THE EFFECTS OF NUTRITION ON THE REPRODUCTIVE PERFORMANCE OF FINN×DORSET EWES

II. POST-PARTUM OVARIAN ACTIVITY, CONCEPTION AND THE PLASMA CONCENTRATION OF PROGESTERONE AND LH

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Summary. After lambing, forty-five ewes were allocated to three groups, two of sixteen and one of thirteen ewes. The lambs of the two groups of sixteen ewes were weaned on Day 1 after lambing and the ewes were fed a diet of 100% (Group H) or 50% (Group R) of maintenance energy requirements. The thirteen ewes in the third group (Group L) suckled twin lambs and were fed freely.

During the first 3 weeks after lambing, oestrus was observed for 11/16 (Group H) and 8/16 (Group R) ewes; of the ewes which had shown oestrus in the two groups, ovulation occurred in 5/8 and 5/7 respectively. Only 1/13 Group-L ewes showed oestrus and ovulated during the same period. The mean plasma concentrations of progesterone and LH were unaffected by the treatments and were around 0.4 and 1.5 ng/ml, respectively.

Restricted feeding had no effect on oestrus, ovulation or the hormone levels during the oestrous cycle following synchronization. The onset of oestrus and the start of the preovulatory discharge of LH were 3 and 6 hr later, respectively, in the lactating ewes (Group L) than in those in Groups H and R. Ewes in Group L also had a higher ovulation rate, 2.8 ± 0.2 versus 2.1 ± 0.2 ($P < 0.05$). Restricted feeding reduced the number of ewes lambing; only 1/11 ewes in Group R, considered to have conceived because of the presence of high progesterone levels 17 days after mating, subsequently lambed compared with 6/12 in Group H and 5/9 in Group L.

INTRODUCTION

Undernutrition is commonly considered to be associated with infertility, although the pathways are not fully understood. Allen & Lamming (1961) concluded that undernutrition of sheep leads to impaired release of pituitary gonadotrophins. This was supported by evidence from the rat (Meites, 1970; Howland, 1971, 1972). Ovarian hypofunction was reported to be related to

the nutritional regimen by Howland, Kirkpatrick, Pope & Casida (1966) in sheep, and by Hill, Lamond, Henricks, Dickey & Niswender (1970) in cows, and it was found to be associated with an increase in plasma LH and decrease in plasma progesterone concentrations in underfed cows and heifers (Hill *et al.*, 1970). Furthermore, it has been suggested that the suppression of fertility by lactation may be mediated by inadequate nutrition (Hunter, 1968), although a recent study with Finn $\times$ Dorset ewes (Shevah, Black, Carr & Land, 1974) indicated that this is not so.

In the present study, the effects of undernutrition on the ovarian activity and the plasma concentrations of progesterone and LH were studied in post-partum lactating and non-lactating Finn $\times$ Dorset ewes.

MATERIALS AND METHODS

Forty-five F₁ Finn $\times$ Dorset ewes which were fed one of two nutritional treatments (high and low energy intake during the last 6 weeks of gestation as described by Shevah *et al.*, 1975) lambed in mid-December 1972, well within the breeding season (Land & McClelland, 1971). After lambing, the ewes were allocated to three groups (two of sixteen, Groups H and R, and one of thirteen, Group L) in which the two prelambling treatments were similarly represented. The lambs of the ewes in Groups H and R were weaned at 1 day of age, whereas the ewes in Group L each suckled two lambs for 56 days. Group-H and -R ewes were housed in individual pens and Group-L ewes in a common pen with access to creep feed for the lambs. A complete ruminant diet (CRD) incorporating 40% straw and containing 1.8 Mcal metabolizable energy (ME)/kg and 9.6% digestible crude protein (DCP) was fed at three different levels. Group H: a maintenance ration based on a recommended intake of 33 Kcal ME/kg live weight of the ewe; Group R: 50% of the above ration; Group L: no dietary restriction. The nutritional state of the ewes was monitored by weekly body weight and blood metabolite determinations.

