ovariectomised ewe found that additional protein (100 g/d) did not reduce the depression in FSH produced by oestradiol-17 β implants of 2 different sizes. In contrast, protein infusion significantly prolonged the period from implant withdrawal until FSH reached the pretreatment level. There is no ready explanation for this delayed recovery but protein intake did not reduce the negative feedback of oestradiol on FSH. Knight *et al.* (1981) showed an elevation in levels of oestradiol-17 β after lupin feeding in one of the few reports investigating the effects of nutrition on peripheral concentrations of oestrogen in intact ewes. However, Adams and Martin (1990) reported that lupin feeding reduced levels of oestradiol and increased levels of FSH in oestrogen-implanted ovariectomised ewes. This conflicting array of data on the effects of nutrition and liveweight on the levels of gonadotrophins suggests that alternative mechanisms of action may be more likely.

Direct Effect of Nutrients on the Ovary

In recent reviews Downing and Scaramuzzi (1990), Scaramuzzi and Campbell (1990) concluded that the changes in follicular dynamics were not due to increased circulating levels of gonadotrophins, but to changes in local (ovarian) effects of growth factors or metabolites. Increased protein and/or energy intakes have been shown to increase the circulating concentrations of insulin (Waghorn *et al.*, 1987) and insulin-like growth factors (IGF-I; Bass *et al.*, 1984). Both insulin and IGF-I have been shown to act synergistically with FSH to increase the aromatase activity and to induce LH receptors in granulosa cells from follicles of a number of species (Adashi *et al.*, 1985). The use of growth hormone (GH) to increase serum IGF concentrations

has been advocated as a possible mechanism to enhance ovulatory activity (Eden *et al.*, 1988). At Ruakura, Davis *et al.*, (1990) treated ewes with recombinant bovine GH for one cycle and increased IGF-I levels more than 2 fold but with no increase in ovulation rate. Other inconclusive data exists for the cow (Butterwick *et al.*, 1988) and pig (Kirkwood *et al.*, 1988).

Downing and Scaramuzzi (1990) reported that the most consistent change associated with the nutritional increases in ovulation rate was an increase in the levels of metabolic hormones, particularly insulin. The potential for insulin to fit the role of a common metabolic hormone whose level is influenced by short and long term nutritional effects has been reviewed by Smith and Stewart (1990). However the data from studies of the ovulatory response following systemic infusion of insulin in the ewe are contradictory. Hinch and Roelofs (1986) have reported an increase in ovulation rate, but others have either failed to record any effect (Paterson, 1989) or observed a negative effect (J.F. Smith unpublished).

CONCLUSIONS AND REMAINING QUESTIONS

It is generally accepted that changes in the level of nutrition both in the short and long term can alter the ovulation rate in ewes. The Ruakura data indicates that there are responses to both energy and protein and that this may be reflected in the levels of BCAA. Any hypothesis for the mechanism of action of nutrition on ovulation rate should take account of the well established liveweight relationships as well as the immediate nutrient effects. All the effects appear to involve increased numbers of follicles available for recruitment or a reduction in follicle atresia. The mechanism by which this increase in active follicles is brought about remains contentious. However, recent results suggest a local (direct) ovarian effect as most likely. The most appealing scenario would be one that involved a common metabolite or nutrient whose levels reflected ewe condition, and changed with increasing or decreasing liveweight and was influenced by both energy and protein intake in the short term. The prime candidates for this action are the BCAA or insulin. Further studies on the effects of an infusion of either insulin or a BCAA directly into the ovary are needed.

Why Do Only Some Animals Respond?

This is a major question having both practical and basic scientific implications. It has been shown (Oldham, 1980) that some ewes repeatably only have one ovulation (non-responders), while others consistently show increases in ovulation rate when given supplements (responders). The proportion of responders varies from flock to flock, but is usually about 30%. What are the physiological, metabolic or endocrinological differences between responders and non-responders? Does the relationship between change in plasma BCAA concentration and increase in ovulation number give some lead to this? If the responders could be identified, then equivalent increases in lamb production could be obtained at the farm level with only a quarter of the present feed cost, as extra feed would not be wasted on non-responders.

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