Plasma progesterone and LH concentrations were determined in samples collected every 3 to 4 days during the first 3 weeks *post partum*, on Day 3 and 10 of the progestagen treatment, on the day of oestrus (every 2 hr) and on Days 8 and 17 of the oestrous cycle after synchronization. The blood samples were withdrawn from the jugular vein into heparinized evacuated tubes.

Oestrus was detected by the introduction twice daily of vasectomized rams from Day 2 after lambing. On Day 21, oestrus was synchronized by the insertion of intravaginal sponges treated with 30 mg Cronolone (G.D. Searle) and 400 mg progesterone as described by Gordon (1971). The sponges were withdrawn after 12 days (Day 33) and, 22 hr later, intact rams were introduced to the ewes for 15 min and then again at 2-hr intervals for further 15-min periods until oestrus was detected up to a limit of 50 hr after sponge withdrawal. During oestrus (Day 34 and 35), the ewes were mated to fertile rams on two occasions approximately 12 hr apart, either individually or in small groups.

Ovulation was studied by counting the number of CL in each ovary at laparoscopy under general anaesthesia (Nembutal: Abbott Laboratories).

Twenty-three ewes were studied on Day 21 and all forty-five ewes 8 days after the synchronization of oestrus.

Biochemical methods

Plasma non-esterified fatty acids (FFA) were determined by the method of Patterson (1963); ketone bodies by single distillation as described by Reid (1960) and plasma glucose by the method of Gutteridge (1968).

Progesterone was determined by a radioimmunoassay technique adapted from the method of Hotchkiss, Atkinson & Knobil (1971) and described in a previous study (Shevah *et al.*, 1975). In the assay, a goat antiserum was incubated with plasma n-hexane extracts. Ovine antiserum (100 μ l/tube) at a dilution of 1:4000 bound 50% of [3 H]progesterone. Samples from a pool of plasma obtained from ewes on the day of parturition were included in every assay and gave a mean concentration of 0.38 ± 0.03 ng progesterone/ml and an inter-assay coefficient of variation between the nine assays of 16.7%.

Levels of LH were determined by a double-antibody radioimmunoassay described by Carr & Land (1975). An equine (anti-bovine LH) antiserum and a purified preparation of ovine pituitary LH labelled with 125 I as a label and NIH-LH-S17 as a standard were used. The preovulatory LH release was determined by a solid phase radioimmunoassay of samples collected on the day of oestrus with the same preparation as above. Polystyrene tubes coated with antibody by the method of Catt & Tregear (1967) were used in the assay.

Statistical analysis

The statistical techniques used were based on methods described by Snedecor (1956).

RESULTS

Nutritional treatment

The effects of the nutritional treatments are summarized in Table 1 and Text-fig. 1. The prelambling feed intake had no effect on the nutritional state or the reproductive activity during the post-partum period and therefore the two sub-groups were pooled within each post-partum treatment. The energy intake of 33 Kcal ME/kg live weight of ewe fed to Group H ewes was found to be adequate to meet the nutritional requirements for maintenance. The ewe live weights were relatively stable, and the weekly determinations of blood metabolites, glucose, FFA and ketone bodies, indicated that the concentrations of these metabolites were all within the normal range (Russel, Doney & Reid, 1967). Undernutrition in the ewes in Group R was indicated by a continuous decline in body weight (about 1 kg/ewe/week) and an increase in plasma FFA up to 650 μ equiv./litre by the 3rd week of the experiment. Group-L ewes consumed an average of 6 Mcal ME/ewe/day and were able to maintain body condition at the initial level for the early part of the experiment, but failed to do so towards the end; in the last 2 weeks, there was a drop in the mean live weight and the plasma concentrations of FFA, and ketone bodies reached the values of 500 μ equiv./litre and 3 mg/100 ml, respectively, both marking the onset of undernutrition in the ewe.

Table 1. Body weight change, feed intake and peripheral blood metabolite concentrations during the first 50 days *post partum* for lactating and non-lactating ewes on various feed levels

Group	No. of ewes	Body wt at parturition (kg)	Daily feed intake		Body wt change (kg)	Plasma glucose (mg/100 ml)	Plasma FFA (μ equiv./litre)	Plasma ketone bodies (mg/100 ml)
			Energy (Mcal ME/ewe)	Protein (g DCP/ewe)				
H	16	64 $\pm$ 1.8	2.1 $\pm$ 0.04	120 $\pm$ 1.6	-1.13 $\pm$ 0.84	60 $\pm$ 0.9	324 $\pm$ 22	1.8 $\pm$ 0.1
R	16	59 $\pm$ 1.8	1.0 $\pm$ 0.04	60 $\pm$ 1.6	-4.50 $\pm$ 0.84	59 $\pm$ 0.9	445 $\pm$ 22	1.9 $\pm$ 0.1
L	13	66 $\pm$ 1.9	6.0 $\pm$ 0.05	320 $\pm$ 1.8	-2.20 $\pm$ 0.93	66 $\pm$ 1.0	459 $\pm$ 24	2.8 $\pm$ 0.1

Overall means $\pm$ S.E. were calculated from the weekly means. ME, metabolizable energy; DCP, digestible crude protein; FFA, free fatty acids.

* $P < 0.05$; ** $P < 0.01$, analysis of variance.

TEXT-FIG. 1. Body weight change and the peripheral plasma concentrations of glucose, free fatty acids (FFA) and ketone bodies measured at weekly intervals during the first 6 weeks after lambing in lactating ewes fed without feed restriction (Group L, $\square$) and non-lactating ewes fed either 100% (Group H, $\bullet$) or 50% (Group R, $\circ$) of the maintenance requirements.

Reproductive activity during the first 3 weeks post partum

The number of ewes which exhibited oestrus and ovulated is given in Table 2. Feed restriction of 50% of the maintenance requirements to ewes in Group R led to a slight and statistically non-significant reduction in the number of ewes showing oestrus, and delayed the day of onset; 8/16 ewes showed oestrus between 8 and 19 days *post partum* (mean interval 16.9 days), compared with 11/16 ewes between 10 and 20 days (mean interval 15.5 days). The ovulation rate, verified by the number of CL observed at laparoscopy on Day 21, of those

Table 2. Ovarian activity before and after synchronization of oestrus 35 days *post partum* in non-lactating ewes on high and low levels of nutrition and in lactating ewes fed without restriction

Group	2 to 21 days after lambing			After sponge withdrawal			
	No. of ewes in oestrus	No. of ewes ovulating/ewe examined†	Mean No. of CL	Onset of oestrus		No. of CL observed on Day 8 of the cycle	Lambing rate
				No. of ewes	Time after withdrawal (hr)		No. of ewes conceiving‡
H	16	11	5/8	13	35.5 ± 1.9§	2.14 ± 0.19§	12
R	16	8	5/7	15	36.3 ± 1.7	2.07 ± 0.19	11
L	13	1	1/8	11	39.3 ± 2.0	2.80 ± 0.21	9
							No. %

* $P < 0.05$, analysis of variance.

† All the ewes examined in Groups H and R had shown oestrus. In Group L, only the one ewe which ovulated had shown oestrus.

‡ Conception was assumed to take place in ewes which had high levels of progesterone on the last day of the synchronized cycle (Day 17).

§ Means ± S.E.

Table 3. Plasma concentrations of progesterone and LH during Days 1 to 21 after lambing, and the characteristics of the preovulatory release of LH at a synchronized oestrus 35 days *post partum* for non-lactating ewes on high and low levels of nutrition and lactating ewes fed without restriction

Group	No. of ewes	Progesterone (ng/ml)	LH (ng/ml)	Start of LH release after onset of oestrus (hr)	Maximum conc. of LH released (ng/ml)	Duration of the LH release (hr)
H	16	0.50 ± 0.09	1.78 ± 0.44	4.8 ± 1.2	118 ± 12	12.6 ± 1.0
R	16	0.44 ± 0.09	1.45 ± 0.44	5.5 ± 1.2	96 ± 12	13.5 ± 1.0
L	13	0.22 ± 0.10	1.04 ± 0.48	8.0 ± 1.3	82 ± 14	9.3 ± 1.1
H+R	32	0.47 ± 0.06	1.61 ± 0.31	5.1 ± 0.8	107 ± 9	13.1 ± 0.7

Values are Means ± S.E.M. * $P < 0.05$, analysis of variance. Statistical comparisons were made between all three treatments, and between lactating and non-lactating ewes.

ewes which showed oestrus was not affected by the nutrition treatment (Table 2). Lactation did, however, inhibit oestrus and ovulation during this period. Only 1/13 ewes in Group L exhibited oestrus and ovulated.

TEXT-FIG. 2. Peripheral plasma levels of progesterone and LH during the first 3 weeks post partum, Days 3 and 10 of the progestagen treatment and Days 1, 8 and 17 of the oestrous cycle after synchronization (Days 35, 43 and 52 post partum), in lactating ewes fed without feed restriction (Group L, $\square$) and non-lactating ewes fed either 100% (Group H, $\bullet$) or 50% (Group R, $\circ$) of the maintenance requirements.

The plasma concentrations of progesterone and LH measured every 3 to 4 days are illustrated in Text-fig. 2, and their over-all means for the 3-week period are given in Table 3. Plasma progesterone was found to increase with time from the very low levels (0.26 ng/ml) measured at parturition to higher average levels in ewes in Groups H and R, but no increase was observed in Group-L ewes. The plasma LH values fluctuated and varied between and within treatments and no trend of change could be seen in the basal LH levels. In some cases, very high levels were measured when blood samples were taken on the day of oestrus. The display of oestrus in Group-H and -R ewes was

reflected by the overall means of progesterone and LH that were higher than those of Group-L ewes. Although the differences between the three groups were not statistically significant ($P > 0.05$), the specific comparison of lactating and non-lactating ewes indicated that the concentration of progesterone in the latter was greater than that of the former ($P < 0.05$).

The effects of the progestagen treatment given from Days 21 to 33 post partum

Insertion of progestagen-impregnated vaginal sponges gradually increased the plasma levels of progesterone in the ewes. This increase was higher in ewes of Group H than in those of Groups R and L. The plasma progesterone levels

TEXT-FIG. 3. Frequency distribution of plasma progesterone concentration 17 days after mating on Day 35 *post partum*, for non-lactating ewes on high (Group H) and reduced (Group R) intake and lactating ewes (Group L) fed without restriction. Hatched columns indicate ewes not considered to be pregnant; x indicates ewes which lambled.

in Group-H ewes increased from 1.3 ng/ml on the 3rd day of the treatment to 3.2 ng/ml by the 10th day. In the three treatments, the rise in plasma progesterone seemed to be related to the existing levels before the ewes were treated with the progestagen (Text-fig. 2).

The LH levels dropped during the progestagen treatment to about 0.2 ng/ml, with negligible differences between treatments.

The progestagen treatment was fully effective in suppressing oestrus in all ewes during the treatment. Following sponge withdrawal on Day 33, oestrus

was observed in 39/45 ewes on Days 34 or 35 *post partum*. Nutrition and lactation treatments had no effect on the number of ewes showing oestrus, but there was an indication that the interval from sponge withdrawal to onset of oestrus was longer in Group-L ewes (Table 2). The ovulation rate was also higher in ewes of Group L (2.8) than in those of Groups H and R (2.1) ($P < 0.05$).

Plasma hormone levels during the synchronized oestrous cycle

Differences in the time interval from the onset of oestrus to the start of LH discharge, the maximum concentration and the time duration of the LH secretion are summarized in Table 3. Although the start of LH release was delayed (up to 22 hr in one ewe) and the maximum LH concentrations were lower in Group-L ewes, the only parameter to be significantly affected by lactation was the duration of the discharge which was shorter. No effects of undernutrition on the secretory pattern of the preovulatory LH were evident in the ewes of Groups H and R.

The plasma LH values measured on Days 8 and 17 of the cycle were very low (0.4 to 0.7 ng/ml) and did not differ significantly between the various treatments or between days.

Fertility

The conception rate, as predicted from the progesterone levels 17 days after mating, averaged 87% for all treatments (ewes which maintained high progesterone concentration, i.e. > 1 ng/ml, were considered to have conceived: Text-fig. 3). The lambing data at the end of gestation (Table 2), however, showed that fertility was markedly affected by the feed intake after the previous lambing; only 1/15 ewes showing oestrus in Group R lambd (one single lamb) compared with 6/13 and 5/11 ewes lambing in Groups H and L, respectively, giving birth to an average of 1.7 lambs each.

Ewes in Groups H and L showed relatively low fertility (38.50% for both groups) when mated after a progestagen treatment 35 days *post partum* within their breeding season.

DISCUSSION

The display of oestrus by only 1/13 lactating ewes compared with 11/16 non-lactating ewes, despite the adequate nutrition of both groups, supports the earlier evidence that suckling has a direct effect on the resumption of reproductive activity following parturition in adequately fed sheep (Shevah *et al.*, 1974), rather than acting indirectly by way of nutrition. Ovarian activity was only slightly affected by a reduction in the diet of non-lactating ewes. The presence of CL observed in ewes of Groups H and R but not in lactating ewes, was associated with higher concentrations of progesterone and possibly LH in the peripheral plasma during the first 3 weeks after lambing. The concentrations of these two hormones were not affected by the state of undernutrition imposed on the ewes in Group R, but remained similar to those of Group-H ewes throughout the period of study. Despite this similarity in the hormone levels observed in the fully fed and diet-restricted groups around the time of mating,

only 1/16 diet-restricted ewes carried a lamb to term, compared to 6/16 fully fed ewes. In sheep, therefore, the present data indicate that the influence of reduced feeding on fertility is not solely through variation in the particular hormones measured in the present experiment around the time of mating.

The low fertility (38.5%) found in the well-fed lactating and non-lactating ewes (Groups L and H) is consistent with previous findings that fertility to natural and artificial matings at synchronized oestrus is lower than normal (Fletcher, 1971), although McClelland & Quirke (1971) obtained good results in Finn × Dorset ewes. The main cause of this low fertility was thought to be a failure of fertilization (Moore, Quinlivan, Robinson & Smith, 1967), but the present data, and those of Gunn, Doney & Russel (1972), suggest that fetal death might also be an important factor, and this may limit the usefulness of progesterone determination on Day 17 after mating for early pregnancy diagnosis as suggested by Shemesh, Ayalon & Lindner (1968).

No relationship was found between progesterone concentration and the number of CL produced, supporting the suggestion of Lamond & Gaddy (1972) that naturally polytocous species maintain blood levels of progesterone within defined limits regardless of the actual number of CL formed. Similarly, the concentration of progesterone was not found to be related to that of LH, an observation consistent with the finding that young CL were not sensitive to LH stimulation (Land, Collett & Baird, 1974), and are probably secreting maximally.

The delay in the onset of oestrus, the longer interval between the onset of oestrus and the release of LH and the shorter duration of the discharge in lactating ewes, although not statistically significant, are consistent with earlier results (Pelletier & Thimonier, 1973; Shevah *et al.*, 1974), and the positive relationship between these intervals and the ovulation rate is consistent with the between-breed findings of Land, Pelletier, Thimonier & Mauléon (1973).

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